RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration

SER SOCIETY FOR ECOLOGICAL RESTORATION

RESEARCH ARTICLE

Does active plant restoration passively restore native fauna community structure and function?

Dean E. Pearson[1,2,3], Yvette K. Ortega[1], Hillary E. Cimino[2], Daniel L. Mummy[4], Philip W. Ramsey[4]

Ecological restoration commonly emphasizes reestablishing native plant communities. Implicit in this approach is the assumption that actively restoring plant communities can passively restore structure and function of other community components like wildlife. However, this assumption is rarely tested. We evaluated how plant restoration in grasslands of the northwestern United States affected the structure (composition and relative abundance) of native small mammal communities and the important functional role they play as seed predators. We quantified vegetation, small mammal community structure, small mammal seed predation, and effects of seed predation on native plant recruitment in comparable grasslands that were either native-dominated, planted with introduced forage grasses, or had undergone restoration treatments to suppress introduced grasses and increase native plants with and without supplemental watering. Native plant cover averaged ≥5 times higher at restoration sites relative to introduced grass sites. Small mammals, primarily deer mice (*Peromyscus maniculatus*), were least abundant in introduced grass sites and most abundant in water-supplemented restoration treatments, with intermediate levels in native and unwatered restoration sites. Seed offerings and seed sowing experiments indicated that seed predation and its effects on plant recruitment correlated with small mammal abundance, with effects generally weakest in introduced grass and strongest in restoration sites. Our results suggest that active plant restoration can passively restore the structure and function of native small mammal communities. While small mammal seed predation is a desired long-term function, it can also inhibit restoration efforts. We discuss emerging strategies for mitigating seed predation during restoration seeding.

Key words: reseeding, restoration seeding, rodents, seed coatings, seed predation, small mammals

Conceptual Implications

- Actively restoring exotic-dominated grasslands to more native plant communities can passively restore the structure and function of some native faunal communities.
- However, restored consumer functions like seed predation can incur undesirable feedbacks like suppressing native plant establishment, which may require temporary mitigation.

Introduction

Ecological restoration has generally focused on reestablishing native plant community composition with an implicit assumption that this approach will restore overall system function (Hobbs & Norton 1996; Young et al. 2001). Of course, fully restoring ecosystems require reestablishing the full complement of system components and their ecological functions across taxa and trophic levels. In theory, because plant communities are basal to higher tropic levels, the more vagile animal species can reestablish once vegetation is in place to provide requisite food and habitat. As stated by Hobbs and Norton (1996), "There is a general perception that the reintroduction of plants into an area will pull the remaining ecosystem components along with it." But as they also note, "This (outcome) is by no means clear." If this idea is valid, then restoration can focus on a "build-it-and-they-will-come" approach wherein active plant restoration passively restores other critical system components. While it is well recognized that certain, more sensitive, wildlife species require targeted restoration strategies that link wildlife responses to vegetation recovery (Fuller et al. 2016), most restoration efforts do not evaluate how other system components like wildlife recover following plant restoration (Young et al. 2001; Wainwright et al. 2018; but see Guiden et al. 2021). If other system

Author contributions: DEP developed small mammal, seed offering, and seed sowing study designs; DLM, PWR developed and executed the restoration treatments; HEC implemented field experiments; YKO executed statistical analyses and coordinated field logistics with HEC; DEP drafted the manuscript; all the authors contributed to assembling and writing the manuscript.

[1]Rocky Mountain Research Station, USDA Forest Service, 800 East Beckwith Avenue, Missoula, MT 59801, U.S.A.
[2]Division of Biological Sciences, University of Montana, Missoula, MT 59801, U.S.A.
[3]Address correspondence to D. E. Pearson, email dean.pearson@usda.gov
[4]MPG Ranch, 19400 Lower Woodchuck Road, Florence, MT 59833, U.S.A.

doi: 10.1111/rec.13481
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.13481/suppinfo

components passively recover following active plant restoration, then the build-it-and-they-will-come approach is justified and efficient. If not, then restoration becomes a more complex and difficult process requiring additional management specifically directed toward recovering other system components. Advancing restoration ecology requires greater understanding of the extent to which active plant restoration facilitates the restoration of higher trophic levels and other community processes.

Primary consumers represent the next level up from plants in the trophic structuring of natural communities. Small mammals are particularly important primary consumers that are prevalent in virtually all terrestrial ecosystems around the world where they play critical roles as herbivores, seed predators, seed and spore dispersers, ecosystem engineers, and food for predators (Wilson & Ruff 1999; Larios et al. 2017; Lacher et al. 2019). As seed predators, small mammals contribute to the structuring of natural plant communities by selectively reducing recruitment of certain plant species relative to others (Brown & Heske 1990; Orrock et al. 2009; Maron et al. 2012; St. Clair et al. 2016; Dylewski et al. 2020). Hence, small mammal seed predators are integral to fully functioning systems. However, small mammal seed predation can also strongly influence restoration success if seed predation inhibits the establishment of important restoration species (Pearson et al. 2019). Therefore, understanding how plant restoration affects small mammal communities and their ecological function as seed predators holds relevance for both executing restoration strategies and for achieving final restoration objectives.

Exotic plant invasions present a global threat to the integrity of natural systems (Mack et al. 2000) and are a major driver of plant restoration efforts (D'Antonio & Meyerson 2002). Exotic plant invasions directly impact native plant communities in a variety of ways that in turn affect native fauna, including small mammals (Litt & Pearson 2013; Steidl et al. 2013). In grasslands of the western United States, exotic wheatgrasses, particularly crested (*Agropyron cristatum*) and intermediate wheatgrass (*Thinopyrum intermedium*), were widely planted for forage production and soil stabilization (Lesica & DeLuca 1996; Lesica & Cooper 2019). These grasses, particularly crested wheatgrass, have subsequently become invasive, reducing cover and richness of native plants (Rogler & Lorenz 1983; Lesica & DeLuca 1996; Christian & Wilson 1999; Scasta et al. 2015), and abundance and richness of small mammals (Reynolds 1980). As a result, crested wheatgrass communities are commonly targeted for vegetation restoration (Hulet et al. 2010; Fansler & Mangold 2011), but whether such efforts may also restore small mammal communities and their ecological roles is unknown.

