Small mammal community maintains stability through compensatory dynamics after restoration of a ponderosa pine forest

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Abstract. 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. Stability is increased when species with similar functional roles compensate for one another by responding differently to environmental change. In restoration projects, the objective is to restore stability by altering ecosystem composition, structure, and function to resemble natural ("reference") conditions. We assessed the success of ecological restoration treatments by examining the structural and functional responses of the small mammal community before and after treatment, and compared to reference conditions. We used Royle density models to examine the responses of eight species of small mammals to restoration (thinning) treatments in ponderosa pine forests to determine if the community maintained total density, biomass, and function (represented by ectomycorrhizal fungi dispersion) after disturbance. Community composition differed in each of 6 years following treatment, but total density and biomass remained constant, suggesting the community is a stable prey base for predators. In addition, golden-mantled ground squirrels (*Spermophilus lateralis*) and gray-collared chipmunks (*Tamias cinereicollis*) appeared to play a similar role in dispersing ectomycorrhizal fungi across different forest structures. Both total species density and biomass were greater after thinning than in unthinned stands, and were similar to reference stands. These results suggest that although species composition changes from year to year after disturbance, restoration treatments can maintain ecosystem stability in terms of small mammal community-level properties.

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Introduction

Ecosystem stability has been of increasing interest in the past several decades as it helps predict the consequences of anthropogenic disturbances on ecosystems (Walker 1995). This may be particularly important in the context of ecological restoration, where humans directly alter an ecosystem with the intention of restoring its composition, structure, and function to that within the natural range of variability that existed prior to human disturbance (Landres et al. 1999). Thus, the benchmark for success in restoration projects is the comparison of the

restored site to "natural conditions," defined as those maintained by natural processes (Society for Ecological Restoration 2004). Although approximating natural conditions should increase ecosystem stability, given the multiple impacts humans have had on the landscape over the past 100 years, such as grazing, altered fire regimes, and climate change (Westerling et al. 2006, Bakker and Moore 2007), we cannot assume restoration treatments will have the intended consequences.

Compensatory population dynamics of interacting species may be one mechanism for maintaining ecosystem stability (Ernest and Brown 2001). Resilient species are those that rebound quickly after an environmental perturbation, as they are usually small bodied and abundant, with high reproductive outputs (Pimm 1991). With these species, assessing population fluctuations as a proxy for stability may not be accurate, as they can exhibit widely fluctuating populations year-to-year but a consistent response over time. Compensation occurs when coexisting species exhibit negative covariances in population dynamics while total resources use, such as total population size or biomass, remains constant (Ernest and Brown 2001). Within a group of species with similar functional roles, density compensation should result in functional compensation, which is the maintenance of ecological processes despite changes in species composition (Frost et al. 1995). Thus, a system with compositional and functional compensation would be able to maintain ecosystem functioning in the face of environmental change (Ehrlich and Walker 1998).

Stability via compensation is difficult to test and prove in the field due to the large demands for data over time, and thus some of the best examples are of zooplankton in lake acidification experiments (Klug et al. 2000, Fischer et al. 2001). A long-term study in the Chihuahuan desert showed 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 pattern 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 compen-

sation can lead to greater stability in certain ecosystem properties. Species compositional changes are useful in assessing ecosystem stability because it is logistically simple to count animals; more difficult is understanding the impacts on species' functional roles within an ecosystem (Naeem and Wright 2003). Furthermore, it is difficult to extrapolate predictions on compensation from one ecosystem to another, due to the food web effects that can come into play (Frost et al. 1995). In the context of ecological restoration, it is important to determine whether functional compensation is maintained during and after treatments that approximate natural disturbances, thus maintaining ecosystem stability.

The southwestern ponderosa pine (Pinus ponderosa) ecosystem is an ongoing experiment in ecological restoration. Historically, ponderosa pine forests experienced frequent disturbance via a natural fire regime, characterized by low-severity understory fires, 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 long-term sustainability. Today, the greatest threat to biological diversity is the loss of evolutionary habitats (Noss and Csuti 1994), which is occurring 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). Thus, there is now an emphasis on ecological restoration in the Southwest, whereby forests are thinned to reduce fuel loads, after which the natural fire regime can be safely reintroduced (Covington 2003). In this case, humans are introducing a perturbation (thinning) in current, dense forest conditions, in an effort to return ecosystems to more open conditions that existed prior to Euro-American settlement.

