Graduate Student Theses, Dissertations, & Professional Papers

Graduate School

2017

A BIOGEOGRAPHIC PERSPECTIVE ON THE IMPACTS AND IMPORTANCE OF RODENT GRANIVORY ON NATIVE VS. INVASIVE PLANTS

Jacob Elias Lucero

A BIOGEOGRAPHIC PERSPECTIVE ON THE IMPACTS AND IMPORTANCE OF

RODENT GRANIVORY ON NATIVE VS. INVASIVE PLANTS

By

JACOB ELIAS LUCERO

B.S. Landscape Management, Brigham Young University, Utah, USA, 2008
M.S. Wildlife and Wildlands Conservation, Brigham Young University, Utah, USA, 2012

Dissertation

presented in partial fulfillment of the requirements for the degree of

Ph.D.
in Organismal Biology, Ecology and Evolution

The University of Montana
Missoula, MT

May 2017

Approved by:

Scott Whittenburg, Dean of the Graduate School
Graduate School

Ragan M. Callaway, Chair
Division of Biological Sciences

John L. Maron
Division of Biological Sciences

Dean E. Pearson
Division of Biological Sciences

Erick Greene
Division of Biological Sciences

Mark Hebblewhite
Ecosystem and Conservation Sciences

ABSTRACT

Lucero, Jacob, Ph.D., Spring 2017　　　　　　　　　*Organismal Biology, Ecology and Evolution*

A biogeographic perspective on the impacts and importance of rodent granivory on native vs. invasive plants

Chairperson: Ragan M. Callaway

One of the most well-known explanations for the success of invasive plants in novel environments is enemy release, which predicts that 1) invasive plants are limited by natural enemies in the native range but not the non-native range, and 2) native competitors in recipient communities remain limited by their natural enemies. Despite considerable empirical attention, very few studies have tested these basic predictions, especially with respect to generalist herbivores. We tested whether invasive cheatgrass (*Bromus tectorum*) has experienced enemy release from granivorous rodents – an important guild of generalists – using exclosures and experimental seed additions in western Asia (where cheatgrass is native) and the Great Basin Desert, USA (where cheatgrass is invasive). Rodent exclusion improved cheatgrass establishment in western Asia but had no effect in the Great Basin (Ch. 1), and rodent exclusion in the Great Basin improved the establishment of a suite of native grasses but not cheatgrass (Ch. 2). Interestingly, rodent exclusion benefited native grasses to the same extent as eliminating cheatgrass competition (Ch. 3). These results suggest that cheatgrass in the Great Basin has experienced enemy release from an important group of generalists, which may help explain its exceptional invasiveness. In addition, seed predation from native rodents and competition from cheatgrass can present equally important barriers to the establishment of native grasses in the Great Basin.

TABLE OF CONTENTS

CHAPTER 1

Invasive *Bromus tectorum* experiences enemy release from generalist granivores

Jacob E. Lucero*[1], Urs Schaffner[2], Ghorban Ali Asadi[3], Alireza Bagheri[4], Toshpulot Rajabov[5], and Ragan M. Callaway[1]

* jacob.lucero@umontana.edu

[1]Division of Biological Sciences, The University of Montana, Missoula, Montana 59812, USA

[2]CABI Switzerland, Chemin des Grillons 1, 2800 Delémont, Switzerland

[3] Department of Agronomy, Ferdowsi University of Mashhad, Mashhad 91775, Iran

[4] Department of Agronomy and Plant Breeding, Razi University, Kermanshah, 67149-67346 Kermanshah Province, Iran

[5] Department of Botany and Plant Physiology, Samarkand State University, University Boulevard 15, 140104, Samarkand, Uzbekistan

ABSTRACT

Perhaps the best-known explanation for the success of exotic, invasive plants in novel environments is enemy release. This hypothesis predicts that invasive plants are more strongly limited by natural enemies in their native ranges than their non-native ranges. Despite considerable empirical attention, very few studies have tested this basic prediction, especially with respect to generalist herbivores. This knowledge gap is significant because escape from generalists is a crucial aspect of the enemy release hypothesis. We tested whether invasive cheatgrass (*Bromus tectorum*) has experienced enemy release from an important guild of generalists (granivorous rodents) using experimental exclosures and seed additions in western Asia (where cheatgrass is native) and in the Great Basin Desert, USA (where cheatgrass is invasive). If enemy release has occurred, native rodents should limit cheatgrass establishment more strongly in western Asia than in the Great Basin. In addition, we examined the food preferences of native rodents in western Asia and the Great Basin with respect to seeds from cheatgrass and a suite of native grasses. If enemy release has occurred, cheatgrass should disproportionately escape granivory relative to native grasses in the Great Basin but not in western Asia. Rodent exclusion significantly improved cheatgrass establishment in western Asia but had no significant effect in the Great Basin, and cheatgrass disproportionately escaped granivory relative to native grasses only in the Great Basin. These results suggest that invasive cheatgrass has experienced some degree of enemy release from a potent guild of generalists at the seed stage.

Key words: biogeography, biological invasion, Bromus tectorum, cheatgrass, enemy release, generalists, granivory, small mammals

INTRODUCTION

Perhaps the best-known explanation for the success of invasive plants in their non-native ranges is the enemy release hypothesis, formalized by Keane and Crawley (2002). This hypothesis states that the translocation of plant species across oceans or continents geographically isolates them from their natural herbivores, resulting in relative freedom from top-down regulation. In turn, such freedom allows exotics to proliferate and become invasive in their non-native ranges, where natives remain subject to regulation via herbivory. This idea can be tested by excluding local herbivores in both the native and non-native ranges of an invader. If enemy release occurs, herbivore exclusion should more strongly benefit populations of the invader in the native range, where enemies have high impacts, than the non-native range, where enemies have low impacts (Maron and Vila 2001, Keane and Crawley 2002).

Many empirical studies have addressed the enemy release hypothesis, but very few have quantified herbivore impacts on invader abundance in both the native and non-native range. Instead, most studies have conducted biogeographic comparisons of herbivore loads and inferred enemy release when fewer herbivorous species attacked invaders in the non-native range than the native range (see review by Roy et al. 2011). Such results may demonstrate biogeographic escape from natural enemies (e.g., Mitchell and Power 2003), but they do not show "release" because reduced enemy loads may or may not translate into improved vital rates for the invader (Beckstead and Parker 2003). A salient example of "release" (*sensu* Maron and Vila 2001, Keane and Crawley 2002) is that of DeWalt et al. (2004). Using paired control and fungicide treatments in both the native (Costa Rica) and non-native (Hawaii) ranges of invasive *Clidemia hirta*, DeWalt and colleagues showed that understory populations of *C. hirta* benefitted from fungus exclusion in the native range, but not in the non-native range. Thus, understory

4

populations of *C. hirta* in Hawaii experienced biogeographic release from pathogenic fungi. Other robust experiments exist (e.g., Williams et al. 2010), but they are rare – an issue frequently noted in reviews (Torchin et al. 2003, Liu and Stilling 2006, Roy et al. 2011).