In this study, we evaluate whether active restoration efforts to restore native plants in grasslands that had been planted with introduced forage grasses (primarily crested and intermediate wheatgrass) results in passive restoration of native small mammal communities and their ecological roles as seed predators. We quantified small mammal abundance by live-trapping for 3 years in three to four replicate sites in each of four habitat conditions: native grasslands, grasslands planted with introduced forage grasses, and planted grasslands that had undergone restoration treatments with or without supplemental watering. In addition, we conducted seed offerings within each habitat over 2 years to evaluate how small mammal seed removal was related to small mammal community responses to the different treatments. Finally, we conducted 2 years of seed addition experiments within each habitat by sowing seeds in paired cages that allowed or precluded small mammal access to assess how seed predation affected the establishment of dominant native plants important for restoration.

Methods

Study System and Overall Study Design

We conducted our research at MPG Ranch, a 6,600 ha private ranch in west-central Montana dedicated to restoration, research, and educational outreach (https://www.mpgranch.com/). The historical and residual native grasslands studied are dominated by bluebunch wheatgrass (*Pseudoroegneria spicata*) and perennial forbs like silky lupine (*Lupinus sericeus*) and balsamroot (*Balsamorhiza sagittata*) with lesser amounts of annual forbs (Mueggler & Stewart 1980). Beginning in the 1980s, crested and intermediate wheatgrasses were planted over 372 ha of the ranch for livestock forage. Additionally, due to invasions of exotic forbs like leafy spurge (*Euphorbia esula*), the broadleaf herbicide Tordon (picloram) was applied periodically to these areas, with the effect of suppressing forbs and favoring monocultures of the planted grasses. By the start of this study, the ranch had not been grazed by cattle for 12 years. In 2015, restoration treatments in planted grasslands were initiated with prescribed burning and then harrowing in preparation for native seed sowing. Residual introduced grasses were killed before seed set using glyphosate. Native grasses and forbs were broadcast and drill seeded (using a rangeland drill) in fall 2015 and spring 2016 (see Table S1 for species list). Areas with low establishment due to drought and an army cutworm (*Euxoa auxiliaris*) outbreak in 2016 were reseeded that fall. Supplemental watering was applied at three restoration sites to facilitate establishment and survival of sown species by watering as needed during low precipitation periods using center-pivots (for two sites visible on map: Fig. 1) or temporary hose arrays (third site). The total area affected by restoration treatments was approximately 1,400 ha. At the time the sampling began for the current study, all restoration sites had mature plants, with most species producing seed and other longer-lived plants approaching seed production.

Sampling was conducted from 2018 to 2020 at fifteen 0.25 ha sites. Each site represented one of four grassland habitats: residual native ($n = 4$), planted with introduced grasses ($n = 4$), and restoration either with ($n = 3$) or without supplemental watering ($n = 4$). At each site, 25 stations were spaced 10 m apart in a 5×5 grid for sampling vegetation and small mammals. In addition, seed offerings and seed sowing experiments were conducted at a subset of stations to assess seed predation rates and their effects on plant recruitment, as detailed below.

Vegetation Sampling

Vegetation sampling was designed to understand the relevance of plant restoration for small mammal communities by focusing on functional components of the plant community. Accordingly, a 1-m radius circular plot was surveyed at each sampling station

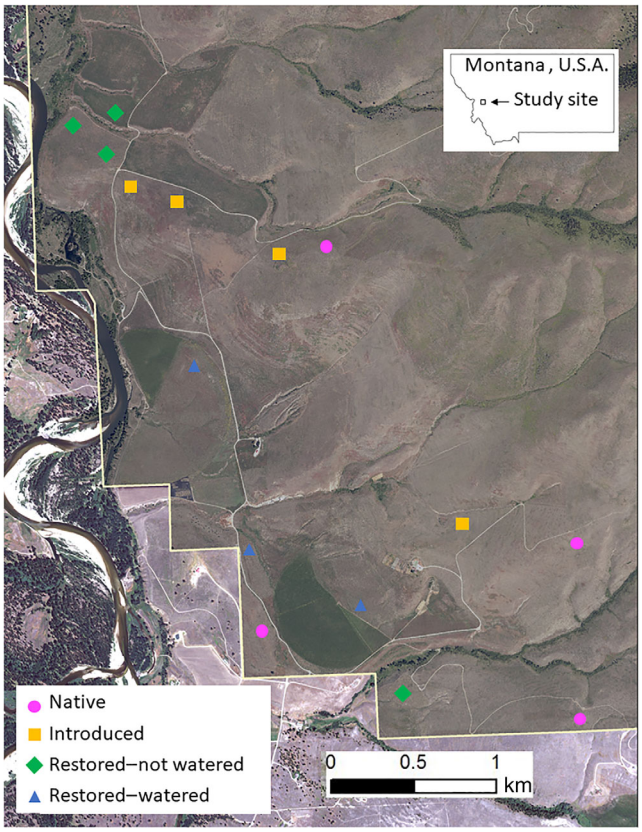

Figure 1. Map of grassland study sites in west-central Montana color-coded by habitat.

during the peak of the growing season (June) in 2019 and 2020. At each station, we visually estimated percent cover of native forbs and grasses, respectively. In addition, we estimated cover of the following exotic groups: introduced forage grasses, consisting of crested wheatgrass and intermediate wheatgrass; annual *Bromus* species consisting of cheatgrass (*B. tectorum*) and Japanese brome (*B. japonicus*), which are aggressive invaders in these systems (Ortega & Pearson 2005; Pearson et al. 2016*a*); other exotic grasses; and forbs.