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 changes in density are within the natural

range of variability in Arizona due to environmental conditions such as drought and fire (Brown et al. 2001), yet these species are sensitive to changes in habitat and are thus good indicators of forest change (Converse et al. 2006). These species have several important ecosystem functions, including acting as prey for mammalian and avian predators, increasing soil aeration, impacting regeneration abundance and patterns, and dispersing fungi (Hooven 1966, Boal and Mannan 1994, Pyare and Longland 2001). In particular, the dispersion of ectomycorrhizal (EM) fungal spores, known as truffles, is largely reliant on small mammals (Johnson 1996). In this study, we examined density responses of eight species of small mammals to thinning ("restoration") treatments. We predicted that although individual species densities would fluctuate in response to treatments, total community density and biomass would remain constant. Density compensation among species would allow EM fungi dispersion to occur in different habitat types by different species at similar levels. Thus, our goal was to assess whether community and ecosystem properties were being maintained by species compensation in response to thinning in a ponderosa pine forest, and if examining these properties could help us ascertain whether restoration treatments were moving the system towards reference conditions. More specifically, our objectives were to: (1) determine if small mammal community total density and biomass remained constant after thinning while tradeoffs occurred among individual species densities (demonstrating stability through compensation); (2) determine if the ecosystem function of fungal dispersion remained constant after thinning (evidence of functional compensation); and (3) compare treated sites to both unthinned and reference conditions to evaluate the efficacy of restoration treatments in restoring small mammal composition and function.

METHODS

Study area

The study area was located 8 km southwest of Flagstaff, Arizona (35°09′37″ N, 111°43′34″ W), in ponderosa pine-dominated forests. This 18,500-ha area experienced a variety of forest management practices, including selective harvesting (early 1900s), commercial thinning (1970–1990s), and fuels reduction and restoration treatments (late 1990s–present). Within a GIS (ArcGIS v9.3, ESRI, Redlands, California, USA), a 500-m resolution lattice was overlaid on the study area to locate prospective sampling points. Points that fell within private lands and non-forested patches >1 ha, or were located >500 m from a road were eliminated. From the remaining points, 100 sampling points were randomly selected, and then a GPS was used to locate and permanently mark the points in the field.

Data collection

Small mammal sampling.—Each of the 100 sampling points was used as the center of a "site." Centered at each site was a 5 × 5 square trap grid which consisted of 25 Sherman (model LNATDG, H.B Sherman Traps, Tallahassee, Florida, USA) traps with 20-m spacing, with a 3 × 3 grid overlaid with 9 Tomahawk (model 202, Tomahawk Live Trap, Hazelhurst, Wisconsin, USA) traps, one at every other grid intersection. The combination of the two trap types ensured the majority of species in the terrestrial small mammal community (animals that weighed <1000 g) were captured. Total site-scale sampling area was 14,400 m^2 (1.4 ha). Small mammals were trapped at each site during the summers of 2006–2009 over a 10-week period from late June to August. Both Sherman and Tomahawk traps were left open overnight, but the Sherman traps were closed during the day to prevent animals from overheating. Traps were checked twice daily, four days per week, which resulted in three nighttime and three daytime trapping sessions. An open-hole test was used to sample for Botta's pocket gopher (*Thomomys bottae*) presence; all gopher mounds located at the site were disturbed with a shovel, and the species was considered present if a mound was repaired within 24 hours (Smallwood and Erickson 1995). We obtained Northern Arizona University Institutional Animal Care and Use Committee approval of our trapping methodology (protocol #06–005).

Vegetation sampling.—To quantify overstory characteristics at each site, an 11.3-m radius circular overstory plot (400 m^2) was established at the site center, and tree species and diameter at

breast height (dbh) were measured. At the site level, our yearly observations and state and federal records were used to determine the age of each treatment and the number of years slash piles were intact. A full description of the trapping and vegetation methods is provided in Kalies et al. (2012).

Fungal sampling.—Fecal sampling was conducted during 2007–2008. Fecal samples were obtained 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, one or two individuals of each of the two species were randomly chosen to sample, however not every animal would provide a fecal sample. Between 30–40 samples per year were chosen for analysis, and a standard protocol (Colgan et al. 1997) was used to prepare five slides per sample. With each slide, five fields of view were randomly chosen under a microscope in which the EM fungal spores were counted. The total number of spores per slide was averaged over five slides for each fecal sample.

Analyses

Covariates.—Four covariates were used to characterize treatments at each site: total basal area per hectare (BA), the number of years since thinning treatment, the number of years since thinning that the slash piles at the site were intact, and the number of years before the piles were burned were also determined. Detection histories from all 4 years of sampling were pooled and "year" was used as a covariate. Within the GIS, the UTM coordinates of each site were obtained in order to derive a unique site-level identifier. Principal components analysis was used to reduce the two UTM coordinates to one variable, similar to an interaction effect. 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 a total of six habitat covariates.