Robust tests of enemy release are particularly scant in the context of *generalist* herbivores. Although several experimental studies have considered release from generalists (Joshi and Vrieling 2005, Schaffner et al. 2011, Halbritter et al. 2012), we know of none that have employed experimental exclosures in a biogeographic setting *sensu* DeWalt et al. (2004). This knowledge gap probably stems from the widely-held notion that effective generalists are ubiquitous in both the native and non-native ranges of exotic plants (Parker and Hay 2005, Parker et al. 2006, Schaffner et al. 2011, Morrison and Hay 2011). Because generalists consume multiple host species, they are not necessarily confined to the geographic distribution of any particular host. Thus, translocated plants could potentially encounter potent generalists in any recipient community. Indeed, generalists often do attack exotic plants in their non-native ranges (Parker and Hay 2005, Parker et al. 2006, Morrison and Hay 2011, Pearson et al. 2011), which can result in population-level suppression (Pearson et al. 2012, St. Clair et al. 2016). However, generalist herbivory does not always suppress exotics (Orrock et al. 2008, Pearson et al. 2011, Maron et al. 2012, Connolly et al. 2014). Thus, escape from generalists is an under-studied aspect of the enemy release hypothesis, despite its theorized importance (Keane and Crawley 2002).

Bromus tectorum (hereafter "cheatgrass") invasion in the Great Basin Desert, USA, presents an excellent opportunity to test the enemy release hypothesis in the context of generalist herbivores. Cheatgrass is an annual species that is native to western Asia and northern Africa, and was first noted in the Great Basin around the turn of the 20th century (Mack 1981). Since

then, cheatgrass has expanded to dominate at least 650,000 km^2 of perennial grassland and shrubland in the central Great Basin (Balch et al. 2013). In both the native and non-native range, cheatgrass spreads exclusively via seed. Importantly, cheatgrass seeds in both ranges are vulnerable to predation by granivorous rodents – generalists that can strongly impact the composition of local plant communities (Brown and Heske 1990, Howe and Brown 2000, Paine et al. 2016). However, several studies have shown that native rodents in the Great Basin avoid cheatgrass seeds relative to seeds from native plants (Kelrick et al. 1986, Lucero et al. 2015). This suggests that cheatgrass in the Great Basin may disproportionately escape the effects of these generalists relative to native plants (but see St. Clair et al. 2016). But testing whether such escape constitutes enemy release requires experimental exclusion of granivorous rodents in both the native and non-native ranges of cheatgrass (Maron and Vila 2001, Keane and Crawley 2002).

Our objective was to explore whether cheatgrass experiences biogeographic release from generalist rodents at the seed stage. To do this, we compared the effects of rodent granivory on cheatgrass establishment in western Asia and the Great Basin using experimental exclosures and seed addition plots. If cheatgrass has experienced enemy release at the seed stage, rodents should limit cheatgrass establishment more strongly in western Asia than in the Great Basin. We also examined the seed preferences of native rodents in western Asia and the Great Basin with respect to cheatgrass to help explain biogeographic differences in the effects of rodent granivory. We expected seed preference to follow rodent effects; if enemy release has occurred, cheatgrass seeds should disproportionately escape granivory in the Great Basin but not in western Asia.

METHODS

Rodent effects

We examined rodent effects on cheatgrass establishment at four study sites in western Asia and five sites in the Great Basin. In western Asia, study sites were in the Razavi Khorasan (n=2) and North Khorasan (n=2) provinces of Iran (Table 1). In the Great Basin, study sites were in Idaho (n=1), Nevada (n=3), and Utah (n=1), USA (Table 1). All study sites in Iran were separated by at least 20 km, and all sites in North America were separated by at least 80 km. These distances are orders of magnitude greater than individual rodents and plants typically disperse over short time periods (Harper et al. 1978, O'Farrell 1978, Jones 1989, Hayssen 1991, Rehmeier et al. 2004). Thus, our study sites in each region were independent from each other. Finally, all sites were located in rural areas in communities dominated by native plants with <5% cover by invasive plants.

We measured the effects of rodent granivory at seven sampling stations per site, each separated by 50 m. Each sampling station consisted of three exclosure treatments. In the first treatment, we sowed 100 cheatgrass seeds into a functional "closed" exclosure that excluded rodents. In the second treatment, we sowed 100 cheatgrass seeds into a non-functional "open" exclosure that admitted rodents. In the third treatment, we installed a functional exclosure that excluded rodents but received no cheatgrass seeds. This third treatment served as a "control" to monitor cheatgrass recruitment from seed banks. Functional (i.e., "closed" and "control") exclosures were constructed of 1 cm-mesh hardware cloth assembled into 30 cm (diameter) x 30 cm (height) cylindrical cages with a floor and a roof. Floors and roofs prevented granivores from burrowing under or climbing into exclosures. These cages were installed by excavating 4 cm of topsoil with a garden hoe and then placing cages in the excavated pits. We secured cages

7

into place by pounding 13 cm (length) sod staples into the ground with a rubber hammer through the cage floor. We then replaced the excavated soil, except for large rocks and plant material. Non-functional (i.e., "open") cages were constructed and installed in a similar fashion, except for one 7 x 7 cm hole cut into the side of the cage at ground level to admit rodent granivores. In cages that received seed additions ("open" and "closed" cages), we gently patted seeds ≈5 mm into the soil. Burying seeds in this manner made them largely inaccessible to invertebrate and avian granivores because only rodents can locate buried seeds via olfaction (Kamil and Balda 1985), and invertebrates do not dig for buried seeds (MacMahon et al. 2000). In Iran, cheatgrass seeds were field-collected by hand during the summer of 2014. In the Great Basin, cheatgrass seeds were field-collected by hand during the summer of 2010. We illustrate this experimental design in Appendix S1: Fig. S1.

We installed this experiment during August 2014 in both Iran and the Great Basin and left cages undisturbed until August 2015, when cheatgrass recruits were counted in all cages. Once counted, cheatgrass plants in the Great Basin were collected and destroyed to prevent the establishment of new populations. Monitoring for potential cheatgrass recruits will continue in the Great Basin until at least 2020. This protocol has successfully prevented cheatgrass invasion following other seed addition experiments in the Great Basin (Lucero et al. 2015).

To quantify the effects of rodent granivory, we compared the average number of cheatgrass individuals established in closed and open cages that received seeds. We employed linear mixed-effects models using the lme package in R (R Development Core Team 2013) to analyze our data. We treated region (Iran vs. the Great Basin) as a fixed factor and study site within each region as a random factor. Treating study sites as random factors statistically accounted for any biologically-relevant differences (e.g., rodent density, *in situ* germination

8

rates, percent plant cover, elevation, temperature, precipitation, etc.) potentially present among study sites. If cheatgrass has experienced enemy release at the seed stage, rodent granivory should have a significant and negative effect on cheatgrass establishment in Iran (i.e., there should be significantly fewer cheatgrass recruits in open cages than closed cages), but rodent granivory should have no significant effect on cheatgrass establishment in the Great Basin (i.e., cheatgrass establishment in open and closed cages should be similar).