Small Mammal Sampling

Small mammal populations were surveyed twice each year in May and August (May only in 2018), which reflect initial spring populations when breeding starts and late summer populations, to determine species composition and estimate relative abundance across habitats. At each of the 25 grid stations, we set out one Sherman folding live trap (7.6 × 8.9 × 22.9 cm; H. B. Sherman Traps, Tallahassee, FL, U.S.A.) baited with peanut butter and rolled oats, provided with polypropylene bedding material, and covered with polyurethane closed cell foam to protect captured animals from precipitation and heat. Traps were left out for 4 days at a time and checked each morning between 07:00 and 10:00 hours. One site from each of the four habitats was sampled during each trapping effort to control for temporal variation. New animals were marked with uniquely numbered ear tags using 1005-1 monel tags (National Band and Tag Company, Newport, KY, U.S.A.) for deer mice (*Peromyscus maniculatus*) and La Pias tags (Muromachi Kikai Company, Tokyo, Japan) for voles (*Microtus montanus*). The former are standard tags used for most small mammal species. The latter we have found to perform better for voles, which have more delicate ears that are prone to tag loss. For each capture, we determined species, sex, and age prior to releasing individuals at the trap station. Voles were identified as montane voles (*M. montanus*) based on dentition of occasional trap mortalities (Foresman 2001). In this system, deer mice are the dominant seed predators, with montane voles being primarily herbivores (Foresman 2012). All animal handling and safety protocols were vetted by the University of Montana IACUC (016-20DPDBS-042420).

Quantifying Seed Removal

To understand how restoration treatments might influence small mammal seed predation, we quantified small mammal seed removal rates by conducting seed offerings using silky lupine seeds (Great Basin Seed, Ephraim, UT, U.S.A.). These seeds provide a good standard for seed removal trials, as *L. sericeus* is a widely distributed native in this system that is readily eaten by mice (Maron & Pearson 2011). Each site was sampled three times (July–August) in 2019 and 2020, with 2–3 weeks between seed offering sessions to represent the primary seed dispersal window. At five grid stations spaced 20 m apart, we set out one petri dish (15 cm diameter × 1.5 cm deep) containing about 150 cc of sand and 40 lupine seeds. Additionally, a 20 × 20 cm square of 1.3-cm mesh hardware cloth (Everbilt, Home Depot Product Authority, Atlanta, GA, U.S.A.) was formed into a half cylinder and placed over each seed tray with approximately a 5-cm spacing above the dish so that small mammals, but not birds, could access trays. After 48 hours, petri contents were collected and passed through a 2-mm gauge sieve to isolate and count the remaining seeds. Seed offerings and trapping sessions never occurred during the same time at a site.

Seed Predation Effects on Plant Recruitment

We evaluated the effects of small mammal seed predation on the recruitment of native plant species that are community dominants and important for restoration by conducting seed sowing experiments. In October 2018 and 2019, paired cages that either allowed or precluded small mammal access were systematically placed at three locations on each grid (90 cages total each year with three replicate pairs on each of 15 grids). Each cage pair was approximately 25 m apart, with cages in each pair spaced 40 cm apart. Cages were 40 × 40 × 20 cm cubes constructed from 1.3 cm mesh hardware cloth (same material used for seed tray covers above), with removable lids secured to the tops. All cages were buried 10 cm into the soil, with small mammal access cages having a 12 × 7 (width × height)–cm hole cut into each side at ground level. New sets of cages were set out in the second year approximately 40 cm from the first year's cages.

In October–November each year, we seeded all cages with 50 seeds each of the perennial forbs *Balsamorhiza sagittata*, *Gaillardia aristata*, *Heterotheca villosa*, and *Lupinus sericeus*; the perennial grass *Pseudoroegneria spicata*; and the shrub *Purshia tridentata*, except that only 30 seeds of *P. tridentata* were sown in 2018 due to a limited supply. All seeds were collected at MPG Ranch the same year they were sown, except *L. sericeus* seeds, which were purchased as noted above. The following May–June, we censused the number of seedlings per species growing in seed cages three times to quantify emergence. Because installation of cages removes vegetation, this method allows us to isolate recruitment from the effects of plant competition, creating conditions similar to those occurring during restoration seeding. Across years, 28 (of 180) cages were compromised (e.g. due to trampling by ungulates) and therefore excluded from analysis.

Statistical Analyses

All analyses were conducted using generalized linear mixed models in SAS (version 9.4, PROC GLIMMIX, SAS Institute 2013). To evaluate vegetation, we treated each cover variable, averaged across stations per site and year, as the response in separate models with a lognormal distribution. Habitat, year, and their interaction were included as fixed factors, with samples per site treated as repeated measures. We followed the same model structure to test for overall differences in the small mammal community among habitats, with the total number of animals captured per site and year averaged across the two sampling sessions as the response variable.

We also conducted more-detailed analysis of relative abundance of each small mammal species in each year, treating the number of animals caught per trapping session as the response variable (McKelvey & Pearson 2001), modeled with a Poisson distribution. This approach of considering each year separately allowed us to use all the data while accounting for repeated sampling within each year. Habitat, trapping session, and their interaction were included as fixed factors, with samples per site treated as repeated measures. We used a similar model structure to examine seed removal rates in each year, with the number of seeds removed per tray and trial as the response; modeled with a negative binomial distribution, site as a random factor, and samples per station as repeated measures and nested within site. To test for correlation between seed removal and abundance of deer mice (the primary seed predator) across years, we treated the mean number of seeds removed per site and year as the response, modeled with a lognormal distribution and a repeated measures structure. We only included seed removal data from the last seed offering trial for this analysis because this period corresponded most closely to the time when natural seed dispersal starts to increase and deer mice being shifting focus from invertebrates to seeds (Pearson et al. 2000); corresponding relative abundance of mice per site and year was represented by the natural log of the number captured in August, treated as a fixed factor in the base model. For simplicity, we did not include year and mouse abundance × year factors in the final model given that they were not significant ($p > 0.7$). We also ran a separate model that included habitat and habitat × mouse abundance as fixed factors to test for variation in the relationship by habitat condition.