Density models.—The single season density modeling framework of Royle et al. (2005) was used 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. Prior to our data collection effort and analyses, 10–15 candidate models were constructed using the six covariates hypothesized would predict density of each species in the small mammal community. The same covariates were used for both density and detection probability. For each species, Program PRESENCE v2.4 (J. Hines, U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland, USA) was used to build models, and they were compared using Akaike's Information Criterion adjusted for small sample sizes (AIC$_c$; Burnham and Anderson 2002). Model importance was ranked from highest to lowest according to differences (Δ) in their AIC$_c$ values. For each species, the best model was used to estimate density. The Appendix presents candidate models and selection results.

Stand structure differences.—Sampling points were categorized by the following stand structural differences: "dense" stands ($N = 105$) were unthinned (>25 years since treatment) and represent postsettlement or current conditions; thinned, including stands 1–6 years post-thinning ($N = 33, 31, 31, 19, 15, 6$, respectively); and "open," meadow-like stands ($N = 38$) that were not recently treated (>25 years) and had low BA (<30 m^2/ha), chosen as reference sites. This resulted in a total of eight "treatments." An unbalanced PERMANOVA procedure in R (R Foundation for Statistical Computing, Vienna, Austria) was used to test for differences in community composition (small mammal species richness and abundance) between treatments. An ANOVA was used to test for differences between treatments in total community density, total community biomass, and mean EM spore count per sample. When differences were found between treatments, the Tukey-Kramer Honestly Significant Difference test was used to identify pairwise differences. A t-test was used to compare mean EM spore count between species and year. For all statistical tests, $\alpha = 0.05$.

RESULTS

Small mammal species densities

A total of 14 sites were sampled in 2006 (pilot year), 96 in 2007, 86 in 2008, and 83 in 2009 ($n = 279$). Each year, we detected the following

species: Mogollon vole (*Microtus mogollonensis*), Mexican woodrat (*Neotoma mexicana*), deer mouse (*Peromyscus maniculatus*), tassel-eared squirrel (*Sciurus aberti*), golden-mantled ground squirrel (*Spermophilus lateralis*), rock squirrel (*Spermophilus variegates*), gray-collared chipmunk (*Tamias cinereicollis*), and Botta's pocket gopher. Terrestrial small mammals we could not detect that could be fairly common in ponderosa pine forests (USDA Forest Service 2005) included the desert cottontail (*Sylvilagus audubonii*), black-tailed jack rabbit (*Lepus californicus*), and dusky shrew (*Sorex monticolus*).

Gray-collared chipmunks and deer mice had the highest overall densities, while the other six species' densities remained near or below two animals/ha (Fig. 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 three species (tassel-eared squirrel, Botta's pocket gopher, Mexican woodrat) slightly decreased during the 6 years post-treatment (Fig. 1). All species, except rock squirrels, had higher densities in the open treatment compared to the dense treatment.

Community density and biomass

Total density and biomass were significantly different between treatments ($P < 0.0001$ and $P = 0.0002$, respectively); but pairwise comparisons indicated that only the dense treatment was significantly different from other treatments (Table 1). The dense treatment had the lowest total density, but following treatment, total community density remained relatively constant at 15–17 animals/ha (Fig. 2). Total community biomass was significantly different between the dense treatments and year 1, but all other treatments were statistically similar to both the dense and year 1 treatments (Fig. 2). However, community composition was significantly different in each of the eight treatments ($P = 0.0001$), with significant differences between 24 of 28 pairs (Table 1).

Fungal dispersal potential

A total of 65 fecal samples (gray collared-chipmunk, $N = 44$; golden-mantled ground squirrel, $N = 21$) were analyzed for mean EM spore count. There was no significant difference in mean EM spore count between treatments ($P = 0.97$) or species ($P = 0.07$), but there was between years ($P = 0.0007$).

