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ABSTRACT.—Cheatgrass (*Bromus tectorum*), Russian thistle (*Salsola kali*), and tall tumblemustard (*Sisymbrium altissimum*) are nonnative plants widely distributed throughout the desert and shrubsteppe communities of the western United States. The impact of these invaders on plant community structure, form, and function has been well documented, but investigations determining the impacts of this cumulative invasion on terrestrial vertebrates have not been undertaken. Our objective was to assess community-level rodent responses to changes in plant community features, with an emphasis on dominance of invasive plant species. We sampled rodent and plant communities in the Great Basin Desert (Utah) over 4 years. Using estimates of rodent species richness and average nightly captures (relative abundance) as our response variables, we developed generalized linear mixed models (GLMMs) to determine the effects of invasive species cover. We found that rodent richness decreased with increasing abundance of invasive plant cover. Contrary to other studies, there was a nonlinear relationship between invasive species cover and rodent abundance, where rodent captures increased with invasive plant cover, reached a threshold, and then exhibited a negative response. This non-linear relationship provides support for the intermediate disturbance hypothesis and suggests that moderate levels of plant invasions, by way of bolstering rodent abundance and rodent biomass, could have bottom-up effects (i.e., positively influencing species that predominantly prey upon rodents). Our findings contradict previous findings on plant invasions in arid portions of the western United States and suggest that the species comprising or dominating a given rodent community may determine the impact of plant invasions.

RESUMEN.—*Bromus tectorum, Salsola kali* y *Sisymbrium altissimum* son plantas no nativas ampliamente distribuidas por todo el desierto y las comunidades de estepas arbustivas del oeste de los Estados Unidos. El impacto de estas especies invasoras en la estructura, forma y función de la comunidad vegetal ha sido bien documentado, sin embargo no se han llevado a cabo investigaciones que determinen los impactos de esta invasión acumulada en vertebrados terrestres. Nuestro objetivo fue evaluar las respuestas de los roedores a nivel comunitario a los cambios en las características de la comunidad vegetal, con énfasis en la dominancia de las especies de plantas invasoras. Muestreamos comunidades de roedores y plantas en el desierto de la Gran Cuenca (Utah) durante cuatro años. Utilizando estimaciones de la riqueza de especies de roedores y las capturas promedio por la noche (abundancia relativa) como nuestras variables de respuesta, desarrollamos modelos lineales generalizados mixtos (GLMM) para determinar el efecto de la cobertura de especies invasoras. Encontramos que la riqueza de los roedores disminuyó con el aumento de la abundancia de la cobertura vegetal invasora. Contrario a otros estudios, encontramos una relación no lineal entre la cobertura de especies invasoras y la abundancia de roedores, donde las capturas de roedores aumentaron con la cobertura de plantas invasoras, alcanzando un umbral y luego presentando una respuesta negativa. Esta relación no lineal proporciona apoyo para la hipótesis de perturbación intermedia y sugiere que los niveles moderados de invasiones de plantas, a modo de reforzar la abundancia de roedores y la biomasa de roedores, podrían tener efectos ascendentes (es decir, influir positivamente en las especies que predominantemente se alimentan de roedores). Nuestros hallazgos contradicen los hallazgos previos sobre invasiones de plantas en zonas áridas del oeste de los Estados Unidos, y sugieren que las especies que comprenden o dominan una determinada comunidad de roedores pueden determinar el impacto de las invasiones de plantas.

Ecosystem viability is often assessed by monitoring community metrics, such as richness and abundance, at differing clades and trophic levels (Tilman et al. 1997, Niemi and McDonald 2004, Balvanera et al. 2014). As invasive plant species colonize native vegetation communities, ecosystems are often dramatically changed (Tilman et al. 1997, Reisner et al. 2013, Steidl et al. 2013). Arid shrublands and grasslands throughout the western United States have been particularly impacted by invasive species, as changes in grazing and fire regimes have buttressed the establishment of annual grass species such as cheatgrass (*Bromus tectorum*), medusahead (*Taeniatherum caput-medusae*), and red brome (*Bromus rubens*) (Knapp 1996, Chambers 2008, Litt and Pearson 2013, Steidl et al. 2013). Of the

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annual grass species, cheatgrass has been a particularly successful invader in the western United States. Since the species' introduction in the early 1900s, cheatgrass has been able to propagate due to its ability to saturate the understory, and continuous cheatgrass monocultures are often the eventual result (Young et al. 1987). This dramatic community alteration decreases plant species richness and abundance (Hejda et al. 2009, Freeman et al. 2014) and reduces functional plant diversity (Hejda et al. 2009, Steidl et al. 2013). Once desiccated, these monocultures act as ideal fuel and increase the frequency of fire, which perpetuates further establishment of the grasses and other invasive forbs across the landscape (Reisner et al. 2013).