Recruitment of sown native species per cage and year was calculated by summing the maximum number of seedlings emerging per species across the three censuses (note that because cages cover a 40 × 40 cm area, results were extrapolated to 1 m^2 for general interpretation). This response variable was modeled with a negative binomial model in a model that tested for the fixed effects of small mammals (i.e. allowed vs. excluded), habitat, and their interaction, for each year separately. Random factors included site and cage pair nested within site. To test for correlation between small mammal effects and their abundance across years, we treated mean recruitment per site and year in cages allowing small mammal access as the response, modeled with a lognormal distribution and a repeated measures structure. Relative abundance of mice per site and year was represented by the natural log of the number captured in May (an estimate of the number accessing seeds overwinter/after seeds were sown), treated as a fixed factor in the base

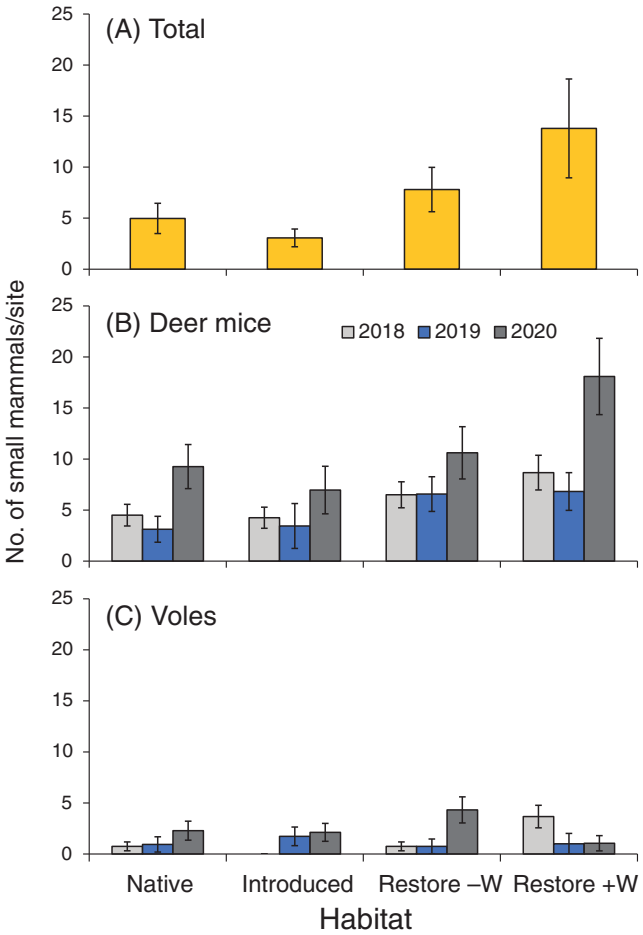

Figure 2. Small mammal composition and abundance by habitat (native, introduced grasses, restoration without watering [−W], restoration with watering [+W]), 2018–2020, as summarized by mean ±1 SE (A) total number of small mammals per site across years, and constituent numbers of (B) deer mice and (C) voles per site and year.

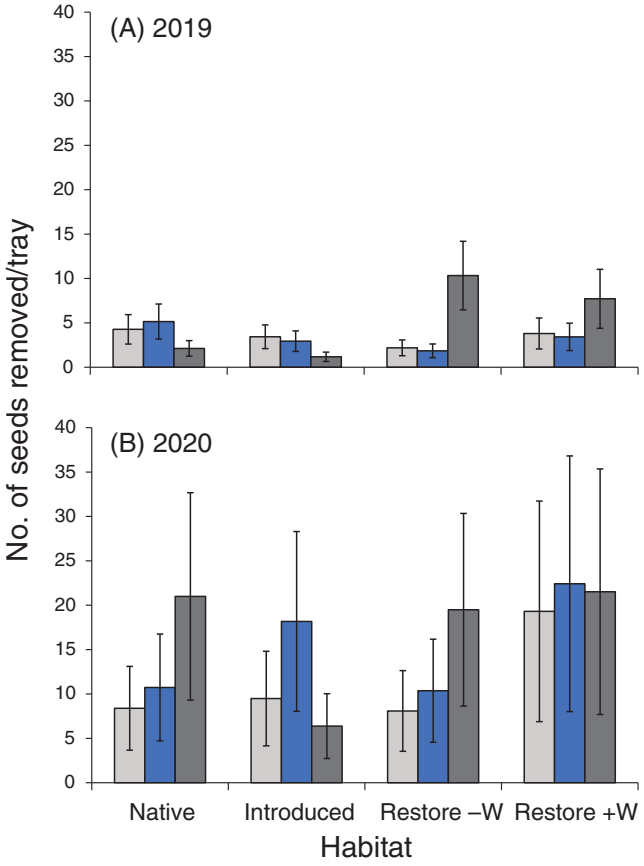

Figure 3. Small mammal seed removal rates (mean ±1 SE) by habitat (native, introduced grasses, restoration without watering [−W], restoration with watering [+W]) in (A) 2019 and (B) 2020. Native lupine seeds ($n = 40$/dish) were offered three times per year during mid-July (trial 1 = light gray bars), late July (trial 2 = blue bars), and mid-August (trial 3 = dark gray bars).

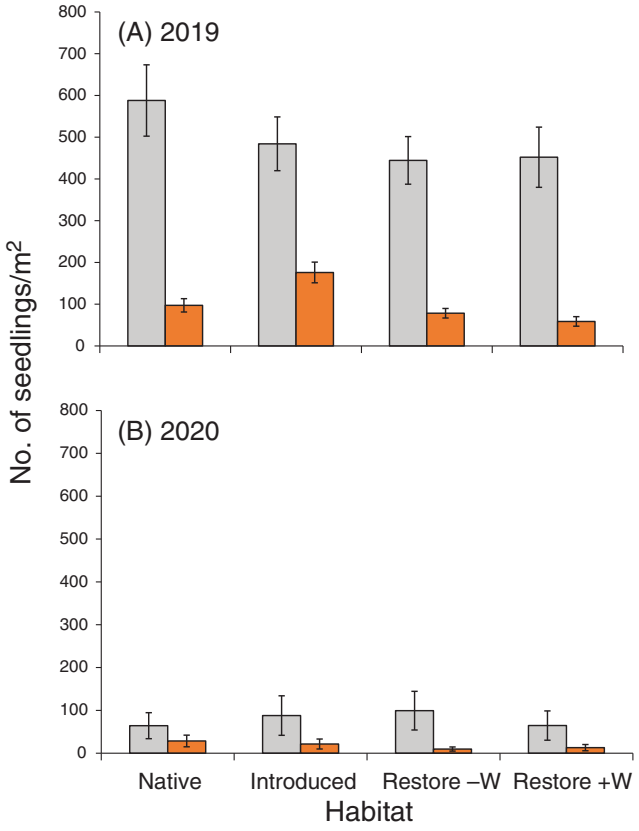

Figure 4. Effects of seed predation on plant recruitment (mean ±1 SE) by habitat (native, introduced grasses, restoration without watering [−W], restoration with watering [+W]) in (A) naturally high and (B) low recruitment years, as measured in seed cages that either allowed (orange bars) or excluded (gray bars) small mammals. Note, seed cages were 40 × 40 cm, but seedling densities were extrapolated to 1 m^2 for easier interpretation.

model. As detailed for seed removal, year effects were not significant ($p > 0.25$) and hence excluded, and a separate model was constructed to test for variation in the abundance relationship by habitat condition.