DISCUSSION

Community structural responses to disturbance

Following thinning and reduction of basal area, ponderosa pine forests experience an increase in understory vegetation in terms of cover and diversity in as little as 2 years post-treatment (Moore et al. 2006). In addition, down wood (slash) is usually left onsite for 1–2 years before being burned, adding a source of cover to an otherwise disturbed site. Our study captured these short-term successional changes (years 1–6 post-thinning) but not the long-term changes that would occur over a longer (~20 year) fire return interval. Nevertheless, species density tradeoffs occurred following thinning treatments. We expected similar responses from the generalist gray-collared chipmunks and deer mice, which are usually found at high densities across different forest structural conditions (Bagne and Finch 2009), but the chipmunks responded more positively than deer mice immediately post-disturbance, likely due to the slash component. We observed opposite responses by tassel-eared squirrels and golden-mantled ground squirrels, as the former is associated with mature pine trees for nesting and foraging (Patton 1977), while the latter uses open meadow-like habitat (Bartels and Thompson 1993); and by woodrats and voles, as woodrats are associated with shrub cover and down wood (Block et al. 2005), while voles use meadow-like understory (Bagne and Finch 2009). Overall, six species responded positively to the disturbance event, which is logical given that ponderosa pine forests and its species historically experienced the natural disturbance of fire every 2–20 years (Covington and Moore 1994), and thinning and fire can effect some habitat features (i.e., understory production) in similar ways (Moore et al. 2006, Schwilk et al. 2009). Two species responded negatively to thinning, including woodrats, which probably experienced a lack of cover at the thinned sites, and pocket gophers, which may have been negatively affected by the soil compaction associated with thinning. Tassel-eared squirrel densities remained fairly constant following thinning, which was contrary to past
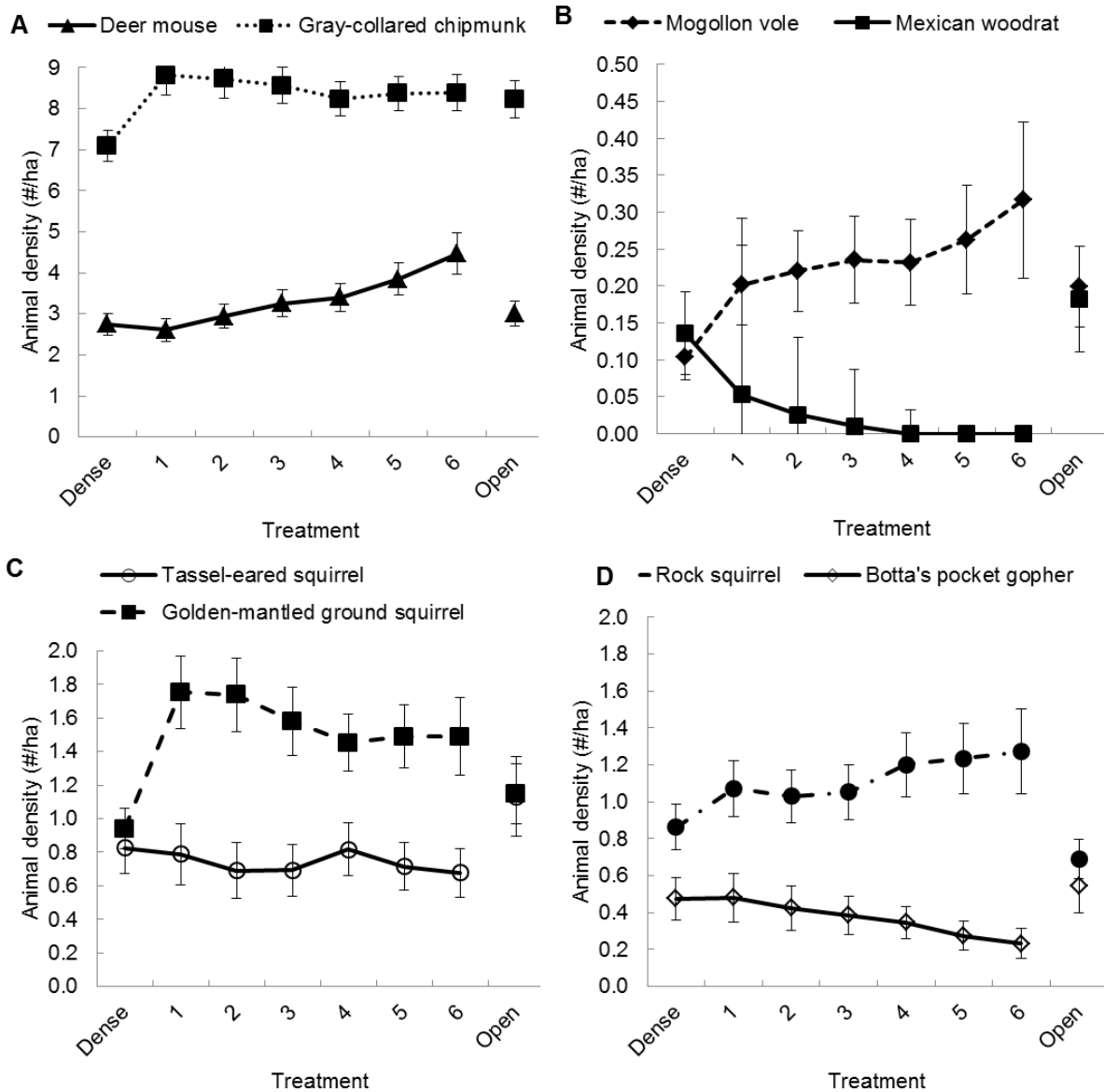
Fig. 1. Densities of each small mammal species averaged over each year since treatment. Dense stands were unthinned, 1–6 indicate time since thinning treatment, and open stands were meadow-like but unthinned.

research suggesting that restoration treatments will have negative consequences (Dodd et al. 2003, Dodd et al. 2006); however, tassel-eared squirrels might be more closely linked to large-diameter trees (Patton 1977, Kalies et al. 2012) which are retained in thinning treatments and do not change in density or size in the short term. Thus, species densities fluctuated in response to various habitat elements, but total community density remained constant following distur-

bance, indicating that the community remained stable through compensation.