Rodent seed preference

To further explore biogeographic differences in the effects of rodent granivory, we examined the region-specific preferences of native rodents with respect to seeds from cheatgrass and seeds from other locally-native grasses using cafeteria-style feeding experiments. We conducted these experiments at the same study sites used to determine rodent effects on cheatgrass establishment (see above), with the addition of three sites in the Nurata District of Uzbekistan (n=7 in western Asia, n=5 in the Great Basin). Thus, except for Uzbekistan, our preference data potentially sampled the same rodents that drove the establishment experiments outlined above. Exact locations of study sites for preference trials are shown in Table 1.

We examined the seed preferences of native rodents at seven sampling stations per site, each separated by 50 m. Each sampling station consisted of four feeding trays, constructed from 150 x 25 mm petri dishes, ¾-filled with on-site soil filtered through a 500 μm sieve. Trays were placed in a rectangular configuration on the ground roughly 7 cm apart from one another. Each feeding tray received 3 g of seed from either cheatgrass or from one of three other locally-common, native grasses. Seed preference can depend on seed size; rodents often prefer large seeds over small ones (Pearson et al. 2011, Maron et al. 2012 and references therein). To account for this, we offered seeds from native grasses that were smaller, similar to, or larger than

cheatgrass seeds. Seeds in one native tray weighed more than those of cheatgrass, seeds in the

second weighed less, and seeds in the third weighed approximately the same. In Iran, we

replaced the "small-seeded" species with a large-seeded species, and in Uzbekistan, the "similar-

sized" species was considerably larger than cheatgrass. These deviations occurred because we

could not find species with ideal seed sizes near the study sites. Table 2 presents the species

offered to rodents at each site, the weights of their seeds, and how seeds were acquired.   We

incorporated all seeds into the filtered soil in feeding trays. Burying seeds in this manner

minimized access to invertebrates and birds (Kamil and Balda 1985, MacMahon et al. 2000).

We left trays undisturbed in the field for 72 consecutive hours, after which they were

collected and processed. Data collection ended on Oct 15, 2013 in Iran; Oct. 22, 2013 in

Uzbekistan; and Oct. 17, 2015 in the Great Basin. We recovered seeds remaining in feeding

trays by passing the trays' contents (filtered soil, debris introduced by foraging rodents,

remaining seeds) through a 500 μm sieve, through which soil passed easily but not seeds. We

removed dirt and/or organic debris associated with recovered seeds and then weighed the sample

to the nearest 0.01 g. We subtracted this weight from the original 3 g to determine the mass of

seeds removed by rodents. We log-transformed these data to improve normality. We assumed

that seed preference and seed removal were positively related (i.e., few remaining seeds

indicated high preference). We illustrate this experimental design in Appendix S1: Fig. S2.

To compare the region-specific seed preferences of granivorous rodents, we employed

three linear mixed-effects models (one for Iran, one for Uzbekistan, and one for the USA) using

the lme package in R (R Development Core Team 2013). We analyzed each country separately

because seed mass for the different species we used varied inconsistently among countries (see

Table 2). Thus, treating seed mass as a covariate in a single analysis that incorporated seed

removal from all three countries could have produced spurious and/or exaggerated seed removal × country interactions. Analyzing each country separately avoided this potential conflict. Within each country, we treated seed mass (i.e., species identity) as a fixed factor and study site as a random factor. If patterns of rodent preference follow predictions made by seed size and the enemy release hypothesis, seed size should explain patterns of seed removal only for the native species. Thus, for cheatgrass, seed size should explain patterns of seed removal in western Asia but not in the Great Basin.

RESULTS

Rodent effects

Rodent granivory limited cheatgrass establishment in Iran but not in the Great Basin (Fig. 1). In Iran, cheatgrass recruited 25.53 ± 2.84 SE individuals in cages closed to rodents that received seeds but only 10.33 ± 3.31 SE individuals in cages open to rodents that received seeds (Z-value = -4.59, $P < 0.001$) (Fig. 1). Thus, rodent granivory reduced cheatgrass establishment by 59.54% in Iran. In the Great Basin, however, cheatgrass recruited 11.20 ± 0.36 SE individuals in cages closed to rodents that received seeds and 10.39 ± 0.40 SE individuals in cages open to rodents that received seeds (Z-value = -0.68, $P = 0.77$). Thus, rodent granivory had no significant effect on cheatgrass establishment in the Great Basin.

Our estimates of rodent effects on cheatgrass establishment were not driven by recruitment from seed banks. Cheatgrass did not recruit appreciably from seed banks in either Iran or the Great Basin (Fig. 2). On average, 2.53 ± 3.21 SE individuals recruited per control cage that received no seed additions in Iran, and 0.02 ± 0.40 SE individuals recruited per control

cage that received no seed additions in the Great Basin. These means did not significantly differ (Z-value = -1.43, P = 0.15), and the 95% confidence intervals of both means ($\pm$ 6.29 in Iran, $\pm$ 0.78 in the Great Basin) included zero, suggesting that cheatgrass recruitment from control cages was not significantly different than zero in either Iran or the Great Basin.

We observed a biogeographic bias in cheatgrass recruitment from cages closed to rodents that received seed additions. More cheatgrass seedlings established in closed cages that received seeds in Iran (25.53 $\pm$ 2.84 SE) than in the Great Basin (11.20 $\pm$ 0.40 SE) (Z-value = -4.05, P < 0.001). Importantly, however, neither of these means had 95% confidence intervals that included zero ($\pm$ 5.57 for Iran and $\pm$ 0.78 in the Great Basin), indicating that average establishment in closed cages that received seeds was greater than zero in both regions. Thus, regardless of biogeographic biases in germination, rodents in both Iran and the Great Basin *could* have impacted cheatgrass establishment.

Rodent seed preference

Patterns of rodent preference generally followed predictions based on seed size and closely followed predictions derived from the enemy release hypothesis (Fig. 3). In Iran, rodents did not discriminate between seeds from cheatgrass and seeds from other native grasses despite variation in seed mass. On average, rodents removed 0.71 ($\pm$ 0.14 SE) g of cheatgrass, 0.93 ($\pm$ 0.16 SE) g *Echinochloa crus-galli*, 0.82 ($\pm$ 0.01 SE) g of *Sorghum halepense,* and 0.73 ($\pm$ 0.04 SE) g of *Lolium rigidum* (all Z-values between 0 and 0.02, all P > 0.05). Thus, although rodents did not remove seeds as predicted by size, cheatgrass seeds in Iran did not disproportionately escape granivory relative to other native species.

In Uzbekistan, rodents responded to seed offerings more or less as predicted by seed size (Fig. 3). On average, rodents removed 0.54 ($\pm$ 0.13 SE) g of *Poa bulbosa*, 0.93 ($\pm$ 0.13 SE) g of cheatgrass, 1.40 ($\pm$ 0.16 SE) g of *Hordeum leporinum,* and 1.10 ($\pm$ 0.18 SE) g of *Eremopyrum bonaepartis.* Rodents preferred the largest seeds (*E. bonaepartis*) over the smallest seeds (*P. bulbosa*) (Z-value = -3.76, *P* < 0.01), and showed an intermediate preference for intermediately-sized cheatgrass seeds. Only *H. leporinum* seeds were preferred above cheatgrass (*H. leporinum* seeds are larger than cheatgrass seeds but smaller than *E. bonaepartis* seeds; Table 1) (Z-value = -2.90, *P* = 0.02). Thus, cheatgrass seeds in Uzbekistan did not disproportionately escape granivory relative to other native species.