Results

Vegetation differed significantly among habitats, as measured by cover of introduced forage grasses and native species, respectively (habitat: $p \leq 0.001$; see Table S2 for details). Mean cover of introduced forage grasses was very high (42%) at sites planted with these species relative to other sites (mean cover <5%). Conversely, mean total cover of native species was relatively high at native sites (42%) and restoration sites with (26%) and without watering (15%) versus sites dominated by introduced grasses (3%); with differences of 14-, 8-, and 5-fold, respectively. Cover of other exotics groups did not differ consistently among habitats (habitat: $p > 0.3$, Table S2).

The total number of small mammals captured across years was significantly different among habitats (habitat: $p = 0.031$, Table S3), and mean levels averaged nearly 5-fold higher at restoration sites with supplemental watering compared to sites dominated by introduced grasses, with intermediate levels at native and unwatered restoration sites (Fig. 2A). This pattern was driven by deer mice, which on average were four times more abundant than voles (Fig. 2B). Deer mouse relative abundance tended to be higher at restoration sites in all years, although differences among habitat types were significant only in 2020 (habitat: $p = 0.049$), when populations more than doubled, and not in 2018 (habitat: $p = 0.12$) or 2019 (habitat: $p = 0.4$, Table S4). Relative abundance of voles differed marginally among habitat types in 2018 (habitat: $p = 0.063$), again tending to peak at watered restoration sites (Fig. 2C), but did not differ significantly among habitats in 2019 or 2020 (habitat: $p > 0.25$, Table S4).

Seed removal rates varied significantly by habitat and trial in both 2019 and 2020 (habitat × trial: $p \leq 0.047$, Table S5). Across years, seed removal tended to be lower at sites planted with introduced grasses compared to restoration sites in the August trial (Fig. 3, dark gray bars) but not necessarily in earlier trails. Removal rates averaged greater than three times higher in 2020 versus 2019, reflecting increases in deer mouse

abundance. Seed removal in the August trial correlated positively with relative abundance of deer mice across years (Fig. S1; $F_{[1,14]} = 7.93$, $p = 0.014$), and this relationship did not vary by habitat (mouse × habitat: $F_{[3,11]} = 0.88$, $p = 0.48$).

Recruitment of sown native plant species was significantly lower in cages allowing versus excluding small mammals in both 2019 and 2020 (small mammal access: $p < 0.0001$ for each year; Table S5; Fig. 4). There were no overall differences in recruitment among habitats in either year (habitat: $p = 0.19$ and $p = 0.8$, respectively), but the magnitude of the small mammal effect varied significantly by habitat in each year (small mammal access × habitat: $p = 0.009$ and $p = 0.007$, respectively; Table S5; Fig. 4). In 2019, a high recruitment year, small mammals reduced mean recruitment by greater than 300 seedlings/m^2 for a reduction of 64% at introduced-grass sites versus greater than 80% at restoration and native sites. In 2020, a low recruitment year, small mammals reduced mean recruitment by only 36–90 seedlings/m^2 such that absolute differences and their variation among habitats were much less pronounced. Variation in the small mammal effect still generally followed that seen in 2019, with a reduction of 76% at introduced-grass sites compared to 80–90% at restoration sites though only 55% at natives sites. Recruitment correlated negatively with deer mouse abundance across years (Fig. S2; $F_{[1,12]} = 9.45$, $p = 0.0097$), and this relationship did not vary by habitat (mouse × habitat: $F_{[3,9]} = 1.07$, $p = 0.41$).

Discussion

Restoring plant communities disrupted by human impacts is presumed to facilitate at least some recovery of higher trophic levels and their ecological functions (Hobbs & Norton 1996), but the extent to which this build-it-and-they-will-come pathway succeeds for wildlife is not well documented (Young et al. 2001; Hilderbrand et al. 2005; Wainwright et al. 2018). In this study, we found that restoration efforts in grasslands formerly planted with introduced forage grasses were linked to similar or higher small mammal abundance compared to native sites, with lowest abundance at sites dominated by introduced grasses. Small mammal seed predation and its effects on native plant recruitment paralleled these patterns. These results suggest that at least some higher trophic levels and their ecological functions can be restored, or even inflated, through plant restoration. Selective seed predation by small mammals is desirable for successful restoration because it plays an important function in structuring natural plant communities around the world (Dylewski et al. 2020). However, during early phases of restoration, seed predation can be at odds with restoration objectives and may need to be managed to achieve desired endpoints. We discuss the implications of these findings below.

Small mammal communities in our system were fairly simple but representative of Intermountain grasslands of the western United States, where deer mice tend to dominate, and montane voles are common but not abundant (Pearson et al. 2001). Functionally, montane voles serve as an important prey base for avian and mammalian predators (Holt & Leroux 1996; Maron et al. 2010) but appear to have weak herbivory effects, possibly due to suppression by predators (Maron & Pearson 2011). However, deer mice are important omnivores who voraciously consume seeds and invertebrates in these systems (Pearson et al. 2000). Hence, recovering mouse populations could have important feedbacks on restoration by elevating mouse predation on native seeds and invertebrate herbivores. Deer mouse predation of invertebrate herbivores could potentially benefit native plants that are suppressed by such herbivores, but these interactions are not well studied and were not a focus of our current work. However, we have shown that deer mice are powerful seed predators capable of suppressing recruitment of larger-seeded plants in these grasslands because of their preference for larger seed sizes (Bricker et al. 2010; Pearson et al. 2011; Maron et al. 2012). This latter function may play an important role in maintaining long-term diversity in these grasslands, given that most community dominants are large-seeded plants. However, in the short-term, successful recovery of mouse populations can create an undesirable feedback that can slow native plant recovery.

