THE EFFECTS OF FOREST MANAGEMENT ON SMALL MAMMAL COMMUNITY DYNAMICS IN SOUTHWESTERN PONDEROSA PINE ECOSYSTEMS

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ABSTRACT

THE EFFECTS OF FOREST MANAGEMENT ON SMALL MAMMAL COMMUNITY DYNAMICS IN SOUTHWESTERN PONDEROSA PINE ECOSYSTEMS

Elizabeth L. Kalies

In the southwestern United States, ponderosa pine (*Pinus ponderosa*) forests have been decreasing in biological diversity for the past century. Today's forests are characterized by dense stands of small-diameter trees that are susceptible to stand-replacing crown fires. There is now an emphasis on ecological restoration in the Southwest, whereby forests are thinned to reduce fuel content so that the natural fire regime can be reintroduced. However, given the multiple impacts humans have had on the landscape over the past 100 years, it is unclear whether thinning and burning treatments will restore all aspects of ecosystem health. Given this uncertainty, managers and stakeholders want information on the impacts of treatments on multiple ecosystem components, including wildlife.

I used meta-analysis to compare effects of restoration treatments on wildlife species in southwestern conifer forests. Thinning and burning treatments had positive effects on most small mammals and passerine bird species reported in 25 studies suitable for meta-analysis; overstory removal and wildfire resulted in an overall negative response. I recommend that managers implement thinning and burning treatments, but that future research efforts focus on long-term responses of species at larger spatial scales and target species for which there is a paucity of data.

No comprehensive analysis of the small mammal community in response to restoration treatments at large scales has been conducted in ponderosa pine forests. Small mammals are important in forest ecosystems in serving as prey, recycling nutrients, dispersing fungal spores and seeds, and aerating soils. During 2006-2009, I trapped eight species of small mammals at 294 sites in northern Arizona, and used occupancy modeling to determine wildlife responses to habitat. The most important habitat variables in predicting small mammal community occupancy were pine basal area, treatment intensity (percent of trees removed and time since treatment), the number and length of time slash piles are left on the ground, rock cover, and snags >40cm diameter. The average occupancy of all species was positively related to thinning treatment and slash. No one treatment benefitted all species, but rather an arrangement of dense and open stands across the landscape with heterogeneity in fine-scale features is likely the best management approach for restoring and maintaining a diverse small mammal community.

Similarly, community composition differed in each of 6 years following treatment, but total density remained constant. Total species densities were significantly lower in stands with dense conditions than in stands with more open structural conditions similar to those of presettlement times, which had similar small mammal densities as the thinning treatments. In addition, tassel-eared squirrels (*Sciurus aberti)*, golden-mantled ground squirrels (*Spermophilus lateralis)*, and gray-collared chipmunks (*Tamias cinereicollis)* appeared to play a functionally redundant role in dispersing ectomycorrhizal fungi across different stand structures. These results suggest that restoration treatments can maintain ecosystem stability in terms of small mammal community structure and function.

Finally, I found that the rapid assessment, occupancy and density modeling approach was highly effective in evaluating the response of the small mammal community to treatment and other habitat attributes. Particularly in the arid Southwest, most small mammal population studies end up primarily tracking precipitation patterns, but I showed a lack of a year effect by all species. Although this study was a big effort, it obtained more reliable, repeatable results for a greater number of species than many equally-intensive small mammal studies with similar objectives, which relied on mark-recapture methods and density estimation. I suggest this design be utilized in other studies that grapple with high variability and large spatial and temporal scales in assessing general impacts of treatments or habitat change on wildlife species.

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PREFACE

This dissertation is an integrated set of research projects designed to answer key questions about the effects of ecological restoration treatments in southwestern ponderosa pine forests on wildlife composition and function. It has been prepared in manuscript format with Chapters 2, 3, and 4 designed as manuscripts for publication, resulting in some redundancy among chapters. Chapter 2, "Wildlife responses to thinning and burning treatments in southwestern conifer forests: A meta-analysis" was published by *Forest Ecology and Management* (259 (2010) 333-342). Chapter 3, "Thinning and slash treatments increase occupancy of the small mammal community in ponderosa pine forests, northern Arizona," will be submitted to *Ecological Applications*. Chapter 4, "Small mammal community maintains stability through compositional and functional compensation in response to disturbance in a southwestern ponderosa pine forest ecosystem," will be submitted to *Ecology*. Chapter 1 is the introduction and literature review, and Chapter 5 presents overall results and conclusions from the entire dissertation. Since each manuscript chapter has its own introduction and conclusions, Chapters 1 and 5 are greatly foreshortened.

CHAPTER 1

INTRODUCTION

After a century of fire suppression, logging, and grazing, ponderosa pine forests in the southwestern United States have undergone a dramatic departure from conditions that existed prior to Euro-American settlement (Cooper 1960, Covington and Moore 1994, Swetnam et al. 1999). Today's ponderosa pine forests are characterized by the over-representation of homogenous, dense, small-diameter stands that are susceptible to stand-replacing crown fires (Fulé et al. 1997). This differs from the natural fire regime that used to occur on a 2-25 cycle at low intensity, which would maintain forests by removing the understory and small diameter trees (Covington 2003). There is now an emphasis on ecological restoration in the Southwest, whereby forests are thinned to approximate presettlement structural conditions so that the natural fire regime can be safely reintroduced.

Today's overly dense ponderosa pine forests not only pose a fire threat to humans, but ecosystems appear to be in general decline (Covington 2000). Changes in biotic and abiotic features include reductions in tree growth (Feeney et al. 1998), rates of decomposition and nutrient cycling (Selmants et al. 2003), water availability and ground water recharge (Baker 2003), and biological diversity (Chambers and Germaine 2003); and increased disease and insect infestation (Kolb et al. 1998). Of greatest concern has been a shift from low intensity surface fires to increasingly large and severe crown fires (Westerling et al. 2006). The intent of ecological restoration is not just to reduce fire risk, but to restore ecosystem biodiversity at all trophic and organizational levels, and in terms of composition, structure, function (Noss 1990).

In the long term, restoration treatments should create forest structures consistent with those that existed before fire exclusion: an open, patchy structure of mostly mature trees with herbaceous ground cover (Moore et al. 1999). This increased spatial and temporal heterogeneity will diversify habitat available for wildlife, and should, in theory, restore the native, diverse assemblage of animal species. However, both ecological restoration treatments and thinning treatments are being implemented across thousands of hectares in the ponderosa pine forests of northern Arizona, with limited quantitative data regarding wildlife responses. The literature that does exist is dominated by avian and single-species studies (e.g., Germaine and Germaine 2002, Germaine et al. 2004, Martin et al. 2005, Wightman and Germaine 2006, Hurteau et al. 2008, Dickson et al. 2009, Pope et al. 2009). Most studies are limited in temporal and spatial scale. A more in-depth review of wildlife responses to restoration and thinning and burning treatments is the topic of Chapter 2.

Small mammals commonly present in ponderosa pine forests of the Southwest include voles (*Microtus spp.)*, woodrats (*Neotoma spp.)*, ground and tree squirrels (*Spermophilus* and *Sciurus spp.)*, mice *(Peromyscus spp.)*, chipmunks (*Tamias spp.),* and gophers *(Thomomys spp.)*. Previous research suggests that tassel-eared squirrels (*Sciurus aberti*) may respond negatively to restoration treatments and the reduction in ponderosa pine tree density and basal area (Patton et al. 1985, Dodd et al. 2003, Dodd et al. 2006). However, species such as the Mogollon vole (*Microtus mogollonensis*) and golden-mantled ground squirrel (*Spermophilus lateralis*) may benefit from the increased understory vegetation cover (Tevis 1956, Converse et al. 2006a, Bagne and Finch 2009). The most comprehensive studies on small mammal community responses to restoration treatments in the Southwest found that mice and chipmunks responded positively to treatments, but other species results were inconclusive and compromised by small temporal and spatial scales (Converse et al. 2006a, Converse et al. 2006b).

Biodiversity of the small mammal community is not truly restored unless composition (abundance and diversity), structure (competition and interspecific relationships), and function (productivity and nutrient cycling) are restored as well. A diverse community should be able to maintain ecosystem functioning in the face of environmental change due to redundancy in their functional roles (Chesson et al. 2002). Small mammals are important in forest ecosystems in 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). Small mammals also provide a substantial part of the prey base for predators including the northern goshawk (*Accipiter gentilis*; a U.S. Fish and Wildlife Service species of concern), Mexican spotted owl (*Strix occidentalis lucida*; federally threatened), and other avian and mammalian predators (Boal and Mannan 1994, Block et al. 2005). The dispersion of ectomycorrhizal (EM) fungi is almost entirely reliant on small mammal disturbance and transfer through feces (Johnson 1996). Tassel-eared squirrels are key players in the dispersal of EM fungi in southwestern ponderosa pine forests (Kotter and Farentinos 1984, States 1984, Dodd et al. 2003), and ground squirrels, chipmunks, and other species may play this role as well (Pyare and Longland 2001). Thus, community members may play redundant functional roles in dispersing EM spores in the different stand structures they occupy, and thus maintain this ecosystem function over different habitat types. While fungal dispersion is not necessarily the most important function the community provides, I used it in this study to represent whether or not functional redundancy occurred within the community.

In designing forest management treatments it is critical to consider the associated impacts on small mammal biodiversity. However, no comprehensive analysis of the small mammal community in response to restoration treatments at large spatial (>16 sites) scales has been conducted in ponderosa pine forests. The broad purpose of this study was to assess changes in the small mammal biodiversity as a result of restoration and fuels reduction treatments in southwestern ponderosa pine forests. During 2006-2009, I trapped eight species of small mammals at 294 sites in northern Arizona, and used occupancy modeling to determine small mammal community responses to thinning treatments and habitat features. In Chapter 3, I analyzed small mammal occupancy responses to thinning treatments, slash piles, overstory and understory composition and structure, and other habitat features. I provided management recommendations for reducing the impact of ecological restoration treatments on small mammals. In Chapter 4, I analyzed density trends within the small mammal community in order to understand community compositional tradeoffs in response to disturbance. I further explored how these tradeoffs related to changes in ecosystem function. Thus, I evaluated impacts of ecological restoration on the small mammal community in terms of compositional, structural, and functional diversity.

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CHAPTER 2

WILDLIFE RESPONSES TO THINNING AND BURNING TREATMENTS IN SOUTHWESTERN CONIFER FORESTS: A META-ANALYSIS

Abstract

After a century of fire suppression, conifer forests in the western United States have dramatically departed from conditions that existed prior to Euro-American settlement, with heavy fuel loads and an increased incidence of wildfire. To reduce this threat and improve overall forest health, land managers are designing landscape-scale treatments that strategically locate thinning and burning treatments to disrupt fuel continuity, allowing managed wildfires to burn the remaining area. A necessary step in designing and evaluating these treatments is understanding their ecological effects on wildlife. We used meta-analysis to compare effects of small-diameter removal (thinnings and shelterwoods) and burning treatments, selective harvesting, overstory removal (including clearcutting), and wildfire on wildlife species in southwestern conifer forests. We hypothesized that small-diameter removal and burning treatments would have minimal effects on wildlife compared to other treatments. We found 33 studies that met our criteria by (1) comparing density or reproductive output for wildlife species, (2) using forest management or wildfire treatments, (3) implementing control-impact or before-after control-impact design using unmanaged stands as controls, and (4) occurring in Arizona or New Mexico ponderosa pine (*Pinus ponderosa*) or mixed conifer (*Abies*/*Picea*/*Pinus*) forest. The 22 studies suitable for meta-analysis occurred ≤20 years post-treatment on sites <400ha. Small-diameter harvest and burning treatments had positive effects but thin/burn and selective harvest treatments had no detectable effect on most small mammals and passerine bird species reported in studies; overstory removal and wildfire resulted in an overall negative response. We examined foraging guild responses to treatments; ground-foraging birds and rodents had no strong response. Aerial-, tree-, and bole-foraging birds had positive or neutral responses to the small-diameter removal and burning treatments, but negative responses to overstory removal and wildfire. Small-diameter removal and burning treatments as currently being implemented in the Southwest do not negatively impact most of the wildlife species in the studies we examined in the short term (≤10 yrs). We believe a combination of treatments in a patchy arrangement across the landscape will result in the highest diversity and density. We recommend that managers implement thinning and burning treatments, but that future research efforts focus on long-term responses of species at larger spatial scales, use reproductive output as a more informative response variable, and target species for which there is a paucity of data.

Key Words: treatment, clearcut, wildfire, density response, meta-analysis, *Pinus ponderosa*, ponderosa pine, mixed conifer, southwestern United States

Introduction

After a century of fire suppression, conifer forests in the western United States have dramatically departed from conditions that existed prior to Euro-American settlement (Covington and Moore 1994, Taylor and Skinner 1998, Fry and Stephens 2006). With the resulting dense forest conditions and heavy fuel loads, wildfires are increasing in frequency and severity (Covington 2000). To reduce this threat and the decline in ecosystem health in frequent fire forests, land managers are devising landscape-scale restoration treatments that would re-establish open forest conditions and allow frequent fire to safely return to its role in regulating tree density and fuel accumulation (Sisk et al. 2005, Noss et al. 2006b). A key assumption in designing landscape-scale treatments is that by strategically locating burning, thinning, and other silvicultural treatments, fuel continuity can be disrupted, allowing managed wildfires to burn the balance of the area (Finney 2001, Agee and Skinner 2005). A necessary step in designing and evaluating these treatments is understanding the ecological effects of silvicultural and fire management treatments on wildlife.

Wildlife responses to forest treatments vary widely; generally, it is assumed that treatments which restore conditions consistent with those they have experienced over evolutionary time will have more beneficial effects than treatments that create novel conditions (Soule 1985, Noss and Csuti 1994, Lindenmayer and Franklin 2002). High severity disturbances such as clearcutting and wildfire (Anthony and Isaacs 1989, Grialou et al. 2000, Cunningham et al. 2002) and unnaturally dense or open conditions (Brown and Davis 1998, Shick et al. 2006) can have negative impacts on animal species, particularly in the short term, because of habitat alteration. Thinning and burning treatments are an effort to return forest structure and composition to within the range of natural variability, which should benefit native wildlife species (Allen et al. 2002).

Southwestern conifer forests of the United States are an ideal system for examining the effects of forest treatments on wildlife, due to historical and current approaches to management. Ponderosa pine (*Pinus ponderosa*) and mixed conifer (*Abies lasiocarpa, P. flexilis, P. ponderosa, Populus tremuloides, Pseudotsuga menziesii*) forests cover >3 million hectares in the southwestern United States (US

Department of Agriculture Forest Service 2009). Due to historical logging and silvicultural practices, fire suppression, and grazing, most frequent fire forests in the Southwest are now characterized by excessive tree densities, low diversity of plant and wildlife species, and high susceptibility to stand-replacing crown fires (Covington et al. 1994, Fulé et al. 1997, Cocke et al. 2005). There is now an emphasis on restoring forests to past conditions using thinning and prescribed fire (Healthy Forests Restoration Act, 2003). These treatments may have negative, short-term effects on wildlife species that do not tolerate disturbance well, or that depend on these structures for nesting or foraging (Bock and Bock 1983, Chambers and Germaine 2003, Converse et al. 2006a). However, in the long term treatments should create forest structures with reduced tree densities and an open, patchy structure of mostly mature trees with herbaceous ground cover maintained by a frequent fire regime (Waltz et al. 2003, Moore et al. 2006). The increase in spatial and temporal heterogeneity should diversify habitat available for wildlife, and, in turn, restore a native, diverse assemblage of animal species (Allen et al. 2002, Noss et al. 2006a).

No consensus exists regarding wildlife responses to forest management in the Southwest. Studies of wildlife responses to thinning and burning treatments vary widely in species studied, response variable (e.g., density, abundance) measured, treatment (e.g., thinning, burning) examined, and temporal and spatial extent of the study design. Existing reviews include summaries of impacts of thinning and burning treatments on birds (Block and Finch 1997, Sallabanks et al. 2000, Bock and Block 2005a, b) and qualitative reviews that described effects of thinning and fire on multiple wildlife species (Lyon et al. 2000, Chambers and Germaine 2003, Pilliod and Bull

2006). A recent meta-analysis examined the impacts of forest treatments on small mammals in North American forests, but focused on clearcutting as a management tool (Zwolak 2009). No review quantitatively examined effects of forest treatments on multiple wildlife species.

To design landscape-scale restoration treatments, managers need to understand what is known about wildlife impacts of treatments that might be used: thinning, prescribed burns, wildfire, and clearcut fuel breaks. The purpose of this study was to synthesize and analyze studies of treatment impacts on wildlife in ponderosa pine and mixed conifer forests in the southwestern United States. We used a both qualitative and quantitative (meta-analysis) techniques. Meta-analysis is an analytical technique used to quantitatively summarize the results of multiple studies by calculating an effect size which compares a response variable between a treatment and control for each study, and then calculates a mean effect size across studies (Hedges and Olkin 1985, Gurevitch and Hedges 1993). We used meta-analysis to assess treatment impacts for vertebrate wildlife species whose density or reproductive output were compared in treated vs untreated forest sites in southwestern forests. Our objectives were to (1) determine which treatments had the greatest effect on wildlife, hypothesizing that thinning and burning treatments, if not eliciting a positive response from wildlife, may have less of a negative impact than clearcutting, selective harvesting, or high severity wildfire, particularly in the short term; (2) determine which species were most and least sensitive to habitat manipulation; and (3) identify species or groups of species for which there was a paucity of field experimentation and data. This analysis serves as a starting point for researchers and resource managers in designing testable hypotheses about impacts of thinning and burning treatments on wildlife, and determining future monitoring and research needs.

Methods

Data selection and extraction

We searched the following databases between September and December 2008: Academic Search Premier, Biological Sciences, BioOne, Environmental Science and Pollution Management, Plant Science, Springer Link, Wiley Interscience, Zoological Record, JSTOR, Forest Science Database, Dissertation and Theses Full Text. We used all combinations of the terms: wildlife, birds, reptiles, amphibians, mammals AND western forest, ponderosa pine AND restoration, thinning, logging, clearcut, prescribed burn, treatment, fuels reduction, fire. Peer-reviewed papers, conference proceedings, government documents, and theses were considered during our search. We also searched online government and institutional libraries including U.S. Forest Service TreeSearch (treesearch.fs.fed.us), Ecological Restoration Institute library at Northern Arizona University (library.eri.nau.edu), and U.S. Fish and Wildlife Service website (library.fws.gov). We spoke to wildlife biologists, public agency personnel, academicians, and authors to obtain additional sources and unpublished studies.

We selected studies that met these 4 criteria:

1. Vertebrate species were compared in terms of either of two response variables: (a) density or (b) reproductive output, as defined by number of successful nests, number of offspring, and/or survival rates of offspring;

2. Treatment was forest harvesting, including thinning, shelterwood, selective harvesting, and clearcutting, and/or burning, including prescribed fire and wildfire;
3. Study design was control-impact (CI) or before-after control-impact (BACI) with a control for comparison (i.e., an unmanaged stand);
4. Study was conducted in the southwestern United States (Arizona or New Mexico) in ponderosa pine or mixed conifer forest.

With the final set of studies, we built a database to record the relevant information. In addition to recording species and their density and reproductive output information, we noted site characteristics that could affect the response, and included these variables as covariates (treatment, time since treatment, and forest type including mixed conifer or ponderosa pine). As treatments were not always defined in silvicultural terms, for the purposes of this analysis we broadly categorized studies into 6 treatments:

1. "Small-diameter removal," where small-to-intermediate diameter trees were removed, including both thinning and shelterwood treatments;
2. "Burning," or low-to-moderate severity burns which were generally prescribed fires with fire-charring roughly 0-1.5 meters above the ground and only a few trees are killed in the understory;
3. "Thin/burn," where a thinning was conducted followed by a low-to-moderate severity prescribed burn;
4. "Selective harvest," where trees, typically of large-diameter, were selectively removed;

5. "Overstory removal," which represents the most intensive treatments, including clearcuts, where >80% of the basal area was removed; and
6. "Wildfire," defined as high severity burns or stand-replacing wildfire where fire charring is greater than 1.5 m above the ground, almost all the understory is killed, and some to all large trees are killed.

Data were separated by year and site whenever possible. We noted methodological variables that we hypothesized could affect the outcome of the study, including study design (BACI or C-I), area sampled, density estimation method (relative density or true density incorporating detection probability), replication, quality of study (peer reviewed or not), and study (identifying the origin of the data). We were unable to account for the season of sampling as a covariate because some studies reported only one density estimate based on a full year of sampling; thus, data from all seasons are pooled.

Meta-analysis

The most commonly used effect sizes in meta-analyses (i.e., Hedges' d, Cohen's d) are calculated based on sample size and variance, assuming that studies with large sample sizes and smaller variances are more reliable (Hedges and Olkin 1985, Rosenberg et al. 2000). However many wildlife studies are not replicated so there is no variance across replicates, nor do many studies report a variance. Often the number of replicates is not an adequate measure of sampling effort because it does not take into account the size of the site. Thus, we used a response ratio as our effect size calculation, defined as ln(treatment mean/control mean) (Hedges et al. 1999). This metric has become more commonly used in meta-analysis (Mosquera et al. 2000, Côté et al. 2001) as it is designed to measure relative differences (often appropriate in ecological studies) and behaves better statistically (Hedges et al. 1999). Since a response ratio cannot be calculated when a treatment or control mean is equal to zero, we performed trials where we added 1, 0.1, 0.001, 0.0001, and 0.00001 to each treatment and control mean before calculating the response ratio (Molloy et al. 2008). We determined that using 0.001 had the smallest impact on the overall (average) effect size.

Effect sizes are usually weighted by the inverse of the sample variance, in order to account for variation between studies in sampling effort. With the wildlife studies we examined, the standard deviation between replicate means is often not (1) reported, (2) available because sample size is one, or (3) meaningful because the size of a replicate varies dramatically from study to study. We used a biologically meaningful weighting scheme where each effect size was weighted by the area sampled (number of plots x plot size) (Mosquera et al. 2000). We also conducted unweighted analyses, as these types of analyses did not differ from traditional weighted analyses (Gardner et al. 2003), produced a more accurate estimate of overall effect size, and reduced Type 1 error (Lajeunesse and Forbes 2003, Marczak et al. 2007).

We built generalized linear models to examine relationships between effect sizes and covariates. We chose 8 models *a priori*, hypothesizing that either ecological or methodological variables, in addition to study, would explain effect size in response to treatment (Table 2-1). We based these hypotheses on our review of the literature and experience with southwestern forest wildlife studies. We compared models using Akaike's Information Criterion adjusted for small sample sizes (AIC_c) to assess the overall strength of each model (Burnham and Anderson 2002). We ranked the models from highest to lowest according to their ΔAIC_c values, and chose those models with $\Delta AIC_c < 2$ as the final set to be used for inference (Burnham and Anderson 2002). We calculated the Akaike weight (w_i) for each candidate model as a measure of model support and selection uncertainty. We performed the model selection analysis separately for weighted (using the total area sampled) and unweighted generalized linear models, and did not detect a difference in the results.

We examined each of the important covariates in the models, as identified by model selection, using Metawin software (v.2, Rosenberg et al. 2000). For categorical variables with ≥2 observations, we calculated a mean effect size (MES) with confidence intervals generated by bootstrapping (Adams et al. 1997), corrected for bias for unequal distribution around the mean. Effect sizes were considered to be different from zero when the confidence interval did not include zero. An effect size of zero, positive, or negative indicated no change between treatment and control, an increase in the response variable compared to the control, or a decrease in the response variable, respectively (Rosenberg et al. 2000). For continuous variables, we regressed effect size against the variable and reported the associated slope which indicates the direction and magnitude of the relationship. We compared unweighted and weighted analyses, found they produced similar results, thus we report only unweighted results.