Rodents in the Great Basin removed native seeds as predicted by size, but not cheatgrass seeds, which experienced less granivory than any native species, regardless of size (Fig. 3). On average, rodents removed 2.38 ($\pm$ 0.15 SE) g of *Festuca idahoensis*, 1.29 ($\pm$ 0.41 SE) g of cheatgrass, 2.65 ($\pm$ 0.11 SE) g of *Pseudoroegneria spicata,* and 2.86 ($\pm$ 0.05 SE) g of *Achnetherum hymenoides* (all Z-values > 3.00, all *P* < 0.02)*.* Thus, even the relatively diminutive seeds of *F. idahoensis* were removed at almost twice the rate of cheatgrass seeds.

DISCUSSION

Our main finding was that rodent granivory significantly reduced cheatgrass establishment in western Asia, but had no significant effect in the Great Basin (Fig. 1). In addition, cheatgrass disproportionately escaped granivory relative to native grasses in the Great Basin but not in western Asia (Fig. 3). Our results suggest that cheatgrass has experienced some

degree of enemy release from a potent guild of generalists at the temporal and spatial scale of our study.

Our main finding challenges the notion that native generalists have similar impacts on invasive plants in both native and non-native communities. In their seminal articulation of the enemy release hypothesis, Keane and Crawley (2002) explicitly stated that biogeographic escape from generalists is an essential aspect of enemy release, and several authors have acknowledged the subject in reviews (Torchin and Mitchell 2004, Liu and Stilling 2006, Blumenthal 2006). However, Keane and Crawley (2002) also hinted that potent generalists could be everywhere. If effective generalists are indeed ubiquitous, then biogeographic release from them would be unlikely. This idea was supported in a global meta-analysis concluding that native generalists actually *preferred* exotic plants over natives and provided meaningful biotic resistance against plant invasions (Parker et al. 2006). Other studies have illustrated the potential for native generalists to suppress exotic plants in recipient communities (Snyder and Ives 2003, Parker and Hay 2005, Joshi and Vrieling 2005, Schaffner et al. 2011, Pearson et al. 2012). However, we now provide evidence that release from generalists can occur (Fig. 1), supporting Keane and Crawley's (2002) original argument (see also Vermeij et al. 2009). In addition to cheatgrass, many other invasive plants appear to be relatively free from generalist herbivory in their non-native ranges (e.g., Cappuccino and Carpenter 2005, Orrock et al. 2008, Pearson et al. 2011, Maron et al. 2012). These systems are ripe for generalist-specific, biogeographically-explicit tests of the enemy release hypothesis.

Biogeographic escape from natural enemies is the conceptual foundation of biocontrol, but our results are not relevant to biocontrol. Biocontrol practitioners seek to curtail plant invasions by introducing effective *specialists*, not generalists, from which invaders have escaped.

14

This practice has led to successful biocontrol in some systems without negative effects on natives (Debach and Rosen 1991). In contrast, generalists have the potential to negatively affect non-target native flora and fauna, which can seriously disrupt native communities (DeBach and Rosen 1991, Snyder and Ives 2001). We do not advocate importing exotic generalists to control exotic invaders.

The germination bias that we observed for cheatgrass in western Asia vs. the Great Basin is somewhat puzzling but does not influence our main finding. On average, cheatgrass recruited approximately 56% better in Iran than in the Great Basin ($P < 0.001$). If cheatgrass universally experienced such comparatively-poor establishment in the non-native range, one might wonder how it could ever establish self-sustaining populations, let alone become invasive (Puth and Post 2005, Blackburn et al. 2011). The germination bias in our study is probably an artifact of the different ages of cheatgrass seeds used in western Iran vs. the Great Basin. In Iran, cheatgrass seeds were collected in 2014, but in the Great Basin, seeds were collected in 2010. Although cheatgrass seeds can remain viable for up to 11 years in storage (Hulbert 1955), the seeds used in Iran may have been generally more viable than seeds used in the Great Basin because they were not as old. Importantly, this does not affect our main finding of enemy release because establishment from closed cages that received seeds was significantly greater than zero in both ranges (avg. establishment from closed cages in Iran = 25.53 ± 2.84 SE; avg. establishment from closed cages in the Great Basin = 11.20 ± 0.40 SE). Thus, rodents in both ranges had the *opportunity* to reduce cheatgrass establishment, but only rodents in Iran actually did so.

Cheatgrass seeds escaped granivory relative to seeds from native species over a broad spatial scale in the Great Basin (Fig. 3). This result is consistent with most other studies of seed preference using cheatgrass in North America (Kelrick et al. 1986, Ostoja et al. 2013, Lucero et

al. 2015). Among these studies, our results are unique because we sampled rodent preferences across roughly 350,000 km^2 – a spatial scale much broader than anything examined previously. However, regardless of scale, our preference results do not provide experimental evidence for enemy release. Our preference results showed that cheatgrass seeds *escaped* granivory in the Great Basin relative to seeds from natives, but only our results from exclosures provided evidence for enemy *release*.

Our preference results add to a growing body of evidence suggesting that native rodents in North America often prefer seeds from native plants over seeds from strong invaders (Orrock et al. 2008, Pearson et al. 2011, Maron et al. 2012, Connolly et al. 2014; but see Blaney and Kotanen 2001). Such preferential foraging for native seeds has favored the establishment of invaders over natives in some systems (Pearson et al. 2011, Connolly et al. 2014), possibly exacerbating local invasions. We do not know from our experiments if disproportionate avoidance of cheatgrass seeds translates into a recruitment advantage for cheatgrass relative to natives. Testing this would require excluding rodents from experimental additions of seeds of natives and cheatgrass at the same time. If rodent preference for natives resulted in a recruitment advantage for cheatgrass, then rodent exclusion should disproportionately benefit the establishment of native species (Connolly et al. 2014).

Cheatgrass seeds did not completely escape predation in the Great Basin. On average, rodents in the Great Basin removed 1.29 ($\pm$ 0.41 SE) g of cheatgrass seed per feeding tray; over a third of the cheatgrass seeds offered (Fig. 3). This is consistent with several studies indicating that cheatgrass seeds are consumed by native rodents in North America (e.g., Flake 1973, Kritzman 1974, St. Clair et al. 2016), even if they are usually less-preferred than seeds from native species (Kelrick et al. 1986, Ostoja et al. 2013, Lucero et al. 2015).