Little is known about the effects of exotic plant invasions on native small mammal communities and less about the effects of plant restoration on small mammals (but see Guiden et al. 2021). Information about the impacts of exotic grasses on small mammals in North America is largely derived from cheatgrass (*Bromus tectorum*) invasions in the Great Basin (Litt & Pearson 2013), with relatively little known about the effects of crested and intermediate wheatgrasses (but see Reynolds 1980). Overall, we found that small mammals were least abundant in introduced grasses and most abundant in watered restoration treatments, with the native sites and unwatered restoration sites being most similar, suggesting unwatered treatments were effective. Faunal community recovery derives from (1) restoration of necessary resource conditions and (2) the capacity of species to reach restored sites as a function of their vagility and the proximity of extant populations (Guiden et al. 2021). In our system, native small mammals persisted in altered habitat and within adjacent native grasslands, facilitating recovery. However, if restoration sites are too far removed from extant fauna, more active measures may be required. Determining the specific mechanisms underlying the small mammal responses we observed was not possible, as they could be due to changes not only in habitat but also in food resources and/or predation, which were not quantified. Teasing out underlying mechanisms requires more comprehensive study designs, but can be very informative (Guiden et al. 2021). If the water-supplemented treatments increased native plant biomass enough to elevate seed production and invertebrate productivity, this may have generated food subsidies that elevated mouse abundance (Yates et al. 2002; Pearson & Fletcher 2008). Elevating mouse populations through whatever mechanism could have important consumer feedbacks on the system, which can only be quantified by experimentally examining consumer effects in conjunction with restoration.

The difference in small mammal abundance we observed translated to differential effects of seed predation across the habitats. Paralleling abundance patterns of deer mice (the primary seed predator), the effects of seed predation on plant recruitment were stronger in the restoration sites relative to sites with

introduced grasses, suggesting these patterns were driven by small mammal density (i.e. more mice equals more seed predation). However, these patterns could also be attributable to changes in foraging behavior, or trait effects (sensu Wootton 1994), linked to different habitat or resource conditions, or a combination of density and trait effects. In examining this question, we found that both seed removal rates (in August when mice begin to shift from insect foods to seeds; Pearson et al. 2000) and seedling recruitment in cages with small mammal access were significantly correlated with deer mouse abundance across years, with no evidence that this relationship differed among habitats, that is, no evidence of behaviors differing sufficiently among habitats to alter these patterns. This is an important finding because it suggests that deer mouse seed predation may be driven primarily by mouse abundance, indicating that simple abundance metrics may predict seed predation and seed predator impacts on restoration. Overall, we found that the build-it-and-they-will-come approach restored small mammal community structure and the important ecological function that small mammals play as seed predators in our system. However, our results also highlight the importance of seed predation as an ecological filter (*sensu* Pearson et al. 2018) that must be addressed for successful restoration.

Although the effects of seed predation on plant recruitment varied among habitat conditions, they were strong across all habitats, even in introduced forage grass stands where mice were least abundant. Moreover, these effects were strong in both years despite large between-year differences in overall recruitment that were attributable to differences in precipitation inputs. Even so, driven by this variation in abiotic factors, seed predation had the greatest impact on absolute plant recruitment in the year when sowing produced the greatest yields, with mice reducing recruitment by as much as 300 seedlings/m^2. Collectively, these findings reinforce the importance of small mammal seed predation for natural plant recruitment and for restoration (Pearson et al. 2019). In fact, strong seed predation pressure may play an important role in inhibiting native plant establishment in introduced forage grass stands, where abundance of native species is very low. Many studies show that selective seed predation can strongly influence plant invasion outcomes (Pearson et al. 2011, 2012, 2014; Mattos 2013; Connolly et al. 2014; Maron et al. 2014; Lucero & Callaway 2018). Importantly, if seed predation pressure increases as restoration progresses, this process can exacerbate the challenge of establishing certain plant species. In our system, rodent seed predation targets larger-seeded plants, which are the community dominants and therefore the species prioritized for restoration. However, size-dependent seed predation varies in its effects on plant recruitment around the world as a function of ecosystem type, with relatively larger-seeded plants suppressed in some systems and smaller seeded plants in others (Dylewski et al. 2020). Therefore, understanding which species are most likely to be targeted by seed predators for a particular system can help inform restoration strategies. Active seeding to reestablish native plants can be an essential tool for both initiating native plant communities and preventing secondary invasions (Pearson et al. 2016*b*). Hence, understanding seed predation as an ecological filter and adapting seeding techniques to circumvent seed predation can be important for restoration success.

Drill seeding can be an effective tool to both reduce seed predation and increase germination and recruitment (Applestein et al. 2018), but it is expensive and not feasible over many terrain types, at large scales, or for all seed types (Davies & Bates 2014). Broadcast seeding is cheaper and more logistically feasible, but this method leaves seeds on the ground surface where they are more susceptible to seed predation and abiotic stress. Seed coating technologies being adapted from agricultural systems for restoration settings show promise for overcoming abiotic stresses that can inhibit seed germination and seedling recruitment (Madsen et al. 2016). More recent advances in these technologies indicate that seed coatings can substantially deter small mammal seed predation (Pearson et al. 2019; Taylor et al. 2020), with field experiments establishing that the resulting increases in plant recruitment can be sufficient to offset the additional costs of coating seeds (Pearson et al. 2019). Understanding seed predation as a biotic filter, similar to abiotic filters, and developing methods for overcoming both types of filters will be key to advancing restoration success. For example, two powerful filters to seedling establishment are water limitation (James et al. 2019) and seed predation (Dylewski et al. 2020). If water limitation is mitigated via good precipitation years or by supplemental watering, this can greatly improve seedling establishment. However, if mouse populations happen to be naturally high in wetter years or are artificially elevated by supplemental watering, seed predation can overshadow the benefits of watering. Hence, manipulating these filters simultaneously by supplemental watering and protecting seeds from predation using seed coatings could dramatically improve restoration reseeding success.

Our finding that active plant restoration may also restore small mammal communities and their ecological functions is heartening. It suggests that the-build-it-and-they-will-come approach holds merit for restoring at least some fauna groups that provide important ecological functions. However, we caution that many small mammals are fairly resilient to perturbations and more work is needed to evaluate how other taxa, such as invertebrates, herps, and birds, may respond to plant restoration (Burger et al. 2003; Rotchés-Ribalta et al. 2018; Wainwright et al. 2018; Pulliam et al. 2020; Guiden et al. 2021). While there will always be some species that are highly specialized and sensitive to specific restoration outcomes, increasing our understandings of the applicability of the build-it-and-they-will-come approach can help bolster the case that restoring plant community structure and function can restore other ecological functions as well.

