Effects of Sagebrush Restoration and Conifer Encroachment on Small Mammal Diversity in Sagebrush Ecosystem ☆

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A B S T R A C T

Conifer encroachment in sagebrush ecosystems reduces habitat heterogeneity, niche space, and resource availability, all of which negatively affect many wildlife populations. Sagebrush restoration is recommended as a management action to mitigate conifer encroachment and restore wildlife across millions of hectares in the Great Basin. Despite this recommendation, the effects of conifer encroachment and sagebrush restoration are unknown for most wildlife species. Small nonvolant mammal communities include keystone species, consumers and prey; facilitate energy flow and ecological function; and provide important ecological goods and services. We assessed causal relationships between conifer encroachment and sagebrush restoration (conifer removal and seeding native plants) on small mammal communities over 11 yr using a Before-After-Control–Impact design. Sagebrush habitat supported an additional small mammal species, twice the biomass, and nearly three times higher densities than conifer-encroached habitat. Sagebrush restoration increased shrub cover, decreased tree cover, and density but failed to increase native herbaceous plant density. Restoration caused a large increase in the non-native, invasive annual cheatgrass (Bromus tectorum L.). Counter to prediction, small mammal diversity did not increase in response to sagebrush restoration, but restoration maintained small mammal density in the face of ongoing conifer encroachment. Piñon mice (Peromyscus truei), woodland specialists with highest densities in conifer-encroached habitat, were negatively affected by sagebrush restoration. Increasing cheatgrass due to sagebrush restoration may not negatively impact small mammal diversity, provided cheatgrass density and cover do not progress to a monoculture and native vegetation is maintained. The consequences of conifer encroachment, a long-term, slow-acting impact, far outweigh the impacts of sagebrush restoration, a short-term, high-intensity impact, on small mammal diversity. Given the ecological importance of small mammals, maintenance of small mammal density is a desirable outcome for sagebrush restoration.

Introduction

Small, nonvolant mammals (hereafter small mammals) play critical ecological roles in sagebrush ecosystems. Seed caching enhances germination of plants such as bitterbrush (Purshia tridentata (Pursh) DC.; Hormay, 1943; Young and Clements, 2002); Mormon tea (Ephedra viridis Coville; Everett et al., 1978; Hollander et al., 2010); and Indian rice grass (Achnatherum hymenoides [Roem. & Schult.] Barkworth; McAdoo et al., 1983). Burrowing by small mammals aerates soils (Huntly and Inouye, 1988), cycles nutrients (Sirotnak and Huntly, 2000), and maintains early seral state plant communities (Kitchen and Jorgensen, 1999). As the prey base for many predators, small mammals are an important trophic link in food webs (Bekoff, 1977; Glaudas et al., 2008). Small mammals also scatter hoard pine nuts, juniper berries, and cheatgrass (Bromus tectorum L.) seed, resulting in the establishment and dispersal of conifers and invasive annual grasses (Chambers et al., 1999; Young and Clements, 2009). Although plant germination is enhanced by scatter hoarding, small mammal herbivory and larder hoarding can also result in significant mortality of seeds and newly established plants (Clements and Young, 1996), both decreasing the establishment of desirable native plants and increasing the prevalence of conifers and cheatgrass. Habitat alteration can disrupt the ecological roles of small mammals in sagebrush ecosystems.

In the past 130 yr, late-successional conifer woodlands have increased 10-fold in the Great Basin (Miller and Tausch, 2001). "Conifer encroachment" describes a successional process of increasing conifer cover and density in sagebrush ecosystems. Historically, conifer encroachment was regulated by periodic natural disturbances, most

importantly high-intensity fire (Miller et al., 2005; Tausch et al., 2009). In recent decades, human-induced factors of fire exclusion (Gruell et al., 1994; Keane et al., 2002), increased atmospheric carbon dioxide concentration, increased winter precipitation, warmer temperatures (Rapp, 2004), and selective herbivory by livestock (Miller et al., 1994) have interacted to increase the rate and scale of conifer encroachment across the Great Basin.

In conifer dominated woodlands, the majority of plant biomass is sequestered as unpalatable cellulose or lignin, which is unavailable to most animals as food. Pine nuts and juniper berries are high in energy and protein, but conifer mast is produced in erratic and unpredictable resource pulses (White et al., 1999; Felicetti et al., 2003). Shrub, grass, and forb production show less interannual variation than conifer mast, produce more palatable seeds and forage, and support higher insect diversity than woodlands, providing a more reliable food source to wildlife than conifer mast (Miller, 2008; McIver and Macke, 2014). Overall conifer encroachment in sagebrush ecosystems reduces habitat heterogeneity, niche space, and resource availability, negatively affecting many wildlife populations, such as sage grouse, pygmy rabbits, and mule deer (Miller et al., 2005; Hanser and Knick, 2011; Baruch-Mordo et al., 2013; Woods et al., 2013).

Conifer removal is the primary restoration tool in conifer-encroached, sagebrush ecosystems. Great Basin coniferous woodlands are dominated by two species: singleleaf piñon pine (Pinus monophylla Torr. & Frém.) and Utah juniper (Juniperus osteosperma [Torr.] Little). Methods of conifer removal include chaining in high-density conifer stands, lop and scatter of low-density conifers, mastication using machinery, prescribed fire, and hand cutting with chainsaws (Bombaci and Pejchar, 2016). To increase shrubs and herbaceous plants, conifer removal projects often incorporate seeding of native shrubs and herbaceous plants into management actions (Weltz et al., 2014).

Despite their critical role in ecosystem function, the effects of conifer encroachment on small mammals have received minimal attention relative to other wildlife species. In a comparison of recent and historic small mammal communities, Rickart et al. (2008) attributed shifts in species composition to increasing conifer woodlands. Changes in species composition included a decrease in sagebrush specialists, Great Basin pocket mice (Perognathus mollpilosus) and least chipmunks (Tamius minimus), and an increase in woodland specialists, piñon mice (Peromyscus truei) and cliff chipmunks (Tamias dorsalis). Sagebrush restoration and conifer removal were suggested as a means to restore sagebrush-dependent small mammal diversity in conifer-encroached ecosystems (Rickart et al., 2008). Similarly, Rodhouse et al. (2010) noted the potential for sagebrush restoration and conifer removal to negatively impact woodland-associated small mammal species, such as piñon mice and cliff chipmunks.