Publication bias and non-independence of data

Publication bias in meta-analysis occurs because studies with significant results are more likely to be published than those without significant results (Arnqvist and Wooster 1995). We minimized bias by limiting the geographic extent of our study area to the Southwest which allowed us to be very complete in our data collection. Most of the studies we used examined multiple (≥3) species that showed a range of responses, and thus species with no response to treatment are reported.

We controlled for the problem of lack of independence in data (i.e., multiple effect sizes can be calculated from the same study using the same control for multiple treatments; a study of 5 bird species in 3 types of treatments over 2 years would generate 30 effect sizes) by including a covariate to identify the origin of the data ("study"), which was an indicator variable to identify each study uniquely. This approach allowed us to analyze the relative importance of "study" compared to the other covariates in our model selection approach.

Results

Overall results

Of 6,908 papers found during our key word literature search, we identified 33 studies that met our criteria. Only 25 studies were usable in our meta-analysis which uses density as the response variable (Appendix 2-A). We then eliminated all species with <5 observations across all studies in order to increase our overall sample size relative to the number of species (n = 1095 observations, 22 studies). Because there were only 8 studies that used reproductive output as a response variable which is insufficient for meta-analysis, we considered these data qualitatively. The wildlife species we examined were limited by the data we obtained; not all species or taxa were equally or well represented (e.g., birds were more studied than other taxa), and most studies were of a limited temporal and spatial scale (≤20 years post-treatment on sites <400ha).

The models ($\Delta AIC_c < 2$) that best predicted wildlife response to treatments included treatment, species, time since treatment, and study (Table 2-1). Other models performed poorly in comparison ($\Delta AIC_c \geq 3.11$) and included the variables forest type, study design, method of density estimation, replication and peer-review status (Table 2-1).

Treatment

The mean effect size differed among treatment types; small-diameter removal and burning treatments had positive effects on densities but the thin/burn and selective harvest treatments did not differ from zero (Figure 2-1a). Species responded negatively to overstory removal and wildfire (Figure 2-1a). We included all species to show the results based on the information currently available (species listed in Table 2-2) and also calculated mean effect sizes for 11 species for which there were data for every treatment (species listed in Table 2-2). The responses to treatments were similar to those for all species combined; however, species responded more positively to selective harvest and less positively to burning, relative to the other treatments (Figure 2-1b).

Species

Species varied in their response to the treatments relative to the controls (Table 2-2), with some species showing strong responses (MES >5 or <-5 and confidence interval does not overlap 0). Two species (house wren (*Troglodytes aedon*)) and red-faced warbler (*Cardellina rubrifrons*)) showed strong negative responses to the small-diameter removal treatments compared to the controls, and 1 species (American robin (*Turdus migratorius)*) had a strong positive response. Two species (western wood-pewee (*Contopus sordidulus)*) and spotted towhee (*Pipilo maculates*)) demonstrated strong positive responses to the burning treatments relative to the controls (Table 2-2). Two species exhibited strong negative responses (hermit thrush (*Catharus guttatus*)) and red-faced warbler) and 3 strong positive responses (American robin, western wood-pewee, and rock wren (*Salpinctes obsoletus*)) in the selective harvest compared to the controls. In contrast, there were 10 species that responded strongly negatively and 3 that responded strongly positively to the overstory removal, and 12 that responded strongly negatively and 8 that responded strongly positively to the wildfire. Mean effect sizes for species calculated across the small-diameter removal, burning, and thin/burn treatments indicated an overall positive response to treatment (MES = 0.5; CI = 0.3 to 0.8). The overall response of species to overstory removal and wildfire was negative (MES = -2.6; CI = -3.1 to -2.0).

Species were grouped into foraging guilds in order to summarize differences between species in response to treatment (Figure 2-2). Ground-foraging birds and rodents had consistently neutral density responses to the treatments, whereas aerial-, tree-, and bole-foraging birds had positive or neutral responses to the small-diameter removal and burning treatments, but negative responses to overstory removal and wildfire. Of the four treatments, woodpeckers and hummingbirds only exhibited a negative density response to overstory removal. Data were limited for raptors (with only 5 observations for American kestrels (*Falco sparverius*)) which responded positively to wildfire, and tree squirrels, which responded neutrally to small-diameter removal.

Time since treatment

Time since treatment across all studies ranged from 1-20 years. Time since treatment had an overall negative effect on species density responses (slope = -0.4); however, this response was driven largely by the overstory removal (slope = -1.0), since burning had a positive response (slope = 0.03) and the other four treatments negative (slope: wildfire = -0.1, selective harvest = -0.2, small-diameter removal = -0.1, thin/burn = -0.1). For guilds with ≥4 years of data, the mean effect sizes across the small-diameter removal, burning, and thin/burn treatments by year demonstrated that some animals responded positively over time (ground-foraging birds, woodpeckers), but others negatively (tree- and bole-foraging birds; Figure 2-3). The longest data set that existed was for the tassel-eared squirrel (*Sciurus aberti*), which responded increasingly positively over time (Figure 2-3).

Study

The presence of study as a variable in our top model (Table 2-1) indicated a lack of independence between observations from the same study. We interpreted this as a site effect, as most observations from the same study also used the same study site.

Reproductive output

Only 8 studies examined reproductive output of animal species in treated versus control sites. Six studies focused on bird responses to treatment (1 on wild turkeys (*Meleagris gallopavo*), 1 on Mexican spotted owls (*Strix occidentalis lucida*), 4 on western bluebirds (*Sialia mexicana*)) and 2 studies examined mammal responses (tassel-eared squirrel, black bear (*Ursus americanus*)).

Wakeling et al. (1998) found that successful wild turkey nests, defined by the hatching of at least one egg, were associated with greater overstory conifer density and time periods longer than 20 years since selective harvest. Battin (2003) found an increase in fledging success for plumbeous vireos (*Vireo plumbeus*) and western tanagers (*Piranga ludoviciana*) within 4 years of treatment in thin/burn versus untreated areas. Germaine and Germaine (2002) found thinning and burning treatments had little effect on the number of eggs or nestlings per nest of western bluebirds within 5 years of treatment, but were associated with a higher number of fledglings per nest and greater probability of fledging at least one young compared to controls. They also found a higher incidence of parasitic infestations by blowflies in nests in thin/burn treatments compared to controls (Germaine and Germaine 2002). Wightman and Germaine (2006) found that successful western bluebird nests, determined by number of young in the nest on the last day prior to fledge, were associated with increased understory and bare ground and lower conifer tree densities found in thinned and burned treatments within ≤7 years post-treatment. Hurteau et al. (in press) show that although nest density for western bluebirds was significantly higher in thinned, burned, and thin/burn treatments versus controls, the number of eggs or nestlings was not significantly different 2-3 years post-treatment. Jenness et al. (2004) found that occupancy and reproduction of Mexican spotted owls, based on sighting of young outside the nest, was higher in unburned versus burned treatments within 4 years of treatment, but the relationship was weak and possibly confounded by the large range in burn severity in the burned sites.

Dodd et al. (2006) found that density, adult survival, and juvenile recruitment, in terms of juveniles/ha, of tassel-eared squirrels was lower in shelterwood treatments versus controls approximately 10 years after treatment. In a four-year study beginning one year after a high-severity wildfire, Cunningham and Ballard (2003) demonstrated that bear densities remained the same before and after fire, and in the burned area versus control; however, the sex ratio in the burned area was skewed towards males compared to the same area prior to fire or the control. Cunningham and Ballard (2003) also found that although 16 cubs were produced in the burn area and 13 in the control, no cubs survived in the burned area versus 36% in the control.

Discussion

The small-diameter removal, burning, and thin/burn treatments had broadly similar effects in terms of small mammal and passerine bird response in the short term (≤10 years). At the guild level, aerial-foraging birds benefit from the small-diameter removal and burning treatments, but have negative responses to overstory removal and wildfire, perhaps due to loss of habitat components or the increased risk of predation by animals that forage in the open. Tree-foliage and bole-foraging birds responded neutrally or positively to the small-diameter removal and burning treatments, but negatively to overstory removal and wildfire, as expected from animals that require trees for foraging. Similar to Zwolak (2009), we found that most ground-dwelling rodents responded positively to small-diameter removal and thin/burn treatments, and that deer mouse (*Peromyscus maniculatus*) densities increased in both treatments and in response to wildfire.

However, although wildfire and overstory removal results in similar, negative impacts on overall species densities, these treatments are not equivalent in their effects. American kestrels (the only raptor represented in our meta-analysis) responded positively to the wildfire treatment, possibly because of their increased ability to spot and catch prey in open sites, or the increase in snags available for nesting (Village 1990). This result would not necessarily hold true for other raptors. Woodpeckers declined in overstory removals, but did not appear to respond to wildfires; we would have expected a positive response due to their well-documented relationship with fire and increased insect foraging opportunities on snags and residual trees (Farris and Zack 2005, Covert-Bratland et al. 2006). Ground/shrub-foraging birds were the only guild that responded positively to overstory removal, suggesting that this treatment was effective in maintaining or enhancing understory and shrub cover (Ffolliott and Gottfried 1989, Yorks et al. 2000). Overstory removal and wildfire have different impacts. With overstory removal, higher levels of biomass are removed, leaving stands with a more uniform structure; wildfire leaves more standing biomass and patches of unburned forest and snags (Spies and Turner 1999). Olive-sided flycatchers (*Contopus cooperi*) responded positively to wildfire but not overstory removal, which could be because these birds forage in open areas with dead trees, but nest high in conifer trees, and thus benefit from a patchy forest structure (McGarigal and McComb 1995).

Similarly, no one treatment benefits all species, at least over the short term. Even within the small-diameter removal treatment, which had the greatest overall positive effect of the six treatments on species densities, house wrens and red-faced warblers responded negatively relative to the controls. This could be due to their need for understory vegetation for foraging (house wrens) and nesting (red-faced warblers) (Wheye et al. 1988). Similarly, the negative response of the Mexican woodrat (*Neotoma mexicana*) to thin/burn treatment is likely caused by a lack of coarse woody debris and downed logs, essential for nest-building and cover (Converse et al. 2006a, Coppeto et al. 2006). Thus, at least in the near term, a combination of various treatments in a patchy arrangement in time and space across the landscape is likely to result in the highest diversity compared to any one treatment (Noss et al. 2006a).

Species responses to time since small-diameter removal or burning treatment were difficult to interpret due to the lack of data beyond 4 years for all species except the tassel-eared squirrel. Ground/shrub-foraging birds demonstrated a positive response to small-diameter removal and burning treatments over the first 4 years post-treatment, which may indicate that the understory and shrub layer is increasing in biomass and diversity during this time (Ffolliott and Gottfried 1989, Yorks et al. 2000). Woodpeckers show a positive response, which is likely due to increased snag decay and insect activity in the years immediately following a thinning or fire (Chambers and Mast 2005, Covert-Bratland et al. 2007). The decreased density of tree- and bole-foraging species suggests that these species emigrate from these areas since the larger trees do not reestablish in this short time frame. The increased density of the tassel-eared squirrel over a 10-year time period, however, may be due to increased growth and vigor of large pine trees (Fajardo et al. 2007) on which they depend (Patton and Green 1970).

The meta-analysis approach worked well in summarizing the density response of multiple species across different treatments over time at a coarse scale. However, a drawback of the approach is that we were unable to quantify fine-scale effects on wildlife. The model selection analysis shows that there are similarities between density responses measured in the same study and using the same site; thus, there must be other important within-site variables that we did not use as covariates in our analysis. Some may include characteristics of the control stands, post-treatment tree density or basal area, treatment intensity, seasonality of treatments, overstory composition, number of snags, and understory characteristics, as these variables were not consistently reported in the literature. For example, our inability to include number of snags as a covariate may be why we did not detect a positive response by woodpeckers to the burning and wildfire treatments. The juxtaposition of treatments on the landscape can also be very important to animals associated with multiple habitat types or edges (Ries and Sisk 2004), such as olive-sided flycatchers (McGarigal and McComb 1995) and spotted towhees (Battin and Sisk 2003), which was not assessed in this analysis.

Meta-analysis was also restrictive in the types of response variables that could be analyzed. Only animal density could be compared in treatments versus controls across different taxa, which eliminated studies that examined other responses such as home range size, diet, or habitat use. Since fitness is often viewed as the best indicator of population performance (Bock and Jones 2004), we compared density and reproductive output results and found that both were consistent in treatments versus controls (either both positive or both negative) for the plumbeous vireo and western tanager (Battin and Sisk 2003), western bluebird (Germaine and Germaine 2002, Wightman and Germaine 2006, Hurteau et al. in press), and tassel-eared squirrel (Dodd et al. 2006). However, black bear had similar densities pre- and post-fire, and in burned areas versus control, but lower reproductive output in the burned areas (Cunningham et al. 2003). It is well-documented in the literature that density is often a misleading indication of habitat quality (Van Horne 1983), for example when the habitat assessed is a seasonal habitat that does not accurately reflect the animal's fitness, as with animals that are more limited by their winter habitat then their summer habitat. Another problem is that territorial behavior often results in the best habitat being claimed by a few, dominant individuals, while the secondary habitat has a higher density of subordinate individuals (Fretwell and Lucas 1970). Thus, assessing wildlife density may not always be meaningful in terms of understanding changes in habitat, yet most studies in our review used this response variable presumably because reproductive output is more difficult, time consuming, and costly to measure.

A final problem is the lack of data for uncommon species. Due to the multi-species approach taken by most bird and small mammal studies, the same common species tend to be measured. Only a few species-specific studies were available (Patton et al. 1985, Cunningham et al. 2003, Dodd et al. 2006, Conway and Kirkpatrick 2007). Thus, these rare species tend to be underrepresented in the meta-analysis.

One outcome of meta-analysis is that it allows us to assess the current state of knowledge on a subject and recommend areas for future research. The vast majority of studies in the analysis were short-term responses of birds to treatment (15 of 22). In particular, recent studies (Berk 2007, Kotliar et al. 2007, Hurteau et al. 2008, Dickson et al. 2009, Pope et al. 2009) thoroughly assess 1-4 year bird responses to prescribed fire and thinning using sophisticated modeling techniques, and we suggest that these studies be carefully consulted before initiating similar research in order to eliminate duplication of effort. There are 7 studies on small mammals but all are short term (<3 years, except for the tassel-eared squirrel) and use small sites (<50 ha). Other underrepresented taxa include reptiles and amphibians, as well as rare birds and small mammals that are not easily assessed using conventional point count and trapping methodologies; for example, shrews (*Sorex*) or wild turkeys. Other species under- or un-represented in this meta-analysis include medium and large mammals, including both predators and ungulates, and birds of prey. However, these species are not entirely ignored in the literature, but rather density is generally not an appropriate response variable for animals with large home ranges. However, the lack of studies that assess reproductive responses of these species indicates a paucity of research on these large and top trophic animals.

Although small mammal and passerine bird species responded positively to small-diameter removal and burning treatments relative to the wildfire and overstory removal, they demonstrated relatively neutral responses relative to the controls, which were unmanaged stands. We expected stronger positive responses, but this could be due to our inability to analyze differences in initial (control) treatments or treatment intensity, which could affect the magnitude of species' responses. The lack of difference between treatments and controls may also reflect the short-term nature of the dataset, as it may take many years to see the positive effects of the altered habitat (Chambers and Germaine 2003). For example, after thinning, deer mice would tend to use this disturbed site in the short term due to the increased foraging opportunities (Bock and Bock 1983), but ultimately golden-mantled ground squirrels (*Spermophilus lateralis*) are probably better suited to the herbaceous habitats that would eventually reestablish (McKeever 1964). Thus, long-term studies are needed to provide a complete picture of species response to treatments and habitat conversion.

Conclusion

This meta-analysis suggests that thinning and prescribed burning of southwestern ponderosa pine and dry mixed conifer forests will benefit passerine birds and small mammals. Based on the existing literature, small-diameter removal and/or burning does not negatively affect species' densities compared to unmanaged forest stands, and is less detrimental than overstory removal or wildfire. These results support the hypothesis that thinning and burning at the landscape level are consistent with ecological restoration objectives for wildlife. However, wildfire and clearcut fuel breaks should be used with caution. In addition, we identified several research needs, the results of which could change these conclusions. We assessed thousands of papers on this topic and found only 25 that produced sufficient information for meta-analysis, revealing a need for greater research coordination. Studies at larger temporal and spatial scales, which examine more informative response variables pertaining to animal fitness for a greater variety of species, are critical to fully understanding the impacts of forest treatments on wildlife.

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Tables

Table 2-1. Model selection analysis; candidate models (model), number of parameters (K), AIC value corrected for small sample size (AIC_c), difference in AIC_c between models (ΔAIC_c), and the relative weight of each model (w_i).

Model	**K**	**AIC_c**	**ΔAIC_c**	**w_i**
Treatment, Species, Time, Study[1]	75	5902.65	0	0.83
Treatment, Species, Time, Study, Study Design	77	5905.76	3.11	0.17
Global: Treatment, Species, Time, Study, Study Design, Forest Type, Density Estimation Method, Replicated, Peer-Reviewed	85	5922.56	19.91	3.93E-05
Treatment, Species, Time	53	5957.85	55.20	8.52E-13
Treatment, Species, Time, Study Design	55	5960.19	57.54	2.64E-13
Treatment, Species	52	5990.33	87.68	7.53E-20
Study	23	6347.46	444.81	2.12E-97
Null	1	6410.10	507.45	5.3E-111

1 Best model ($\Delta AIC_c<2$). Parameter estimates and standard errors for this model are reported in Appendix 2-B.

Table 2-2. Mean effect size (number of observations) for wildlife species in each of the six treatments, organized by guild. Bolding indicates the confidence interval did not overlap zero[1].

Species	Small-diameter removal	Burn	Thin/ burn	Selective harvest	Overstory removal	Wildfire
Aerial-foraging birds						
Common nighthawk (*Chordeiles minor)*	0 (3)			0 (4)	**-7.3 (2)**	**8.2 (2)**
Cordilleran flycatcher (*Empidonax occidentalis)*	0.08 (4)	**-0.9 (6)**		**-4.2 (12)**	**-5.5 (5)**	**-5.2 (5)**
Olive-sided flycatcher (*Contopus cooperi)*						**7.2 (4)**
Violet-green swallow (*Tachycineta thalassina)*	0.2 (4)	**-1.0 (3)**		**-3.2 (12)**	**-4.3 (5)**	**-7.2 (11)**
Western wood-pewee (*Contopus sordidulus)*	3.4 (4)	**8.2 (4)**	0.3 (8)	**7.8 (6)**		-0.8 (12)
Hummingbirds						
Broad-tailed hummingbird (*Selasphorus platycercus)*	3.7 (4)	**0.5 (4)**		**2.0 (5)**	**-4.0 (4)**	**3.5 (8)**
Ground/shrub-foraging birds						
American robin[2] (*Turdus migratorius)*	**5.8 (5)**	-0.4 (4)	0.5 (8)	**5.3 (12)**	**4.8 (3)**	**-4.8 (12)**
Brown-headed cowbird (*Molothrus ater)*						**-6.9 (10)**
Chipping sparrow[2] (*Spizella passerine)*	**0.8 (4)**	**-1.3 (4)**	0.3 (9)	**3.3 (6)**	-4.6 (3)	**5.4 (6)**
Dark-eyed junco[2] (*Junco hyemalis)*	**0.4 (7)**	0.07 (6)	**0.4 (11)**	-0.07 (12)	-0.9 (5)	**-1.0 (12)**
Green-tailed towhee						**8.0 (4)**

Species	Small-diameter removal	Burn	Thin/ burn	Selective harvest	Overstory removal	Wildfire
(*Pipilo chlorurus)*						
Hermit thrush (*Catharus guttatus)*	-0.3 (4)	**-0.7 (4)**		**-5.0 (8)**	**-4.1 (5)**	**-5.7 (5)**
House wren (*Troglodytes aedon)*	**-7.0 (2)**	-0.3 (6)		**4.5(8)**	**1.7 (2)**	**5.2 (4)**
Mountain bluebird (*Sialia currucoides)*				0.6 (4)	**6.7 (2)**	**7.6 (2)**
Mourning dove (*Zenaida macroura)*	0 (3)	2.1 (3)		-3.4 (4)	**-7.3 (2)**	-1.0 (11)
Rock wren (*Salpinctes obsoletus)*				**7.8 (6)**	**7.8 (3)**	
Spotted towhee (*Pipilo maculates)*		**5.4 (4)**			**8.1 (3)**	0.5 (2)
Western bluebird[2] (*Sialia mexicana)*	**0.6 (7)**	**0.9 (15)**	**1.2 (11)**	**0.5 (10)**	-1.9 (5)	0.07 (13)
Tree foliage-foraging birds						
Black-headed grosbeak (*Pheucticus melanocephalus)*	0.2(4)	**4.5 (4)**		**-4.2 (4)**	**-7.4 (3)**	4.9 (3)
Grace's warbler (*Dendroica graciae)*	**0.7 (4)**		0.2 (9)	-0.04 (6)	**-8.4 (4)**	**-6.0 (7)**
Mountain chickadee[2] (*Poecile gambeli)*	2.3 (6)	-0.1 (17)	-0.2 (11)	-0.8 (11)	**-4.4 (4)**	**-7.2 (13)**
Pine sisken (*Spinus pinus)*				**4.6 (2)**	**-0.6 (2)**	**-9.8 (3)**
Plumbeous vireo (*Vireo plumbeus)*	**4.3 (4)**		0.9 (9)	**1.0 (6)**	**-7.1 (3)**	**-6.1 (10)**
Red-faced warbler	**-7.2 (4)**			**-5.4 (8)**	**-6.3 (5)**	

Species	Small-diameter removal	Burn	Thin/ burn	Selective harvest	Overstory removal	Wildfire
(*Cardellina rubrifrons)*						
Steller's jay[2] (*Cyanocitta stelleri)*	0.04 (5)	**0.8 (4)**	**0.2 (8)**	0.7 (7)	**-4.1 (4)**	**-2.4 (12)**
Virginia's warbler (*Vermivora virginiae)*		**4.2 (4)**				**-5.5 (5)**
Warbling vireo (*Vireo gilvus)*		**-0.8 (4)**		0.2 (2)	**0.6 (2)**	**-2.9 (2)**
Western tanager[2] (*Piranga ludoviciana)*	**2.4 (4)**	0.1 (4)	**0.4 (9)**	2.2 (7)	-2.1 (3)	-2.6 (10)
Yellow-rumped warbler[2] (*Dendroica coronate)*	**3.8 (7)**	-0.02 (6)	-0.02 (11)	2.0 (7)	**-2.6 (3)**	**-5.9 (12)**
Bole-gleaning birds						
Brown creeper (*Certhia Americana)*		-0.07 (2)		**-3.1 (6)**	**-6.6 (2)**	**-6.9 (10)**
Pygmy nuthatch[2] (*Sitta pygmaea)*	0.3 (7)	-0.2 (14)	0.1 (10)	**-2.4 (12)**	**-6.8 (5)**	**-5.3 (11)**
White-breasted nuthatch[2] (*Sitta carolinensis)*	**0.8 (5)**	-0.05 (16)	-0.06 (9)	-0.5 (12)	**-7.6 (5)**	**-4.9 (13)**
Woodpeckers						
Acorn woodpecker (*Melanerpes formicivorus)*		0.1 (2)				**7.4 (2)**
American three-toed woodpecker (*Picoides dorsalis)*					-0.3 (2)	-4.7 (3)
Downy woodpecker (*Picoides pubescens)*				-0.7 (4)	0.06 (2)	
Hairy woodpecker[2] (*Picoides villosus)*	0.2 (5)	**0.8 (15)**	**0.9 (8)**	-0.2 (12)	**-4.4 (5)**	-0.5 (12)