Exotic forbs such as Russian thistle (*Salsola kali*) and tall tumblemustard (*Sisymbrium altissimum*) are also widely distributed across the Great Basin (Yensen 1981). Commonly known as tumbleweeds, the prolific seeding habits of these forbs make them successful invaders with the potential to outcompete native plants, especially in previously disturbed sites (Yensen 1981). The combined invasion of the aforementioned species is responsible for the elimination of large areas of sagebrush-bunchgrass and mixed shrublands throughout the western United States (Yensen 1981, Knapp 1996, Chambers 2008, Litt and Pearson 2013, Reisner et al. 2013).

Plant invasions can cause cascading effects for higher trophic levels, especially in sagebrush-bunchgrass habitats (Ostoja and Schupp 2009, Steidl et al. 2013, Freeman et al. 2014). Monocultures often alter habitat heterogeneity (Knapp 1996) and reduce quality of available forage for rodents and other herbivores (Reisner et al. 2013). This reduction in habitat and forage can cause a bottom-up effect, lowering animal diversity and abundance at higher trophic levels (Knapp 1996, Ostoja and Schupp 2009, Fischer et al. 2012, Litt and Pearson 2013, Steidl et al. 2013, Freeman et al. 2014, Zeng et. al. 2014). However, relaxed competition resulting from declines in diversity of invader-affected rodent species may shift rodent community assemblages, allowing remaining species to better utilize the resources and habitat characteristics provided by invasive plants (Kelt 2011). Investigations have revealed that plant invasions can increase the abundance of animal species that prefer dense vegetation or are able to utilize seed resources provided by invasive plants (Mattos and Orrok 2010, Malick et al. 2012, Malo et al. 2013, Litt and Pearson 2013, Steidl et al. 2013). Increasing our understanding of the effects of biological invasions on higher-trophic-level species and communities is vital to informing decisions concerning wide-scale management and conservation actions, as exotic species invasions are forecast to increase (Sax et al. 2007, Litt and Pearson 2013, Steidl et al. 2013).

Rodent studies are often used as a tool for quantifying overall ecosystem function, since species in this clade are relatively easy to capture and quantify, have a large influence on the distribution of plants, and act as a pivotal food source for mammalian and avian predators (Sieg 1987, Kelt 2011). In addition to serving as prey, rodents act as ecosystem engineers by disturbing soil, caching and dispersing seeds, and preferentially consuming seeds (Olff and Ritchie 1998, Steidl et al. 2013). As a primarily granivorous guild, desert rodent communities are not exempt from the myriad changes caused by plant invasions (Freeman et al. 2014). Typically, diverse communities have been observed in areas with high levels of structural heterogeneity, with less dense groundcover and a mosaic plant community (Ostoja and Schupp 2009, Hall 2012, Steidl et al. 2013, Thompson and Gese 2013). This is of particular concern because structural heterogeneity is reduced by plant invasions (Litt and Pearson 2013, Reisner et al. 2013). A recent study across the Great Basin Desert found that total rodent abundance and richness decreased linearly with increasing cheatgrass cover, though total abundance was highly driven by the most ubiquitous species, the deer mouse (*Peromyscus maniculatus*) (Freeman et al. 2014). Similarly, Hall (2012) observed a negative linear relationship between cheatgrass density and abundance of deer mice.