Acknowledgments

We thank Brandon Davis, Kendell Norcott, and Solomon Ziegert for their efforts in the field. Funding for this research was provided by MPG Ranch and the Rocky Mountain Research Station, USDA Forest Service. We also greatly appreciate staff support from MPG Ranch, Rocky Mountain Research Station, and the University of Montana.

LITERATURE CITED

Applestein C, Bakker J, Delvin E, Hamman ST (2018) Evaluating seeding methods and rates for prairie restoration. Natural Areas Journal 38:347–355

Bricker M, Pearson D, Maron J (2010) Small-mammal seed predation limits the recruitment and abundance of two perennial grassland forbs. Ecology 91: 85–92

Brown JH, Heske EJ (1990) Control of a desert-grassland transition by a keystone rodent guild. Science 250:1705–1707

Burger JC, Redak RA, Allen EB, Rotenberry JT, Allen MF (2003) Restoring arthropod communities in coastal sage scrub. Conservation Biology 17: 460–467

Christian JM, Wilson SD (1999) Long-term ecosystem impacts of an introduced grass in the northern Great Plains. Ecology 80:2397–2407

Connolly BM, Pearson DE, Mack RN (2014) Granivory of invasive, naturalized, and native plants in communities differentially susceptible to invasion. Ecology 95:1759–1769

D'Antonio C, Meyerson LA (2002) Exotic plant species as problems and solutions in ecological restoration: a synthesis. Restoration Ecology 10: 703–713

Davies KW, Bates JD (2014) Attempting to restore herbaceous understories in Wyoming big sagebrush communities with mowing and seeding. Restoration Ecology 22:608–615

Dylewski Ł, Ortega YK, Bogdziewicz M, Pearson DE (2020) Seed size predicts global effects of small mammal seed predation on plant recruitment. Ecology Letters 23:1024–1033

Fansler VA, Mangold JM (2011) Restoring native plants to crested wheatgrass stands. Restoration Ecology 19:16–23

Foresman KR (2001) Key to the mammals of Montana. University of Montana Bookstore, Missoula, Montana

Foresman KR (2012) Mammals of Montana. Mountain Press Publishing, Missoula, Montana

Fuller R, Marshall M, Eversham B, Wilkinson P, Wright K (2016) The increasing importance of monitoring wildlife responses to habitat management. British Wildlife 27:175–186

Guiden PW, Barber NA, Blackburn R, Farrell A, Fliginger J, Hosler SC, et al. (2021) Effects of management outweigh effects of plant diversity on restored animal communities in tallgrass prairies. Proceedings of the National Academy of Sciences 118:e2015421118

Hilderbrand RH, Watts AC, Randle AM (2005) The myths of restoration ecology. Ecology and Society 10:1

Hobbs RJ, Norton DA (1996) Towards a conceptual framework for restoration ecology. Restoration Ecology 4:93–110

Holt DW, Leroux LA (1996) Diets of northern pygmy-owls and northern saw-whet owls in west-central Montana. The Wilson Bulletin 108:123–128

Hulet A, Roundy BA, Jessop B (2010) Crested wheatgrass control and native plant establishment in Utah. Rangeland Ecology and Management 63: 450–460

James JJ, Sheley RL, Leger EA, Adler PB, Hardegree SP, Gornish ES, Rinella MJ (2019) Increased soil temperature and decreased precipitation during early life stages constrain grass seedling recruitment in cold desert restoration. Journal of Applied Ecology 56:2609–2619

Lacher TE Jr, Davidson AD, Fleming TH, Gómez-Ruiz EP, McCracken GF, Owen-Smith N, Peres CA, Vander Wall SB (2019) The functional roles of mammals in ecosystems. Journal of Mammalogy 100:942–964

Larios L, Pearson DE, Maron JL (2017) Incorporating the effects of generalist seed predators into plant community theory. Functional Ecology 31: 1856–1867

Lesica P, Cooper SV (2019) Selecting high-dispersal species for precision prairie reconstruction on the northwestern Great Plains. Ecological Restoration 37: 211–213

Lesica P, DeLuca TH (1996) Long-term harmful effects of crested wheatgrass on Great Plains grassland ecosystems. Journal of Soil and Water Conservation 51:408–409

Litt AR, Pearson DE (2013) Non-native plants and wildlife in the Intermountain West. Wildlife Society Bulletin 37:517–526

Lucero JE, Callaway RM (2018) Native granivores reduce the establishment of native grasses but not invasive *Bromus tectorum*. Biological Invasions 20:3491–3497

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10:689–710

Madsen MD, Davies KW, Boyd CS, Kerby JD, Svejcar TJ (2016) Emerging seed enhancement technologies for overcoming barriers to restoration. Restoration Ecology 24:S77–S84

Maron JL, Auge H, Pearson DE, Korell L, Hensen I, Suding KN, Stein C (2014) Staged invasions across disparate grasslands: effects of seed provenance, consumers and disturbance on productivity and species richness. Ecology Letters 17:499–507

Maron JL, Pearson DE (2011) Vertebrate predators have minimal cascading effects on plant production or seed predation in an intact grassland ecosystem. Ecology Letters 14:661–669

Maron JL, Pearson DE, Fletcher R Jr (2010) Counterintuitive effects of large-scale predator removal on a midlatitude rodent community. Ecology 91: 3719–3728

Maron JL, Pearson DE, Potter T, Ortega YK (2012) Seed size and provenance mediate the joint effects of disturbance and seed predation on community assembly. Journal of Ecology 100:1492–1500

Mattos KJ (2013) Rodent granivores generate context-specific seed removal in invaded and uninvaded habitats. The American Midland Naturalist 169: 168–178

McKelvey KS, Pearson DE (2001) Population estimation with sparse data: the role of estimators versus indices revisited. Canadian Journal of Zoology 79:1754–1765

Mueggler WF, Stewart WL (1980) Grassland and shrubland habitat types of western Montana. U.S. Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report