Species	**Small-diameter removal**	**Burn**	**Thin/ burn**	**Selective harvest**	**Overstory removal**	**Wildfire**
Northern flicker (*Colaptes auratus)*	0.2 (5)	-1.8(6)		**-0.2 (12)**	**-3.1 (5)**	-0.6 (12)
Williamson's sapsucker (*Sphyrapicus thyroideus)*				**-0.6 (6)**	0 (2)	
Yellow-bellied sapsucker (*Sphyrapicus varius)*				2.5 (4)	**0.5 (2)**	
Raptors						
American kestrel (*Falco sparverius)*				**4.3 (4)**		**7.4 (5)**
Arboreal rodents						
Tassel-eared squirrel (*Sciurus aberti)*	-0.2 (5)		**-2.1 (3)**	-0.1 (2)		
Ground rodents						
Deer mouse (*Peromyscus maniculatus)*	0.4 (4)		**1.9 (13)**			**0.9 (2)**
Golden-mantled ground squirrel *(Spermophilus lateralis)*	-0.4 (3)		0.7 (8)			
Gray-collared chipmunk *(Tamias cinereicollis)*	**1.1 (4)**		0.1 (9)			
Mexican woodrat *(Neotoma mexicana)*	**0.7 (2)**		-3.3 (7)			

1 Bootstrapped confidence intervals for each mean effect size are shown in Appendix 2-C.

2 Species data were available for all six treatments.

Figures

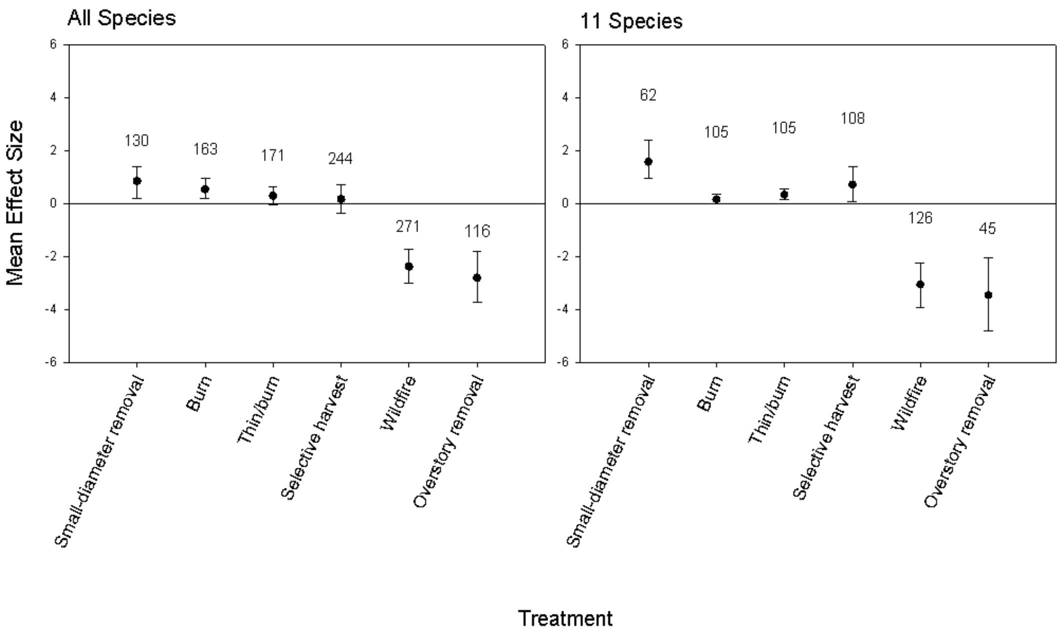

Figure 2-1. Mean effect size (ln treatment mean density/control mean density), with bootstrapped confidence intervals and number of observations, a) across all available species for the 6 forest treatment types, and b) for the 11 species for which data were available in each of the 6 forest treatment types. See Table 2-2 for the list of species included in each treatment.

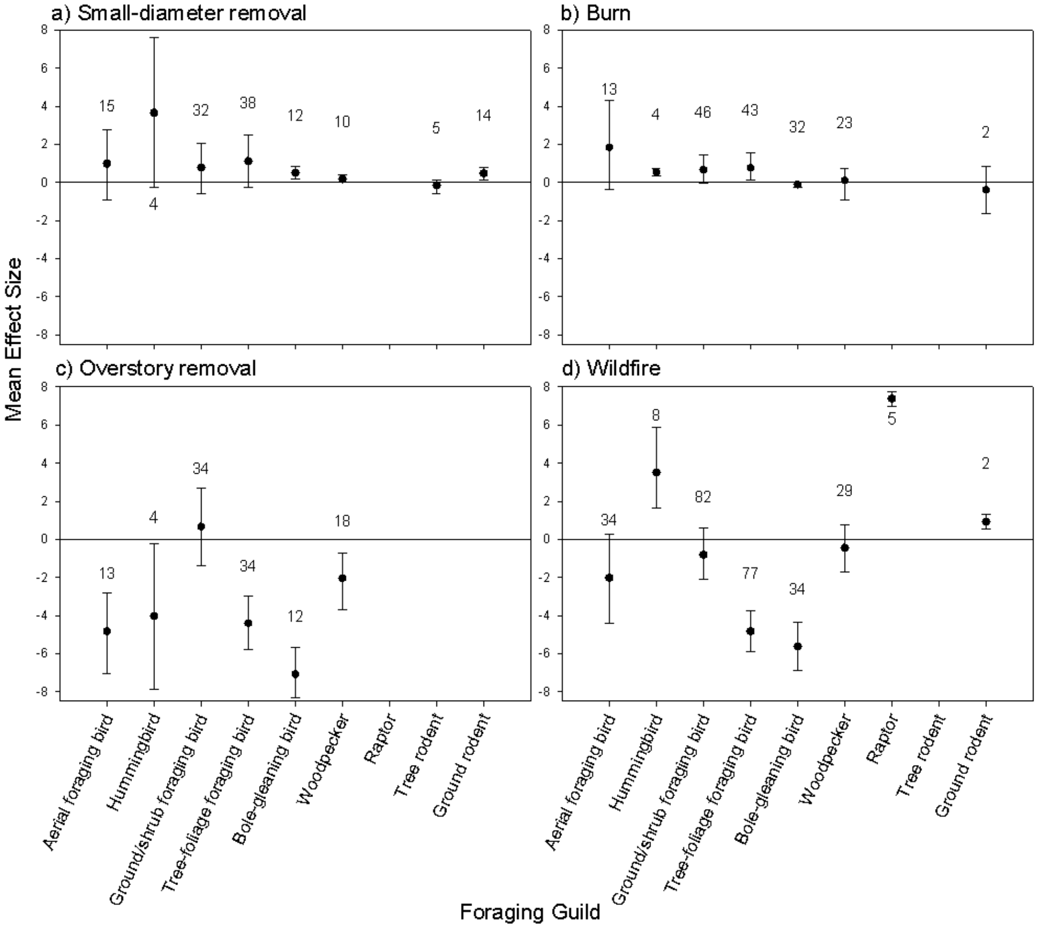

Figure 2-2. Mean effect size (ln treatment mean density/control mean density), with bootstrapped confidence intervals and number of observations, by foraging guild in the a) small-diameter removal, b) burning, c) overstory removal, and d) wildfire treatments. See Table 2-2 for the list of species included in each treatment and guild.

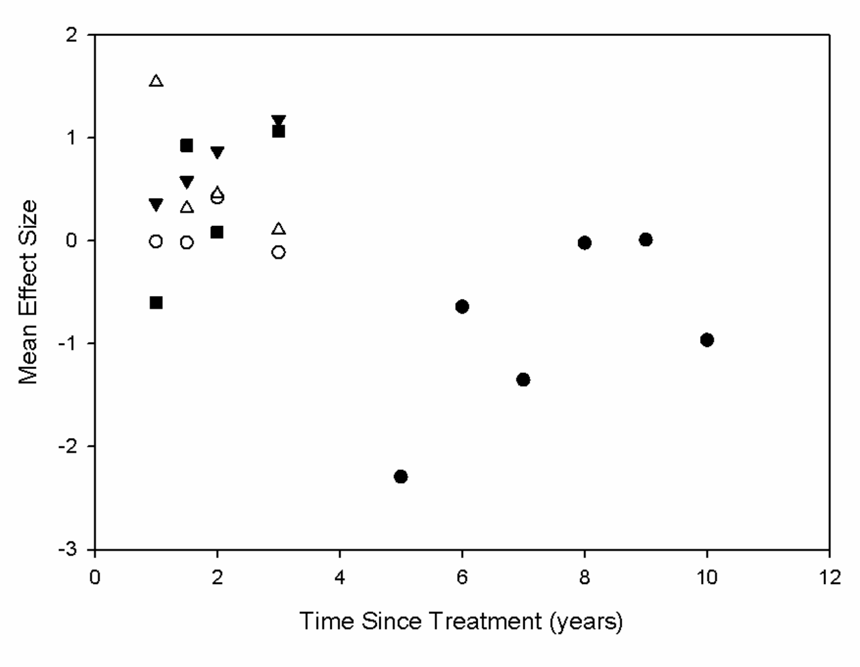

Figure 2-3. Mean effect size (ln treatment mean density/control mean density) versus time since treatment by foraging guild for the small-diameter removal, burning, and thin/burn treatments. Foraging guilds include ground/shrub-foraging birds (▼), tree-foliage foraging birds (△), bole-gleaning birds (○), woodpeckers (■), and arboreal rodents (●). See Table 2-2 for a list of species included in each guild.

Appendix 2-A

References and covariates used in the meta analysis

Reference	Region	Treatment	Species	Time since treatment[1] (years)	Area sampled[2] (ha)	Study design	Forest type	Density estimation method	Repli-cated?	Source
Wightman and Yarborough, 2006	Northern AZ	Thin/burn	Lizards[3] (5 species)	6, 7	4	C-I	PIPO	Based on abundance data	Y	Agency report
Wightman and Rosenstock, unpublished data	Northern AZ	Thin/burn	Tassel-eared squirrel (*Sciurus aberti)*	6, 7	2	C-I	PIPO	Clippings	Y	Unpub-lished
Battin, 2003	Northern AZ	Thin/burn	Birds (9 species)	1-4 (combined)	16	C-I	PIPO	Transects; based on abundance data	Y	Dissertation
Berk, 2007	Northern & eastern AZ, western NM	Low-to-moderate prescribed fire	Birds (5 species)	3	872 total (4 sites)	BACI and C-I	PIPO	Point counts, detection probabilities, distance sampling	Y	Thesis
Burgoyne, 1980	Northern AZ	Shelterwood	Birds (10 species)	2	110	C-I	PIPO	Older version of distance sampling (Emlen 1971)	Y	Dissertation
Converse et al., 2006	Northern AZ	Thin (3 levels), thin/burn	Small mammal (4 species)	1 (thin); 1, 2, 3, (thin/burn)	15 (3 treatments)	C-I	PIPO	Mark-recapture	Y	Forest Ecology and Manage-ment

Reference	Region	Treatment	Species	Time since treatment[1] (years)	Area sampled[2] (ha)	Study design	Forest type	Density estimation method	Replicated?	Source
Converse et al., 2006b	Northern AZ, northern NM	High intensity wildfire, thin	Small mammal (3 species)	1	44 (burn), 75 (thin AZ)	C-I	PIPO	Mark-recapture	Y	Journal of Wildlife Management
Conway and Kirkpatrick, 2007	Southern AZ	High, moderate-low wildfire	Buff-breasted flycatcher[3] (*Empidonax fulvifrons*)	6	10,800 (high); 11,668 (mod-low)	C-I	PIPO, MC	Point counts, detection probabilites	Y	Journal of Wildlife Management
Cunningham et al., 2003	Southern AZ	Crown fire	Black bear[3] (*Ursus americanus)*	1-2 (combined)	24,000	BACI and C-I	PIPO	Petersen estimate	N	Wildlife Society Bulletin
Dickson et al., 2009	Northern & eastern AZ, western NM	Low-to-moderate intensity prescribed burn	Birds (14 species)	1-2 (combined)	872 (4 sites)	BACI and C-I	PIPO	Point counts, detection probabilities, DISTANCE	Y	Ecological Applications
Dodd et al., 2006	Northern AZ	Shelterwood	Tassel-eared squirrel	10 (combined 4 years of data at ~10-year old treatments)	3	C-I	PIPO	Clippings	Y	Restoration Ecology
Dwyer & Block (Dwyer and Block 2000)	Northern AZ	High and moderate-low wildfire	Birds (5 species)	1	217 (2 sites)	C-I	PIPO	Point counts, simple density calc based on abundance	Y (moderate), N (high)	Conference proceedings (peer-reviewed)

Reference	**Region**	**Treatment**	**Species**	**Time since treatment^1 (years)**	**Area sampled^2 (ha)**	**Study design**	**Forest type**	**Density estimation method**	**Repli-cated?**	**Source**
Franzreb and Ohmart, 1978	Eastern AZ	Overstory removal	Birds (47 species)	1, 2	31	C-I	MC	Census	N	The Condor
Horton and Mannan, 1988	Southern AZ	Moderate-low prescribed fire	Birds (16 species)	1	95	BACI and C-I	PIPO	Point counts, modified distance sampling	Y	Wildlife Society Bulletin
Hurteau et al., 2008	Northern AZ	Moderate-low prescribed fire, thin, thin/burn	Birds (5 species)	2	180 (3 sites)	BACI and C-I	PIPO	Point counts, DISTANCE	Y	Journal of Wildlife Management
Kotliar et al., 2007	Northern NM	High, moderate-low wildfire	Birds (21 species)	1, 2	315 (3 sites)	BACI and C-I	PIPO, MC	Point counts, DISTANCE	Y	Ecological Applications
Kyle and Block, 2000	Northern AZ	High and moderate-low wildfire	Deer mouse (*Peromyscus maniculatus*), gray-collared chipmunk (*Tamias cinereicollis*)	1	64 (2 sites)	C-I	PIPO	Mark-recapture, CAPTURE	N	Conference proceeding (peer-reviewed)
Lowe et al., 1978	Northern AZ	High severity wildfire	Birds (31 species)	1, 3, 7, 20	188 (4 sites)	C-I	PIPO	Census	N	Government document
Overturf, 1979	Northern AZ	High severity wildfire	Birds (33 species)	1, 2, 7, sampled for 2 years	62 (3 sites)	C-I	PIPO	Census	N	Thesis

Reference	**Region**	**Treatment**	**Species**	**Time since treatment[1] (years)**	**Area sampled[2] (ha)**	**Study design**	**Forest type**	**Density estimation method**	**Repli-cated?**	**Source**
Patton et al., 1985	Northern AZ	Selective harvest	Tassel-eared squirrel	1-2 (combined)	240	BACI and C-I	PIPO	Census	Y	Journal of Wildlife Management
Pope et al., 2009	Northern AZ	Low-to-moderate intensity prescribed burn	Birds (3 species)	1-2 (combined)	533	C-I	PIPO	Point counts, detection probabilities, DISTANCE	Y	Journal of Wildlife Management
Roberts, 2003	Northern AZ	Thin/burn	Pinyon mouse[3] (*Peromyscus truei*), deer mouse	1, 2	32	BACI and C-I	PIPO	Mark-recapture, CAPTURE	N	Thesis
Scott and Gottfried, 1983	Eastern AZ	Selective harvest	Birds (23 species)	1-2 (combined)	296	BACI and C-I	MC	Census	N	Government document
Scott, 1979; Scott and Oldemeyer, 1983	Eastern AZ	Selective harvest	Birds (18 species)	1-2 (combined)	68	BACI and C-I	MC	Census	N	7 species in Journal of Forestry; 11 species in government document
Szaro and Balda, 1979	Northern AZ	multiple (see below)	Birds (30 species)	1, 3, 4, 6, sampled for 3 years	150 (4 sites)	BACI and C-I	PIPO	Census	N	Studies in Avian Biology
		clearcut		6						
		thin		4						
		strip cut (thin)		3						

Reference	Region	Treatment	Species	Time since treatment[1] (years)	Area sampled[2] (ha)	Study design	Forest type	Density estimation method	Repli-cated?	Source
		silvicultur-ally cut (thin)		1						

1 Different years were considered individual observations, except when the author combined results over multiple years; in these cases, we used the mean number of years as our time variable.

2 Area sampled is per species per year per study type. If there were different sites/treatments analyzed separately, that is noted in parenthesis.

3 Omitted from meta-analysis because there were < 5 total observations per species.

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Appendix 2-B

Parameter estimates and standard errors for best model (Table 2-1)

Parameter	**Estimate**	**Standard Error**
Intercept	0.838	0.612
Species[Tassel-eared squirrel]	-5.101	5.828
Species[Acorn woodpecker]	4.013	1.565
Species[American kestrel]	6.365	1.098
Species[American robin]	0.586	0.577
Species[Black-headed grosbeak]	-1.039	0.850
Species[Broad-tailed hummingbird]	1.428	0.734
Species[Brown creeper]	-4.843	0.803
Species[Brown-headed cowbird]	-4.958	1.120
Species[Chipping sparrow]	0.404	0.670
Species[Common nighthawk]	0.293	1.064
Species[Cordilleran flycatcher]	-3.990	0.655
Species[Dark-eyed junco]	-0.772	0.544
Species[Deer mouse]	4.269	1.861
Species[Downy woodpecker]	-1.422	1.415
Species[Golden-mantled ground squirrel]	4.269	2.293
Species[Grace's warbler]	-2.459	0.688
Species[Gray-collared chipmunk]	4.073	2.225
Species[Green-tailed towhee]	9.121	1.540
Species[Hairy woodpecker]	-0.918	0.532
Species[Hermit thrush]	-4.019	0.727
Species[House wren]	0.876	0.767
Species[Mexican woodrat]	1.761	2.308
Species[Mountain bluebird]	4.017	1.223
Species[Mountain chickadee]	-2.679	0.519
Species[Mourning dove]	-1.035	0.762
Species[Northern flicker]	-1.108	0.597
Species[American three-toed woodpecker]	-1.664	1.546
Species[Olive-sided flycatcher]	6.831	1.543
Species[Pine sisken]	-2.994	1.319
Species[Plumbeous vireo]	-1.556	0.670
Species[Pygmy nuthatch]	-2.847	0.533
Species[Red-faced warbler]	-6.819	0.877
Species[Rock wren]	8.827	1.130

Parameter	**Estimate**	**Standard Error**
Species[Spotted towhee]	5.807	1.183
Species[Steller's jay]	-1.303	0.608
Species[Violet-green swallow]	-4.106	0.634
Species[Virginia's warbler]	-0.856	1.119
Species[Warbling vireo]	-2.290	1.122
Species[Western bluebird]	-0.285	0.524
Species[Western tanager]	-0.814	0.628
Species[Western wood-pewee]	2.056	0.652
Species[White-breasted nuthatch]	-2.512	0.524
Species[Williamson's sapsucker]	-1.924	1.232
Species[Yellow-bellied sapsucker]	0.881	1.415
Total Trmt[wildfire]	0.565	0.995
Total Trmt[burn]	1.398	0.883
Total Trmt[overstory removal]	-4.459	0.708
Total Trmt[harvest]	0.426	0.627
Total Trmt[small-diameter removal]	1.310	0.540
Time yrs	-0.189	0.046
Ref[AZGF in review]	3.584	5.542
Ref[Battin 2003]	0.533	1.602
Ref[Berk 2007]	0.604	1.606
Ref[Burgoyne 1980]	0.182	1.287
Ref[Converse 2006]	-5.289	1.975
Ref[Converse 2006a]	-4.919	2.805
Ref[Dickson 2006]	0.107	1.155
Ref[Dodd et al 2006]	3.876	5.897
Ref[Dwyer & Block 2000]	-0.604	1.870
Ref[Franzreb & Ohmart 1978]	4.884	0.846
Ref[Horton & Mannan 1988]	-0.375	1.669
Ref[Hurteau 2007]	0.192	1.117
Ref[Kotliar et al 2007]	-0.428	1.539
Ref[Kyle & Block 2000]	-5.803	3.001
Ref[Lowe et al 1978]	-0.615	1.684
Ref[Overturf 1979]	-3.391	1.635
Ref[Patton et al 1985]	4.101	5.940
Ref[Pope 2008]	0.670	2.497
Ref[Roberts 2003]	0.000	0.000
Ref[Scott & Gottfried 1983]	1.990	0.727
Ref[Scott 1979]	0.000	0.000

Appendix 2-C

Number of observations (N), mean effect sizes (MES), lower confidence intervals (LCI), and upper confidence intervals (UCI) for wildlife species in each of the six treatments. Bolding indicates that confidence interval did not overlap zero.