Community functional responses to disturbance

Biomass is both a measure of ecosystem stability, as well as an indicator of the amount of prey available to predators, which is an important function of the small mammal community. Through a concurrent study, we observed that coyotes (*Canis latrans*) and gray foxes

Table 1. Results of pairwise comparisons of treatments for community composition, total density, and total biomass; asterisks (*) indicate that the response variable was significantly different between treatments ($P < 0.05$).

Treatment pairs†	Community composition (P)	Total density (P)	Total biomass (P)
Dense vs. 1	0*	0*	0.0016*
Dense vs. 2	0*	0*	0.062
Dense vs. 3	0*	0*	0.1534
Dense vs. 4	0*	0*	0.0504
Dense vs. 5	0*	0*	0.1613
Dense vs. 6	<0.0001*	<0.0001*	0.6528
Dense vs. open	0*	0*	0.278
1 vs. 2	0.1790	1	0.9924
1 vs. 3	0.0024*	1	0.9553
1 vs. 4	0.0001*	1	1
1 vs. 5	<0.0001*	0.9709	1
1 vs. 6	0.0001*	0.6073	1
1 vs. open	<0.0001*	0.4528	0.7774
2 vs. 4	0.0011*	1	0.9995
2 vs. 5	<0.0001*	0.9775	1
2 vs. 6	0.0002*	0.6307	1
2 vs. open	<0.0001*	0.4446	0.9973
3 vs. 2	0.2301	1	1
3 vs. 4	0.0887	1	0.9943
3 vs. 5	0.0033*	0.9739	0.9991
3 vs. 6	0.0034*	0.6181	0.9998
3 vs. open	<0.0001*	0.4673	0.9999
4 vs. 5	0.0324*	0.9582	1
4 vs. 6	0.0039*	0.5865	1
5 vs. 6	0.1816	0.9722	1
Open vs. 4	<0.0001*	0.7941	0.9487
Open vs. 5	<0.0001*	0.1463	0.9858
Open vs. 6	<0.0001*	0.0676	0.9977

†Dense stands were unthinned, 1–6 indicate time since thinning treatment, and open stands were meadow-like but unthinned.

(*Urocyon cinereoargenteus*) commonly used our sites, and raccoons (*Procyon lotor*) and ringtails (*Bassariscus astutus*) were occasional visitors (Barrett et al. 2012). These predators tend to be prey generalists (Hoffmeister 1986), and thus likely would not be negatively affected by changes in species composition so long as adequate prey biomass was available. We found that biomass remained constant following treatment, suggesting that small mammals continued to provide this function and at similar levels as those at reference sites. However, without measurements of predator density or occurrence following treatments, we cannot confirm that this ecosystem function is being maintained. For example, avian predators are also likely present at our sites, and some species such as the federally threatened Mexican spotted owl (*Strix occidentalis lucida*) may have preferences for specific prey species (e.g., woodrats; Ganey 1992), and thus could be negatively affected by fluctuations in individual species' densities. In addition, we were unable to trap rabbits during

our study, which can be an important prey item for mammalian and avian predators (Fritzell and Haroldson 1982, Boal and Mannan 1994).