Although nonnative plant invasions appear to lead ubiquitously to decreases in native fauna richness (Ostoja and Schupp 2009, Hall 2012), recent investigations have challenged the widely held viewpoint that invasive species invasions uniformly lead to reduced abundance of native animal populations. The intermediate disturbance hypothesis predicts an observable increase in species richness or total abundance following a moderate level of

disturbance (Roxburgh et al. 2004). Several vertebrate communities have been found to respond in accordance with the intermediate disturbance hypothesis. For example, riparian bird communities responded positively to Russian olive (*Elaeagnus angustifolia*) invasion up to a threshold (Fischer et al. 2012), and reptile communities responded with increased total abundance following logging, with the highest abundance found around a median time since disturbance (Hu et al. 2013). Studies addressing this topic for rodent species and communities are mixed. Freeman et al. (2014) found that rodent abundance decreased with increasing cheatgrass cover. Conversely, a study on the influence of spotted knapweed (*Centaurea stoebe*) on a rodent community dominated by deer mice found that invasion had an indirect positive influence on rodent abundance because of an increase in food resources (Pearson and Fletcher 2008, Malick et al. 2012). Others have suggested that the effects of cheatgrass invasion on rodent abundance are species-dependent, whereby some species were more adversely affected than others (Ostoja and Schupp 2009, Litt and Pearson 2013, Steidl et al. 2013). These findings suggest that further examination of the impact of plant invasions on rodent communities is warranted.

The overall objective of our study was to further elucidate the influence of invasive plant species on rodent communities in the Great Basin Desert. Specifically, we aimed to determine (1) the impact of invasive plant species on rodent species richness and (2) the impact of invasive plant species on total rodent abundance. We predicted that we would observe linear decreases in rodent species richness and abundance in response to plant invasion severity.

METHODS

Study Area

We sampled rodent and plant communities throughout the summers of 2010 through 2013 within 266 km^2 of the eastern portion of the U.S. Army Dugway Proving Ground, located approximately 128 km southwest of Salt Lake City in Tooele County, Utah, USA. Elevations ranged from 1349 to 2021 m. The area was characterized as a cold desert: winters were cold, summers were hot and dry, with the majority of precipitation occurring in the spring. Average maximum temperatures on DPG ranged from 3.3 °C in January to 34.7 °C in July (Arjo et al. 2007). Average minimum temperatures ranged from –8.8 °C in January to 16.3 °C in July. Mean annual precipitation was 20.07 cm. The study area consisted of a predominately flat playa punctuated with steep mountain ranges. The lowest areas consisted of sparsely vegetated salt playa flats. Slightly higher-elevation areas were less salty and supported a cold desert chenopod shrub community dominated by greasewood (*Sarcobatus vermiculatus*). Higher elevations consisted of vegetated sand dunes. Near the bases of the higher, steep mountains were shrub-steppe communities of big sagebrush (*Artemisia tridentata*). The highest elevation was a Utah juniper (*Juniperus osteosperma*) community including black sagebrush (*Artemisia nova*) and bluebunch wheatgrass (*Pseudoroegneria spicata*). Exotic herbaceous vegetation, primarily cheatgrass, tall tumblemustard, and Russian thistle, had replaced approximately 40% of historical juniper woodland and shrub communities (Emrick and Hill 1999). These exotic plant species were also interspersed within communities dominated by sagebrush, rabbitbrush (*Chrysothamnus* sp.), greasewood, and juniper (Arjo et al. 2007).