	Small-diameter removal				**Burn**				**Thin/burn**				**Selective harvest**				**Overstory removal**				**Wildfire**			
Species	**N**	**MES**	**LCI**	**UPI**	**N**	**MES**	**LCI**	**UPI**	**N**	**MES**	**LCI**	**UPI**	**N**	**MES**	**LCI**	**UPI**	**N**	**MES**	**LCI**	**UPI**	**N**	**MES**	**LCI**	**UPI**
Aerial-foraging birds																								
Common nighthawk	3	0.00	-7.31	4.88									4	0.00	0.00	0.00	2	**-7.31**	-7.31	-7.31	2	**8.17**	7.82	8.52
Cordilleran flycatcher	4	0.08	-0.19	0.43	6	**-0.93**	-1.88	-0.06					12	**-4.22**	-6.18	-2.12	5	**-5.50**	-7.75	-2.73	5	**-5.16**	-7.31	-2.96
Olive-sided flycatcher																					4	**7.22**	6.62	7.82
Violet-green swallow	4	0.16	0.00	0.31	3	**-1.04**	-1.39	-0.66					12	**-3.16**	-5.31	-1.14	5	**-4.33**	-8.38	-0.28	11	**-7.19**	-9.51	-4.52
Western wood-pewee	4	3.44	-0.08	6.97	4	**8.16**	6.95	8.98	8	0.31	-0.03	0.74	6	**7.85**	7.48	8.21					12	-0.77	-3.75	2.96
Hummingbirds																								
Broad-tailed hummingbird	4	3.66	-0.27	7.59	4	**0.53**	0.33	0.74					5	**2.04**	0.49	4.83	4	**-4.03**	-8.14	-0.20	8	**3.51**	1.72	6.01
Ground-shrub-foraging birds																								
American robin	5	**5.84**	2.90	7.31	4	-0.42	-0.87	0.02	8	0.47	0.00	0.82	12	**5.33**	3.57	7.05	3	**4.78**	0.92	7.19	12	**-4.78**	-6.81	-2.86
Brown-headed cowbird																					10	**-6.85**	-7.70	-5.16
Chipping sparrow	4	**0.83**	0.41	1.31	4	**-1.29**	-2.51	-0.26	9	0.27	-0.83	1.50	6	**3.31**	0.92	6.43	3	-4.65	-7.31	0.00	6	**5.41**	1.35	9.11

	Small-diameter removal				**Burn**				**Thin/burn**				**Selective harvest**				**Overstory removal**				**Wildfire**			
Species	**N**	**MES**	**LCI**	**UPI**	**N**	**MES**	**LCI**	**UPI**	**N**	**MES**	**LCI**	**UPI**	**N**	**MES**	**LCI**	**UPI**	**N**	**MES**	**LCI**	**UPI**	**N**	**MES**	**LCI**	**UPI**
Dark-eyed junco	7	**0.42**	0.15	0.78	6	0.07	-0.54	0.69	11	**0.39**	0.14	0.64	12	-0.07	-0.42	0.28	5	-0.90	-1.99	0.20	12	**-1.05**	-1.45	-0.48
Green-tailed towhee																					4	**8.06**	6.90	9.03
Hermit thrush	4	-0.35	-5.21	4.34	4	**-0.67**	-1.23	-0.25					8	**-5.04**	-6.62	-2.71	5	**-4.18**	-6.58	-1.71	5	**-5.68**	-7.31	-4.04
House wren	2	**-7.05**	-7.05	-7.05	6	-0.26	-0.62	0.35					8	**4.49**	2.13	6.81	2	**1.72**	1.10	2.33	4	**5.21**	0.63	9.80
Mountain bluebird													4	0.62	-0.10	1.34	2	**6.68**	6.22	7.15	2	**7.65**	7.47	7.82
Mourning dove	3	0.00	-7.31	7.31	3	2.07	-0.61	7.24					4	-3.38	-7.31	0.55	2	**-7.31**	-7.31	-7.31	11	-1.04	-5.32	3.11
Rock wren													6	**7.85**	7.54	8.09	3	**7.82**	7.72	7.92				
Spotted towhee					4	**5.44**	1.09	9.77									3	**8.07**	7.92	8.20	2	0.53	-7.78	8.84
Western bluebird	7	**0.65**	0.41	0.98	15	**0.87**	0.26	1.85	11	**1.24**	0.53	2.93	10	**0.49**	0.26	0.84	5	-1.87	-7.73	4.05	13	0.07	-1.71	2.36
Tree foliage-foraging birds																								
Black-headed grosbeak	4	0.24	-0.30	0.69	4	**4.51**	0.27	8.55					4	**-4.21**	-7.52	-0.79	3	**-7.39**	-7.72	-7.21	3	4.94	-0.49	8.01
Grace's warbler	4	**0.67**	0.48	1.01					9	0.23	-0.25	0.71	6	-0.04	-0.49	0.31	4	**-8.43**	-8.73	-8.12	7	**-6.05**	-8.16	-1.83
Mountain chickadee	6	2.35	-0.50	6.41	17	-0.14	-0.46	0.13	11	-0.21	-0.61	0.17	11	-0.83	-3.07	1.22	4	**-4.38**	-7.77	-0.82	13	**-7.24**	-9.16	-4.64
Pine sisken													2	**4.61**	1.30	7.92	2	**-0.61**	-1.11	-0.10	3	**-9.83**	-9.83	-9.83
Plumbeous vireo	4	**4.35**	0.69	8.01					9	0.89	-0.06	2.71	6	**0.96**	0.73	1.19	3	**-7.08**	-7.31	-6.62	10	**-6.13**	-7.58	-3.98

	Small-diameter removal				**Burn**				**Thin/burn**				**Selective harvest**				**Overstory removal**				**Wildfire**			
Species	**N**	**MES**	**LCI**	**UPI**	**N**	**MES**	**LCI**	**UPI**	**N**	**MES**	**LCI**	**UPI**	**N**	**MES**	**LCI**	**UPI**	**N**	**MES**	**LCI**	**UPI**	**N**	**MES**	**LCI**	**UPI**
Red-faced warbler	4	**-7.24**	-7.62	-6.79									8	**-5.41**	-7.28	-3.40	5	**-6.31**	-7.92	-3.58				
Steller's jay	5	0.04	-0.42	0.52	4	**0.78**	0.26	1.31	8	**0.25**	0.01	0.53	7	0.71	-0.52	2.97	4	**-4.13**	-8.31	-0.04	12	**-2.41**	-4.62	-0.25
Virginia's warbler					4	**4.21**	0.92	7.70													5	**-5.53**	-6.62	-3.36
Warbling vireo					4	**-0.81**	-1.10	-0.56					2	0.21	-0.10	0.51	2	**0.58**	0.34	0.81	2	**-2.92**	-4.00	-1.85
Western tanager	4	**2.43**	0.41	6.19	4	0.13	-0.42	0.45	9	**0.42**	0.13	0.74	7	2.19	-2.19	5.23	3	-2.14	-7.31	0.54	10	-2.60	-5.38	0.92
Yellow-rumped warbler	7	**3.81**	1.10	7.36	6	-0.02	-0.30	0.31	11	-0.03	-0.37	0.34	7	2.05	-2.13	5.23	3	**-2.58**	-7.31	-0.16	12	**-5.92**	-7.82	-3.61
Bole-gleaning birds																								
Brown creeper					2	-0.07	-0.22	0.08					6	**-3.12**	-6.19	-0.93	2	**-6.57**	-9.20	-3.93	10	**-6.87**	-8.40	-4.67
Pygmy nuthatch	7	0.30	-0.02	0.56	14	-0.21	-0.39	0.02	10	0.15	-0.08	0.47	12	**-2.36**	-4.46	-0.96	5	**-6.79**	-8.86	-3.63	11	**-5.34**	-7.77	-2.92
White-breasted nuthatch	5	**0.80**	0.05	1.47	16	-0.05	-0.21	0.13	9	-0.06	-0.33	0.25	12	-0.49	-1.17	0.21	5	**-7.59**	-8.25	-6.98	13	**-4.89**	-6.97	-2.72
Woodpeckers																								
Acorn woodpecker					2	0.12	-0.38	0.62													2	**7.37**	6.91	7.82
American three-toed woodpecker																	2	-0.33	-0.66	0.00	3	-4.71	-7.31	0.51
Downy woodpecker													4	-0.69	-5.18	3.80	2	0.06	-0.28	0.40				
Hairy woodpecker	5	0.19	0.00	0.58	15	**0.85**	0.56	1.13	8	**0.85**	0.56	1.18	12	-0.17	-0.56	0.36	5	**-4.41**	-7.31	-1.51	12	-0.54	-2.16	0.46

	Small-diameter removal				Burn				Thin/burn				Selective harvest				Overstory removal				Wildfire			
Species	**N**	**MES**	**LCI**	**UPI**	**N**	**MES**	**LCI**	**UPI**	**N**	**MES**	**LCI**	**UPI**	**N**	**MES**	**LCI**	**UPI**	**N**	**MES**	**LCI**	**UPI**	**N**	**MES**	**LCI**	**UPI**
Northern flicker	5	0.16	0.00	0.48	6	-1.75	-5.02	0.02					12	**-0.18**	-0.38	-0.02	5	**-3.06**	-5.99	-0.15	12	-0.59	-2.09	0.23
Williamson's sapsucker													6	**-0.59**	-0.73	-0.46	2	0.00	0.00	0.00				
Yellow-bellied sapsucker													4	2.52	-0.69	5.73	2	**0.55**	0.40	0.70				
Raptors																								
American kestrel													4	**4.33**	1.59	5.98					5	**7.38**	6.90	7.72
Arboreal rodents																								
Tassel-eared squirrel	5	-0.16	-0.59	0.13					3	**-2.15**	-2.50	-1.54	2	-0.11	-0.68	0.45								
Ground rodents																								
Deer mouse	4	0.38	0.00	0.80					13	**1.91**	0.45	4.05									2	**0.93**	0.56	1.29
Golden-mantled ground squirrel	3	-0.44	-0.96	0.36					8	0.74	-3.25	4.17												
Gray-collared chipmunk	4	**1.09**	0.89	1.41					9	0.11	-0.06	0.24												
Mexican woodrat	3	**0.67**	0.27	1.12					7	-3.27	-6.78	1.47												

CHAPTER 3

THINNING AND SLASH TREATMENTS INCREASE OCCUPANCY OF THE SMALL MAMMAL COMMUNITY IN PONDEROSA PINE FORESTS, NORTHERN ARIZONA

Abstract

In the southwestern United States, ponderosa pine (*Pinus ponderosa*) forests have been decreasing in biological diversity for the past century. Today's forests are characterized by dense, stands of small-diameter trees that are susceptible to stand-replacing crown fires. There is now an emphasis on ecological restoration in the Southwest, whereby forests are thinned to reduce fuel content and crown fire risk, after which the natural fire regime is reintroduced. Small mammals are important in forest ecosystems in serving as prey for multiple predators, recycling nutrients, dispersing fungal spores and seeds, and aerating soils. However, no comprehensive analysis of the small mammal community in response to restoration treatments at large spatial (>16 sites) scales has been conducted in ponderosa pine forests. During 2006-2009, we trapped eight species of small mammals at 294 sites in northern Arizona, and used occupancy modeling to determine wildlife responses to thinning treatments and habitat features. The most important habitat variables in predicting small mammal community occupancy were pine basal area, treatment intensity (percent of trees removed and time since treatment), the number and length of time slash piles are left on the ground, rock cover, and snags >40cm diameter. Five species (*Microtus mogollonensis*, *Peromyscus maniculatus*, *Spermophilus lateralis*, *Spermophilus variegates*, *Tamias cinereicollis*) responded positively to treatment and 3 (*Neotoma mexicana, Sciurus aberti*, *Thomomys* *bottae*) negatively; the average occupancy of all species combined was positively related to treatment. All but 2 species (*P. maniculatus*, *Thomomys bottae*) responded positively to slash piles, and average occupancy of all species was positively related to slash. For all habitat attributes, we found tradeoffs in the response of each species which illustrated that no one treatment benefitted all species, but rather an arrangement of dense and open stands across the landscape with heterogeneity in fine-scale features is likely the best management approach for small mammals. Compared to studies with similar objectives, the occupancy modeling approach was effective in detecting treatment effects while accounting for year effects; this design can be used in other studies that grapple with high variability and large spatial and temporal scales.

Key Words: *Microtus mogollonensis*, *Neotoma mexicana*, *Peromyscus maniculatus*, *Sciurus aberti*, *Spermophilus lateralis*, *Spermophilus variegates*, *Tamias cinereicollis*, *Thomomys bottae*, ecological restoration, occupancy modeling, detection probability, *Pinus ponderosa*

Introduction

In the southwestern United States, ponderosa pine (*Pinus ponderosa*) forests have been decreasing in biological diversity for the past century. Due to fire suppression, logging, and grazing, these forests have undergone a dramatic departure from conditions that existed prior to Euro-American settlement (Covington and Moore 1994b, Swetnam et al. 1999). Today's southwestern ponderosa pine forests are characterized by homogenous, dense, small-diameter stands and heavy litter and fuel accumulation that are susceptible to stand-replacing crown fires (Fulé et al. 1997). These forests not only pose a fire threat to humans, but the ecosystems appear to be in general decline (Covington 2000). Changes in biotic and abiotic features include reductions in tree growth (Feeney et al. 1998), rates of decomposition and nutrient cycling (Selmants et al. 2003), water availability and ground water recharge (Baker 2003), and biological diversity (Chambers and Germaine 2003); and increased disease and insect infestation (Kolb et al. 1998). Wildlife populations have been affected as well; Brown and Davis (1998) determined that 34 grassland species have experienced extirpation or reduction of their ranges in the Southwest since 1890, perhaps due to the reduction of open forest stand structure. Thus, there is now an emphasis on ecological restoration in the Southwest, whereby forests are thinned to reduce fuels and crown fire risk, after which the natural fire regime is reintroduced. Prescribed fire use in ecological restoration is designed to mimic the natural fire regime that used to occur on a 2-25 cycle at low intensity, which would maintain forests by removing the understory and small diameter trees (Covington 2003). In the long term, restoration treatments should create forest structures with an open, patchy structure of mostly mature trees with herbaceous ground cover (Waltz et al. 2003).

A landscape maintained by frequent fire constituted the southwestern ponderosa pine forest's evolutionary environment, defined as the range of conditions that have exerted selection pressure on animals which they now depend on for their survival (Noss and Csuti 1994). Today's thinning and burning treatments are designed to increase spatial and temporal heterogeneity of habitat, and, in turn, will likely restore a native, diverse assemblage of animal species (Allen et al. 2002, Noss et al. 2006). However, given the multiple impacts humans have had on the landscape over the past 100 years, including grazing, altered fire regimes, and climate change (Fry and

Stephens 2006, Westerling et al. 2006, Bakker and Moore 2007), it is unclear whether thinning and burning treatments will restore all aspects of ecosystem health. Additionally, habitat components such as Gambel oak *(Quercus gambelii)*, large-diameter trees, snags, and down wood are thought to be important to wildlife, but there is debate about treatment targets on the landscape (Abella et al. 2006, Noss et al. 2006). Given this uncertainty, managers and stakeholders want information on the impacts of treatments on multiple ecosystem components, including wildlife (Sisk et al. 2006).

Of particular concern is wildlife in the wildland-urban interface, the area where human developments lie adjacent to natural areas, which tend to be the source of social tension due to the conflicting priorities of land preservation and resource use (Marzluff and Bradley 2003). These areas are also often prioritized for treatment in order to reduce fire risk close to cities and towns. Although the interface may experience an increase in species diversity via supplemental feeding and reduced predation due to human activities, it is likely to lose ground-nesting and forest-interior species because of increased edge effects and disturbance; thus, interface communities tend to be dominated by generalists (Marzluff and Bradley 2003). Evaluating wildlife communities in these areas may be of particular importance because settlement of southwestern ponderosa pine forests has increased over the last half century (Block and Finch 1997).

A recent meta-analysis summarizing wildlife responses to thinning and burning treatments in southwestern conifer forests found that these treatments had overall positive effects on small mammal and passerine bird densities, with the literature dominated by avian and single-species studies (Kalies et al. 2010). In addition, most of these studies were limited in temporal and spatial scale, which further hindered the development of consistent conclusions. Only a handful of studies examined small mammal community response to forest management practices in the Southwest (Converse et al. 2006a, Converse et al. 2006b, Wampler et al. 2008, Bagne and Finch 2009). The most heavily-studied small mammal in southwestern ponderosa pine forests is the tassel-eared squirrel (*Sciurus aberti*), which is a Management Indicator Species for many national forests and may experience negative effects due to restoration treatments because of their dependence on high basal area and continuous canopy cover (Patton et al. 1985, Dodd et al. 2006, Prather et al. 2006). However, no comprehensive analysis of the small mammal community has been conducted in ponderosa pine forests at large spatial (>16 sites) scales.

Small mammals commonly present in ponderosa pine forests of the Southwest include voles (*Microtus spp.)*, woodrats (*Neotoma spp.)*, ground and tree squirrels (*Spermophilus* and *Sciurus spp.)*, mice *(Peromyscus spp.)*, chipmunks (*Tamias spp.),* and gophers *(Thomomys spp.)*. Small mammals are important in forest ecosystems in 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). Small mammals also provide a substantial part of the prey base for predators including the northern goshawk (*Accipiter gentilis*; a US Fish and Wildlife Service species of concern), Mexican spotted owl (*Strix occidentalis lucida*; federally threatened), and other avian and mammalian predators (Boal and Mannan 1994, Block et al. 2005). Research suggests that tassel-eared squirrels may respond negatively to restoration treatments and the reduction in ponderosa pine trees (Patton et al. 1985, Dodd et al. 2003, Dodd et al. 2006), but species such as the Mogollon vole (*Microtus mogollonensis*) and golden-mantled ground squirrel (*Spermophilus lateralis*) may benefit from the increased understory vegetation cover (Tevis 1956, Converse et al. 2006a, Bagne and Finch 2009). Thus, small mammals can be indicators of changes in forest structure that result from restoration treatments.

In designing forest management treatments it is critical to consider the associated compositional changes of the small mammal community. In this study, we used occupancy modeling; a relatively new 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 may be more appropriate for assessing wildlife at large spatial and temporal scales compared to traditional mark-recapture methods, due to its lesser demands for field data. We examined small mammal community responses to thinning only, as this is the treatment most commonly used in the wildland-urban interface in Arizona. Our objectives were to: 1) estimate a detection probability for each small mammal species; 2) quantify the importance of treatment and habitat attributes on occupancy for each individual species and collectively; 3) make inferences from the relationships between key attributes and species occupancy to better inform management decisions, and 4) assess the efficacy of occupancy modeling by determining if thinning treatments and habitat attributes would affect species occupancy more than background interannual variation, at a comparable level of effort to other similar studies.

Methods

Study area

Our primary study area was located 8km southwest of Flagstaff, Arizona, in the ponderosa pine-dominated forests of the wildland-urban interface (Appendix 3-A). Historically, this 18,500-ha area experienced a variety of forest management practices, including high grading (early 1900s), commercial thinning (1970-1990s), and fuels reduction and restoration treatments (late 1990s-present), resulting in a range of stand structures in terms of tree basal area and density. We established an additional 4,800-km study area on the Kaibab National Forest north of Grand Canyon National Park, Arizona, to represent old-growth forest structure conditions. 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 used this distance to ensure spatial independence in sampling points (i.e., eliminate autocorrelation) based on the larger home range of tassel-eared squirrels (Hoffmeister 1986). We eliminated points that fell within private lands and non-forested patches >1ha, or were located >500m 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 treated and half in untreated stands, and then located and permanently marked them in the field using a global positioning system.

Data collection

Small mammal sampling- We used each of the 110 sampling points as the center of a "site." We obtained Northern Arizona University Institutional Animal Care and Use Committee approval of our trapping methodology (protocol #06-005). At each site we centered a 5x5 square trap grid which consisted of 25 Sherman (model LNATDG) traps with 20m spacing, with a 3x3 grid overlaid with 9 Tomahawk (model 202) traps, one at every other grid intersection; the combination of the 2 trap types ensured we captured the majority of species in the small mammal community (animals that weighed <1000g). Total site-scale sampling area was 14,400m^2 (1.4ha). We trapped small mammals at each site during the summers of 2006-2009 over a 10-week period late June to 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 4 days per week, which resulted in 3 nighttime and 3 daytime trapping sessions. We sampled for Botta's pocket gopher (*Thomomys bottae*) 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 determined the number of surveys and relevant habitat and detection covariates at each site using data from our first year (2006).

Vegetation sampling- At each site, we quantified overstory and understory characteristics that we hypothesized could affect occupancy (i.e., habitat covariates). We established an 11.3m-radius circular overstory plot (400m^2) at the site center, and measured slope (degrees), total number of stumps, and species and diameter at breast height (dbh) for trees ≥1.4m. At the site center, we also established a nested subplot of 3.6-m radius (40m^2) and assessed species, percent cover, and height class for herbaceous plants, shrubs, and trees <1.4m. At each subplot and 4 additional 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 randomly established a 20-m transect and measured each piece of wood >7.5 cm in diameter (Brown et al. 1982). At the site level we counted the number of slash piles, and used our yearly 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 4 years of thinning treatment. All vegetation sampling was conducted in June of each year, prior to small mammal sampling activities.

Data analysis

Habitat and detection covariates- For each site, we calculated slope, pine and oak BA/ha, big trees (>40, 50, and 60cm dbh)/ha, snags (all snags and >40, 50, 60 cm dbh)/ha, and the proportion of trees/ha removed by any method of harvesting (Table 3-1). We also calculated understory plant species richness, percent of vegetation >40cm in height, average percent cover of each substrate, and volume of down wood at the site level. We determined the number of slash piles/site, the number of years piles were left intact, and the time (years) since treatment. Because spatial location (i.e., latitudinal and longitudinal position) can serve as a surrogate for unmeasured habitat variables (Rahbek and Graves 2001), we obtained the Universal Transverse Mercator (UTM) coordinates of each site in order to derive a unique site-level identifier and consider the role of spatial location in our estimates of occupancy. We pooled detection histories from all 4 years of sampling and used “year” as an occupancy covariate.

Covariates that we hypothesized could cause heterogeneity in detection probability (i.e. detection covariates) included temperature, precipitation, year, week, and individual survey event. Temperature and precipitation can affect activity levels of animals, making it more or less likely they will encounter a trap (Getz 1961). Year and week can capture this variability plus other attributes that are difficult to measure, such as changing resource availability. Survey event 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 maximum daily temperature, minimum daily temperature, humidity, and precipitation as detection covariates, and obtained these data from the Flagstaff Airport weather station which is within 30km of our farthest site on the Coconino, and Fredonia, Arizona which is within 50km of our farthest site on the Kaibab (Weather Underground Inc. 2009).

We standardized all continuous habitat and detection covariates, and diagnosed univariate correlations and multicolinearity 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.).

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). 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, for each small mammal species. We conducted all analyses using Program PRESENCE v2.4 (Hines 2007).

Prior to our data collection effort and analyses, we identified covariates that we hypothesized would predict occupancy of small mammal species, based on the literature and our own field experience. In order to focus on the variables that most impacted overall community occupancy and to avoid overparameterizing our models (i.e., Moore and Swihart 2005), we reduced this list of variables by building univariate models of each covariate and comparing them against the null model of occupancy for each species.

Using only variables that performed better than the null for at least 3 species, we then developed 15 candidate models of occupancy and detection. We included null models (i.e., intercept-only) that predicted detection or occupancy probabilities assuming probabilities are constant across the sites. For each species, we ran occupancy models using PRESENCE and compared models 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 considered models with ΔAIC_c values ≤ 2 to have considerable support. We also computed weights of evidence and model selection uncertainty using AIC weights (w_i; (Burnham and Anderson 2002)). We ranked relative variable importance by summing the AIC weights across all models in which a given variable occurred, and considered cumulative weights ($w_+(j)$) ≥ 0.50 to be strong evidence for a species response (Barbieri and Berger 2004, Dickson et al. 2009).

Efficacy of occupancy modeling approach- To compare the level of effort and quality of results between our study and similar efforts, we obtained all peer-reviewed studies that met these criteria: 1) the objective was to assess small mammal population responses to forest management treatments, 2) it was conducted in southwestern US conifer forest, 3) the response variable was abundance, density, or a fitness parameter (not raw counts of captures), and 4) the sampling methodology used was live-trapping. We compared studies based on the response variable, number of species assessed, area sampled, duration of study, and total trap nights.

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, etc.), sampling effort varied somewhat 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 (*Neotoma mexicana*), deer mouse (*Peromyscus maniculatus*), tassel-eared squirrel, golden-mantled ground squirrel, rock squirrel (*Spermophilus variegates*), gray-collared chipmunk (*Tamias cinereicollis*), and Botta's pocket gopher.

Habitat and detection covariates

Our univariate analysis identified 8 out of 21 initial covariates that did not perform better than the null model for at least 3 species, including understory vegetation height and richness, slope, down wood volume, 2 size classes of large trees, and 2 size classes of snags (Table 3-1). This resulted in 11 habitat covariates: pine BA (m^2/ha), oak BA (m^2/ha), understory vegetation (% cover), rock (% cover), trees >50cm dbh/ha, snags/ha, snags >40cm dbh/ha, slash (high values indicate high number of slash piles and long duration slash piles were present), treatment (high values indicate a high percentage of trees/ha were removed and treatment was recently implemented), year, and UTMs (higher values indicate southeastern sites) (Table 3-1).

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 variables from further analysis.

Detection probabilities

Detection probabilities for the 8 species of small mammals ranged from 0.3–0.9 over 4 years (Figure 3-1), which are considered adequate for occupancy analysis (MacKenzie and Royle 2005). The most parsimonious models of detection probability included survey, year, week, or none of the covariates (Table 3-2).

Occupancy probabilities

Each of the 11 habitat covariates except year appeared in at least one model with $\Delta AIC_c \leq 2$ (Table 3-2). Covariates for which $w_+(j) \geq 0.50$ for at least 3 species included pine BA, treatment, slash, rock cover, snags >40cm/ha, and UTMs (Table 3-3).

Gray-collared chipmunks had the highest rates of occupancy and Mexican woodrats the lowest across all sites (Figure 3-2). Sites with higher pine BA (m^2/ha) elicited a positive response from only Mexican woodrats and tassel-eared squirrels

(Figure 3-2). "Treatment" represents a range from old treatments (negative values) to recent treatments (positive values); the older treatments were selective harvesting or pre-commercial thinning with relatively low tree-per-hectare removal, while the new treatments were fuels reduction or restoration treatments with high tree-per-hectare removal. Five species (Mogollon vole, deer mouse, golden-mantled ground squirrel, rock squirrel, gray-collared chipmunk) responded positively to treatment and three negatively (Mexican woodrat, tassel-eared squirrel, Botta's pocket gopher; Table 3-3). The average occupancy of all species indicated a positive trend (slope = 0.01).