We evaluated the relationships between conifer encroachment, sagebrush restoration, and small mammal diversity in a sagebrush ecosystem over 11 yr. We hypothesized that conifer encroachment has negatively impacted small mammal diversity and that sagebrush restoration could mitigate this loss of diversity. We made four predictions about the effects of conifer encroachment and sagebrush restoration on small mammal diversity: 1) Small mammal diversity is lower in conifer encroached habitat than in sagebrush habitat; 2) Native shrub cover and herbaceous plant density will increase in response to sagebrush restoration; 3) Sagebrush restoration will increase small mammal density, richness, biomass, and evenness; and 4) Small mammal community responses to sagebrush restoration will be species specific. We expected sagebrush specialists to increase in response to sagebrush restoration and woodland specialists to decrease.

Methods

Study Site

The study was conducted in Great Basin National Park, South Snake Range, White Pine County, Nevada (38.98°N, −114.30°W; Fig. 1). Elevations in the South Snake Range vary from 1 621 m in the town of Baker to 3 982 m at the summit of Wheeler Peak. The climate is cool and arid and varies with elevation. The elevation of the study site is 2 832 m, annual precipitation 33 cm, and the mean annual temperature is 9°C
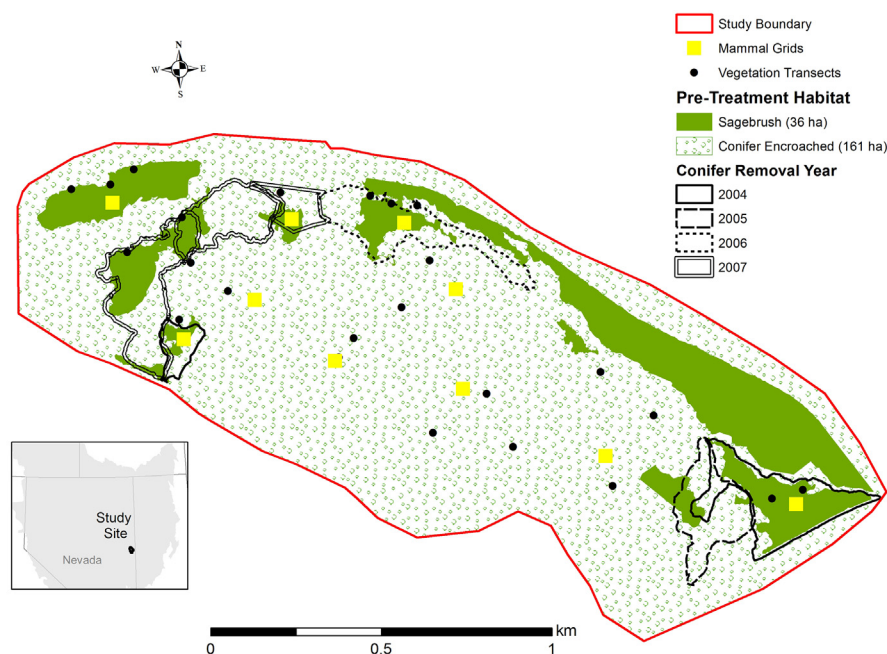

Figure 1. Study site map, showing small mammal grids, vegetation transects, habitat, and areas and year of sagebrush restoration treatments. Inset map shows the study site in the context of the larger Great Basin desert (gray shading).

(Western Regional Climate Center, unpublished data for Lehman Caves). The frost-free period ranges from 60 to 90 d.

Sagebrush Restoration

Treatment goals were to reduce conifer cover from pre-treatment levels of $20 - 30\%$ to $< 10\%$ cover. Quantitative outcomes for shrubs and herbaceous vegetation were not defined, but an overall project goal was to increase native shrubs and native herbaceous vegetation (graminoids and forbs), without increasing cheatgrass, a non-native invasive annual grass. Singleleaf piñon and Utah juniper trees were cut with chainsaws on a total area of 32 ha over the duration of the project (see Fig. 1). Staggered at different sites over several years, conifers were removed only once at a given location (see Fig. 1; $2004 - 2007$). Conifer slash was disposed of through a combination of pile burning, chipping, and fuel wood disposal. To promote the restoration of shrub and herbaceous vegetation, a native seed mix consisting of mountain big sagebrush, Sandberg bluegrass (*Poa secunda* J. Presl), bluebunch wheatgrass, basin wildrye (*Leymus cinereus* [Scribn. & Merr.] Á. Löve), squirreltail (*Elymus elymoides* [Raf.] Swezey), Lewis flax (*Linum lewisii* Pursh), and Indian rice grass was broadcast on the conifer removal units with belly spreaders at ≈ 9 kg of pure live seed per ha.

Study Design

Our study was set up as a Before-After-Control–Impact (BACI) design, a common, quasiexperimental study design widely used to compare environmental conditions before and after human disturbance (de Lucas et al., 2005). The BACI design predicts different patterns of change for impact sites relative to control sites following a disturbance. Hereafter, we use the terms "impact" and "treatment" interchangeably and use "reference" synonymously with "control." A statistically significant interaction between time relative to treatment and treatment (Underwood, 1992) strongly infers a causal relationship between impact and effect (Block et al., 2001). Although reference sites should be closely matched to the impact sites, the absolute similarity between impact and the reference sites is less important than the trajectory of the sites relative to each other, with respect to treatments (Underwood, 1994).

Before sagebrush restoration, habitats were stratified into two habitat types: sagebrush or conifer encroached. Stratification was based on visual assessment and pre-treatment global positioning system (GPS) mapping of habitat patches. Twenty-four vegetation transects were randomly located: 12 in sagebrush habitat and 12 in conifer-encroached habitat, conditional on a minimum separation of 50 m between transects (see Fig. 1). Five small mammal trapping grids were randomly chosen from conifer-encroached habitat. Sagebrush habitat was limited, so the five sagebrush grids were located remotely using a global information system to maximize grid fit (see Fig. 1). Although vegetation transects were not colocated exactly with trapping grids, seven grids were intersected by vegetation transects. The mean distance between vegetation transects and small mammal grids was 6.4 m (range = $0 - 36$ m). Given this close proximity, we consider vegetation transects strongly linked to and representative of small mammal grids (see Fig. 1).