Data Collection

We used stratified random sampling (see Kluever et al. 2016) to establish sixteen 50 × 50-m sampling plots throughout the study area (Fig. 1). We evaluated the plant community using seven 60-m line transects following the axis of the plot and spaced 10 m apart. The orientation of vegetation transects (e.g., east to west, north to south) was randomly chosen for each sampling event, such that the transects still overlapped the rodent trapping grid. Using the line-point intercept method (Herrick et al. 2005), we catalogued cover type, species encountered, and plant height at 1-m intervals. We sampled vegetation on plots twice per summer on the day prior to the onset of rodent sampling. This vegetation sampling protocol has been previously used to determine the effect of vegetation characteristics on rodent communities (Thompson and Gese 2013, Freeman et al. 2014). Parameters estimated from transects were percent bare ground, percent litter cover, mean plant height, percent
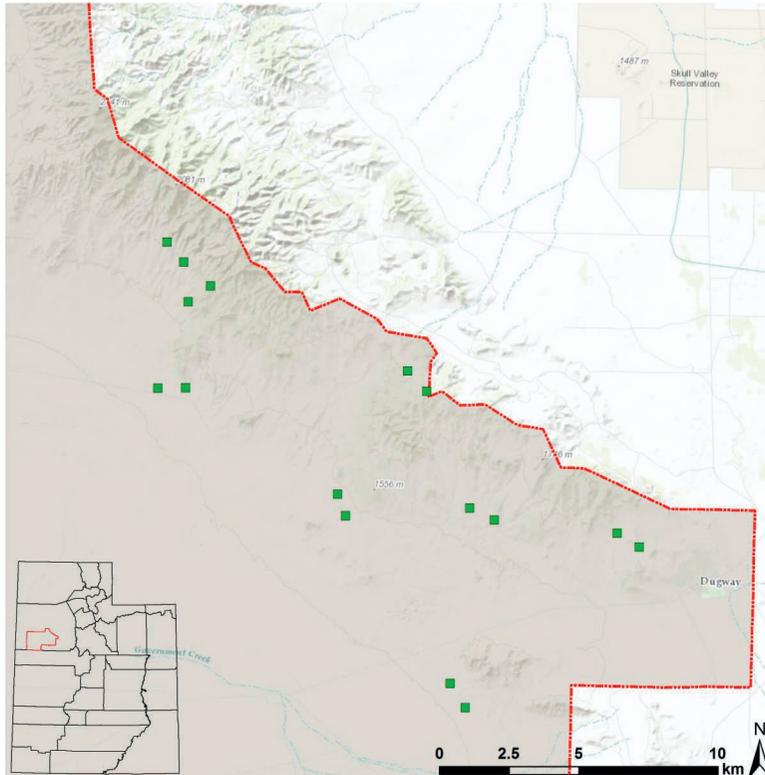
Fig. 1. Study area and sample plots (map created using ArcGIS, Esri, Redlands, CA). Green boxes denote the locations of sixteen 50 × 50-m trapping plots that were sampled for rodents on the U.S. Army Dugway Proving Ground, Utah, 2010–2013.

shrub cover, percent cheatgrass cover, and percent invasive species cover. We determined the percent cover of invasive species by using the combined occurrence of cheatgrass, tall tumblemustard, and Russian thistle.

We sampled rodents at each plot for 4 consecutive nights (i.e., one trapping session). Two trapping sessions took place each summer, typically with one in late spring/early summer (1 May to 30 June) and the other in late summer/early autumn (1 August to 30 September). During the first year of the study, 3 sampling sessions took place at each site, with 2 trapping sessions occurring during all other years. We established a 7 × 7 trapping grid (8.3-m spacing per trap) with Sherman live traps (5.08 × 6.35 × 22.86 cm; H.B. Sherman Traps, Inc., Tallahassee, FL) at each site. We were more interested in obtaining estimates of rodent community metrics at the scale of specific grids than an inventory of species at the landscape level. Thus, we followed the recommendations of Conard et al.

(2008) and used high-density Sherman live trap grids (≤11-m spacing) and a moderate sampling duration (4 nights).

We baited traps with a mixture of black sunflower and mixed bird seed. All captured rodents were identified to species and standard morphometric measurements (e.g., mass, tail length, hind foot length) were recorded. Because moon brightness can influence foraging behavior and activity patterns of desert rodents (Kaufman and Kaufman 1982, Kotler et al. 2010, Upham and Hafner 2013), we recorded moon brightness for each trapping session as percent moon illuminated, following the methods described by Upham and Hafner (2013). We estimated species richness for all rodent plots by using the maximum number of species encountered during a given trapping session. We estimated rodent abundance by using the average number of nightly captures per session per grid, a metric often used as a reliable surrogate for abundance (Bowman et al. 2001, Thompson and Gese 2013, Young et al. 2016).

Fieldwork was approved and sanctioned by the USDA National Wildlife Research Center and the U.S. Army Dugway Proving Ground. Permission to access land on the Dugway Proving Ground was obtained from the U.S. Army. Capture and handling protocols were reviewed and approved by the Institutional Animal Care and Use Committees (IACUC) at the USDA National Wildlife Research Center (QA-1734) and Utah State University (#1438). All applicable institutional and national guidelines for the care and use of animals were followed.

Data Analyses

We assessed the effects of the predictor variables (percent invasive species cover, plant species richness, percent shrub cover, percent bare ground, mean plant height, moon illumination, percent cheatgrass cover, and percent litter cover) on rodent richness and abundance using generalized linear mixed models (GLMMs) from the GLIMMIX procedure in SAS/STAT 13.2 in the SAS® System for Windows 9.4 TS1M2 (McCulloch and Neuhaus 2005, SAS Institute Inc. 2013). The trapping plot was used as the sampling unit for analysis, with 16 independent replications.