"Slash" can be interpreted as a range of sites with no or low numbers of slash piles left onsite for a very short period of time (negative values), to sites with many slash piles left on the ground for up to 3 years (positive values). All species responded positively to slash quantity and duration except for the deer mouse and pocket gopher (Table 3-3). The average occupancy of all species indicated a positive trend (slope = 0.02).

Sites with higher rock cover elicited a positive response from 4 species (Mexican woodrat, deer mouse, rock squirrel, gray-collared chipmunk) and a negative response from 4 species (Mogollon vole, tassel-eared squirrel, rock squirrel, Botta's pocket gopher; Table 3-3). Snags >40cm produced a positive response from 5 species (Mogollon vole, Mexican woodrat, deer mouse, tassel-eared squirrel, gray-collared chipmunk) and a negative response from 3 species (golden-mantled ground squirrel, rock squirrel, Botta's pocket gopher; Table 3-3). UTMs indicate a site effect for 4 species (Mexican woodrat, tassel-eared squirrel, golden-mantled ground squirrel, rock squirrel; Table 3-3).

Efficacy of occupancy modeling approach

Of the 9 small mammal studies that have been conducted in the Southwest using live-trapping to assess response to forest management, our study is the only one that used occupancy as the response variable (Table 3-4). Our study required the 6th greatest level of effort (trap nights); however, our study area was the 7th largest, and we assessed 8 species whereas the maximum was previously 4. We were able to sample two species that had not previously been assessed (rock squirrel and Botta's pocket gopher).

Discussion

Response of small mammal community to forest treatments and habitat attributes

Thinning and restoration treatments are implemented to reduce tree density so prescribed fire can be introduced. Restoration treatments (i.e., treatments with high tree-per-hectare removal and recent implementation) resulted in increased occupancy for all species except tassel-eared squirrels and Mexican woodrats; Botta's pocket gopher responded positively to low pine basal area but negatively to treatment. 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 open stand structure as their evolutionary environment. It is well-documented that tassel-eared squirrel and Mexican woodrat are associated with higher density stands (Block et al. 2005, Dodd et al. 2006), and it is possible that they were found less commonly on the landscape during presettlement times. Botta's pocket gopher likely benefit from decreased pine basal area as it leads to increased understory vegetation for foraging (Huntly and Reichman 1994), and fewer obstacles in digging their tunnel systems (Reichman et al. 1982). These results support the inference that open stand structure as well as dense stands naturally occurred, and creating both stand types on the landscape is likely to lead to higher overall species diversity (Allen et al. 2002, Noss et al. 2006).

No single habitat feature increased occupancy of all species; this 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), leaving 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. 2006), and regulating litter and understory vegetation levels. Our sites were not treated with prescribed fire, but we assessed species responses to fine-scale features across the variety of habitat sampled. Large trees are features of presettlement forests that have decreased in density due to fire suppression and logging (Cooper 1961, Covington and Moore 1994a). Our results support the inference that this features was part of the evolutionary environment, as we found that all but one species responded positively to large trees (>50cm). In comparison, trees ≥40cm (proposed as a diameter cap in the Southwest; Abella et al. 2006) did not have a strong effect on the community. Similarly, only 2 species responded positively to snags but 5 responded positively to snags >40cm, likely because big snags provide larger cavities for nesting and cover (Chambers and Mast 2005).

Changes in oak basal area, rock percent cover, and herbaceous vegetation cover also resulted in tradeoffs in occupancy among species within the small mammal community. Greater herbaceous vegetation cover, which was correlated with increased vegetation height and species richness, benefitted most species (5 of 8), which fits with the theory that the community is adapted to an open forest structure with low tree density and a herbaceous ground cover, which provides both food and cover (Allen et al. 2002). Species that responded negatively to vegetation cover included the tassel-eared squirrel, which forages for fungi in moist litter environments generally associated with dense stands, and uses the tree canopies as cover (States and Gaud 1997, Dodd et al. 2003), and the Mexican woodrat and rock squirrel which are more strongly associated with rock as cover. Six species responded positively to oaks or rock; rocky outcrops of oak are a unique habitat feature on the ponderosa pine landscape, providing cover, burrowing spaces, and food for a variety of wildlife (Rosenstock 1998).

The overall positive response by the small mammal community to the number and duration of slash piles may be because the animals are using the piles as cover, given that thinned sites often lose down wood, understory vegetation, and snags in the short term (Chambers and Germaine 2003). The piles, acting as surrogate habitat, may give the animals an opportunity to reestablish while the site is otherwise recovering from disturbance. The exceptions are deer mouse and Botta's pocket gopher; deer mouse tend to populate recently disturbed areas (Zwolak 2009) and thus may be outcompeted by other animals that thrive in an otherwise highly disturbed site due to the slash piles. However, deer mouse occupancy probabilities remained close to 0.8 even with slash piles. Botta's pocket gopher also responded negatively to slash, likely because it lives underground and derives no benefits from slash, and may instead be negatively impacted by the ground disturbance caused by treatment. Overall, however, slash is one of the few habitat variables that can be relatively easily manipulated with such positive results across the community.

For the UTM covariate, the direction of the response is not informative, however a strong response indicates site influence (i.e., species was found at the same site over multiple years). The four largest and long-lived species (Mexican woodrat, tassel-eared squirrel, golden-mantled ground squirrel, rock squirrel; Hoffmeister 1986) responded strongly to this covariate. These species may be more susceptible to the long-term effects of habitat alteration than the short-lived, more transient species.

Management and research implications

The goal of restoration treatments in the Southwest is not to maximize or increase the occupancy of species, but rather to restore the ecosystem and associated wildlife to the composition, structure, and function of presettlement conditions. We are not advocating increasing occupancy of any or all species across the Southwest, but rather leave it to managers to determine desired conditions in a particular landscape. In addition, we caution that the tradeoffs we see among small mammal species are likely to exist among other mammals, birds, and invertebrates, and all other species that live in ponderosa pine forests.

Forest management in the Southwest tends to promote retention of big ponderosa pine trees, snags, and oak trees. Our results showed that these attributes are good for some species, but like stand structure there is no “one-size-fits-all” solution for the small mammal community. A diversity of these features across the landscape will restore and maintain the diversity of the small mammal community. As some of these features (i.e., snags and big trees) have decreased in prevalence on the landscape (Cooper 1961), managers may choose to make efforts to retain them. However, more is not always necessarily better; for example, managers in the Southwest protect Gambel oak when implementing treatments, and thus this tree species has been increasing in density since presettlement times (Abella and Fulé 2008). Although oak retention may be important for other animals, our results showed that increasing oak BA is not necessarily better for the small mammal community, particularly because only one species responded strongly to it (rock squirrel).

We also showed that the size of a “big tree” matters in predicting small mammal occupancy, as trees >40cm dbh had little effect but trees >50cm dbh had an overall positive effect. This may be useful to managers attempting to establish diameter caps for thinning or harvesting treatments. The retention of slash piles on the landscape for several years (piles in our sites were burned after no more than 3 years) should lead to increased occupancy of all small mammal species, but some management agencies choose to burn the piles immediately. However, the immediate removal of fuel reduces fire risk, a concern which often supersedes wildlife issues.

The tassel-eared squirrel has been highlighted as a species that will be negatively impacted by thinning and restoration treatments (Patton et al. 1985, Dodd et al. 2006). Our results uphold this inference. However, the fact that the majority of the small mammal community increased in occupancy due to thinning and slash treatments should not be overlooked. Furthermore, restoration treatments should, in the long term, promote the growth of large trees to which tassel-eared squirrels responded positively. Thus, although tassel-eared squirrel remain an indicator of the negative effects of treatment, we offer golden-mantled ground squirrel as an indicator of the positive effects, as it had a strong response to treatment, slash, and reduced pine basal area. Similarly, the Mogollon vole showed a dramatic response to understory vegetation cover, with occupancy probabilities ranging from 0 in sites with no vegetation and 0.6 at sites with high cover (65%); thus, this species may be a good indicator of a recovered site.

Finally, we found that the rapid assessment, occupancy modeling approach was highly effective in evaluating the response of the small mammal community to treatment and other habitat attributes. Small mammal studies are commonly confounded by high year-to-year variability, because r-selected species with short life spans and high reproductive rates react quickly and dramatically to environmental and climatic changes (MacArthur and Wilson 1967). Particularly in the arid Southwest, most small mammal population studies end up primarily tracking precipitation patterns (Bagne and Finch 2009). We showed a lack of a year effect by all species. We attribute this to the fact that we measured occupancy, which should be more resistant to yearly changes, rather than density.

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 this study was a big effort, it obtained more reliable, repeatable results for a greater number of species than many of the equally-intensive small mammal studies with similar objectives, which relied on mark-recapture methods and density estimation. The volume of data we collected and the spatial scale at which we designed this study resulted in clear patterns in response to habitat attributes with relatively small standard errors. We suggest this design be utilized in other studies that grapple with high variability and large spatial and temporal scales in assessing general impacts of treatments or habitat change on wildlife species. Our study occurred at the stand level because that is currently the scale at which treatments are being planned and implemented in the Southwest ponderosa pine forests. However, management is moving towards landscape-scale projects (i.e., the Four Forests Initiative in Arizona) and better ecological information at larger spatial scales is needed to inform these efforts. This necessitates scaling up of studies of small mammals and other species, which could be achieved using occupancy approaches more readily than demographic methods. We see this approach as having great potential for wildlife assessment and monitoring at the landscape level in an extremely cost efficient manner.

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Tables

Table 3-1. Descriptions and summary statistics for habitat covariates measured in northern Arizona (*n* = 294).

Habitat covariate	**Calculation**	**Range**	**Median**	**Average**	**Standard deviation**	**Final variable abbreviation**
Pine BA (m^2/ha)	Sum(((dbh/100/2)^2)*3.14)*40	0-109.5	28.6	33.4	20.2	**Pine**
Oak BA (m^2/ha)	Sum(((dbh/100/2)^2)*3.14)*40	0-42	0	1.8	5.0	**Oak**
Veg (% cover)	Average of 5 plots per site	0-65	19.1	21.4	13.6	**Veg**
Veg >40cm high (% cover)	Average of 5 plots per site	0-43	0	1.0	3.5	(Omitted from analysis)
Veg richness (# 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 5 plots per site	0-47	10.2	12.3	9.3	**Rock**
Down wood volume (m3/m2)	9.869*((sum of diameters of wood pieces in plot)^2))/8*20m)) (Harmon and Sexton 1996)	0-1910.6	3.5	54.5	201.1	(Omitted from analysis)
Trees >40cm dbh (#/ha)	(#/plot)*40	0-240	45.0	68.0	58.1	(Omitted from analysis)
Trees >50cm dbh (#/ha)	(#/plot)*40	0-240	0	25.2	36.6	**Bigtrees**
Trees >60cm dbh (#/ha)	(#/plot)*40	0-160	0	10.8	25.7	(Omitted from analysis)
Snags (#/ha)	(#/plot)*40	0-1120	0	54.3	124.7	**Snags**
Snags >40cm (#/ha)	(#/plot)*40	0-40	0	2.6	9.7	**Snags16**
Snags >50cm (#/ha)	(#/plot)*40	0-40	0	1.4	7.3	(Omitted from analysis)
Snags >60cm (#/ha)	(#/plot)*40	0-40	0	0.75	5.3	(Omitted from analysis)
Slash piles (#)	#/site	0-38	0	1.4	4.9	**Slash** (combined using PCA)
Time of intact slash piles (yrs)	Years	0-3	0	0.4	0.7	
Trees/ha removed (%)	(Stumps/ha)/(total trees/ha + stumps/ha)	0-97.9	37.5	38.5	30.5	**Treatment** (combined using PCA)
Time since treatment (yrs)	Years	1-109	12	24.3	36.1	
Year[1]	2006-2009 equals years 1-4	-	-	-	-	**Year**
UTMs[1]	UTM coordinates of each site	-	-	-	-	**UTM** (combined using PCA)

1 Summary statistics are not meaningful for these covariates; see methods for covariate descriptions.

Table 3-2. Species code, occupancy (ψ) models with $\Delta AIC_c \leq 2$, number of parameters (K), AIC value corrected for small sample size (AIC_c), difference in AIC_c between models (ΔAIC_c), and the relative weight of each model (w_i). A period (.) indicates the null model. For each species the most parsimonious model of detection (p) was used.

Species	**Model**[1]	**K**	**AIC_c**	**ΔAIC_c**	**w_i**
Mogollon vole	ψ (veg + snags16) p(week)	5	300.34	0	0.65
	ψ (rock + veg) p(week)	5	301.71	1.37	0.33
Mexican woodrat	ψ (pine + treatment + slash + UTM) p(.)	6	150.96	0	0.81
Deer mouse	ψ (rock + bigtrees + snags16) p(year)	6	1152.63	0	0.83
Tassel-eared squirrel	ψ (pine + treatment + slash + UTM) p(year)	7	690.33	0	0.58
	ψ (pine + bigtrees + treatment + UTM) p(year)	7	691.41	1.08	0.34
Golden-mantled ground squirrel	ψ (pine + treatment + slash + UTM) p(survey)	12	929.34	0	0.84
Rock squirrel	ψ (oak + rock + UTM) p(.)	5	579.95	0	1.00
Gray-collared chipmunk	ψ (pine + snags + snags16) p(.)	5	606.29	0	0.57
Botta's pocket gopher	ψ (rock + veg) p(week)	5	380.42	0	0.55
	ψ (veg + snags16) p(week)	5	380.87	0.45	0.44

1 Abbreviations for covariates are defined in Table 3-1.

Table 3-3. Cumulative AIC weights ($w_+(j)$) for assessing the relative importance of habitat covariates used to predict occupancy of 8 species of small mammals, followed by the direction of the response in parenthesis. Bolded values indicate $w_+(j) \geq 0.50$ and were considered strong evidence for a species response to the habitat covariate. For each species the most parsimonious model of detection probability was used (Table 3-2).

Species	**Pine BA (m2/ha)**	**Oak BA (m2/ha)**	**Rock (% cover)**	**Understory Vegetation (% cover)**	**Trees >50 cm dbh (#/ha)**	**Snags (#/ha)**	**Snags >40cm (#/ha)**	**Treatment**	**Slash**	**Year**	**UTM**
Mogollon vole	0.018 (-)	0.000 (-)	0.329 (-)	**0.981 (+)**	0.001 (-)	0.016 (-)	**0.669 (+)**	0.002 (+)	0.001 (+)	0.001 (-)	0.002 (+)
Mexican woodrat	**0.887 (+)**	0.112 (+)	0.112 (+)	0.000 (-)	0.075 (+)	0.000 (-)	0.000 (+)	**0.887 (-)**	**0.812 (+)**	0.075 (-)	**0.925 (-)**
Deer mouse	0.004 (-)	0.040 (+)	**0.989 (+)**	0.125 (+)	**0.829 (+)**	0.002 (+)	**0.830 (+)**	0.003 (+)	0.000 (-)	0.000 (+)	0.043 (+)
Tassel-eared squirrel	**0.925 (+)**	0.073 (+)	0.074 (-)	0.001 (-)	0.341 (+)	0.000 (-)	0.001 (+)	**0.925 (-)**	**0.584 (+)**	0.000 (-)	**0.998 (+)**
Golden-mantled ground squirrel	**0.842 (-)**	0.158 (+)	0.000 (-)	0.000 (+)	0.001 (+)	0.158 (-)	0.000 (-)	**0.842 (+)**	**0.999 (+)**	0.160 (-)	**0.842 (-)**
Rock squirrel	0.000 (-)	**1.000 (+)**	**1.000 (+)**	0.000 (-)	0.000 (+)	0.000 (+)	0.000 (-)	0.000 (+)	0.000 (+)	0.000 (-)	**1.000 (+)**
Gray-collared chipmunk	**0.704 (-)**	0.036 (-)	0.069 (+)	0.190 (+)	0.150 (+)	**0.598 (-)**	**0.718 (+)**	0.137 (+)	0.031 (+)	0.168 (-)	0.142 (-)
Botta's pocket gopher	0.002 (-)	0.000 (-)	**0.555 (-)**	**0.998 (+)**	0.002 (+)	0.000 (-)	0.443 (-)	0.002 (-)	0.000 (-)	0.002 (-)	0.002 (-)

Table 3-4. Summary of peer-reviewed studies that assess small mammal population responses (using live-trapping) to forest management practices in the southwestern U.S.

	Roberts (2003)	Dodd et al. (2006)	Kyle & Block (2000)	Converse et al. (2006a)	Wampler et al. (2008)	**Kalies**	Converse et al. (2006b)	Bagne & Finch (2009)	Patton et al. (1985)
Response variable	Density, abundance	Recruitment, survival	Density	Density	Abundance, survival	**Occupancy**	Density	Density, abundance	Density
# species	3	1	2	4	3	**8**	2	4	1
Total area per year (ha)	24	558	48	168	20	**135**	125	5	84
Duration of study (yrs)	3	1	1	6	2	**4**	3	5	8
Total trap nights	**4,586**	**5,760**	**10,277**	**15,840**	**27,440**	**29,988**	**32,400**	**42,000**	**44,280**

Figures

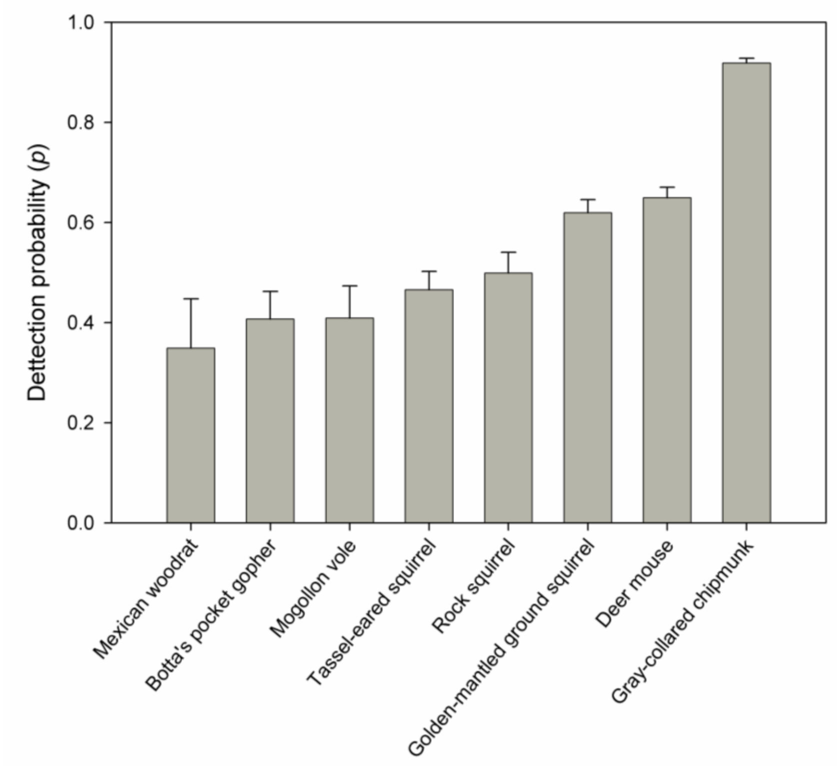


Figure 3-1. Detection probabilities (± SE) (*n* = 294) for 8 species of small mammals over the 4 years of the study. Each model uses the most parsimonious model of occupancy for each species (Table 3-2).

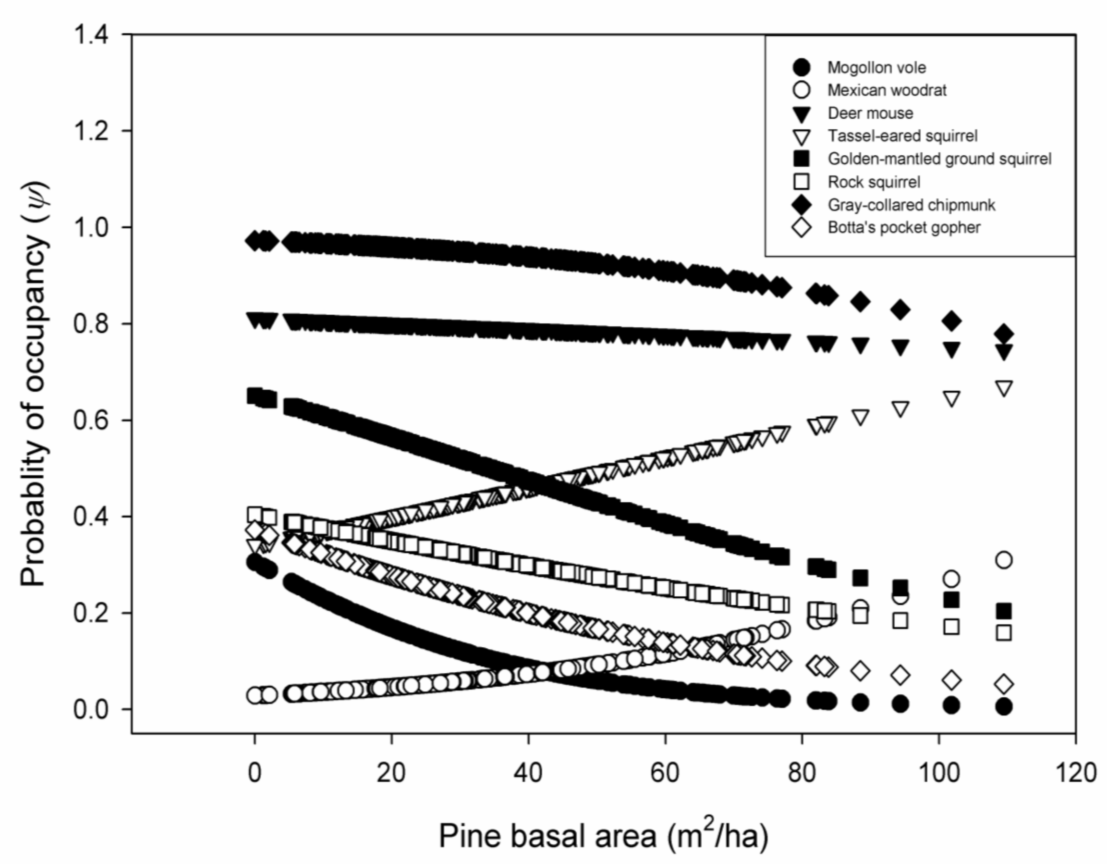
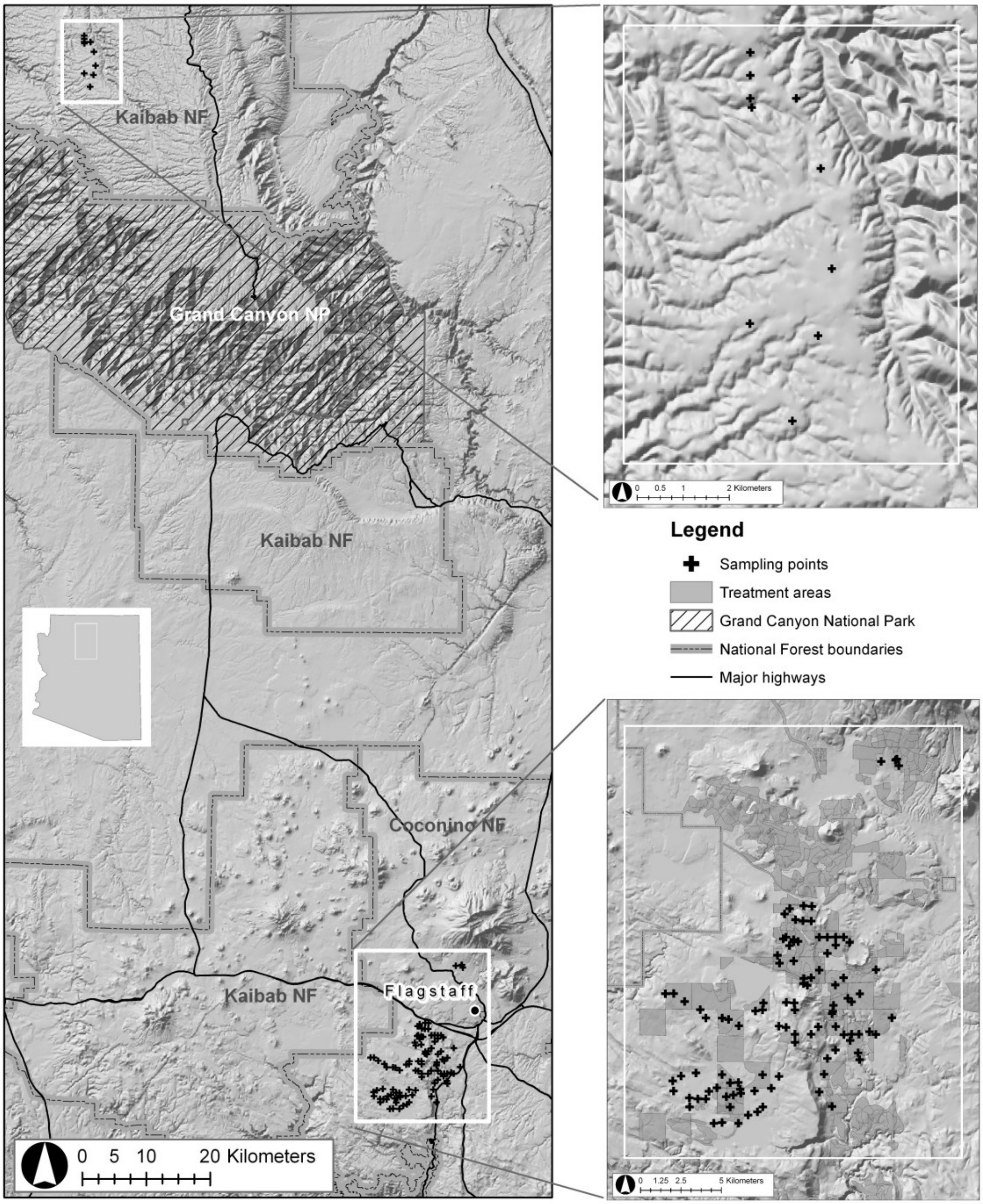


Figure 3-2. Probability of occupancy (*n* = 294) for 8 species of small mammals in response to pine basal area. Error bars are not shown to increase readability; see Appendix 3-B and 3-C for SEs. Each model uses the most parsimonious model of detection probability for each species (Table 3-2).