Conifer encroachment occurs on a continuum of increasing tree cover and density described with three woodland phases (Tausch et al., 2009). Conifers occur at low cover and density in phase I woodlands, with shrubs and herbaceous vegetation dominating the understory. In contrast, phase III woodlands have high conifer cover and density, with little shrub or understory vegetation. Phase II woodlands are codominated by conifers and shrubs and provide biological and structural attributes of both woodland and sagebrush habitats (Tausch et al., 2009). We considered post hoc framing of our results into woodland phases but ultimately used our a priori habitat stratification, as the woodland phase paradigm did not exist at the onset of our study. Retrospectively, our conifer-encroached habitat was similar to phase III

woodlands and sagebrush habitat similar to phase II woodlands. We recommend that inferences of our results be limited to sagebrush restoration in phase II woodlands, using similar restoration methods (i.e., cutting conifers with chainsaws and seeding with native plant species).

Four small mammal grids and nine vegetation plots served as impact sites. All impact sites were in sagebrush habitat, where the impact consisted of conifer removal and seeding native vegetation (see "Sagebrush Restoration" earlier). Six small mammal grids and 15 vegetation transects served as untreated, reference sites. Of these reference sites, 1 small mammal grid and 3 vegetation transects were in sagebrush habitat and 5 grids and 12 transects were in conifer-encroached habitat. Habitat was considered a fixed effect, so treated sagebrush sites were still considered sagebrush habitat following treatments.

Time was considered in three ways. "Year" was a continuous variable of calendar year and was incorporated into models as a random effect to account for interannual variation. Pre-treatment and post-treatment were categorical variables (e.g., before and after treatments). Time relative to treatment was the number of years from treatment. As the treatments were staggered over different years, time relative to treatment occurred in different calendar years for the different sites. Reference sites were assigned time relative to treatment on the basis of their proximity to the treated sites, with control sites paired with their closest treated sites.

Vegetation Sampling

Each vegetation transect was sampled before and after sagebrush restoration treatments in June of 2004, 2010, and 2014. Pre-treatment cover (2004) was assessed using a line intercept method (Bonham, 1989). A major weakness of the line intercept method is that annual grass cover is poorly sampled. Cheatgrass is the only ecologically important annual grass on our site. As a non-native invasive species, cheatgrass was critical to monitor. To improve sampling of cheatgrass cover, we adjusted our methodology from a line intercept to a line–point intercept in 2010 and 2014 (Herrick et al., 2005). To justify this change in sampling, we ran seven comparative transects and found tree and shrub cover strongly correlated ($r = 0.993$ and 0.944, respectively) between methods. Herbaceous cover, which included cheatgrass, all other grasses, graminoids, and forbs, was weakly correlated between methods ($r = 0.675$). Given the strong correlations for tree and shrub cover, we used cover to assess treatment effects on shrubs, density on herbaceous vegetation, and both cover and density to address treatment effects on trees. Herbaceous plant density was measured in four quadrats per transect (35 cm $\times$ 35 cm). Quadrats, combined by transect for analysis, were oriented on the east side of transects every 10 m, sampling a total area of 0.5 m^2 per transect. Tree density was sampled on larger plots (2 m $\times$ 100 m), one plot per transect (Herrick et al., 2005). All trees with stems wholly or partially within the plot were tallied.

Small Mammal Sampling

Small mammals were sampled with Sherman live traps arranged in a grid configuration. Grids were sampled each July from 2004 to 2014. Each grid consisted of 49 Sherman live traps (SFAL; 5 cm $\times$ 6 cm $\times$ 23 cm or LFA; 8 cm $\times$ 9 cm $\times$ 23 cm) separated by 15 m, in a 7×7 pattern, sampling an area of approximately 1 ha. Individual trap locations were relocated with GPS ($\pm$ 1 m). Traps were locked open and prebaited for $3 - 4$ d before sampling, then rebaited and set. Millet and sunflower seeds were used as bait. Traps were set each evening between 17:00 and 20:00, checked each morning between 05:00 and 10:00, and shut during the day. Trapping sessions consisted of 4 consecutive nights. Trapping was interrupted on two occasions for 1 night but resumed the following day. Captured small mammals were ear tagged, identified to species, visually assessed for sex, weighed, and released. Recaptured individuals were weighed and assessed for ear tag number, species, and

Table 1

Small mammal captures by species for sagebrush and conifer-encroached habitats in Great Basin National Park, White Pine County Nevada. Small mammals were sampled from 2004 to 2014 for a total of 20 920 trap nights in 10, one-ha grids.

Common name	Species	Sagebrush	Conifer encroached
Deer mouse	*Peromyscus maniculatus*	1 228	369
Western harvest mouse	*Reithrodontomys megalotis*	144	0
Cliff chipmunk	*Tamias dorsalis*	75	80
Piñon mouse	*Peromyscus truei*	22	103
Montane vole	*Microtus montanus*	8	0
Long-tailed vole	*Microtus longicaudus*	14	1
Great Basin pocket mouse	*Perognathus mollipilosus*	13	1
Sagebrush vole	*Lemmiscus curtatus*	5	0
Uinta chipmunk	*Tamias umbrinus*	1	1
Least chipmunk	*Tamias minimus*	1	0

sex and then released. After accounting for sprung traps, trap effort consisted of 20 920 trap nights. Ten species and 2 066 individuals were captured over the 11 yr of sampling (Table 1). Small mammal densities fluctuated widely across years in both impact and reference grids (Fig. 2). Fluctuations were qualitatively synchronous across impact and reference sites (see Fig. 2). Small mammal sampling was conducted according to the guidelines of Brigham Young University's Institutional Animal Care and Use Committee, project code 07-0301, scientific research permits from Great Basin National Park (GRBA-2007-SCI-0002) and Nevada Department of Wildlife (S35631), and the American Society of Mammalogists (Sikes et al., 2011).

Data Analysis (Vegetation)

To quantify pre-treatment differences in mean tree, shrub, and herbaceous cover between sagebrush and conifer-encroached transects, we used Student's *t*-tests with unequal variances and *f*-tests to examine differences in variability. We examined the response of vegetation to conifer removal, using a BACI design (as described earlier) implemented in a generalized linear mixed-model framework. For vegetation analyses, time was binned into two categories: pre-treatment or post-treatment. Tree and shrub cover and herbaceous and tree density were treated as fixed effects in separate models. Cover was modeled with a negative binomial distribution and density with a Poisson distribution, both using log links. Transect was incorporated into models as a random effect. Chi-squared tests were used to test for differences in observed versus expected herbaceous density and percent composition of annual grasses between treated and untreated sites, pre-treatment and post treatment. Expected density, the statistical null hypothesis, was defined as equal distribution across time and treatments.
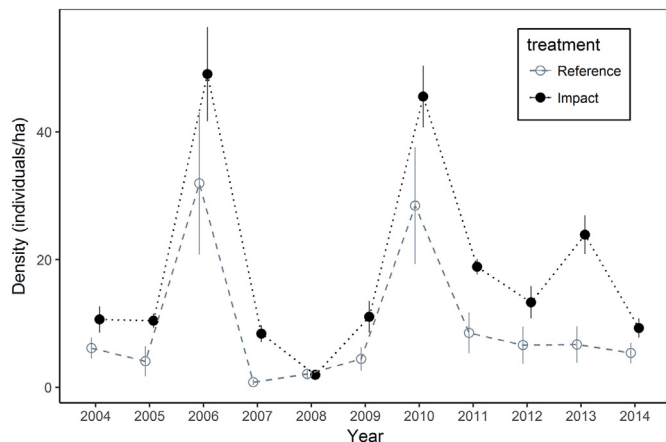