In an effort to evaluate another functional role of the small mammal community, we quantified EM spores found in small mammal feces. Due to the physical size of truffles, only animals such as ungulates, mammals, or turkeys can unearth them, and thus their dispersal may be limited by the presence of these animals, although this has not been empirically proven (Johnson 1996). In addition, although animals may release spores into the air when preying upon the truffle, probably of greater importance is that spores are ingested and dispersed via feces (Johnson 1996). Several studies showed not only that spores are viable after passing through the animals' guts, but this process may actually promote germination (Kotter and Farentinos 1984, Cork and Kenagy 1989). We found that mean EM spore counts in the feces of two species of small mammals remained constant across treatments. Korb et al. (2003) showed that
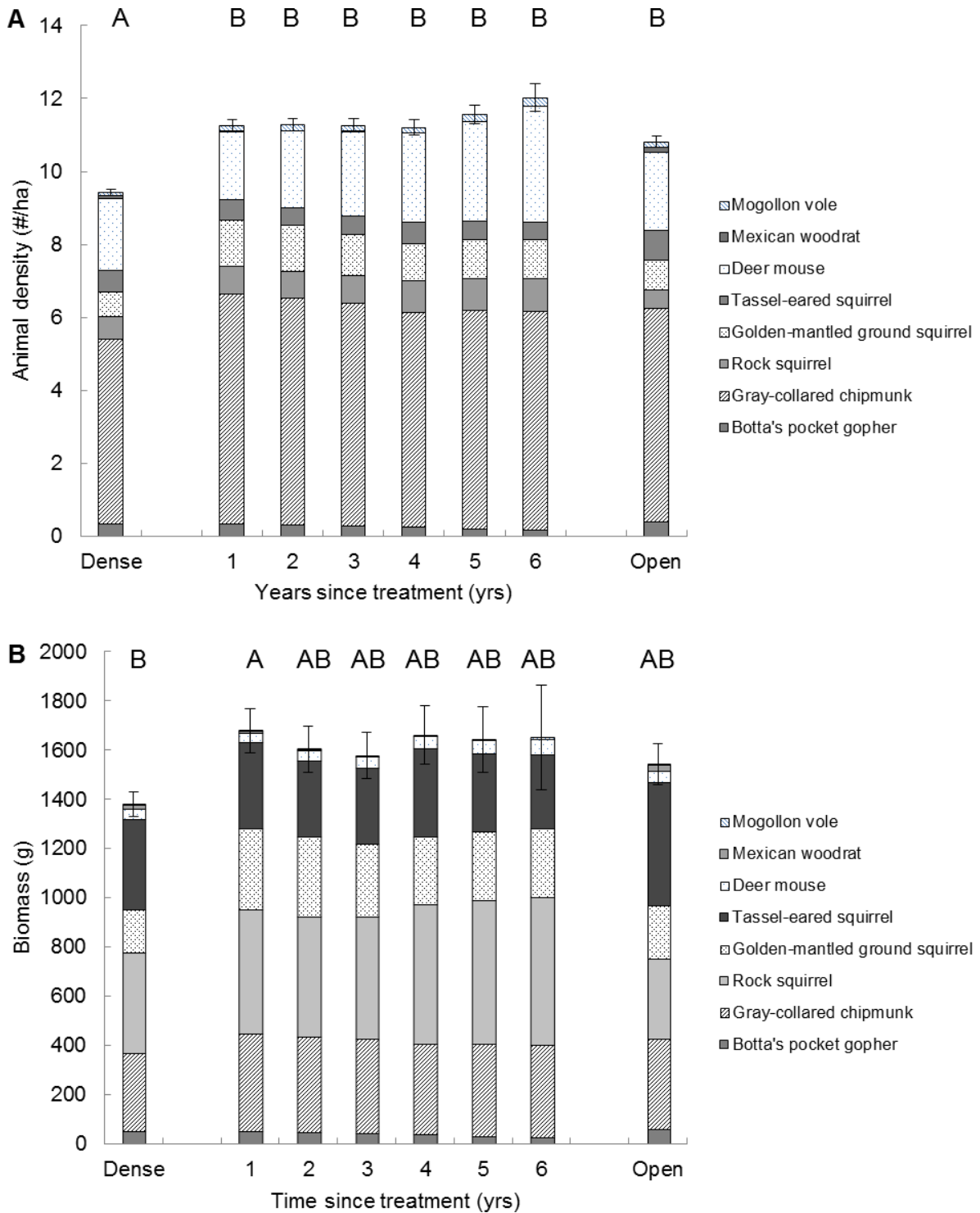
Fig. 2. Average (A) density and (B) biomass of small mammal species each year since treatment. Dense stands were unthinned, 1–6 indicate time since thinning treatment, and open stands were meadow-like but unthinned. Dense stands were different from other treatments in terms of total density, but community composition was significantly different in each of the eight treatments ($P = 0.0001$). In terms of biomass, the dense stand and year 1 were significantly different, but were each similar to all other treatments.

restoration treatments in ponderosa pine forests did not decrease the relative amount of EM fungi propagules compared to unmanaged sites, and thus we assume that EM availability was relatively constant. 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 golden-mantled ground squirrels and gray-collared chipmunks carried similar amounts of EM spores in their feces. We were particularly interested in these species because they were found to be major players in consuming truffles in other systems (Pyare and Longland 2001) and were the most abundant small mammals in our study (excluding deer mice). Furthermore, we wanted to understand the role of species associated with open forest structure, because abundant research on tassel-eared squirrels confirms that the species disperses EM fungi and suggests the role is tied to dense forest conditions (Kotter and Farentinos 1984, States et al. 1988, Dodd et al. 2003). Thus, golden-mantled ground squirrels, chipmunks, and tassel-eared squirrels may compensate for one another in providing this ecosystem function. However, the presence of EM fungi in the feces of small mammals only confirms their potential to disperse fungi; we were unable to measure EM fungi presence or availability following treatments. In addition, we were unable to quantify EM spore counts for the less abundant species that could disperse truffles, including rock squirrels, pocket gophers, voles, and woodrats. Finally, we examined fungi abundance but not diversity, and other studies suggest that small mammal species may not play functionally redundant roles in terms of the species of fungi they disperse (Pyare and Longland 2001).