Because the same 16 plots were sampled over time (multiple times per year for 4 years), plot was fit as a random effect in all models. We checked continuous variables for collinearity using correlational analysis (we eliminated all pairs of variables with Pearson's r indicating more than 30% correlation; Zar 2009). Mean plant height, percent shrub cover, and percent litter cover were arcsine square-root transformed to improve normality. We included rodent richness and rodent abundance as continuous response variables in separate models, and the parameters percent invasive cover, mean plant height, percent shrub cover, percent moon illumination, percent litter cover, and plant richness were included as continuous predictor variables. Both models used a lognormal distribution. Effects of predictor variables were considered significant at a probability (P) of <0.05; however, we also considered P values in terms of relative evidence of difference and acknowledged this for P values just above the cutoff of P < 0.05 (Ramsey and Schafer 2002). Because the predictor variable *invasive cover* was of primary interest, we tested for a nonlinear relationship between response variables and invasive cover by including a quadratic (invasive cover × invasive cover interaction) term (Zar 2009) if invasive cover alone was not significant.

RESULTS

Between May 2010 and September 2013, we conducted 9 trapping sessions and accumulated 4987 rodent captures over 28,224 trap nights. A total of 12 species were captured. In decreasing order of abundance, the following species were captured: Ord's kangaroo rat (*Dipodomys ordii,* 70.3%), deer mouse *(Peromyscus maniculatus,* 15.6%), chisel-toothed kangaroo rat (*Dipodomys microps,* 5.9%), long-tailed pocket mouse (*Chaetodipus formosus,* 3.2%), northern grasshopper mouse (*Onychomys leucogaster,* 1.9%), western harvest mouse (*Reithrodontomys megalotis,* 1.4%), Great Basin pocket mouse (*Perognathus parvus,* 0.8%), desert woodrat (*Neotoma lepida,* 0.2%), piñon mouse (*Peromyscus truei,* 0.1%), antelope ground squirrel (*Ammospermophilus leucurus,* 0.1%), sagebrush vole (*Lemmiscus curtatus,* <0.1%), and little pocket mouse (*Perognathus longimembris,* <0.1%). There was an average of 8.8 nightly captures per plot, ranging from 0 to 29 nightly captures per plot. Plot richness ranged from 0 to 8 species with a mean richness of 2.6 species.

We detected 119 unique plant species across the 16 sampling plots. The percentage of invasive cover at these sites ranged from 3% to 99% with an average percent invasive cover of 48.8% (SD 29.27). In decreasing order of abundance, the following invasive plant species were encountered: cheatgrass (59.5%), tall tumblemustard (6.97%), and Russian thistle (5.02%). The most commonly encountered noninvasive plant species were big sagebrush (7.48%), *Poa* spp. (2.93%), and Indian ricegrass (*Achnatherum hymenoides,* 1.9%). Thus, the 3 invasive species comprised the first, second, and fourth most commonly observed plant species during the study.

Percent bare ground and percent cheatgrass cover were removed from the models due to collinearity with percent invasive cover. Percent invasive cover ($t = -2.6$, df = 120, $P = 0.011$; Fig. 2) and moon brightness were found to be significant drivers of rodent richness (Table 1). There was suggestive evidence that rodent richness may have been influenced
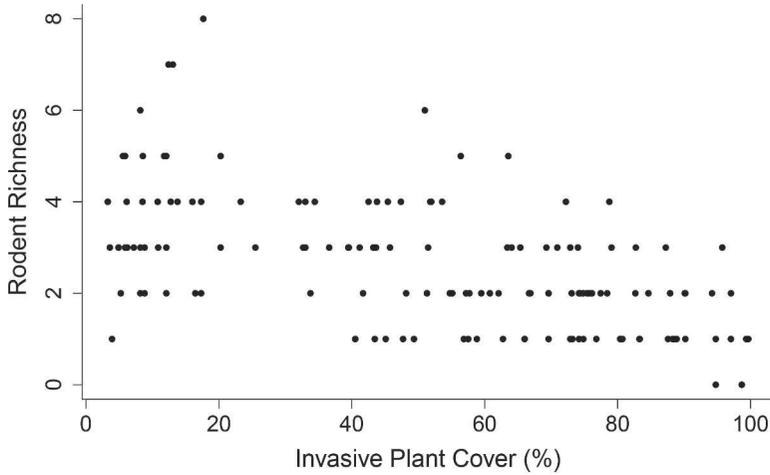
Fig. 2. Relationship between rodent richness (number of species encountered) and percent invasive plant cover on U.S. Army Dugway Proving Grounds, Utah, 2010–2013 (n = 144 plots).