Figure 2. Annual small mammal densities ($\overline{x} \pm$ SE) in July for reference and impact grids in Great Basin National Park, White Pine County, Nevada. Small mammal densities were estimated from spatially explicit capture recapture models.

Data Analysis (Small Mammals)

Species richness was the number of species per grid by year. Our evenness metric was the inverse of the Simpson index (SI) calculated as: SI $= 1/[\sum (n_i * (n_i - 1)/N(N - 1)]$; where $n_i =$ the number of individuals of the ith species; and $N =$ the total number of individuals (Magurran, 2004). As SI decreases, community evenness also decreases. Total biomass was the sum of the mean weights of all individuals captured per grid by year.

Total density and density of individual species (deer mice, piñon mice, cliff chipmunks, voles, Great Basin pocket mice, and western harvest mice) were calculated using spatially explicit capture recapture (SECR) models. Spatially explicit capture recapture models relate the spatial relationships of traps (detectors) and the movement of animals between traps through a combination of a state model and an observation model (Efford et al., 2009). The state model describes the distribution of the animal home ranges on the landscape. The observation model (spatial detection model) relates the probability of detecting an individual at a particular detector to the distance of the detector to a central point in each animal's home range. The distribution of home range centers is treated as a homogenous Poisson point process. Buffer width was set at 150 m. The detection function describes the decline in detection probability with distance from the home range center using a half-normal detection function. Detector types were single, as traps were generally capable of catching only one animal. Full likelihood was used to fit all models. Detection was modeled as a function of distance between the trap and the individual's latent activity center.

Eight candidate SECR models were analyzed to calculate density. Each year was treated as a session, and each grid was analyzed separately by species. Density was always fit as a function of session (year). Detection (g0) and movement (σ) were modeled as 1) constant detection probability across occasions and detectors; 2) learned response affecting detection; 3) trap response to time; 4) trap response with a time trend; 5) trap response model-transient; 6) site learned response; 7) site transient response; and 8) heterogeneity model, finite mixture model, with two latent classes. All SECR models were computed in the R package secr (Efford, 2018). Density estimates were highly correlated with raw captures ($r = 0.90$).

The heterogeneity model (8) was highly favored by Akaike Information Criterion, corrected for small sample size (AIC$_c$) when enough animals were captured to support the model structure (Δ AIC$_c$ <2) (Burnham and Anderson, 2002). Otherwise, the null model was preferred. When there was competing weight of evidence, we used model averaging to calculate density (individuals ha^{-1}). When there was a clear top model (Δ AIC$_c$ < 2), that model was used to estimate density. Year-specific density estimates by sampling grid were incorporated as response variables into the mixed models.

We assessed the effects of habitat and sagebrush restoration treatments on small mammal communities using the BACI design as described earlier. Generalized linear mixed models were used to assess the effects of sagebrush restoration and habitat on small mammal diversity (species richness, total biomass, evenness, total density, and individual species density). Habitat (sagebrush or conifer-encroached) and sagebrush restoration effects (interaction between treatment and time) were the primary independent variables. Time was defined in years from treatment or binned into pre-treatment or post treatment. For most dependent variables we compared five models: 1) treatment × time (pre, post) + habitat; 2) treatment × time (year relative to treatment) + habitat; 3) habitat only; 4) treatment × time (pre, post); and 5) null model. Site and year were included as additive random effects in models. Richness and evenness were modeled using a Gaussian distribution and identity link function. A negative binomial distribution was used to model biomass and a Poisson distribution to model density, both using log link functions (Table 2).

Zero-inflated models were used to analyze the effect of sagebrush restoration and habitat on piñon mouse, cliff chipmunk, vole, pocket

Table 2
Model comparisons of sagebrush restoration and habitat effects on small mammal diversity in Great Basin National Park.

	Model	Parameters	AICc	Delta AICc	Model weight
Richness	Habitat	6	284.77	0.00	0.91
	Treatment × time + habitat	9	290.76	5.99	0.05
	Treatment × time	8	291.83	7.07	0.03
	Null	5	292.63	7.87	0.02
	Treatment × yr + habitat	25	312.52	27.76	0.00
Total biomass	Habitat	6	1419.76	0.00	0.93
	Treatment × time + habitat	9	1424.90	5.13	0.07
	Treatment × time	8	1433.56	13.80	0.00
	Null	5	1434.50	14.74	0.00
	Treatment × yr + habitat	25	1458.13	38.36	0.00
Evenness	Null	5	221.73	0.00	0.55
	Habitat	6	222.49	0.77	0.37
	Treatment × time	8	226.13	4.40	0.06
	Treatment × time + habitat	9	228.51	6.78	0.02
	Treatment × yr + habitat	25	264.19	42.46	0.00
Total density	Treatment × time + habitat	8	689.21	0.00	0.39
	Habitat	5	689.51	0.30	0.33
	Treatment × time	7	690.07	0.86	0.25
	Null	4	694.60	5.39	0.03
	Treatment × yr + habitat	24	700.01	10.80	0.00

Richness indicates number of species/grid/yr; Evenness, inverse of Simpson index (SI), where lower values indicate lower evenness; Total biomass, sum of mean weights for all individuals captured/ grid/yr; Total density, sum of estimated densities for all species/yr, estimated through spatially explicit capture recapture models. Time (pre_post), time binned into pre-treatment or post-treatment periods; time (yrs elapsed), time binned into yrs elapsed post treatment; habitat, habitat type, either sagebrush or conifer encroached.

mouse, and western harvest mouse densities. The proportion of grids with no captures for these species ranged from 35% to 88%. Long-tailed and montane vole densities were combined for analysis. Models for piñon mice, cliff chipmunks, voles, pocket mice, and harvest mice could support time only as pre-treatment, post-treatment in the treatment time interaction. To allow model convergence, random effects for piñon mice only included year and random effects were excluded from density models for cliff chipmunks, voles, pocket mice, and harvest mice. Total and deer mouse densities did not require zero-inflated models.