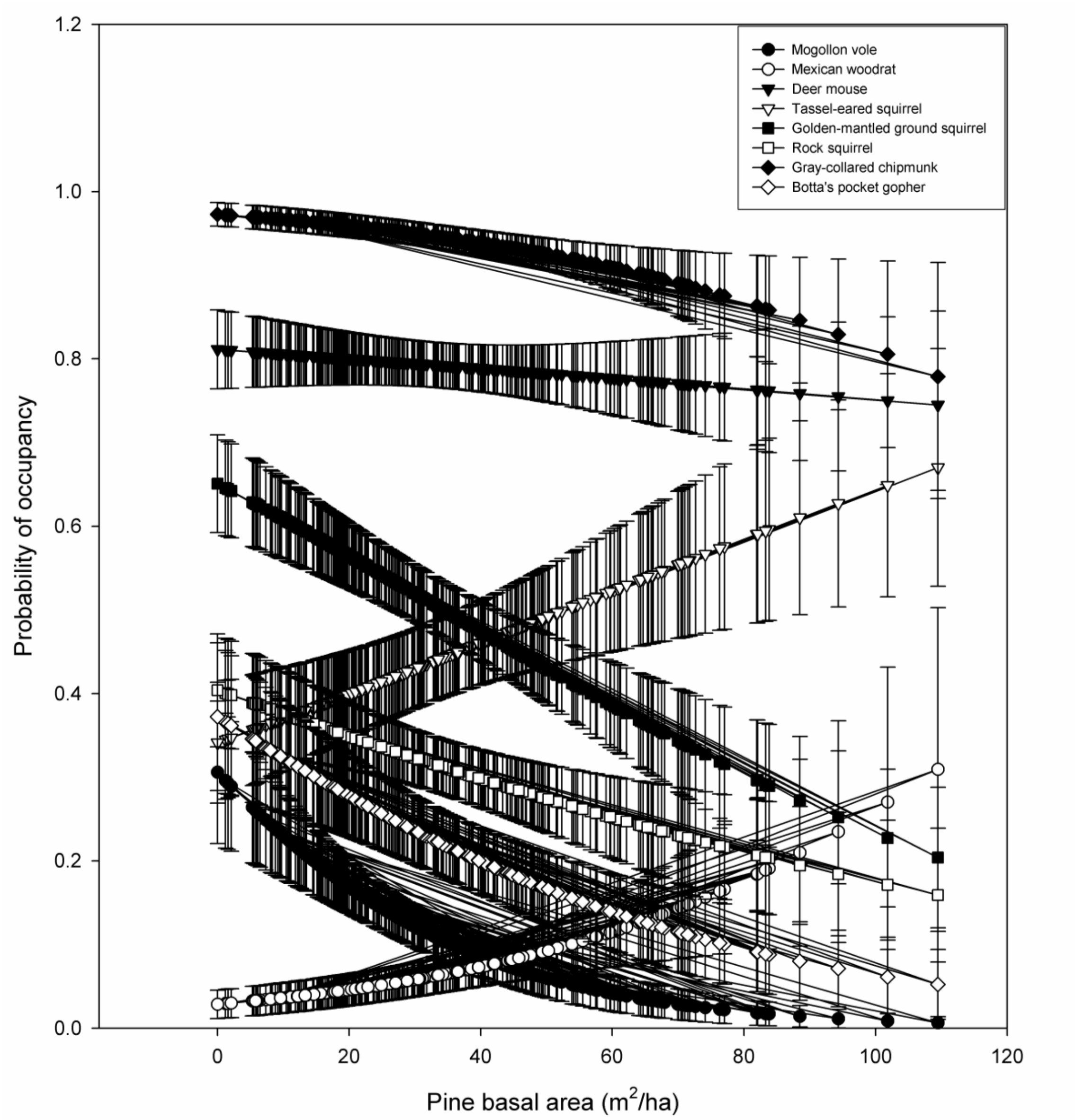
Appendix 3-A

Figure of study areas



Appendix 3-B

Probability of occupancy for 8 species of small mammals in response to pine basal area (Figure 3-2) with error bars



Appendix 3-C

Occupancy probabilities (*ψ*) and standard errors (SE) for each species for pine basal area (Figure 3-2, Appendix 3-B)

Pine BA	Mogollon vole		Mexican woodrat		Deer mouse		Tassel-eared squirrel		Golden-mantled ground squirrel		Rock squirrel		Gray-collared chipmunk		Botta's pocket gopher	
	Ψ	SE	Ψ	SE	Ψ	SE	Ψ	SE	Ψ	SE	Ψ	SE	Ψ	SE	Ψ	SE
0	0.306	0.085	0.028	0.017	0.811	0.047	0.341	0.072	0.651	0.058	0.404	0.068	0.973	0.014	0.372	0.088
1	0.296	0.081	0.029	0.017	0.811	0.046	0.345	0.071	0.646	0.057	0.400	0.066	0.972	0.014	0.366	0.085
2	0.293	0.079	0.030	0.017	0.811	0.046	0.346	0.070	0.644	0.057	0.399	0.065	0.972	0.014	0.364	0.085
5	0.264	0.066	0.032	0.018	0.809	0.043	0.356	0.066	0.629	0.053	0.389	0.059	0.970	0.014	0.346	0.076
6	0.262	0.066	0.032	0.018	0.808	0.042	0.357	0.066	0.628	0.053	0.388	0.059	0.970	0.014	0.345	0.075
7	0.249	0.060	0.034	0.018	0.807	0.041	0.362	0.064	0.620	0.051	0.383	0.056	0.968	0.014	0.336	0.072
8	0.244	0.058	0.035	0.018	0.807	0.040	0.364	0.063	0.617	0.050	0.381	0.055	0.968	0.014	0.332	0.070
9	0.234	0.054	0.036	0.018	0.806	0.039	0.368	0.062	0.611	0.049	0.378	0.053	0.967	0.014	0.326	0.067
10	0.233	0.053	0.036	0.018	0.806	0.039	0.369	0.062	0.611	0.049	0.377	0.053	0.967	0.014	0.325	0.067
11	0.222	0.049	0.037	0.018	0.805	0.038	0.373	0.060	0.604	0.047	0.373	0.050	0.966	0.014	0.318	0.064
12	0.218	0.047	0.038	0.018	0.805	0.037	0.375	0.059	0.601	0.047	0.371	0.050	0.965	0.014	0.315	0.062
13	0.208	0.044	0.039	0.019	0.804	0.036	0.380	0.058	0.594	0.045	0.367	0.048	0.964	0.014	0.307	0.060
14	0.207	0.043	0.039	0.019	0.804	0.036	0.380	0.058	0.593	0.045	0.366	0.047	0.964	0.014	0.307	0.059
15	0.195	0.039	0.041	0.019	0.803	0.035	0.386	0.056	0.585	0.043	0.362	0.045	0.963	0.014	0.298	0.056
16	0.194	0.039	0.041	0.019	0.803	0.035	0.386	0.056	0.584	0.043	0.361	0.045	0.963	0.014	0.297	0.056
17	0.184	0.036	0.043	0.019	0.802	0.033	0.391	0.054	0.577	0.041	0.356	0.043	0.961	0.014	0.290	0.053
18	0.182	0.035	0.043	0.019	0.802	0.033	0.392	0.054	0.575	0.041	0.356	0.042	0.961	0.014	0.288	0.053
19	0.172	0.032	0.045	0.019	0.801	0.032	0.398	0.052	0.567	0.040	0.351	0.040	0.960	0.014	0.280	0.050
20	0.171	0.032	0.045	0.019	0.801	0.032	0.398	0.052	0.567	0.039	0.350	0.040	0.959	0.014	0.279	0.050
21	0.161	0.030	0.048	0.019	0.800	0.031	0.404	0.051	0.558	0.038	0.345	0.038	0.958	0.014	0.271	0.047
22	0.160	0.030	0.048	0.019	0.799	0.031	0.404	0.051	0.558	0.038	0.345	0.038	0.958	0.014	0.271	0.047
23	0.154	0.028	0.049	0.019	0.799	0.030	0.408	0.050	0.552	0.037	0.342	0.037	0.957	0.014	0.265	0.046

Pine BA	Mogollon vole		Mexican woodrat		Deer mouse		Tassel-eared squirrel		Golden-mantled ground squirrel		Rock squirrel		Gray-collared chipmunk		Botta’s pocket gopher	
	Ψ	SE	Ψ	SE	Ψ	SE	Ψ	SE	Ψ	SE	Ψ	SE	Ψ	SE	Ψ	SE
24	0.150	0.028	0.050	0.020	0.798	0.030	0.410	0.050	0.548	0.036	0.340	0.037	0.956	0.014	0.262	0.045
25	0.141	0.027	0.052	0.020	0.797	0.029	0.416	0.049	0.540	0.035	0.335	0.035	0.954	0.014	0.255	0.043
26	0.141	0.026	0.052	0.020	0.797	0.029	0.416	0.049	0.540	0.035	0.335	0.035	0.954	0.014	0.254	0.043
27	0.132	0.025	0.055	0.020	0.796	0.028	0.422	0.048	0.531	0.034	0.330	0.034	0.952	0.014	0.247	0.042
28	0.132	0.025	0.055	0.020	0.796	0.028	0.422	0.048	0.531	0.034	0.330	0.034	0.952	0.014	0.246	0.042
29	0.126	0.025	0.057	0.020	0.795	0.028	0.427	0.048	0.525	0.034	0.326	0.034	0.951	0.014	0.241	0.041
30	0.123	0.025	0.058	0.020	0.795	0.027	0.428	0.047	0.522	0.034	0.324	0.033	0.950	0.014	0.238	0.041
31	0.115	0.024	0.060	0.021	0.794	0.027	0.434	0.047	0.513	0.033	0.320	0.033	0.948	0.014	0.231	0.040
32	0.114	0.024	0.061	0.021	0.794	0.027	0.435	0.047	0.512	0.033	0.319	0.033	0.948	0.014	0.229	0.040
33	0.110	0.024	0.062	0.021	0.793	0.027	0.438	0.047	0.507	0.033	0.316	0.033	0.947	0.014	0.226	0.039
34	0.105	0.024	0.064	0.022	0.792	0.027	0.443	0.048	0.500	0.033	0.312	0.033	0.945	0.014	0.220	0.039
35	0.103	0.024	0.065	0.022	0.792	0.027	0.444	0.048	0.498	0.033	0.311	0.033	0.945	0.014	0.218	0.039
36	0.097	0.024	0.068	0.022	0.791	0.027	0.449	0.048	0.491	0.033	0.307	0.033	0.943	0.014	0.212	0.039
37	0.097	0.024	0.068	0.022	0.791	0.027	0.450	0.048	0.490	0.033	0.307	0.033	0.943	0.014	0.212	0.039
38	0.091	0.024	0.071	0.023	0.790	0.028	0.456	0.049	0.482	0.034	0.302	0.034	0.941	0.014	0.205	0.039
39	0.090	0.024	0.071	0.023	0.790	0.028	0.456	0.049	0.481	0.034	0.302	0.034	0.941	0.015	0.205	0.039
40	0.085	0.024	0.074	0.024	0.789	0.028	0.462	0.050	0.473	0.035	0.297	0.034	0.938	0.015	0.198	0.039
41	0.084	0.024	0.074	0.024	0.789	0.028	0.462	0.051	0.472	0.035	0.297	0.035	0.938	0.015	0.198	0.039
42	0.079	0.024	0.077	0.025	0.788	0.029	0.467	0.052	0.464	0.036	0.293	0.035	0.936	0.015	0.192	0.040
43	0.078	0.024	0.078	0.025	0.787	0.029	0.468	0.052	0.463	0.036	0.292	0.036	0.936	0.015	0.191	0.040
44	0.073	0.024	0.081	0.026	0.786	0.030	0.475	0.054	0.454	0.037	0.287	0.037	0.933	0.016	0.184	0.040
45	0.072	0.024	0.082	0.026	0.786	0.031	0.475	0.054	0.453	0.038	0.287	0.037	0.933	0.016	0.184	0.041
46	0.068	0.024	0.085	0.027	0.785	0.032	0.481	0.056	0.446	0.039	0.283	0.038	0.931	0.017	0.178	0.041
47	0.067	0.024	0.086	0.028	0.785	0.032	0.482	0.056	0.444	0.039	0.282	0.038	0.930	0.017	0.177	0.041
48	0.064	0.024	0.089	0.029	0.784	0.033	0.486	0.058	0.438	0.040	0.279	0.039	0.928	0.018	0.173	0.042

Pine BA	Mogollon vole		Mexican woodrat		Deer mouse		Tassel-eared squirrel		Golden-mantled ground squirrel		Rock squirrel		Gray-collared chipmunk		Botta’s pocket gopher	
	Ψ	SE	Ψ	SE	Ψ	SE	Ψ	SE	Ψ	SE	Ψ	SE	Ψ	SE	Ψ	SE
49	0.063	0.024	0.089	0.029	0.784	0.033	0.488	0.058	0.436	0.041	0.278	0.040	0.927	0.018	0.171	0.042
50	0.059	0.023	0.093	0.031	0.783	0.035	0.493	0.060	0.428	0.042	0.273	0.041	0.925	0.019	0.166	0.042
51	0.057	0.023	0.095	0.032	0.782	0.036	0.496	0.061	0.423	0.043	0.271	0.042	0.923	0.020	0.163	0.043
52	0.056	0.023	0.096	0.032	0.782	0.036	0.497	0.062	0.422	0.043	0.271	0.042	0.923	0.020	0.162	0.043
54	0.052	0.023	0.101	0.034	0.781	0.038	0.504	0.064	0.412	0.046	0.266	0.044	0.920	0.021	0.156	0.044
55	0.050	0.023	0.103	0.035	0.780	0.038	0.507	0.066	0.409	0.047	0.264	0.044	0.918	0.022	0.153	0.044
56	0.049	0.023	0.104	0.036	0.780	0.039	0.509	0.067	0.405	0.047	0.262	0.045	0.917	0.023	0.151	0.044
57	0.047	0.022	0.107	0.038	0.779	0.040	0.513	0.068	0.400	0.049	0.259	0.046	0.915	0.024	0.148	0.045
58	0.045	0.022	0.110	0.039	0.778	0.041	0.516	0.070	0.396	0.050	0.257	0.047	0.913	0.025	0.145	0.045
59	0.043	0.022	0.113	0.041	0.777	0.043	0.520	0.072	0.390	0.051	0.254	0.048	0.911	0.026	0.142	0.045
60	0.042	0.022	0.114	0.042	0.777	0.044	0.522	0.072	0.387	0.052	0.253	0.049	0.910	0.026	0.140	0.045
61	0.040	0.021	0.119	0.044	0.776	0.045	0.527	0.075	0.381	0.053	0.249	0.050	0.907	0.028	0.136	0.046
62	0.038	0.021	0.121	0.046	0.776	0.046	0.530	0.076	0.376	0.054	0.247	0.051	0.906	0.029	0.134	0.046
64	0.036	0.020	0.126	0.049	0.774	0.048	0.536	0.079	0.369	0.056	0.243	0.052	0.902	0.031	0.129	0.047
65	0.034	0.020	0.130	0.051	0.774	0.050	0.540	0.081	0.363	0.057	0.240	0.053	0.900	0.033	0.126	0.047
66	0.034	0.020	0.130	0.051	0.773	0.050	0.540	0.081	0.362	0.057	0.240	0.054	0.899	0.033	0.125	0.047
67	0.032	0.019	0.134	0.054	0.773	0.052	0.545	0.083	0.356	0.059	0.237	0.055	0.897	0.035	0.122	0.047
68	0.031	0.019	0.136	0.055	0.772	0.053	0.546	0.084	0.354	0.059	0.236	0.055	0.896	0.036	0.121	0.047
70	0.028	0.018	0.145	0.061	0.770	0.056	0.555	0.089	0.342	0.062	0.230	0.058	0.890	0.040	0.114	0.048
71	0.028	0.018	0.145	0.062	0.770	0.056	0.556	0.089	0.341	0.063	0.229	0.058	0.889	0.040	0.114	0.048
72	0.027	0.018	0.149	0.064	0.770	0.058	0.559	0.091	0.337	0.064	0.227	0.059	0.887	0.042	0.111	0.048
73	0.026	0.018	0.152	0.066	0.769	0.059	0.562	0.092	0.333	0.064	0.225	0.059	0.885	0.043	0.109	0.048
74	0.024	0.017	0.157	0.070	0.768	0.061	0.567	0.094	0.327	0.066	0.222	0.061	0.882	0.046	0.106	0.048
76	0.022	0.017	0.164	0.075	0.767	0.064	0.573	0.098	0.318	0.068	0.218	0.062	0.877	0.050	0.102	0.048
77	0.022	0.016	0.166	0.077	0.766	0.065	0.576	0.099	0.316	0.068	0.216	0.063	0.875	0.051	0.101	0.048

Pine BA	Mogollon vole		Mexican woodrat		Deer mouse		Tassel-eared squirrel		Golden-mantled ground squirrel		Rock squirrel		Gray-collared chipmunk		Botta’s pocket gopher	
	Ψ	**SE**	**Ψ**	**SE**	**Ψ**	**SE**	**Ψ**	**SE**	**Ψ**	**SE**	**Ψ**	**SE**	**Ψ**	**SE**	**Ψ**	**SE**
82	0.018	0.015	0.184	0.091	0.763	0.071	0.591	0.106	0.297	0.072	0.207	0.066	0.863	0.061	0.091	0.048
83	0.017	0.014	0.189	0.095	0.762	0.073	0.595	0.108	0.292	0.073	0.204	0.067	0.860	0.063	0.089	0.048
84	0.017	0.014	0.191	0.097	0.762	0.074	0.596	0.109	0.290	0.073	0.203	0.067	0.859	0.065	0.088	0.048
89	0.014	0.013	0.210	0.112	0.759	0.081	0.610	0.116	0.273	0.076	0.195	0.070	0.846	0.075	0.080	0.047
94	0.011	0.011	0.235	0.132	0.755	0.089	0.627	0.124	0.252	0.079	0.184	0.074	0.829	0.090	0.071	0.046
102	0.009	0.009	0.270	0.162	0.750	0.100	0.649	0.133	0.227	0.082	0.171	0.077	0.806	0.112	0.061	0.044
109	0.006	0.008	0.309	0.194	0.745	0.112	0.670	0.142	0.204	0.084	0.159	0.080	0.779	0.136	0.052	0.042

CHAPTER 4

SMALL MAMMAL COMMUNITY MAINTAINS STABILITY THROUGH COMPOSITIONAL AND FUNCTIONAL COMPENSATION IN RESPONSE TO DISTURBANCE IN A SOUTHWESTERN PONDEROSA PINE FOREST ECOSYSTEM

Abstract

Understanding ecosystem stability has been of increasing interest in the past several decades as it helps predict the consequences of anthropogenic disturbances on ecosystems. Species may exhibit stability through compensation, with greatly fluctuating populations year-to-year but a consistent density response over time in the face of multiple disturbances. Stability is increased by functional redundancy, where species with similar functional roles compensate for one another by responding differently to environmental change. Historically, the southwestern ponderosa pine ecosystem experienced repeated disturbance in the form of frequent fire. Due to fire suppression, today's forests have become unnaturally dense; there is now an emphasis on ecological restoration, whereby forests are thinned so that the natural fire regime can be safely reintroduced in an effort to restore ecosystem function to historical conditions. Using Royle density models and multi-model inference, we examined responses of 8 species of small mammals to restoration (thinning and slash) treatments to determine if the community maintains total density and function (represented by ectomycorrhizal fungi dispersion) after disturbance. Community composition differed in each of 6 years following treatment, but total density remained constant. Total species densities were significantly lower in stands with dense conditions than in stands with more open structural conditions similar to those of presettlement times, which had similar small mammal densities as the thinning treatments. In addition, tassel-eared squirrels (*Sciurus aberti*), golden-mantled ground squirrels (*Spermophilus lateralis*), and gray-collared chipmunks (*Tamias cinereicollis*) appeared to play a functionally redundant role in dispersing ectomycorrhizal fungi across different stand structures. These results suggest that restoration treatments are maintaining ecosystem stability in terms of small mammal community structure and function.

Key Words: small mammal community, *Microtus mogollonensis*, *Neotoma mexicana*, *Peromyscus maniculatus*, *Sciurus aberti*, *Spermophilus lateralis*, *Spermophilus variegates*, *Tamias cinereicollis*, *Thomomys bottae*, ectomycorrhizal fungi dispersal, restoration treatment, thinning, Royle density models, ponderosa pine, *Pinus ponderosa*

Introduction

The relationship between species composition and ecosystem stability has been of increasing interest. While research often focuses on biodiversity as a stabilizing mechanism, an alternative theory proposes that ecosystem stability is a result of compensatory population dynamics of interacting species (Ernest and Brown 2001, Hughes et al. 2002). For example, long-term studies on the Chihuahuan desert show that composition of small mammal species changes in response to disturbance, but richness, total population size, and biomass remain relatively constant (Ernest and Brown 2001). A similar result was found in Tanzania, where individual ungulate grazer species changed in population size over time, but overall herbivore biomass remained constant (Prins and Douglas-Hamilton 1990). Thus, species compensation seems to lead to greater stability.