TABLE 1. Results of GLMM for predictor variable effects on rodent richness, Dugway Proving Ground, Utah, 2010–2013 (n = 144).

Predictor variable	Estimate	SE	t	P
Mean plant height	0.069	0.035	1.96	0.053
Percent invasive	−0.006	0.002	−2.60	0.011*
Percent shrubs	0.076	0.039	1.98	0.053
Moon brightness	−0.199	0.098	−2.03	0.045*
Percent litter	0.013	0.014	0.93	0.354
Plant richness	0.002	0.013	0.13	0.895

*Denotes significant P values when α = 0.05.

TABLE 2. Results of GLMM for predictor variable effects on rodent abundance, Dugway Proving Ground, Utah, 2010–2013 (n = 144).

Predictor variable	Estimate	SE	t	P
Mean plant height	−0.013	0.097	−0.13	0.893
Percent invasive	−0.005	0.006	−0.84	0.402
Percent invasive (quadratic)	−0.001	0.0002	−4.07	<0.0001*
Percent shrubs	0.063	0.115	0.55	0.585
Moon brightness	−0.663	0.248	−2.67	0.009*
Percent litter	0.004	0.003	1.41	0.160
Plant richness	−0.002	0.036	−0.06	0.953

*Denotes significant P values when α = 0.05.

by mean plant height ($t = 1.96$, df = 120, $P = 0.053$; Table 1) and percent shrub cover ($t = 1.98$, df = 120, $P = 0.053$; Table 1). Other vegetation structure parameters did not appear to influence rodent richness (Table 1). We found evidence of a nonlinear relationship between percent invasive cover and rodent abundance ($t = -4.07$, df = 120, $P < 0.001$; Table 2, Fig. 3). Rodent abundance increased with increasing levels of invasive plant cover until a threshold was reached at approximately 48% invasive cover, after which rodent abundance decreased (Fig. 3). Moon illumination was a significant predictor of rodent relative abundance and exhibited a negative relationship ($t = -2.67$, df =120, $P = 0.009$; Table 2). Other parameters were nonsignificant in the model (Table 2).

DISCUSSION

Our results confirmed our prediction that invasive plant species would have a negative
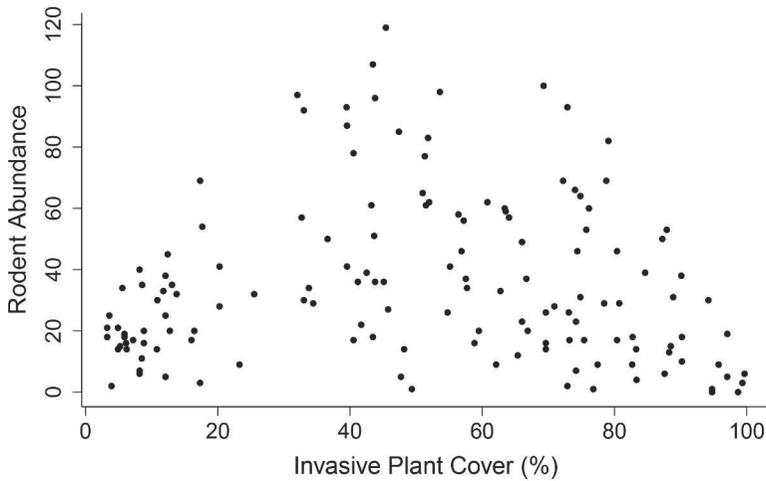
Fig. 3. Nonlinear relationship between rodent abundance (average nightly captures per session per plot) and percent invasive plant cover on U.S. Army Dugway Proving Grounds, UT, 2010–2013 (n = 144 plots).