To validate model fit, we plotted residuals versus fitted values, residuals versus covariates, and examined histograms of residuals for normality. We also compared models with treatment and habitat effects to null models using Akaike Information Criterion (AIC_c) to guide model selection (Burnham and Anderson, 2002). Models differing by < 2 AIC_c units were considered equivalent. Alpha (α) was set at 0.05. Effect sizes are given following statistical results, calculated from highest-ranked model coefficients, model averaging, or mean differences between groups. Analyses were done with Program R (R Core Team, 2016), generalized linear mixed models in the R package glmmADMB (Skaug et al., 2014), and model averaging with the R package "MuMIn" (Barton, 2018).

Results

Vegetation (pre-treatment)

Before sagebrush restoration, transects classified as sagebrush habitat had higher herbaceous (t = 4.20, d.f. = 13.1, P = 0.001; 5.3%) and shrub cover (t = 5.75, d.f. = 11.25, P = 0.0001; 13.4%) than conifer-encroached transects (Fig. 3). Total plant cover did not differ between habitats (t = 1.03, d.f. = 15.3, P = 0.32). Conifer-encroached habitat was higher in tree cover (t = 2.69, d.f. = 16.89, P = 0.015; 13%) and had lower variance in herbaceous (ratio of variances = 0.09), shrub (ratio of variances = 0.01), and tree cover (ratio of variances = 0.29) than sagebrush habitat (P < 0.05 for all tests). Tree density was higher in conifer-encroached relative to sagebrush habitat by a factor of 2 (t = 4.80, d.f. = 18, P < 0.0001; 7 975 vs. 4 071 trees ha^{-1}). All conifer-encroached transects had < 2.6% shrub cover, and all sagebrush transects had > 2.6% shrub cover. Singleleaf pinyon was the dominant tree, accounting for 84% of tree cover and 93% of tree density. Utah juniper was less abundant and comprised 15% of tree cover and 5% of tree density. Curleaf mountain mahogany (*Cercocarpus ledifolius* Nutt.), aspen (*Populus tremuloides* Michx.), and chokecherry (*Prunus virginiana* L.) occurred on sagebrush transects but were rarely sampled.

Vegetation (post treatment)

Sagebrush restoration reduced tree cover from 28.7% to 2.2%, while tree cover was unchanged on untreated plots (z = 11.81, P < 0.0001).
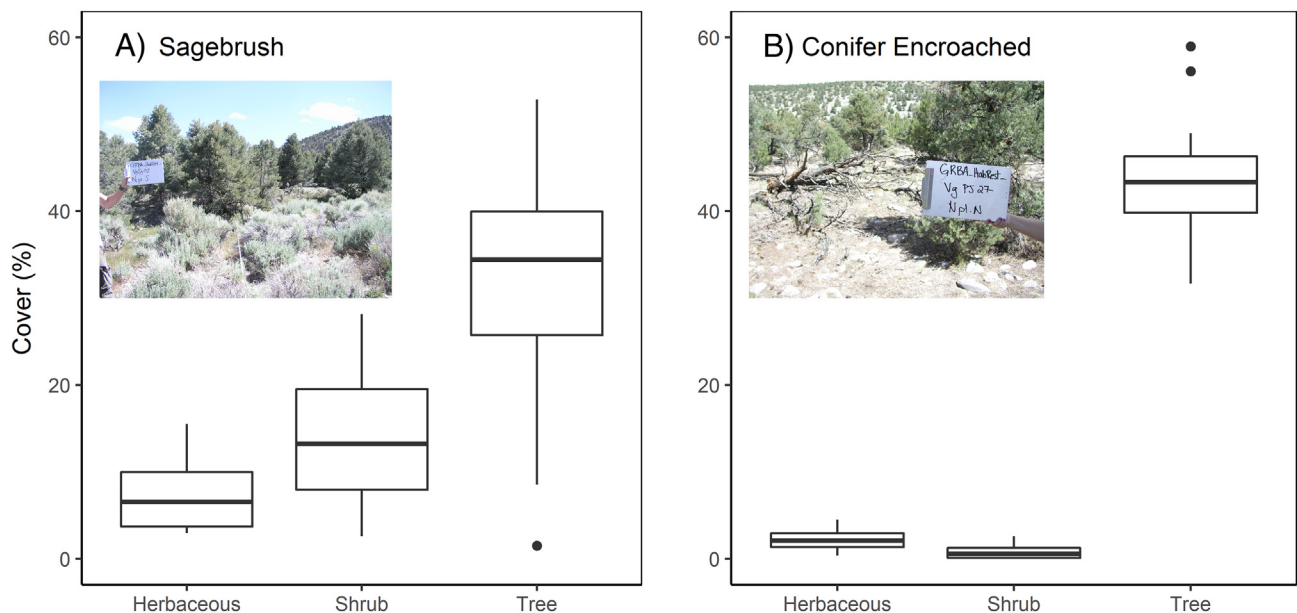