So why did native rodents in the Great Basin limit cheatgrass establishment to a lesser extent than native rodents in western Asia? One potential explanation is that native rodents in the Great Basin are less-effective granivores than rodents in western Asia. To test this, we compared the average mass of seeds removed per feeding tray (all species combined) in Iran, Uzbekistan, and the Great Basin using a linear mixed-effects model with region (Iran vs. Uzbekistan vs. Great Basin) as a fixed factor and site within each region as a random factor. If native rodents in the Great Basin are generally less-effective than rodents in western Asia, seed removal should be significantly lower in the Great Basin than in Iran or Uzbekistan. This was not the case. Rodents removed 0.80 g ($\pm$ 0.09 SE) of seed per tray in Iran, 0.99 g ($\pm$ 0.14 SE) in Uzbekistan, and 2.18 g ($\pm$ 0.12 SE) in the Great Basin. Thus, on average, rodents in the Great Basin removed over twice as much seed from feeding trays as rodents in either Iran or Uzbekistan ($P < 0.01$ for both Iran-Great Basin and Uzbekistan-Great Basin; Fig. 4). This suggests that rodents in the Great Basin were probably more, not less, effective than rodents in western Asia.

Instead, we propose that evolutionary naivety may leave native rodents in the Great Basin relatively under-equipped to exploit cheatgrass seeds. It has long been appreciated that plants and herbivores can evolve in response to one another (Ehrlich and Raven 1964, Janz 2011). In this context, herbivores – including polyphagous generalists like rodents – may be well-equipped to exploit the plant species with which they evolved, but under-equipped to exploit exotic plants with unfamiliar traits (Schaffner et al. 2011). For example, Cappuccino and Carpenter (2005) have suggested that some invasive plant species in northeastern North America may disproportionately escape herbivory in recipient communities because they possess biogeographically-novel phytochemicals (i.e., "novel weapons"; Callaway and Aschehoug 2000)

that render them unpalatable to local consumers. Initial observations suggest that novel weapons may also help cheatgrass seeds escape granivory in the Great Basin. In the lab, we have noticed that the water-soluble leachates of cheatgrass seeds dye water a deep purple color. Leachates from seeds of native species (including all species used in this study) have never produced this color, as far as we have yet observed (J.E. Lucero, R.M. Callaway, *unpublished data*). Although preliminary, these observations hint that the water-soluble phytochemicals of cheatgrass seeds could be biogeographically novel.

Cheatgrass seeds do not always escape the effects of rodent granivory in the Great Basin. Recently, St. Clair et al. (2016) reported that native rodents thwarted cheatgrass establishment following experimentally-induced disturbance events (fire) in a Great Basin ecosystem, resulting in meaningful biotic resistance. Interestingly, the study of St. Clair et al. (2016) was conducted only ≈30 km from our study site near Vernon, UT (see Table 1 for exact location), where we observed no significant effects of rodent granivory on cheatgrass establishment (Appendix S1: Fig. S3). What can explain such context dependence?

Rodent impacts on cheatgrass establishment may depend on the local availability of more-preferred seed resources. A number of independent studies, including ours (Fig. 3), report that native rodents in the Great Basin generally prefer seeds from native plants over seeds from cheatgrass (Kelrick et al. 1986, Ostoja et al. 2013, Lucero et al. 2015). However, selective consumers become less choosy when preferred resources are scarce (Pulliam 1974). For example, Krebs et al. (1977) showed that great tits (*Parus major*) increased consumption of inferior prey as the frequency of preferred prey decreased. Similarly, native rodents in the Great Basin may suppress less-preferred cheatgrass only when more-preferred native species are locally rare. The disturbance treatments imposed by St. Clair et al. (2016) virtually eliminated

native species from study plots, potentially leaving local rodents with few foraging alternatives to cheatgrass. In contrast, our experiments occurred in habitats dominated by native species where preferred resources may have been relatively abundant (However, we note that spatial association with more-preferred native seeds can increase predation risk for cheatgrass seeds [Ostoja et al. 2013]). Hence, the divergent outcomes reported in our study vs. the study of St. Clair et al. (2016) could result from stark differences in the local availability of more-preferred seed resources. Accordingly, we recognize that our experiments may have produced different results had they been conducted at a time and/or place in which native seeds were extremely limited (e.g., during an exceptionally dry year or near a large-scale disturbance).

Finally, we emphasize that biogeographic release from rodent granivory probably cannot entirely explain the invasiveness of cheatgrass in the Great Basin. For an exotic plant to become invasive, it must be translocated to a novel environment, establish self-sustaining populations, successfully spread, and impact native populations (Puth and Post 2005, Blackburn et al. 2011). Biogeographic release from generalist rodents at the seed stage probably decreases local barriers to cheatgrass establishment and facilitates the local accumulation of cheatgrass propagules. However, many other factors operating at multiple temporal and spatial scales also influence the success of cheatgrass and other invasive plants in their non-native ranges (e.g., disturbance, propagule pressure, feedbacks with the abiotic environment, biotic interactions with native species, etc.; D'Antonio and Vitousek 1992, Mitchell et al. 2006, Catford et al. 2009, Blackburn et al. 2011). These factors are by no means mutually exclusive, and some factors are probably more important than others under different conditions. In order to explain the invasiveness of a particular invader, the relative importance (*sensu* Brooker et al. 2005) of these factors must be addressed by elucidating their individual and collective effects on the invader's impacts in the

non-native range. Experiments that assess the relative importance of multiple factors are rare

(but see Williams et al. 2010, Orrock et al. 2015) but needed. In this context, we suggest that

biogeographic release from rodent granivory contributes to the success of cheatgrass in the Great

Basin, but the importance of enemy release relative to other factors remains unclear.

ACKNOWLEDGEMENTS

LITERATURE CITED

Balch, J.K., B.A. Bradley, C.M. D'Antonio and J. Gomez-Dans. 2013. Introduced annual grass

increases regional fire activity across the arid western USA (1980-2009). Global Change

Biology 19:173-183.

Beckstead, J., and I.M. Parker. 2003. Invasiveness of *Ammophila arenaria*: release from soil-

borne pathogens? Ecology 84:2824-31.

Blackburn, T.M., P. Pysek, S. Bacher, J. Carlton, R.P. Duncan, V. Jarosik, J.R.U. Wilson and

D.M. Richardson. 2011. A proposed unified framework for biological invasions. Trends

in Ecology and Evolution 26:333-339.

Blaney, C.S. and P. M. Kotanen. 2001. Post-dispersal losses to seed predators: an experimental

comparison of native and exotic old field plants. Canadian Journal of Botany 79:284-

292.

Blumenthal, D. M. 2006. Interactions between resource availability and enemy release in plant invasion. Ecology Letters 9:887-895.

Brooker, R., Z. Kikvidze, F.I. Pugnaire, R.M. Callaway, P. Choler, C.J. Lortie and R. Michalet. 2005. The importance of importance. Oikos 109:63-70.

Brown, J.H. and E.J. Heske. 1990. Control of a desert–grassland transition by a keystone rodent guild. Science 250: 1705–1707.

Callaway, R.M. and E.T. Aschehoug. 2000. Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. Science 290:521–523.

Cappuccino, N. and D. Carpenter. 2005. Invasive exotic plants suffer less herbivory than non-invasive exotic plants. Biology Letters 1:435-438.

Catford, J.A., R. Jansson and C. Nilsson. 2009. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. Diversity and Distributions 15:22-40.

Connolly, B.M., D.E. Pearson and R.N. Mack. 2014. Granivory of invasive, naturalized, and native plants in communities differentially susceptible to invasion. Ecology 95:1759-1769.