influence on rodent species richness. This relationship was likely largely attributable to increasing cheatgrass cover, the most consistently dominant observed invasive, which homogenized habitat and reduced suitability for most rodent species. Researchers have repeatedly observed that rodent richness decreases with increasing cheatgrass cover throughout the Great Basin (Ostoja and Schupp 2009, Hall 2012, Freeman et al. 2014), but the additional effects of forbs such as Russian thistle and tall tumblemustard have not been examined exclusively. Percent cover of Russian thistle and tall tumblemustard in our plots was as high as 26% and 52%, respectively. These invasive species may have had an additional effect on our observations. Although deer mice and Ord's kangaroo rat have demonstrated the ability to utilize habitat dominated by Russian thistle (Groves and Keller 1983), our findings suggest that invaded sites were not a suitable substitute for native habitat. These forbs are able to utilize soils with extremely low moisture (White 1985), and such dry soils can inhibit burrowing rodents (Sjoberg et al. 1984). Additionally, the observed pattern of reduced openness with increasing invasive species cover likely inhibited the movement of most species (Ostoja and Schupp 2009, Rieder et al. 2010, Hall 2012), which could have impacted vital rates, such as recruitment and survival, if individuals remained in the area. Alternatively, or concomitantly, generalists (such as deer mice) or species more transient in

nature (Supp et al. 2015) may have emigrated to less invaded areas. Given that invasive cover was autocorrelated with bare ground and total cheatgrass cover, it is possible that one or both of these factors, rather than or in addition to invasive cover, could have driven our observed rodent responses.

Rodent forage availability was likely affected by the exotic plant invasion. Studies have shown that invaded sites feature reduced forage availability and habitat for rodent species (Knapp 1996, Ostoja and Schupp 2009). Kangaroo rats and deer mice are able to consume and cache cheatgrass seeds, but studies have shown that native consumers preferentially forage on native seeds over those of cheatgrass (Kelrick et al. 1986 [but see Jenkins 1988], Beard et al. 2013, Lucero et al. 2015). Similarly, some rodent species can utilize forage provided by Russian thistle, but will preferentially target easily available native forage when possible (McAdoo et al 1983, Longland 2007). Our vegetation data was not robust enough to examine the influence of each invasive plant species on rodent richness, nor did our investigation explicitly track seed consumption by rodents.

Although invasive cover appeared to be the strongest predictor of rodent richness, plant height and percent shrub cover may have also influenced this metric. Thompson and Gese (2013) linked landscape heterogeneity to community richness and found that plant height positively influenced rodent richness. Many

quadruped rodents prefer to forage in areas with large amounts of cover, which is found in areas with higher plant height (Freeman et al. 2014). Thus, our observed decrease in species richness appeared to be driven by the changes prompted by the exotic invasion, including subsequent decreased cover (Knapp 1996), reduced heterogeneity (Thompson and Gese 2013), and reduced niche space for less abundant species (Freeman et al. 2014).

Our prediction that invasive plant cover would influence rodent abundance in a negative linear manner was not met. We feel our finding of a nonlinear relationship between invasive plant species and abundance of rodents supports the idea that rodent abundance in our study area actually increased with moderate levels of disturbance in the form of a cumulative plant invasion. This provides evidence for the intermediate disturbance hypothesis, given that a higher relative abundance was observed with moderate invasive cover. Due to the changes in cover and forage availability, along with a host of other changes to habitat composition, exotic plants are a large mechanism of disturbance (Knapp 1996, Thompson and Gese 2013, Freeman et al. 2014). Support for the intermediate disturbance hypothesis has been observed for several bird communities (Malavasi et al. 2009, Fischer et al. 2012, MacGregor-Fors et al. 2013), but rarely in rodent communities (Malick et al. 2012). We feel our observed increase may have been driven by Ord's kangaroo rat, the most abundant species during the study. Studies have shown that as an exotic plant invasion occurs, more intershrub space is created, which is commonly used more frequently by bipedal rodents, such as Ord's kangaroo rat, than by quadrupeds like the deer mouse (Thompson 1982, Freeman et al. 2014). In the same study area as ours and by using satellite-based landscape-level cover type classifications, Kluever et al. (2016) observed that rodents were more abundant in areas where exotic herbaceous vegetation was the dominant cover type compared to sagebrush-dominated areas.