Figure 3. Vegetation structure in sagebrush and conifer-encroached habitats in Great Basin National Park, White Pine County, Nevada. Herbaceous vegetation included cheatgrass, graminoids, and forbs. Boxes show median and interquartile ranges, whiskers extend 1.5 times the interquartile ranges, and dots show data falling outside the 1.5 interquartile ranges.
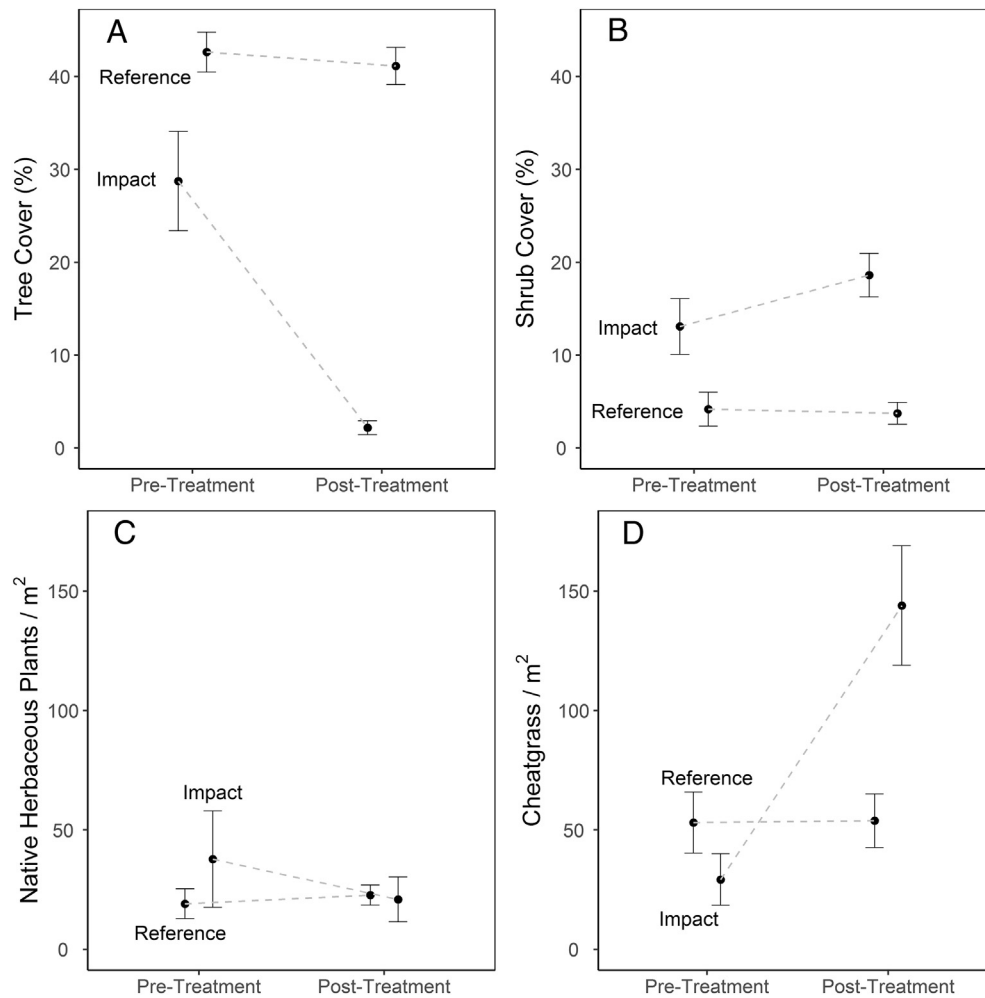
Figure 4. Percent cover of trees (**A**), percent cover of shrubs (**B**), density of native herbaceous plants (**C**), and density of cheatgrass (**D**) before and after sagebrush restoration at control and treatment sites in the Great Basin National Park. Values are means and standard errors.

Tree density was reduced from 4 194 to 1 805 trees ha^{-1} on treated plots while tree density increased from 7 120 to 7 374 trees ha^{-1} on untreated plots ($z =$, $P < 0.0001$). Sagebrush restoration increased shrub cover from 13.1% to 18.6% on treated plots while shrub cover decreased slightly on untreated plots from 4.2% to 3.7% ($z = 2.50$, $P = 0.0123$). Herbaceous plant density increased by 146% on treated plots and was unchanged on untreated plots ($z = 4.94$, $P < 0.0001$). The increase in herbaceous density was driven by cheatgrass, which increased fourfold on treated plots (Fig. 4). As a proportion of herbaceous density, cheatgrass density nearly doubled, increasing from 42% to 81% on treated plots while decreasing from 66% to 42% on untreated plots. When cheatgrass was removed from the model, the increase in herbaceous density due to conifer removal was not statistically significant ($z = 1.32$, $P = 0.20$). Cheatgrass also increased in percent composition on treated plots. Following sagebrush restoration treatments, cheatgrass density was higher than expected on treated plots, while noncheatgrass herbaceous density was less than expected (see Fig. 4; $\chi^2 = 619$, $P < 0.0001$). Total cheatgrass cover on post-treated transects ranged from 7% to 59% ($\bar{x} = 33\% \pm 15\%$).

Small Mammal Diversity

Sagebrush restoration did not affect total biomass (yr, $z < 1.06$, $P > 0.36$; pre-, post-, $z = 0.81$, $P = 0.42$); richness (yr, $z < 1.06$, $P > 0.287$; pre-, post-, $z = 0.49$, $P = 0.62$); or evenness (yr, $z < 1.13$, $P > 0.260$;

pre-, post, $z = 0.40$, $P = 0.69$). When time was binned into years relative to treatment, the treatment effect was significant for total density at 8 yr post treatment ($z = 2.25$, $P > 0.024$). When time was binned into pre-treatment or post-treatment, sagebrush restoration maintained density
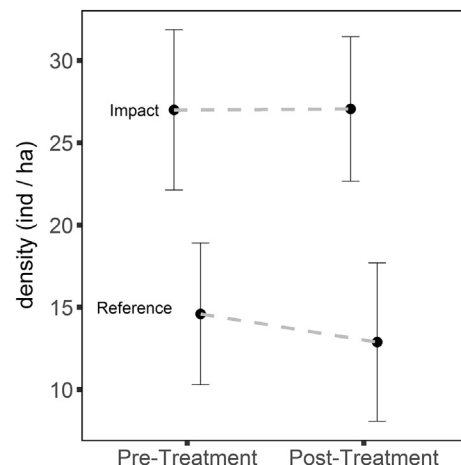

Figure 5. Total density of small mammals for impact and reference grids before and after sagebrush restoration. Restoration maintained density on treated grids while density fell on untreated grids ($P = 0.0097$).

Table 3

Metrics of small mammal diversity for sagebrush and conifer-encroached habitats in Great Basin National Park. Sites were sampled annually from 2004 to 2014.

	Sagebrush	Encroached
Richness*	2.5 ± 9.0	1.7 ± 12.4
Evenness	1.52 ± 0.65	1.41 ± 0.70
Biomass (g)*	447.8 ± 347.0	187.6 ± 213.1
Density (ind./ha)*	27.5 ± 23.3	10.1 ± 12.9

Asterisk (*) indicates significant differences ($P < 0.01$).

on treated grids, while density dropped on untreated grids ($z = 2.59$, $P = 0.0097$; Fig. 5). Model comparisons supported habitat-only models for richness and biomass, indicating that treatment effects can be discarded in favor of the simpler habitat-only models (see Table 2). Habitat had large effects on richness, biomass, and density ($z > 3.27$, $P < 0.001$; Table 3). Sagebrush habitat supported an additional species, 2.3 times more biomass, and 2.7 times the number of individuals than conifer-encroached grids (see Table 3). Habitats did not differ in evenness ($z = 1.26$, $P = 0.21$).