Resistance is defined as the ability of species to withstand change (Pimm 1991). For vertebrates, this may mean that despite a reduction in numbers, the population remains viable. The other strategy in the face of disturbance is resilience, or the ability to rebound quickly after an environmental perturbation (Pimm 1991). These two strategies are associated with different life histories; resistant species tend to be long-lived and far-ranging, with large body sizes and low reproductive outputs, and resilient species are usually small bodied, abundant, with high reproductive outputs (MacArthur and Wilson 1967, Hairston et al. 1970). Therefore, assessing population fluctuations as a proxy for stability may not be accurate; resilient species may exhibit widely fluctuating populations year-to-year, but a consistent response over time. For example, fluctuating populations of rodents seems to be within the natural range of variability in desert environments (Brown and Ernest 2002). Klinger (2006) showed that in response to floods in Belize, species of small mammals retained ecosystem stability via resilience, with a high degree of variability of population size.

When species have similar functional roles but respond somewhat differently to environmental change, this creates functional redundancy. Functional redundancy has never been demonstrated empirically with vertebrates, although Naeem and Li (1997) showed it held in an experiment using microbes. However, there is strong theoretical evidence in support of this hypothesis (Naeem 1998, Yachi and Loreau 1999, Hughes et al. 2002). This is an important concept in terms of environmental perturbations, in that it would indicate that a diverse system would be able to maintain ecosystem functioning in the face of environmental change (Ehrlich and Walker 1998).

Historically, the southwestern ponderosa pine ecosystem experienced frequent disturbance via a natural fire regime with a 2-20 year interval (Covington and Moore 1994, Fulé et al. 1997). The resulting heterogeneity in time and space is the natural range of variability to which wildlife in ponderosa pine is adapted and may depend on for their long-term sustainability. Noss and Csuti (1994) state that the greatest threat to biological diversity is the loss of evolutionary habitats, which is precisely what is happening in today's ponderosa pine forests due to fire suppression and crown fire, which have created dense, homogenous forest stands very different from historical conditions (Moore et al. 1999, Westerling et al. 2006). Thus, there is now an emphasis on ecological restoration in the Southwest, whereby forests are thinned to reduce fuel loads and the risk of crown fire, after which the natural fire regime can be safely reintroduced. In this case, humans are introducing a perturbation meant to emulate natural disturbance; current conditions are outside of historical conditions or the "natural range of variability" (Landres et al. 1999). Thus, restoration treatments seek to restore ecosystem stability and function.

Small mammals commonly present in ponderosa pine forests of the Southwest include voles (*Microtus spp.)*, woodrats (*Neotoma spp.)*, mice *(Peromyscus spp.)*, ground and tree squirrels (*Spermophilus* and *Sciurus spp.)*, chipmunks (*Tamias spp.),* and gophers *(Thomomys spp.)*. As with other small mammal communities, year-to-year variability in density occurs due to environmental conditions such as drought and fire (Brown and Ernest 2002, Converse et al. 2006). These species may play similar roles in ecosystem functioning, including serving as prey for predators, increasing soil aeration, impacting regeneration abundance and patterns, and dispersing fungi (Hooven 1966, Cork and Kenagy 1989, Boal and Mannan 1994, Pyare and Longland 2001). In particular, the dispersion of hypogeous fungi is largely reliant on small mammal disturbance and transfer through feces (Johnson 1996). Due to the physical size of ectomycorrhizal (EM) fungal spores, known as truffles, dispersal occurs primarily by ungulates and small mammals.

In ponderosa pine forests, tassel-eared squirrels (*Sciurus aberti*) are dispersers of EM fungi (States et al. 1988, Dodd et al. 2003), but the contribution of other small mammal species is unknown. Research in other forest types shows that voles, woodrats, ground squirrels, chipmunks, and pocket gophers can potentially disperse EM fungi (Claridge et al. 1999, Pyare and Longland 2001, Taylor et al. 2009). Although tassel-eared squirrels are closely linked with dense stands of trees, other animals, including golden-mantled ground squirrels (*Spermophilus lateralis)* and Mogollon voles (*Microtus mogollonensis),* are associated with open stands (Chapter 3). Meanwhile, generalists such as gray-collared chipmunks (*Tamias cinereicollis)* and deer mice *(Peromyscus maniculatus)* are found throughout various stand densities (Chapter 3). In ponderosa pine forests, various members of the small mammal community may play similar functional roles, including that of fungal dispersion, in the different habitat types they occupy. While fungal dispersion is not necessarily the most important function the community provides, we used it in this study to represent whether or not functional redundancy occurred within the community.

We examined density responses of 8 species of small mammals to thinning and slash treatments in order to understand how they responded to disturbance. Typically, two disturbances occur during restoration treatments in southwestern ponderosa pine forests: first, the stand is thinned and the non-merchantable wood is stacked into slash piles, and second, the piles are burned after 0-3 years. We predicted that although individual species densities would fluctuate in response to treatments, total community density would remain constant. However, we predicted that slash would alter species compositions depending on the length of time the piles were left intact. Density compensation among species would allow EM fungi dispersion to occur in different habitat types by different species at similar levels. The objectives of this study were to 1) determine if small mammal community total density remained constant after thinning while tradeoffs occurred among individual species densities (demonstrating stability through compensation); 2) examine how surrogate habitat in the form of slash piles and their subsequent burning (2nd disturbance) affected community composition; and 3) determine if the ecosystem function of fungal dispersion was associated with species in different habitat types (evidence of functional redundancy).

Methods

Study area- Our study area was located 8 km southwest of Flagstaff, Arizona, in ponderosa pine-dominated forests (Appendix 4-A). Historically, this 18,500-ha area experienced a variety of forest management practices, including high grading (early 1900s), commercial thinning (1970-1990s), and fuels reduction and restoration treatments (late 1990s-present). Within a geographic information system (GIS; ArcGIS v9.3, ESRI, Redlands, California, USA), we overlaid a 500-m resolution lattice on the study area to locate prospective sampling points. We used this distance to ensure spatial independence in sampling points (i.e., eliminate autocorrelation) based on the larger home range of tassel-eared squirrels (Hoffmeister 1986). 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 100 sampling points, with approximately half in treated and half in untreated stands, and then located and permanently marked them in the field using a global positioning system.

Data collection

Small mammal sampling- We used each of the 100 sampling points as the center of a "site." We obtained Northern Arizona University Institutional Animal Care and Use Committee approval of our trapping methodology (protocol #06-005). At each site we centered a 5x5 square trap grid which consisted of 25 Sherman (model LNATDG) traps with 20m spacing, with a 3x3 grid overlaid with 9 Tomahawk (model 202) traps, one at every other grid intersection; the combination of the 2 trap types ensured we captured the majority of species in the small mammal community (animals that weighed <1000 g). Total site-scale sampling area was 14,400 m^2 (1.4 ha). We trapped small mammals at each site during the summers of 2006-2009 over a 10-week period late June to 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 4 days per week, which resulted in 3 nighttime and 3 daytime trapping sessions. We sampled for Botta's pocket gopher (*Thomomys bottae*) 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 determined the appropriate number of surveys following power analysis using data from our first year of sampling (2006).

Vegetation sampling- To quantify overstory characteristics at each site, we established an 11.3m-radius circular overstory plot (400m^2) at the site center, and measured tree species and diameter at breast height (dbh). At the site level we counted the number of slash piles, and used our yearly observations and state and federal records to determine the age of each treatment and the number of years the slash piles were intact. See Chapter 3 for a full description of the trapping and vegetation methods.

Fungal sampling- We attempted fecal sampling during 2007-08. We obtained fecal samples directly from golden-mantled ground squirrels and gray-collared chipmunks while in hand. Other species were either too large to handle or did not provide samples, and we were unable to locate fecal samples in traps after their capture. At each site, we randomly chose 1or 2 individuals of each of the 2 species to sample, however not every animal would provide a fecal sample. We froze samples until they were processed. We randomly chose 30-40 samples per year to analyze, and made 5 slides per sample using a standard protocol (Colgan et al. 1997). With each slide, we randomly chose 5 fields of view under a microscope in which we counted the EM fungal spores. We added the total number of spores per slide and averaged over the 5 slides for each fecal sample.

Data analysis

Covariates- Based our previous analysis of this dataset, we determined that thinning and slash pile burning treatments were important variables for predicting occupancy of most species in the small mammal community (Appendix 4-B); thus, we focused on 4 covariates that characterized treatments. For each site, we calculated total basal area per hectare (BA). We determined the number of years since thinning treatment (thin), the number of years since thinning that the slash piles at the site have been intact (slash), and the number of years since the piles were burned (burn). Within the GIS, we obtained the Universal Transverse Mercator (UTM) coordinates of each site in order to derive a unique site-level identifier and consider the role of spatial location (i.e., latitudinal and longitudinal position) in our estimates of occupancy. We reduced the 2 UTM coordinates into one variable using principal components analysis, similar to an interaction effect. In addition, we pooled detection histories from all 4 years of sampling and used "year" as a covariate. UTM and year were included so that any heterogeneity due to a site or year effect would be modeled and incorporated into the density estimates. This resulted in 6 covariates: thin, slash, burn, BA, year, and UTM.

Royle density models and multi-model inference- Simple, or "naïve," estimates of abundance can be calculated for a given site by simply averaging the number of counts of a species over the repeated visits to the site; 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). We used the density modeling framework of Royle (2004) to estimate both detection probability, defined as the probability of detecting the species at a site if it is present, and density, defined as the number of animals per site, for each small mammal species. We fit all models using Program PRESENCE v2.4 (Hines 2007).

Prior to our data collection effort and analyses, we identified 10-15 candidate models using the 6 covariates that we hypothesized would predict density of each species in the small mammal community. We used the same covariates for both density and detection probability. We included a null model (i.e., intercept-only) for each species that assumed density was constant across the sites. For each species, we built models using PRESENCE and compared them 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 considered models with ΔAIC_c values ≤2 to have considerable support. We also computed weights of evidence and model selection uncertainty using AIC weights (w_i; Burnham and Anderson 2002).

For each species, we used density estimates derived using the best model for comparison with treatments. We categorized treatments in terms of time since treatment: "dense" stands (N = 105) were unthinned (>25 years since treatment) stands that represent postsettlement or current conditions; 1-6 were stands in years post-thinning (N = 33, 31, 31, 19, 15, 6, respectively); and "open," meadow-like stands (N = 38) were not recently treated (>25 years) and had low BA ($<30m^2$/ha), chosen to resemble presettlement or restored conditions. This resulted in a total of 8 "treatments."

We used a Tukey-Kramer Honestly Significant Difference (HSD) test to compare total community density, and an unbalanced PERMANOVA procedure in R (Version 2.9.1, 2009) to test for differences in community composition across each treatment as a categorical variable ($\alpha = 0.05$).

Fungal analysis- We built generalized linear models for all possible combinations of the 3 variables that we hypothesized predicted EM spore count: the year the sample was collected (year), the basal area of the site from which the sample was collected (BA), and the species that produced the sample (species; either golden-mantled ground squirrel or gray-collared chipmunk). We compared the models using the multi-model inference methods described above. We graphed pine basal area versus mean EM spore count for the two species we sampled and for tassel-eared squirrels, using fecal data from Dodd et al. (2006).

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, etc.), sampling effort varied somewhat among years. We sampled 14 sites in 2006 (pilot year), 96 in 2007, 86 in 2008, and 83 in 2009 (n = 279). Each year, we detected the Mogollon vole, Mexican woodrat (*Neotoma mexicana*), deer mouse, tassel-eared squirrel, golden-mantled ground squirrel, rock squirrel, gray-collared chipmunk, and Botta's pocket gopher.

Species density responses to thinning

Each species responded to treatment (Table 4-1). Gray-collared chipmunks and deer mice had the highest overall densities, while the other 6 species' densities remained near or below 2 animals/ha (Figure 4-1). Five species (gray-collared chipmunk, deer mouse, golden-mantled ground squirrel, rock squirrel, Mogollon vole) showed increased densities in response to thinning (years 1-6), but 3 species (tassel-eared squirrel, Botta's pocket gopher, Mexican woodrat) slightly decreased during the 6 years post-treatment (Figure 4-1). All species had higher densities in the open treatment compared to the dense treatment except rock squirrels.

Community density responses to thinning

Overall density remained relatively constant following treatment at 15-17 animals/ha (Figure 4-2). The dense treatment had a significantly lower total density than stands years 1-6 after thinning or the open treatment (q = 3.05; Figure 4-2). However, community composition was significantly different in each of the 8 treatments ($p = 0.0001$, $R^2 = 0.30$). Pairwise comparisons indicated that while the dense treatment differed from all other treatments for both community composition and total density, 17 of the other 21 treatment pairs were significantly different in terms of community composition, but none were significantly different in terms of total density (Table 4-2).

Species density responses to slash piles and burning

Slash appeared in a top model (either independently or as part of the global model) for 4 species; tassel-eared squirrels, golden-mantled ground squirrels, Mexican woodrats, and Botta's pocket gopher. Mexican woodrats decreased in density after treatment but remained at higher densities in the presence of slash piles, decreasing after piles were burned (Figure 4-3). Similarly, golden-mantled ground squirrels increased in density during the years the piles were intact and decreased after the piles were burned; the species reached its highest density after slash piles were intact for 3 years at >2 animals/ha (Figure 4-3). Tassel-eared squirrels had a variable density response to the presence of slash piles but increased after they were burned in all scenarios except when the piles were burned immediately after treatment (Figure 4-3). Botta's pocket gophers decreased in density while the slash piles were present but increased after each year slash piles were burned (Figure 4-3).

Fungal dispersal potential in resulting stand types

We analyzed 69 fecal samples for mean EM spore count. The best model (w_i = 0.70) that predicted mean EM spore count used the year and BA covariates (Table 4-3). Both golden-mantled ground squirrel and gray-collared chipmunk EM counts were positively correlated with BA (Figure 4-4). The species from which the sample was collected did not affect mean spore count (Table 4-3).

Discussion

Species density tradeoffs occurred following thinning treatments. These findings are consistent with the literature; tassel-eared squirrels and Mexican woodrats should respond negatively to thinning because of their positive relationship with basal area and canopy cover (Patton 1977, Dodd et al. 2006) and shrub cover and down wood (Block et al. 2005, Converse et al. 2006), respectively. Golden-mantled ground squirrels, Botta's pocket gophers, and Mogollon voles are associated with increased understory cover and reduced tree density (Tevis 1956, Huntly and Inouye 1988, Bagne and Finch 2009). Deer mice and gray-collared chipmunks are generalists that are found in most habitats (Hoffmeister 1986, Coppeto et al. 2006). Thus, species densities fluctuated but overall community density remained constant following treatment, indicating that the community remained stable through compensation.

Three species that decreased in density after thinning (Mexican woodrat, tassel-eared squirrel, Botta's pocket gopher) had higher densities in open stands than in any previous scenario, suggesting that if restoration treatments can achieve this desired endpoint, it will benefit these species despite short-term losses. Furthermore, total species densities were higher in the open treatments than the dense sites, and the dense sites had significantly lower total densities than the other treatments. Thus, the thinning treatments produced community compositions that more closely emulated presettlement conditions. However, while the open stands provide a reference point by which to judge the effectiveness of treatments, these stand structures differ from true presettlement conditions. Due to logging near Flagstaff during the late 1800's, trees at our study sites tended to be small (less than 2% of the trees we measured were ≥60 cm) unlike presettlement conditions which contained low densities of large trees (quadratic mean diameter of 42 cm) (Fulé et al. 1997).

The differing species density responses to slash piles and burning similarly showed tradeoffs due to disturbance. For some species, slash piles may have provided supplemental habitat in the form of cover. Golden-mantled ground squirrels and Mexican woodrats clearly responded to this additional resource, as they are often associated with down wood and shrub cover (Goodwin and Hungerford 1979, Smith and Maguire 2004, Block et al. 2005); however, in all scenarios their density by year 6 was approximately the same, so the benefit of the supplemental habitat did not permanently increase the species' density. Meanwhile, tassel-eared squirrels and pocket gophers had lower densities as the duration of slash piles increased, perhaps due to competition with other species since they do not benefit as much from the slash piles, nesting and foraging primarily in trees and underground, respectively (Hoffmeister 1986). Again, these results demonstrated a tradeoff between individual species densities even in the presence of a supplemental resource.

Species compositional changes are usually studied in assessing ecosystem stability because it is logistically simpler to count animals than to investigate changes in function (Prins and Douglas-Hamilton 1990, Ernest and Brown 2001, Naeem and Wright 2003). However, although total small mammal species density increased after thinning treatment and then remained constant over time, we cannot simply assume that ecosystem function improved or remained stable. Although all species in our community can potentially disperse EM fungi (with the possible exception of the deer mouse; Pyare and Longland 2001), we showed that tassel-eared squirrels, golden-mantled ground squirrels, and gray-collared chipmunks were functionally redundant in that they carried similar amounts of EM spores in their feces in different stand structural types. The increase in average EM counts with pine basal area was likely because there was increased availability, since EM are associated with increased canopy cover of intermediate-aged ponderosa pines (States and Gaud 1997); however, Korb et al. (2003) showed that restoration treatments did not decrease the relative amount of EM fungi propagules. Thus, fungi dispersion is likely important across open and dense stands, and the two specialist squirrel species and one generalist chipmunk may compensate in terms of providing this ecosystem function.

We conclude that in this ecosystem, species compensated for one another in response to treatment in terms of density, while the community remained at an overall stable density. Our results suggest that EM fungal dispersion is a functionally redundant role that many of the small mammal species fill across different stand structural types. Total community density was higher and more stable following thinning treatment, and similar to species composition in presettlement stand structures, suggesting that restoration treatments are maintaining ecosystem stability in terms of small mammal community structure and function.

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Tables

Table 4-1. Species code, density (λ) models with $\Delta AIC_c \leq 2$, number of parameters (K), AIC value corrected for small sample size (AIC_c), difference in AIC_c between models (ΔAIC_c), and the relative weight of each model (w_i) for 8 species of small mammals (N=279). For each model the same covariates for density and detection were used. The λ estimates from each species' best model were used in further analysis.

Species	**Model**[1]	**K**	**AIC_c**	**ΔAIC_c**	**w_i**
Mogollon vole	λ(burn, BA)	4	330.07	0.00	0.35
	λ(BA)	3	330.83	0.76	0.24
	λ(thin, slash, burn, BA, year)	7	331.19	1.12	0.20
Mexican woodrat	λ(burn, UTM)	4	146.88	0.00	0.36
	λ(GLOBAL)	8	147.05	0.17	0.33
	λ(burn, BA, UTM)	5	147.39	0.51	0.28
Deer mouse	λ(burn, year, UTM)	5	2164.90	0.00	0.68
Tassel-eared Squirrel	λ(thin, slash, BA, year, UTM)	7	878.03	0.00	0.62
	λ(GLOBAL)	8	879.54	1.51	0.29
Golden-mantled ground squirrel	λ(GLOBAL)	8	1527.82	0.00	0.78
Rock squirrel	λ(burn, year, UTM)	5	1072.72	0.00	0.85
Gray-collared chipmunk	λ(BA, UTM)	4	3746.77	0.00	0.59
	λ(burn, BA, UTM)	5	3747.66	0.89	0.38
Botta's pocket gopher	λ(GLOBAL)	8	570.29	0.00	0.34
	λ(UTM)	3	571.18	0.89	0.22
	λ(burn, UTM)	4	571.23	0.94	0.21
	λ(burn, year, UTM)	5	571.73	1.44	0.17

1 Covariates include total basal area per hectare (BA), the number of years since thinning treatment (thin), the number of years since thinning that the slash piles at the site were intact (slash), the number of years since the piles were burned (burn), UTM coordinates of each site (UTM), and year of sampling (year). GLOBAL indicates that all 6 covariates were used in the model.

Table 4-2. Pairwise comparisons of treatments (p-values; $\alpha = 0.05$) for community composition (using PERMANOVA; overall $p = 0.0001$) and for total density (using Tukey-Kramer HSD; overall $q = 3.05$); bolded values indicate that the response variable was significantly different between treatments.

Treatment pairs	**Community composition (p-value)**	**Total density (p-value)**
0 vs. 1	**0**	**0**
0 vs. 2	**0**	**0**
0 vs. 3	**0**	**0**
0 vs. 4	**0**	**0**
0 vs. 5	**0**	**0**
0 vs. 6	**<0.0001**	**<0.0001**
0 vs. 20	**0**	**0**
1 vs. 2	0.1790	1.0000
1 vs. 3	**0.0024**	1.0000
1 vs. 4	**0.0001**	1.0000
1 vs. 5	**<0.0001**	0.9709
1 vs. 6	**0.0001**	0.6073
1 vs. 20	**<0.0001**	0.4528
2 vs. 4	**0.0011**	1.0000
2 vs. 5	**<0.0001**	0.9775
2 vs. 6	**0.0002**	0.6307
2 vs. 20	**<0.0001**	0.4446
3 vs. 2	0.2301	1.0000
3 vs. 4	0.0887	1.0000
3 vs. 5	**0.0033**	0.9739
3 vs. 6	**0.0034**	0.6181
3 vs. 20	**<0.0001**	0.4673
4 vs. 5	**0.0324**	0.9582
4 vs. 6	**0.0039**	0.5865
5 vs. 6	0.1816	0.9722
20 vs. 4	**<0.0001**	0.7941
20 vs. 5	**<0.0001**	0.1463
20 vs. 6	**<0.0001**	0.0676

Table 4-3. Model selection analysis for generalized linear models predicting EM spore counts in golden-mantled ground squirrels and chipmunks; candidate models (model), number of parameters (K), AIC value corrected for small sample size (AIC_c), difference in AIC_c between models (ΔAIC_c), and the relative weight of each model (w_i) (N=69) are shown.

Model[1,2]	**K**	**AIC_c**	**ΔAIC_c**	**w_i**
Year, BA	4	637.47	0	0.70
GLOBAL	6	641.09	3.63	0.11
Year	3	640.94	3.47	0.12
BA	2	643.95	6.48	0.03
Species, Year	5	645.44	8.00	0.01
NULL	1	646.19	8.72	0.009
Species, BA	4	647.09	9.62	0.006
Species	3	648.16	10.70	0.003

1 Covariates include the year the sample was collected (Year), the basal area of the site from which the sample was collected (BA), and the species that produced the sample (Species; either golden-mantled ground squirrel or gray-collared chipmunk).

2 GLOBAL indicates that all 3 covariates were used in the model; NULL indicates that no covariates (intercept only) were used in the model.