Orrock JL, Witter MS, Reichman OJ (2009) Native consumers and seed limitation constrain the restoration of a native perennial grass in exotic habitats. Restoration Ecology 17:148–157

Ortega YK, Pearson DE (2005) Weak vs. strong invaders of natural plant communities: assessing invasibility and impact. Ecological Applications 15:651–661

Pearson DE, Callaway RM, Maron JL (2011) Biotic resistance via granivory: establishment by invasive, naturalized and native asters reflects generalist preference. Ecology 92:1748–1757

Pearson DE, Fletcher RJ Jr (2008) Mitigating exotic impacts: restoring deer mouse populations elevated by an exotic food subsidy. Ecological Applications 18:321–334

Pearson DE, Hierro JL, Chiuffo M, Villarreal D (2014) Rodent seed predation as a biotic filter influencing exotic plant abundance and distribution. Biological Invasions 16:1185–1196

Pearson DE, McKelvey KS, Ruggiero LF (2000) Non-target effects of an introduced biological control agent on deer mouse ecology. Oecologia 122: 121–128

Pearson DE, Ortega YK, Eren Ö, Hierro JL (2016a) Quantifying "apparent" impact and distinguishing impact from invasiveness in multispecies plant invasions. Ecological Applications 26:162–173

Pearson DE, Ortega YK, Eren Ö, Hierro JL (2018) Community assembly theory as a framework for biological invasions. Trends in Ecology & Evolution 33:313–325

Pearson DE, Ortega YK, McKelvey KS, Ruggiero LF (2001) Small mammal communities and habitat selection in Northern Rocky Mountain bunchgrass: implications for exotic plant invasions. Northwest Science 75:107–117

Pearson DE, Ortega YK, Runyon JB, Butler JL (2016b) Secondary invasion: the bane of weed management. Biological Conservation 197:8–17

Pearson DE, Potter T, Maron JL (2012) Biotic resistance: exclusion of native rodent consumers releases populations of a weak invader. Journal of Ecology 100:1383–1390

Pearson DE, Valliant M, Carlson C, Thelen GC, Ortega YK, Orrock JL, Madsen MD (2019) Spicing up restoration: can chili peppers improve restoration seeding by reducing seed predation? Restoration Ecology 27: 254–260

Pulliam JP, Somershoe S, Sather M, Mcnew LB (2020) Habitat targets for imperiled grassland birds in northern mixed-grass prairie. Rangeland Ecology and Management 73:511–519

Reynolds TD (1980) Effects of some different land management practices on small mammal populations. Journal of Mammalogy 61:558–561

Rogler GA, Lorenz RJ (1983) Crested wheatgrass – early history in the United States. Journal of Range Management 36:91–93

Rotchés-Ribalta R, Winsa M, Roberts SP, Öckinger E (2018) Associations between plant and pollinator communities under grassland restoration respond mainly to landscape connectivity. Journal of Applied Ecology 55:2822–2833

SAS Institute (2013) SAS 9.4 user's guide: survey data analysis. SAS Institute Inc., Cary, North Carolina

Scasta JD, Engle DM, Fuhlendorf SD, Redfearn DD, Bidwell TG (2015) Meta-analysis of exotic forages as invasive plants in complex multi-functioning landscapes. Invasive Plant Science and Management 8:292–306

St. Clair SB, O'Connor R, Gill R, Mcmillan B (2016) Biotic resistance and disturbance: rodent consumers regulate post-fire plant invasions and increase plant community diversity. Ecology 97:1700–1711

Steidl RJ, Litt AR, Matter WJ (2013) Effects of plant invasions on wildlife in desert grasslands. Wildlife Society Bulletin 37:527–536

Taylor JB, Cass KL, Armond DN, Madsen MD, Pearson DE, St. Clair SB (2020) Deterring rodent seed-predation using seed-coating technologies. Restoration Ecology 28:927–936

Wainwright CE, Staples TL, Charles LS, Flanagan TC, Lai HR, Loy X, et al. (2018) Links between community ecology theory and ecological restoration are on the rise. Journal of Applied Ecology 55:570–581

Wilson DE, Ruff S (1999) The Smithsonian book of North American mammals. Smithsonian Institution Press, Washington, District of Columbia

Wootton JT (1994) The nature and consequences of indirect effects in ecological communities. Annual Review of Ecology and Systematics 25: 443–466

Yates TL, Mills JN, Parmenter CA, Ksiazek TG, Parmenter RR, Vande Castle JR, et al. (2002) The ecology and evolutionary history of an emergent disease: hantavirus pulmonary syndrome: evidence from two El Niño episodes in the American southwest suggests that El Niño–driven precipitation, the initial catalyst of a trophic cascade that results in a delayed density-dependent rodent response, is sufficient to predict heightened risk for human contraction of hantavirus pulmonary syndrome. BioScience 52:989–998

Young TP, Chase JM, Huddleston RT (2001) Community succession and assembly comparing, contrasting and combining paradigms in the context of ecological restoration. Ecological Restoration 19:5–18

Supporting Information

The following information may be found in the online version of this article:

Table S1. Restoration plantings involved the following species.

Table S2. Vegetation cover variables compared among habitats (native, introduced grasses, restoration without watering [-W], restoration with watering [+W]), 2019-2020, via generalized linear mixed effects models.

Table S3. Results of a generalized linear mixed effects model testing for overall differences in the small mammal community among habitats, 2018-2020.

Table S4. Results of generalized linear mixed effects models comparing the relative abundance of small mammals among habitats for each species and sampling year.

Table S5. Results of generalized linear mixed effects models comparing small mammal seed removal rates among habitats in each sampling year, 2019-2020.

Table S6. Results of generalized linear mixed effects models testing for the effect of small mammals on recruitment of sown native species by habitat in each sampling year, 2019-2020.

Figure S1. Relationship between seed removal rates and relative abundance of deer mice across habitats (native, introduced grasses, restoration without watering [-W], restoration with watering [+W]) and years, 2019-2020.

Figure S2. Relationship between recruitment of sown native seeds and relative abundance of deer mice across habitats (native, introduced grasses, restoration without watering [-W], restoration with watering [+W]) and years, 2019-2020.

Coordinating Editor: Loralee Larios

Received: 13 February, 2021; First decision: 1 April, 2021; Revised: 10 June, 2021; Accepted: 10 June, 2021