In addition to movement strategies, Ord's kangaroo rats create deep burrow complexes which are used to larder-hoard food (Jenkins and Breck 1998, Beck and Vander Wall 2010, White and Geluso 2012), escape physical weather conditions (White and Geluso 2012),

and escape predation (Edelman 2011). Conversely, deer mice create nests above ground (Witmer and Moulton 2012) or use short burrows for protection (Hu and Hoekstra 2017) and scatter-hoard food (Beck and Vander Wall 2010). Large burrow complexes, such as those utilized by kangaroo rats, are energetically costly to create (Vleck 1979), and kangaroo rats may inhabit invaded areas for longer due to an unwillingness to abandon an established burrow. Additionally, Ord's kangaroo rats have been shown to regularly consume and cache cheatgrass seeds (McMurray et al. 1997, Jenkins and Breck 1998). These seeds contain less protein but more carbohydrates than some native seeds (e.g., Indian ricegrass) and become far more abundant than native seeds as cheatgrass becomes established (Kelrick et al. 1986 [but see Jenkins 1988], Lucero et al. 2015). As such, the influx of low-quality but high-quantity forage available at intermediate levels of invasion may have resulted in increased resource availability for Ord's kangaroo rats. This resource influx, however, likely becomes overshadowed by the deleterious effects that accompany invasion severity once an invasion exceeds an intermediate level. It is also possible that a larger niche for Ord's kangaroo rat was created as shrub cover decreased with plant invasion and as other rodent species, primarily quadruped rodents from the Cricetidae family, experienced a marked reduction in abundance, emigrated to higher-quality habitat, or faced local extirpation.

Moon illumination was also a significant predictor of rodent abundance and richness. This result correlates with previous findings suggesting changes in foraging activity based on perceived vulnerability to predation (Orrock et al. 2004, Perea et al. 2011, Upham and Hafner 2013). In our study, moon illumination was not correlated with percent invasive cover, and moon illumination did not differ by plot or sampling session. As such, our results showed that the percentage of invasive cover was still a major driver of rodent community dynamics even after accounting for moon illumination.

Our study provides evidence that exotic invasions in the Great Basin Desert may have differential impacts on rodent community metrics at moderate levels of invasion. Freeman et al. (2014) and Ostoja and Schupp (2009) reported similar findings for species richness but observed a negative linear relationship for

abundance of Great Basin rodents. Similarly, Hall (2012) observed a negative linear relationship between deer mouse abundance and exotic plant invasion. These somewhat contradictory findings appear to be driven by our study area being dominated by a bipedal rodent, whereas in other areas, Freeman et al. (2014) showed dominance of the deer mouse and Hall (2012) focused solely on the deer mouse. The deer mouse is likely more apt to vacate its burrow for more suitable habitat, which may be the reason for trends observed in prior studies. We speculate that the subsequent decrease in rodent abundance following a threshold of invasive disturbance was likely caused by the cumulative effects of decreased forage diversity and quality, obstruction and hindrance of movement, different seed-caching strategies, and raised predation risk—all factors that the remaining species could not cope with after invasive plants became the dominating plant feature. As such, there is a need for future rodent investigations to employ more experimentally robust designs that catalog rodent community metrics while manipulating invasive plant pervasiveness. Thus, careful consideration of the species comprising and dominating a rodent community is warranted when undertaking rodent–invasive plant investigations.

To our knowledge, we are the first to provide evidence for an intermediate response of a rodent community to exotic herbaceous invasion in a desert system. Because rodent biomass was highly correlated to rodent abundance in our study area, the prey base available to higher-trophic-level organisms that regularly consume Ord's kangaroo rats, like the kit fox (*Vulpes macrotis*; Kozlowski et al. 2008), a species of conservation concern, may peak in areas that have been moderately disturbed by invasive plant species. As such, if high total rodent abundance (i.e., biomass) is deemed an important ecological component or management/conservation goal for a community, the magnitude of invasive plant species eradication should be carefully considered in areas where kangaroo rats are or have the potential to be the most abundant rodent. However, if maintaining rodent diversity is considered more important, invasive plant species eradication and native species restoration should be a priority. Further, due to the tendency of invasive plant species

encroachments to increase the frequency of fire disturbance and create complete monocultures, it is unlikely that a vegetation community intermediately disturbed by exotics could be maintained.

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