Implications for ecological restoration

Three species that decreased in density after thinning (Mexican woodrat, tassel-eared squirrel, Botta's pocket gopher) reached their highest densities at reference stands, suggesting that if restoration treatments can achieve this desired endpoint, it will benefit these species despite short-term losses. Furthermore, although total biomass was relatively constant across all treatments, total density was higher in reference than dense sites. However, community composition differed among years, and was significantly different in reference sites compared with each year of thinning; thus, we have no evidence that the thinning treatments will eventually produce community compositions that emulate natural conditions. In addition, while the open stands provide a reference point by which to judge the effectiveness of treatments, these stand structures differ from true natural conditions. Due to logging near Flagstaff during the late 1800s, trees at our study sites tended to be small (less than 2% of the trees we measured were $\geq$60 cm in diameter) unlike natural conditions which contained low densities of large trees (approximately 10% were $\geq$60 cm in diameter; Fulé et al. 1997). Relict sites with intact fire history would be a better indicator of "natural" communities than the sites we sampled. Thus, our results suggest that restoration treatments are maintaining small mammal community-level properties, but it is unclear if community composition is on a trajectory toward restoration in the long term.

LITERATURE CITED

Bagne, K. E. and D. M. Finch. 2009. Response of small mammal populations to fuel treatment and precipitation in a ponderosa pine forest, New Mexico. Restoration Ecology 18:409–417.

Bakker, J. D. and M. M. Moore. 2007. Controls on vegetation structure in southwestern ponderosa pine forests, 1941 and 2004. Ecology 88:2305–2319.

Barrett, K. J., E. L. Kalies, and C. L. Chambers. 2012. Predator occupancy rates in a thinned ponderosa

pine forest, Arizona: a pilot study. Wildlife Society Bulletin 36:232–239.

Bartels, M. A. and D. P. Thompson. 1993. *Spermophilus lateralis*. Mammalian Species 440:1–8.

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

Boal, C. W. and R. W. Mannan. 1994. Northern goshawk diets in ponderosa pine forests on the Kaibab Plateau. The Northern Goshawk: Ecology and Management. Studies in Avian Biology 16:97–102.

Brown, J. H., S. K. M. Ernest, J. M. Parody, and J. P. Haskell. 2001. Regulation of diversity: maintenance of species richness in changing environments. Oecologia 126:321–332.

Burnham, K. P. and D. Anderson. 2002. Model selection and multi-model inference. Second edition. Springer-Verlag, New York, New York, USA.

Colgan, W., III., A. B. Carey, and J. M. Trappe. 1997. A reliable method of analyzing dietaries of mycophagous small mammals. Northwestern Naturalist 78:65–69.

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

Cork, S. J. and G. J. Kenagy. 1989. Rates of gut passage and retention of hypogeous fungal spores in two forest-dwelling rodents. Journal of Mammalogy 70:512–519.

Covington, W. W. 2003. The evolutionary and historical context. Pages 26–47 *in* P. Friederici, editor. Ecological restoration of southwestern ponderosa pine forests. Island Press, Washington, D.C., USA.

Covington, W. W. and M. M. Moore. 1994. Southwestern ponderosa forest structure: changes since Euro-American settlement. Journal of Forestry 92:39–47.

Dodd, N. L., R. E. Schweinsburg, and S. Boe. 2006. Landscape-scale forest habitat relationships to tassel-eared squirrel populations: implications for ponderosa pine forest restoration. Restoration Ecology 14:537–547.

Dodd, N. L., J. S. States, and S. S. Rosenstock. 2003. Tassel-eared squirrel population, habitat condition, and dietary relationships in north-central Arizona. Journal of Wildlife Management 67:622–633.

Ehrlich, P. and B. Walker. 1998. Rivets and redundancy. BioScience 48:387.

Ernest, S. K. M. and J. H. Brown. 2001. Homeostasis and compensation: the role of species and resources in ecosystem stability. Ecology 82:2118–2132.

Fischer, J. M., T. M. Frost, and A. R. Ives. 2001. Compensatory dynamics in zooplankton community responses to acidification: measurement and mechanisms. Ecological Applications 11:1060–1072.

Fritzell, E. K. and K. J. Haroldson. 1982. *Urocyon cinereoargenteus*. Mammalian Species 189:1–8.

Frost, T. M., S. R. Carpenter, A. R. Ives, and T. K. Kratz. 1995. Species compensation and complementarity in ecosystem function. Pages 224–239 *in* C. G. Jones and J. H. Lawton, editors. Linking species and ecosystems. Chapman and Hall, New York, New York, USA.