D'Anotonio, C.M. and P.M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23:63-87.

Debach, P. and D. Rosen. 1991. Biological control by natural enemies. Cambridge University Press, New York, New York, USA.

DeWalt, S.J., J.S. Denslow and K. Ickes. 2004. Natural-enemy release facilitates habitat expansion of the invasive tropical shrub *Clidemia hirta*. Ecology 85:471-483.

Ehrlich, P.R. and P.H.Raven. 1964. Butterflies and plants: a study in coevolution. Evolution
18:586-608.

Flake, L.D. 1973. The food habits of four species of rodents on a short-grass prairie in
Colorado. Journal of Mammalogy 54:636-647.

Halbritter, A.H., G.C. Carroll, S. Gusewell and B.A. Roy. 2012. Testing assumptions of the
enemy release hypothesis: generalist versus specialist enemies of the grass *Brachypodium*
sylvaticum. Mycologia 104:34-44.

Harper, K.T., D.C. Freeman, W.K. Ostler and L.G. Klikoff. 1978. The flora of Great Basin
mountain ranges: diversity, sources, and dispersal ecology. The Great Basin Naturalist
Memoirs 2:81-103.

Hayssen, V. 1991. *Dipodomys microps*. Mammalian Species 389:1-9.

Howe, H.F. and J.S. Brown. 2000. Early consequences of rodent granivory on synthetic dicot
communities. Ecological Applications 10:917-924.

Hulbert, L.C. 1955. Ecological studies of *Bromus tectorum* and other annual bromegrasses.
Ecological Monographs. 25:181-213.

Janz, N. 2011. Ehrlich and Raven revisited: Mechanisms underlying codiversification of plants
and enemies. Annual Review of Ecology and Systematics 42:71-89.

Jones, W.T. 1989. Dispersal distance and the range of nightly movement in Merriam's
kangaroo rats. Journal of Mammalogy 70:27-34.

Joshi, J. and K. Vrieling. 2005. The enemy release and EICA hypothesis revisited:
incorporating the fundamental difference between specialist and generalist herbivores.
Ecology Letters 8:704-714.

Kamil, A.C. and R.P. Balda. 1985. Cache recovery and spatial memory in Clark's nutcracker

(*Nucifraga colombiana*). Journal of Experimental Psychology: Animal Behavior

Processes 11:95-111.

Keane, R.M. and M.J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis.

Trends in Ecology and Evolution 17:164-170.

Kelrick, M.I., J.A. MacMahon, R.R. Parmenter and D.V. Sisson. 1986. Native seed preferences

of shrub-steppe rodents, birds and ants: the relationships of seed attributes and seed use.

Oecologia 68:327-337.

Krebs, J.R., J.T. Erichsen, M.I. Webber and E.L. Charnov. 1977. Optimal prey selection in the

great tit (*Parus major*). Animal Behaviour 25:30-38.

Kritzman, E.B. 1974. Ecological relationships of *Peromyscus maniculatus* and *Perognathus

parvus* in Eastern Washington. Journal of Mammalogy 55:172-188.

Liu, H. and P. Stilling. 2006. Testing the enemy release hypothesis: a review and meta-analysis.

Biological Invasions. 8:1535-1545.

Lucero, J.E., P.S. Allen and B.R. MacMillan. 2015. Increased primary production from an

exotic invader does not subsidize native rodents. PLoS ONE 10(8):e 0131564.

Mack, R.N. 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological

chronicle. Agro-Ecosystems 7:145–165.

MacMahon, J.A., J.F. Mull and T.O. Crist. 2000. Harvester ants (*Pogonomyrmex* spp.): their

community and ecosystem influences. Annual Review of Ecology and Systematics

31:265-291.

Maron, J.L. and M. Vila. 2001. When do herbivores affect plant invasion? Evidence for the

natural enemies and biotic resistance hypotheses. Oikos 95:361-373.

Maron, J.L., Pearson, D.E., Potter, T., Ortega, Y. (2012) Seed size and provenance mediate the

joint effects of disturbance and seed predation on community assembly. Journal of

Ecology, 100:1492-1500.

McCullough, E.L., P.R. Weingarden and D.J. Emlen. 2013. Costs of elaborate weapons in a

rhinoceros beetle: how difficult is it to fly with a big horn? Behavioral ecology 23:1042-

1048.

Mitchell, C.E. and A. G. Power. 2003. Release of invasive plants from fungal and viral

pathogens. Nature 625-627.

Mitchell, C.E., A.A. Agrawal, J.D. Bever, G.S. Gilbert, R.A. Hufbauer, J.N. Klironomos, J.L.

Maron, W.F. Morris, I.M. Parker, A.G. Power, E.W. Seabloom, M.E. Torchin and D. P.

Vasquez. 2006. Biotic interactions and plant invasions. Ecology Letters 9:729-740.

Morrison, W.E. and M.E. Hay. 2011. Herbivore preference for native vs. exotic plants:

generalist herbivores from multiple continents prefer exotic plants that are evolutionarily

naïve. PLoS One 6: e17227.

O'Farrell, M.J. 1978. Home range dynamics of rodents in a sagebrush community. Journal of

Mammalogy 59:657-668.

Orrock, J.L., M.S. Witter and O.J. Reichman. 2008. Apparent competition with an exotic plant

reduces native plant establishment. Ecology 89:1168-1174.

Orrock, J.L., H.P. Dutra, R.J. Marquis and N. Barber. 2015. Apparent competition and native

consumers exacerbate the strong competitive effect of an exotic plant species. Ecology

96:1052-1061.

Ostoja, S.M., E.W. Schupp, S. Durham and R. Klinger. 2013. Seed harvesting is influenced by

associational effects in mixed seed neighbourhoods, not just by seed density. Functional

Ecology 27: 775-785.

Paine, C.E.T., H. Beck and J. Terborgh. 2016. How mammalian predation contributes to

    tropical tree community structure. Ecology 97:3326-3336.

Parker, J.D. and M.E. Hay. 2005. Biotic resistance to plant invasions? Native herbivores prefer

    non-native plants. Ecology Letters 8:959-967.

Parker, J.D., D.E. Burkpile and M.E. Hay. 2006. Opposing effects of native and exotic

    herbivores on plant invasions. Science 311:1459-1461.

Pearson, D.E., R.M. Callaway and J.L. Maron. 2011. Biotic resistance via granivory:

    establishment by invasive, naturalized, and native asters reflects generalist preference.

    Ecology 92:1748-1757.

Pearson, D.., T.E. Potter and J.L. Maron. 2012. Biotic resistance: exclusion of native rodent

    consumers releases populations of weak invader. Journal of Ecology 100:1383-1390.

Pulliam, H.R. 1974. On the theory of optimal diets. *The American Naturalist* 108:59-74.

Puth, L.M. and D.M. Post. 2005. Studying invasion: have we missed the boat? Ecology Letters

    8:715-721.

R Development Core Team (2013) R: a language and environment for statistical computing. R

    Foundation for Statistical Computing, Vienna, Austria.

Rehmeier, R.L., G.A. Kaufman and D.W. Kaufman. 2004. Long distance movements of the

    deer mouse in tallgrass prairie. Journal of Mammalogy 85:562–568.