Species-Specific Effects

Deer mice were the most abundant species in both habitats, making up 77% of captures (see Table 1). The effects of sagebrush restoration on deer mice mirrored total density, where restoration treatments maintained density on treated grids and density fell on untreated grids (yr 1 post treatment, $z = 2.26$, $P < 0.0238$; pre-treatment and post-treatment, $z = 1.94$, $P = 0.0519$). Deer mice were 3.8 times more abundant in sagebrush than conifer-encroached habitat ($P < 0.0001$). Vole densities (*Microtus* sp.) were unaffected by conifer removal ($z = 0.50$, $P = 0.612$) and were higher in sagebrush habitat by a factor of 22 ($P = 0.0042$). Great Basin pocket mouse density was not affected by conifer removal ($z = 1.78$, $P = 0.076$). Pocket mouse density was higher on sagebrush than conifer-encroached grids by a factor of 16 ($z = 2.42$, $P = 0.0155$). Western harvest mice occurred only in sagebrush habitat, and we were unable to model habitat effects. Harvest mice increased in density in sagebrush habitat from 2004 to 2014 ($z = 4.63$, $P < 0.001$), and there was no effect of sagebrush restoration ($z = 0.00$, $P = 1.00$). We could not test for habitat or treatment effects for sagebrush vole density, but we note that the only observations of sagebrush voles occurred on a sagebrush grid following conifer removal. Piñon mouse density was significantly reduced by sagebrush restoration treatments while density increased on

Figure 6. Total density of piñon mice for impact and reference grids before and after sagebrush restoration. Restoration decreased density on treated grids while density increased on untreated grids ($P = 0.0036$).

untreated sites (pre-treatment and post-treatment; $z = 2.91$, $P = 0.0036$; Fig 6). Piñon mouse density was 5.9 times higher on conifer-encroached than sagebrush habitat ($z = 4.73$, $P = 0.00531$). There were no treatment effects ($z = 1.32$, $P = 0.350$) on cliff chipmunk density. Cliff chipmunks were more abundant (1.6 times) in sagebrush than conifer-encroached habitat ($z = 2.38$, $P = 0.02621$).

Discussion

Sagebrush restoration is recommended on millions of hectares across the Great Basin (Wisdom et al., 2002). As the scale and rate of these projects increase, site-specific understanding of sagebrush restoration effects on wildlife communities is a major research need (Knick et al., 2014; Bombaci and Pejchar, 2016). Small mammals are excellent models for assessing the effects of conifer encroachment and restoration. With their small home ranges, small mammals are closely tied to local changes in resource availability (Stephens et al., 2017). Additionally, small mammal communities include keystone species; habitat specialists and generalists; a diverse guild of feeding ecologies; and are both consumers and prey. Thus, small mammal community response is a window into ecosystem function, the understanding of which is a fundamental goal of land management and restoration. This study is the first to assess the relationships between conifer encroachment and sagebrush restoration (conifer removal and seeding) on small mammal communities using a BACI design to assign causal relationships and random effects to increase inferential scope. In addition, the 11 yr of monitoring effort is substantially longer than most BACI studies.

Conifer encroachment into sagebrush habitat has dramatically reduced small mammal abundance and biomass. Sagebrush restoration (conifer removal and seeding of native plants) increased native shrub cover and invasive, non-native cheatgrass density but did not increase native herbaceous plant densities. Sagebrush restoration reduced the density of the woodland specialist piñon mouse. Overall, sagebrush restoration treatments had few effects on small mammal diversity but restoration effectively maintained small mammal densities in the face of conifer encroachment.

Large-scale ecological experiments, such as this study, are difficult to implement but are critical to address management and conservation questions (Soanes et al., 2018). We used the strongest possible methods and study design, given the constraints of management and habitat on the study site (Soanes et al., 2018). However, it is important to acknowledge the limitations of our study. Due to limited sagebrush habitat, our study did not capture the entire successional range of sagebrush ecosystems (e.g., phase I, II, and III woodlands). We recommend that inferences of our results be limited to sagebrush restoration in phase II woodlands, using similar restoration methods (i.e., cutting conifers with chainsaws and seeding with native plant species).

Conifer Encroachment and Small Mammal Diversity

We observed large differences in small mammal richness, biomass, and density between conifer-encroached and sagebrush habitats (see Table 3) that support our prediction that conifer encroachment has reduced small mammal diversity. Comparison of sagebrush and conifer-encroached habitats can be viewed as a space for time substitution. Several lines of evidence support the hypothesis that our study site was historically more open and sagebrush dominated, and that conifer density and cover have increased over the last century (sensu Tausch et al., 2009). Soils on our study site are in the Badena series, a mollisol with glacial outwash parent material (USDA Natural Resources Conservation Service, 2009). Characterized by a mollic epipedon, mollisols develop in the absence of conifers, primarily from organic matter derived from grasses and shrubs (USDA Natural Resources Conservation Service, 2009). In addition, historic photos of the study site document lower tree densities and higher shrub cover than currently occur (Appendix 1). We also regularly observed shrub skeletons under conifers, further
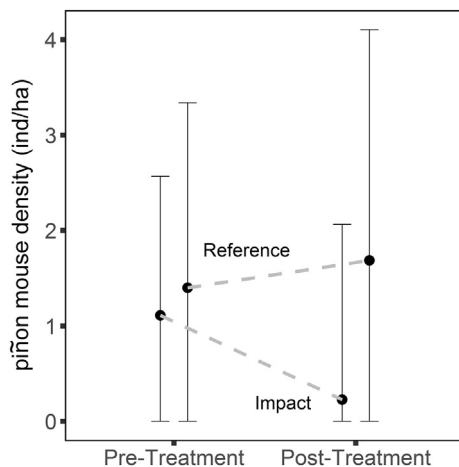
indication of recent conifer encroachment (Appendix 2; Austin, 1999; Miller et al., 2008; Tausch et al., 2009). Assuming an increase in tree density and cover over the past century, small mammal diversity has been lost from formerly open sagebrush habitat as a result of conifer encroachment.

Similar negative relationships between conifer encroachment and small mammal diversity were also found in northern Nevada sagebrush ecosystems. Coincident with regional woodland expansion, small mammal communities declined by 50% in abundance, biomass, and energy use between 1920 and 2008 (Rowe et al., 2011). We found threefold lower density and twofold lower small mammal biomass in conifer-encroached habitat relative to sagebrush habitat, results consistent with the Rowe et al. (2011) historic comparison.