Fulé, P. Z., W. W. Covington, and M. M. Moore. 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. Ecological Applications 7:895–908.

Ganey, J. L. 1992. Food habits of Mexican spotted owls in Arizona. Wilson Bulletin 104:321–326.

Hoffmeister, D. F. 1986. Mammals of Arizona. The University of Arizona Press, Tucson, Arizona, USA.

Hooven, E. F. 1966. Pine regeneration in Oregon: habits and control of seed-eating mammals. Research Paper 5. Forest Research Laboratory, Oregon State University, Corvallis, Oregon, USA.

Johnson, C. N. 1996. Interactions between mammals and ectomycorrhizal fungi. Trends in Ecology and Evolution 11:503–507.

Kalies, E. L., B. G. Dickson, C. L. Chambers, and W. W. Covington. 2012. Small mammal community occupancy responses to restoration treatments in ponderosa pine forests, northern Arizona, USA. Ecological Applications 22:204–217.

Klug, J. L., J. M. Fischer, A. R. Ives, and B. Dennis. 2000. Compensatory dynamics in planktonic community responses to pH perturbations. Ecology 81:387–398.

Korb, J. E., N. C. Johnson, and W. W. Covington. 2003. Arbuscular mycorrhizal propagule densities respond rapidly to ponderosa pine restoration treatments. Journal of Applied Ecology 40:101–110.

Kotter, M. M. and R. C. Farentinos. 1984. Formation of ponderosa pine ectomycorrhizae after inoculation with feces of tassel-eared squirrels. Mycologia 76:758–760.

Landres, P. B., P. Morgan, and F. J. Swanson. 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecological Applications 9:1179–1188.

Moore, M. M., C. A. Casey, J. D. Bakker, J. D. Springer, P. Z. Fulé, W. W. Covington, and D. C. Laughlin. 2006. Herbaceous vegetation responses (1992–2004) to restoration treatments in a ponderosa pine forest. Rangeland Ecology and Management 59:135–144.

Moore, M. M., W. W. Covington, and P. Z. Fulé. 1999. Reference conditions and ecological restoration: a southwestern ponderosa pine perspective. Ecological Applications 9:1266–1277.

Naeem, S. and J. P. Wright. 2003. Disentangling biodiversity effects on ecosystem functioning:

deriving solutions to a seemingly insurmountable problem. Ecology Letters 6:567–579.

Noss, R. F. and B. Csuti. 1994. Habitat fragmentation. Pages 237–264 in G. K. Meffe and C. R. Carroll, editors. Principles of conservation biology. Sinauer, Sunderland, Massachusetts, USA.

Patton, D. R. 1977. Managing southwestern ponderosa pine for the Abert squirrel. Journal of Forestry 75:264–267.

Pimm, S. L. 1991. The balance of nature? The University of Chicago Press, Chicago, Illinois, USA.

Prins, H. H. T. and I. Douglas-Hamilton. 1990. Stabililty in a multi-species assemblage of large herbivores in East Africa. Oecologia 83:392–400.

Pyare, S. and W. S. Longland. 2001. Patterns of ectomycorrhizal-fungi consumption by small mammals in remnant old-growth forests of the Sierra Nevada. Journal of Mammalogy 82:681–689.

Royle, J. A., J. D. Nichols, and M. Kery. 2005. Modelling occurence and abundance of species when detection is imperfect. Oikos 110:353–359.

Schwilk, D. W. et al. 2009. The national fire and fire surrogate study: Effects of fuel reduction methods on forest vegetation structure and fuels. Ecological Applications 19:285–304.

Smallwood, K. S. and W. A. Erickson. 1995. Estimating gopher populations and their abatement in forest plantations. Forest Science 41:284–296.

Society for Ecological Restoration. 2004. The SER international primer on ecological restoration. Society for Ecological Restoration International Science & Policy Working Group, Tucson, Arizona, USA.

States, J. S., W. S. Gaud, W. S. Allred, and W. J. Austin. 1988. Foraging patterns of tassel-eared squirrels in selected ponderosa pine stands. Pages 425–431 in R. C. Szaro, K. E. Severson, and D. R. Patton, editors. Symposium proceedings on management of amphibians, reptiles, and small mammals in North America, Flagstaff, Arizona, July 19–21, 1988. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

USDA Forest Service. 2005. Mammals of the Coconino National Forest: a checklist. MR-R3-04-1. USDA Forest Service, Southwest Region, Albuquerque, New Mexico, USA.

Walker, B. 1995. Conserving biological diversity through ecosystem resilience. Conservation Biology 9:747–752.

Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. Science 313:940–943.

SUPPLEMENTAL MATERIAL

APPENDIX

Table A1. Model selection results for eight species of small mammals. 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 eight 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†	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

†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 six covariates were used in the model.