Roy, H.E., L. J. L. Handley, K. Schonrogge, R. L. Poland and B. V. Purse. 2011. Can the

    enemy release hypothesis explain the success of invasive alien predators and parasitoids?

    BioControl 56:451-468.

Schaffner, U., W.M. Ridenour, V.C. Wolf, T. Bassett, C. Muller, H. Muller-Scharer, S.

Sutherland, C.J. Lortie and R.M. Callaway. 2011. Plant invasions, generalist herbivores, and novel defense weapons. Ecology 92:829-835.

Snyder, W.E. and A.R. Ives. 2001. Generalist predators disrupt biological control by a specialist parasitoid. Ecology 82:705-716.

Snyder, W.E. and A.R. Ives. 2003. Interactions between specialist and generalist natural enemies: parasitoids, predators, and pea aphid biocontrol. Ecology 84:91-107.

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

Tobalske, B.W., Hedrick, T. L., Dial, K.P. and Biewener, A.A. 2003. Comparative power curves in bird flight. Nature 421:363-366.

Torchin, M.E. and C.E. Mitchell. 2004. Parasites, pathogens, and invasions by plants and animals. Frontiers in Ecology and the Environment 2:183–190.

Vermeij, M.J.A., T.B. Smith, M.L. Dailer and C.M. Smith. 2009. Release from native herbivores facilitates the persistence of invasive marine algae: a biogeographical comparison of the relative contribution of nutrients and herbivory to invasion success. Biological Invasions 11:1463.

Williams, J.L., H. Auge and J.L. Maron. 2010. Testing hypotheses for exotic plant success: parallel experiments in the native and introduced ranges. Ecology 91:1355-1366.

TABLES

Table 1. Locations of study sites used to infer rodent impacts on plant establishment ("E") and

seed preference ("P") with respect to cheatgrass (*Bromus tectorum*).

Region	Country	Nearest town	GPS coordinates	Experiments conducted
Western Asia	Iran	Shirvan	37°23'46.15"N, 58°11'37.15"E	E, P
		Shirvan	37°38'34.13"N, 57°39'24.38"E	E, P
		Mashhad	36°12'57.33"N, 60° 4'2.26"E	E, P
		Mashhad	36° 3'30.41"N, 59°39'8.79"E	E, P
	Uzbekistan	Nurota	40°41'14.82"N, 65°36'36.16"E	P
		Nurota	41° 4'35.52"N, 63° 0'9.86"E	P
		Nurota	43°25'47.98"N, 64°37'27.36"E	P
North America	USA	Challis	44°12'8.65"N, 113°56'9.88"W	E, P
		Jackpot	41°55'28.70"N, 114°43'44.96"W	E, P
		McGill	39°58'26.51"N, 114°40'10.10"W	E, P
		Baker	39° 1'6.34"N, 114°25'53.44"W	E, P
		Vernon	40° 6'54.99"N, 112°32'4.37"W	E, P

Table 2. Species offered to rodents during preference trials, mass of their respective seeds (per seed), and mode of seed accession. Species offered were consistent across all sites within each country. We specify the number and location of study sites in each country in Table 1. "Purchased" seeds were field-produced and distributed by Granite Seed Co., Lehi, UT, USA.

Region	Country	Species offered	Seed mass	Mode of accession
Western Asia	Iran	*Bromus tectorum*	3.1 mg	Field-collected
		Echinochloa crus-galli	3.2 mg	Field-collected
		Sorghum halepense	3.8 mg	Field-collected
		Lolium rigidum	3.8 mg	Field-collected
	Uzbekistan	*Poa bulbosa*	1.3 mg	Field-collected
		Bromus tectorum	3.1 mg	Field-collected
		Hordeum leporinum	3.9 mg	Field-collected
		Eremopyrum bonaepartis	4.2 mg	Field-collected
North America	USA	*Festuca idahoensis*	1.4 mg	Purchased
		Bromus tectorum	3.1 mg	Field-collected
		Pseudoroegneria spicata	3.2 mg	Purchased
		Achnatherum hymenoides	3.9 mg	Purchased

FIGURE LEGENDS

Fig. 1. Mean number of cheatgrass (*Bromus tectorum*) individuals established in open (exposed to rodents) and closed (protected from rodents) cages that received seed additions in Iran vs. the Great Basin Desert, USA ("USA"). Error bars show one standard error. Means that do not share letters differ significantly (i.e., $P < 0.05$).

Fig. 2. Mean number of cheatgrass (*Bromus tectorum*) individuals established from seed banks in Iran and the Great Basin Desert, USA ("USA"). Error bars show one standard error.

Fig. 3. Seed preferences of native rodents in Iran, Uzbekistan, and the Great Basin Desert, USA ("USA"). Species offered to rodents in each region are arranged along x-axes in ascending order of seed weight (see Table 2 for species names and seed weights). Error bars show one standard error. Means that do not share letters differ significantly (i.e., $P < 0.05$).