Although these arguments are correlative, direct observation and establishment of a true causal relationship between conifer encroachment and small mammal diversity is unlikely. More than 100 yr are required for the development of woodlands similar to the conifer-encroached habitat we studied (Tausch et al., 2009). Given limitations of funding for long-term monitoring, correlative relationships, space for time substitutions, and historic comparisons provide the strongest available evidence of negative effects of conifer encroachment on small mammal communities.

If conifer encroachment causes a loss of small mammal diversity, what mechanisms drive the process? Small mammal abundance and biomass reflect resource availability (Rowe et al., 2011). Conifer encroachment has resulted in the severe reduction of native understory shrubs and herbaceous vegetation, structural complexity and variability, plant productivity, habitat heterogeneity and an overall reduction of resource and niche space availability to the small mammal community (see Fig. 3).

Sagebrush Restoration and Vegetation

Sagebrush restoration increased shrub cover and decreased tree cover and density but failed to increase native herbaceous plant density. Restoration treatments also caused an increase in the non-native, invasive, annual grass cheatgrass (see Fig. 4). Despite the increase in cheatgrass associated with sagebrush restoration, there were no negative effects on small mammal diversity in our study. Some studies have correlated reduced small mammal diversity with high cheatgrass cover (Ostoja and Schupp, 2009; Freeman et al., 2014). Other work has shown that species richness was not affected by cheatgrass cover, but species responses were related to their functional traits (Ceradini and Chalfoun, 2017). Cover values of cheatgrass on our treated sites were modest (33%) compared with studies linking reduced small mammal diversity and cheatgrass (47 − 100% cover; Freeman et al., 2014; monoculture and 90% standing biomass; Ostoja and Schupp, 2009). In addition, these studies on small mammal diversity and cheatgrass were conducted at lower elevations than our study, below the zone of conifer encroachment, where Heteromyids formed a larger component of the small mammal community (Ostoja and Schupp, 2009; Freeman et al., 2014; Ceradini and Chalfoun, 2017). Native shrubs and native herbaceous plants were also maintained on our treated sites. Thus, an increase in cheatgrass resulting from sagebrush restoration may not negatively impact small mammal diversity, provided cheatgrass density and cover do not progress to an annual grass monoculture.

Increases in cheatgrass often occur following sagebrush restoration projects (Bates et al., 2005; Baughman et al., 2010), and seeding alone may not restore native perennial grasses and forbs (Baughman et al., 2010). To avoid cheatgrass monocultures, sagebrush restoration projects should target resilient and resistant sites (Pellant et al., 2004; Weltz et al., 2014), anticipate post-treatment increases in annual grasses, and incorporate several years of seeding and herbicide treatments following conifer removal into restoration prescriptions.

Sagebrush Restoration and Small Mammal Communities

Contrary to prediction, small mammal diversity did not increase in response to sagebrush restoration. With the exception of total density, treatments did not affect diversity. However, sagebrush restoration *maintained* small mammal densities in the face of conifer encroachment. In contrast to the short-term, high-intensity, "pulse" impact of restoration, the slow conversion of sagebrush habitat to conifer-encroached habitat is a long-term, slow-acting "press" impact with a negative and, presumably, slow effect on small mammal communities (see Underwood, 1994 for definitions of press and pulse impacts). Restoration resets succession and reduces tree cover, increasing shrub cover and herbaceous plants. In untreated sites, shrub and herbaceous cover continued to be lost to conifer encroachment, as tree cover increased. Restoration delayed conversion of sagebrush habitat to conifer-encroached habitat, effectively maintaining small mammal densities.

Species-Specific Effects

Piñon mice showed a strong and negative response to sagebrush restoration. We anticipated this response, as piñon mice are true woodland obligates (Hoffmeister, 1981; Rodhouse et al., 2010). Piñon mice were also the only species more abundant in conifer-encroached habitat than sagebrush (by a factor of 7). These habitat preferences are consistent with historically expanding populations of piñon mice in response to woodland expansion (Rickart et al., 2008).

Counter to expectation, cliff chipmunks, also associated with conifer woodlands (Rodhouse et al., 2010), were not affected by conifer removal and were slightly more abundant in sagebrush habitat. We initially speculated that the larger cliff chipmunks had correspondingly larger home ranges than piñon mice and dispersed into treated sites from the conifer-encroached matrix. However, the two species have similar home range sizes of approximately 1 ha (Hoffmeister, 1981; Hart, 1992; this study). Our methods restricted captures of diurnal species, such as cliff chipmunks, which may have influenced our results. Assessment of treatment effects on diurnal species will require daytime sampling.

Due to low capture rates, large annual fluctuations in density, and unbalanced occurrence across habitats and treatments, species-specific effects of sagebrush restoration and habitat were difficult to model for most species. This is a common theme in conservation biology; species of management concern are generally uncommon, habitat specialists and seldom captured in sufficient numbers to make strong, statistically valid inferences with adequate power to detect treatment effects. While we found no treatment effects for voles, pocket mice, or harvest mice, we noted that these species were much more abundant in sagebrush than conifer-encroached habitat. Harvest mice and sagebrush voles include annual grasses in their range of habitat preferences, and our study found those species only on treated sites post sagebrush restoration. Future studies should test the hypothesis that some small mammal species may increase in density or occupancy as a result of sagebrush restoration and increased annual grasses. Additional work should focus on functional and aggregate diversity and attempt to model restoration effects on rarer species, particularly sagebrush specialists. Future questions should be addressed across the successional range of conifer encroachment in sagebrush ecosystems and, ideally, replicated regionally.

Management Implications

Negative consequences of conifer encroachment on small mammals far outweigh the short-term, minor impacts of sagebrush restoration. Given the ecological significance of small mammals as keystone species, consumers, and prey species, maintenance of small mammal density is a desirable ecological outcome for sagebrush restoration. Unless woodland specialists such as piñon mice and cliff chipmunks are species of management concern, sagebrush restoration is an appropriate tool for

maintenance of small mammal diversity in the face of conifer encroachment. Moderate increases in cheatgrass as a result of sagebrush restoration may not negatively affect small mammal communities, provided native shrubs and herbaceous plants are maintained and cheatgrass cover values are low. However, sagebrush restoration projects should anticipate increased annual grasses and plan for several years of herbicide application and seeding following restoration treatments.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.rama.2018.08.004.

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