Figures

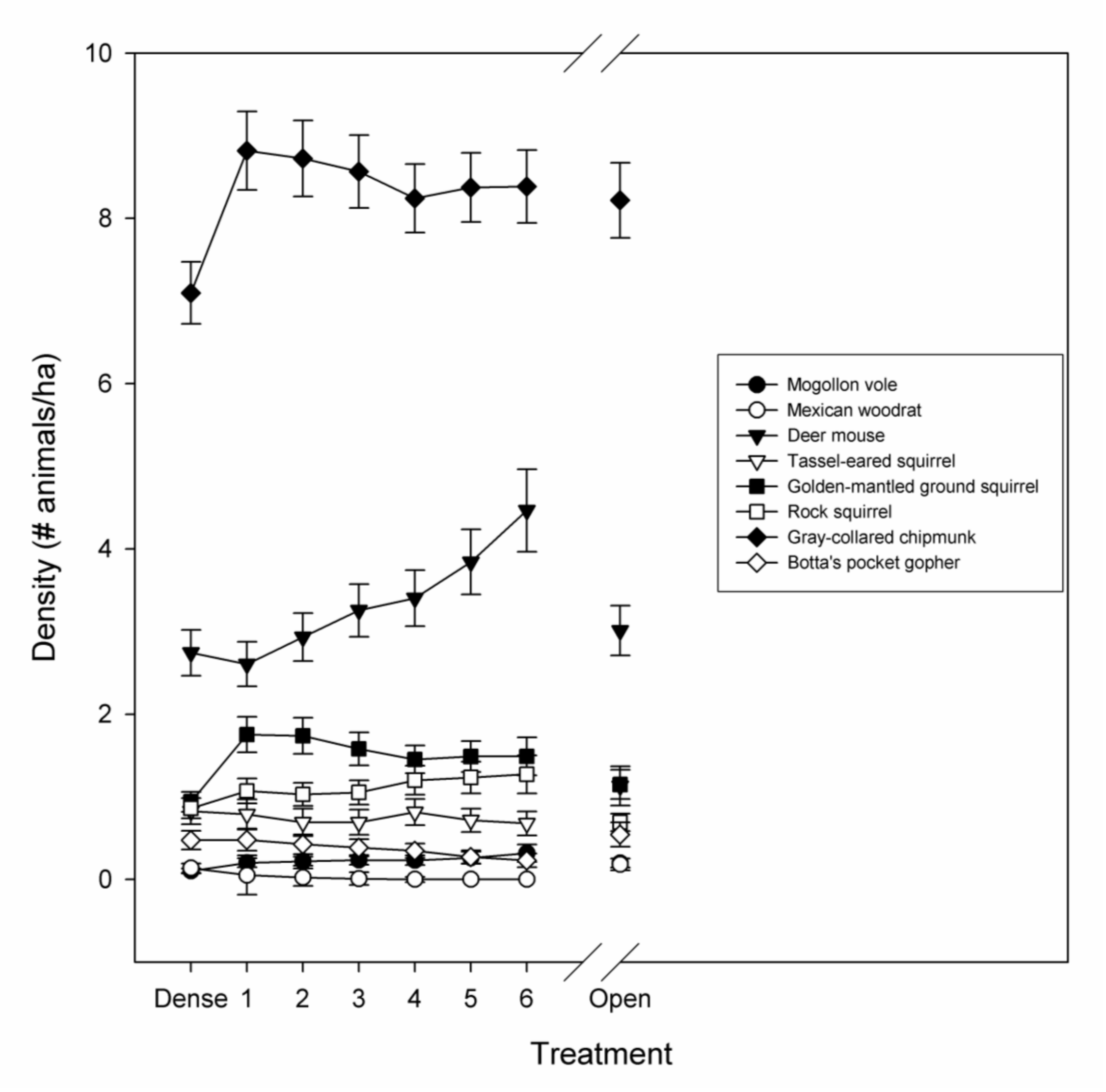


Figure 4-1. Densities of small mammal species averaged over each year since treatment. Dense stands were unthinned, 1-6 indicate time since thinning treatment, and open stands were meadow-like but unthinned.

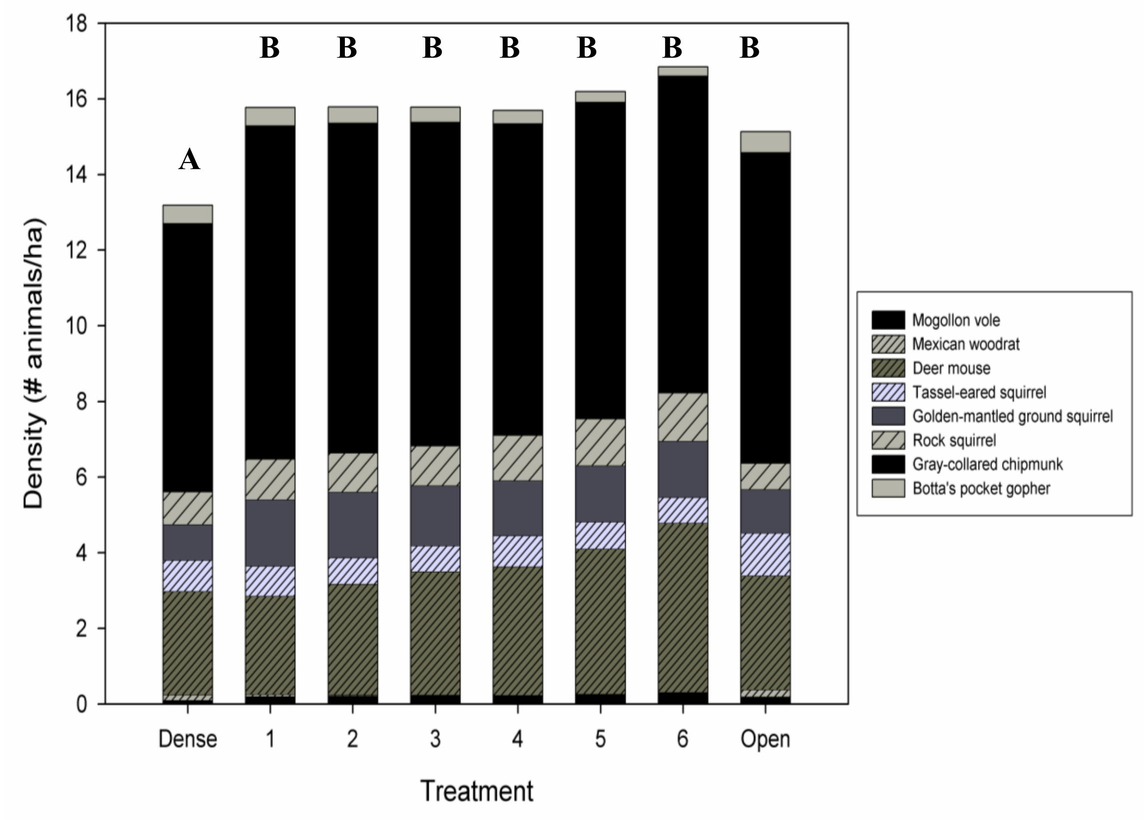


Figure 4-2. Densities of small mammal species averaged over each year since treatment. Dense stands were unthinned, 1-6 indicate time since thinning treatment, and open stands were meadow-like but unthinned. Dense stands were different from other treatments (q = 3.05) in terms of total density, but community composition was significantly different in each of the 8 treatments (p = 0.0001).

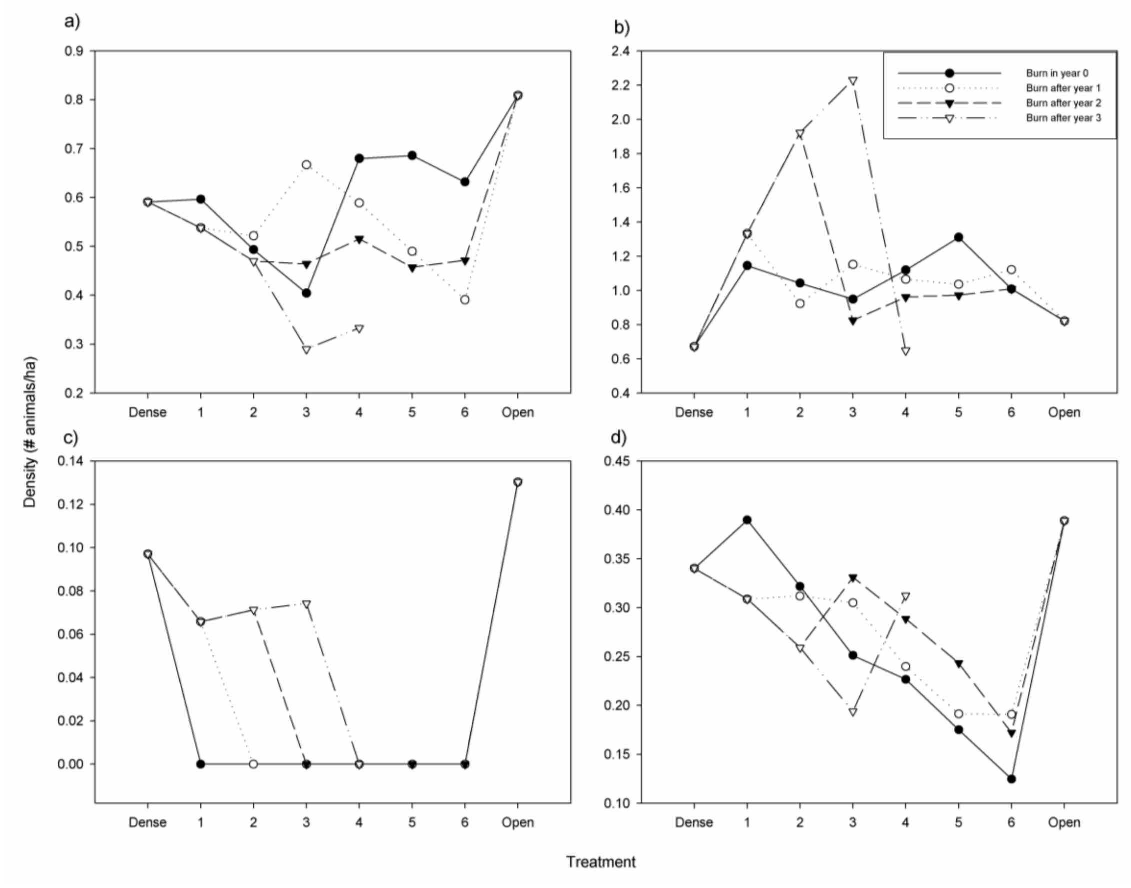


Figure 4-3. Densities of a) tassel-eared squirrels, b) golden-mantled ground squirrels, c) Mexican woodrats, and d) Botta's pocket gophers in response to 4 scenarios, in which slash piles were burned either the same year thinning occurred, or after 1, 2, or 3 years post-thinning. Dense stands were unthinned, 1-6 indicate time since thinning treatment, and open stands were meadow-like but unthinned. To increase graph readability, standard errors are provided in Appendix 4-C.

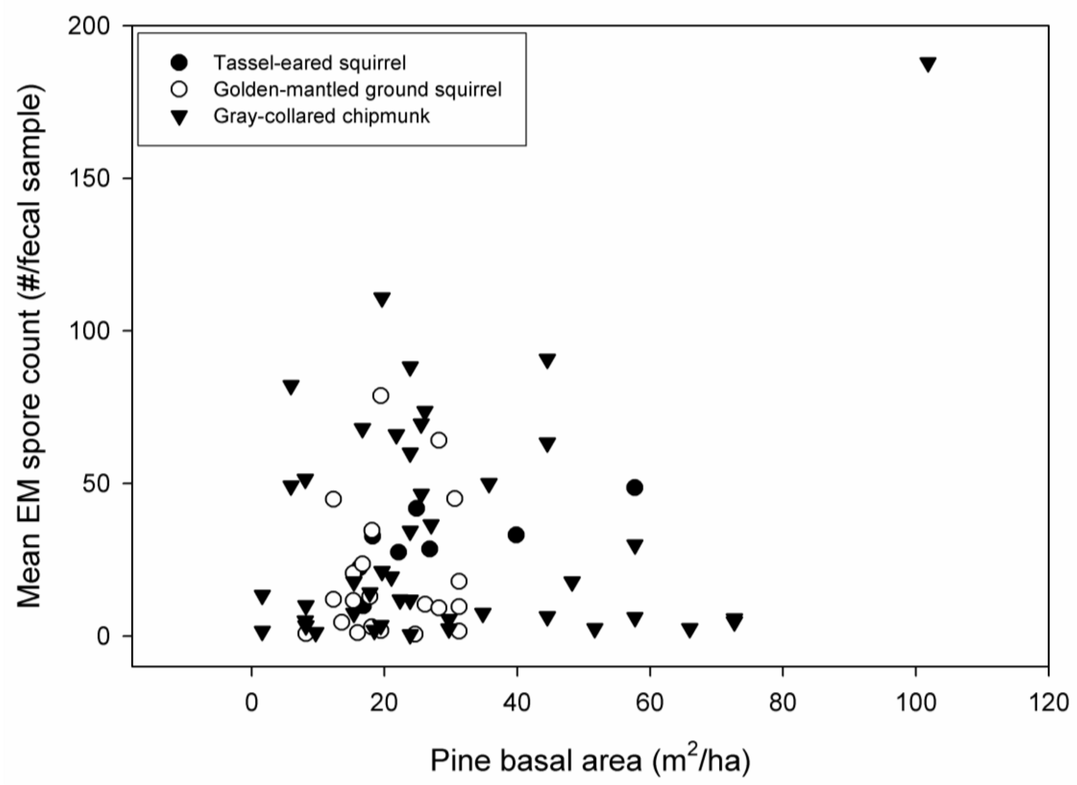
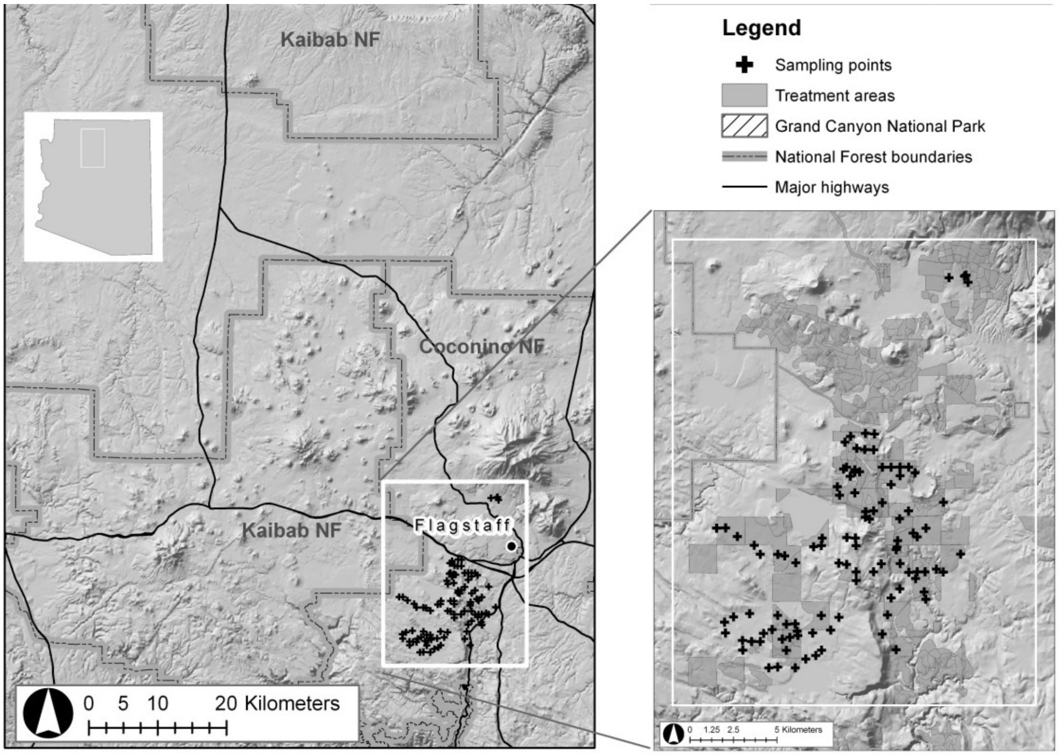


Figure 4-4. Mean EM fungi content of fecal samples from tassel-eared squirrels, golden-mantled ground squirrels, and gray-collared chipmunks in stands with varying amounts of pine basal area. Tassel-eared squirrel data were from Dodd et al. (2003).

Appendix 4-A

Figure of study area



Appendix 4-B

Cumulative AIC weights for assessing the relative importance of habitat covariates used to predict occupancy of 8 species of small mammals (Chapter 3)

Species	Pine BA (m2/ha)	Oak BA (m2/ha)	Rock (% cover)	Understory Vegetation (% cover)	Trees >50 cm dbh (#/ha)	Snags (#/ha)	Snags >40cm (#/ha)	Treatment	Slash	Year	UTM
Mogollon vole	0.018 (-)	0.000 (-)	0.329 (-)	**0.981 (+)**	0.001 (-)	0.016 (-)	**0.669 (+)**	0.002 (+)	0.001 (+)	0.001 (-)	0.002 (+)
Mexican woodrat	**0.887 (+)**	0.112 (+)	0.112 (+)	0.000 (-)	0.075 (+)	0.000 (-)	0.000 (+)	**0.887 (-)**	**0.812 (+)**	0.075 (-)	**0.925 (-)**
Deer mouse	0.004 (-)	0.040 (+)	**0.989 (+)**	0.125 (+)	**0.829 (+)**	0.002 (+)	**0.830 (+)**	0.003 (+)	0.000 (-)	0.000 (+)	0.043 (+)
Tassel-eared squirrel	**0.925 (+)**	0.073 (+)	0.074 (-)	0.001 (-)	0.341 (+)	0.000 (-)	0.001 (+)	**0.925 (-)**	**0.584 (+)**	0.000 (-)	**0.998 (+)**
Golden-mantled ground squirrel	**0.842 (-)**	0.158 (+)	0.000 (-)	0.000 (+)	0.001 (+)	0.158 (-)	0.000 (-)	**0.842 (+)**	**0.999 (+)**	0.160 (-)	**0.842 (-)**
Rock squirrel	0.000 (-)	**1.000 (+)**	**1.000 (+)**	0.000 (-)	0.000 (+)	0.000 (+)	0.000 (-)	0.000 (+)	0.000 (+)	0.000 (-)	**1.000 (+)**
Gray-collared chipmunk	**0.704 (-)**	0.036 (-)	0.069 (+)	0.190 (+)	0.150 (+)	**0.598 (-)**	**0.718 (+)**	0.137 (+)	0.031 (+)	0.168 (-)	0.142 (-)
Botta's pocket gopher	0.002 (-)	0.000 (-)	**0.555 (-)**	**0.998 (+)**	0.002 (+)	0.000 (-)	0.443 (-)	0.002 (-)	0.000 (-)	0.002 (-)	0.002 (-)

Appendix 4-C

Means and standard errors (SE) of species densities (#animals/ha) in response to slash treatments (Figure 4-3)

Treatment	Year slash burned	Mexican woodrat		Tassel-eared squirrel		Golden-mantled ground squirrel		Botta’s pocket gopher	
		Density	SE	Density	SE	Density	SE	Density	SE
Dense	NA	0.136	0.056	0.827	0.157	0.940	0.121	0.476	0.115
1	0	0.000	0.507	0.835	0.194	1.603	0.201	0.545	0.148
2	0	0.000	0.000	0.690	0.152	1.459	0.166	0.450	0.110
3	0	0.000	0.000	0.566	0.124	1.327	0.159	0.352	0.091
4	0	0.000	0.000	0.952	0.191	1.566	0.231	0.317	0.097
5	0	0.000	0.000	0.960	0.183	1.834	0.282	0.245	0.086
6	0	0.000	0.000	0.884	0.183	1.412	0.275	0.175	0.075
1	1	0.092	0.041	0.753	0.176	1.865	0.227	0.432	0.124
2	1	0.000	0.418	0.730	0.156	1.292	0.148	0.437	0.105
3	1	0.000	0.000	0.934	0.188	1.613	0.179	0.427	0.104
4	1	0.000	0.000	0.824	0.154	1.491	0.160	0.336	0.083
5	1	0.000	0.000	0.686	0.137	1.449	0.178	0.268	0.078
6	1	0.000	0.000	0.547	0.122	1.568	0.221	0.267	0.090
1	2	0.092	0.041	0.753	0.176	1.865	0.227	0.432	0.124
2	2	0.100	0.043	0.658	0.205	2.691	0.383	0.363	0.148
3	2	0.000	0.565	0.650	0.136	1.155	0.126	0.464	0.100
4	2	0.000	0.000	0.722	0.147	1.346	0.133	0.404	0.085
5	2	0.000	0.000	0.640	0.130	1.361	0.141	0.341	0.080
6	2	0.000	0.000	0.660	0.134	1.413	0.167	0.241	0.067
1	3	0.092	0.041	0.753	0.176	1.865	0.227	0.432	0.124
2	3	0.100	0.043	0.658	0.205	2.691	0.383	0.363	0.148
3	3	0.104	0.044	0.406	0.171	3.122	0.561	0.272	0.158
4	3	0.000	0.624	0.466	0.099	0.909	0.102	0.437	0.092
Open	NA	0.182	0.072	1.133	0.238	1.150	0.178	0.544	0.147

CHAPTER 5

CONCLUSIONS

This dissertation was designed to assist managers in developing ecological restoration treatments, advance our ecological understanding of how communities respond to disturbance, and reveal additional research needs.

Management recommendations

In Chapter 2, I showed that small-diameter harvest and burning treatments had positive effects but thin/burn and selective harvest treatments had no detectable effect on most small mammals and passerine bird species reported in studies suitable for meta-analysis; overstory removal and wildfire resulted in an overall negative response. Thus, small-diameter removal and burning treatments as currently being implemented in the Southwest do not negatively impact most of the wildlife species in the studies I examined, at least in the short term (≤10 yrs). These results support the hypothesis that thinning and burning at the landscape level are consistent with ecological restoration objectives for wildlife.

In Chapter 3, I found that the average occupancy of all small mammal species in the community was positively related to thinning treatment and slash. The most important habitat variables in predicting small mammal community occupancy were pine basal area, treatment intensity (percent of trees removed and time since treatment), the number and length of time slash piles are left on the ground, rock cover, and snags >40cm diameter. Five species (*Microtus mogollonensis*, *Peromyscus maniculatus*, *Spermophilus lateralis*, *Spermophilus variegates*, *Tamias cinereicollis*) responded positively to treatment and three (*Neotoma mexicana, Sciurus aberti*, *Thomomys bottae*) negatively; the average occupancy of all species combined was positively related to treatment. All but two species (*P. maniculatus*, *Thomomys bottae*) responded positively to slash piles, and average occupancy of all species was positively related to slash. For all habitat attributes, I found tradeoffs in the response of each species which illustrated that no one treatment benefitted all species, but rather an arrangement of dense and open stands across the landscape with heterogeneity in fine-scale features is likely the best management approach for small mammals.

Ecological conclusions

In Chapter 4, I found that small mammal community composition differed in each of 6 years following treatment, but total density remained constant. Total species densities were significantly lower in stands with dense conditions than in stands with more open structural conditions similar to those of presettlement times, which had similar small mammal densities as the thinning treatments. In addition, tassel-eared squirrels, golden-mantled ground squirrels, and gray-collared chipmunks appeared to play a functionally redundant role in dispersing ectomycorrhizal fungi across different stand structures. These results suggest that restoration treatments are maintaining ecosystem stability in terms of small mammal community structure and function.

Future research needs

Although I assessed thousands of papers on restoration impacts on wildlife, I found only 25 studies that produced sufficient information for meta-analysis, revealing a need for greater coordination of research efforts. The vast majority of studies in the analysis were short-term responses of birds to treatment. Underrepresented taxa include reptiles and amphibians; rare birds and small mammals that are not easily assessed using conventional point count and trapping methodologies; medium and large mammals, including both predators and ungulates; and birds of prey. Many of these species are not entirely ignored in the literature, but rather density is generally not an appropriate response variable for animals with large home ranges. However, the lack of studies that assess reproductive responses of these species indicates a paucity of research on these large and top trophic animals. Studies at larger temporal and spatial scales, which examine more informative response variables for a greater variety of species, are critical to fully understanding the impacts of forest treatments on wildlife.

To fill some of the data gaps revealed by the meta-analysis, I trapped eight species of small mammals at 294 sites in northern Arizona over four years, in what is now the largest study of its kind. I found that the rapid assessment, occupancy modeling approach was highly effective in evaluating the response of the small mammal community to treatment and other habitat attributes. Particularly in the arid Southwest, most small mammal population studies end up primarily tracking precipitation patterns, but I showed a lack of a year effect by all species. Although this study was a big effort, it obtained more reliable, repeatable results for a greater number of species than many of the equally-intensive demographic studies with similar objectives. I suggest this design be utilized in other studies that grapple with high variability in assessing general impacts of treatments or habitat change on wildlife species. This will be particularly important as management moves towards landscape-scale projects, and better ecological information at larger spatial scales is needed to inform these efforts.