Fig. 4. Average seed removal by native rodents per feeding tray (all species combined) in Iran, Uzbekistan, and the Great Basin Desert, USA ("USA"). Error bars show one standard error. Means that do not share letters differ significantly (i.e., $P < 0.05$).
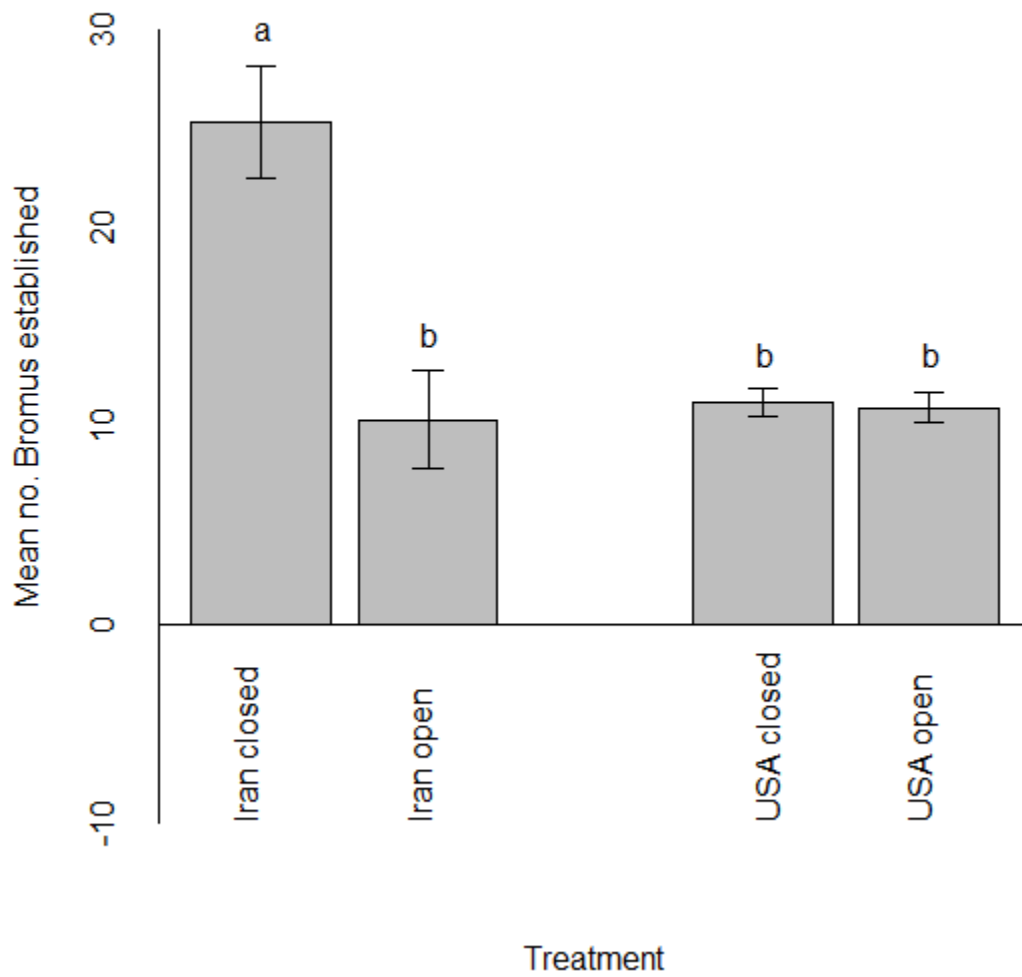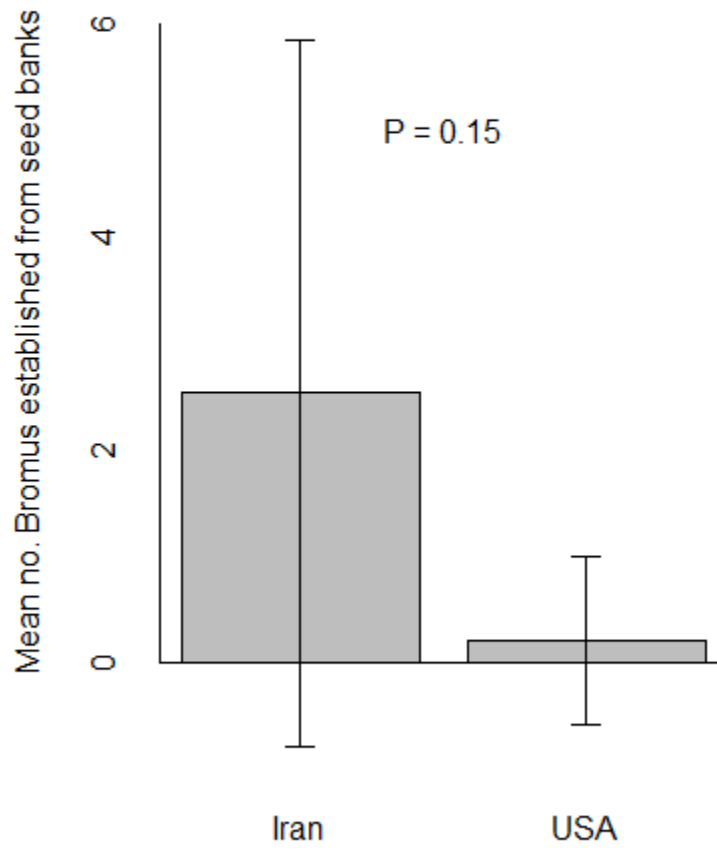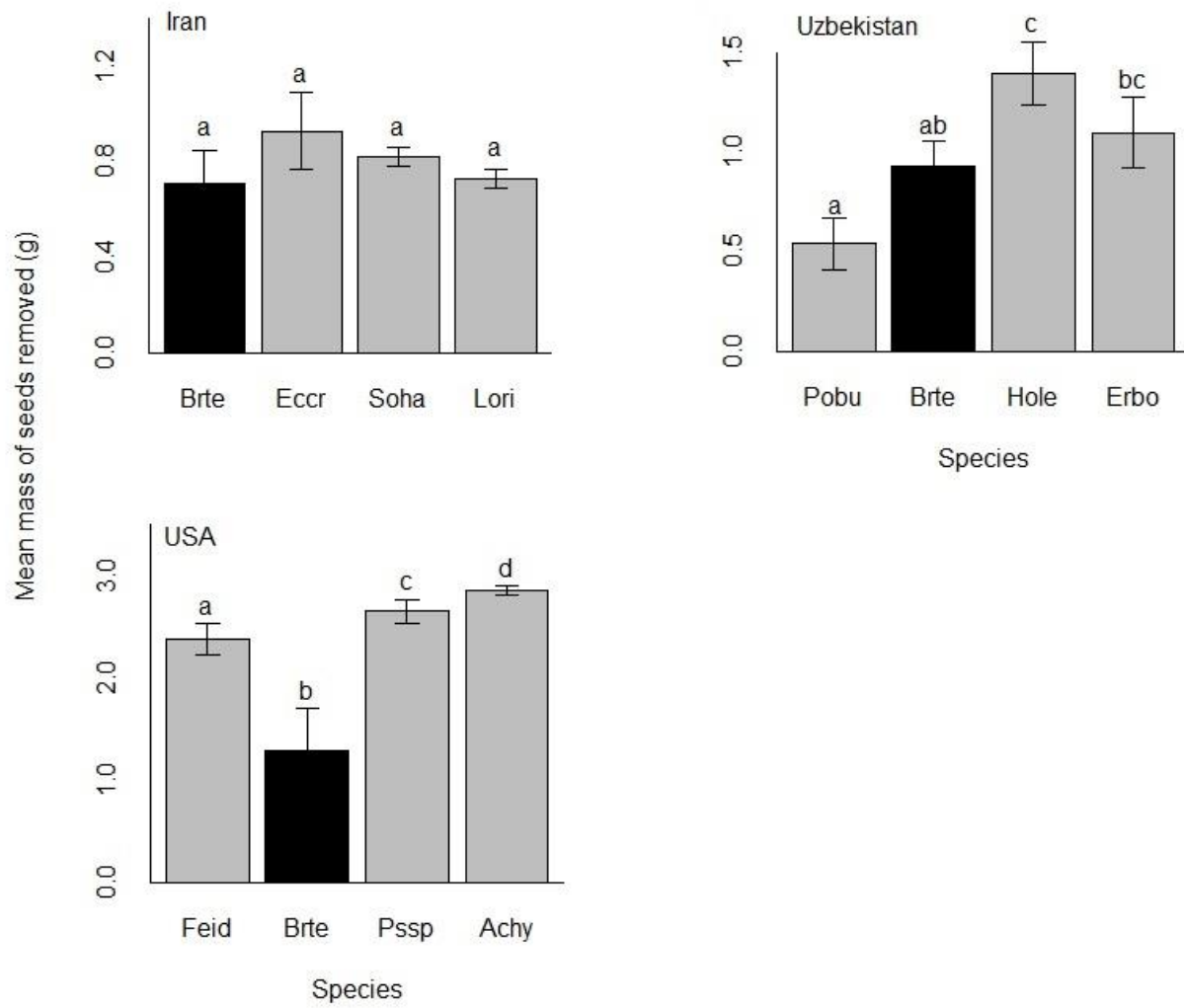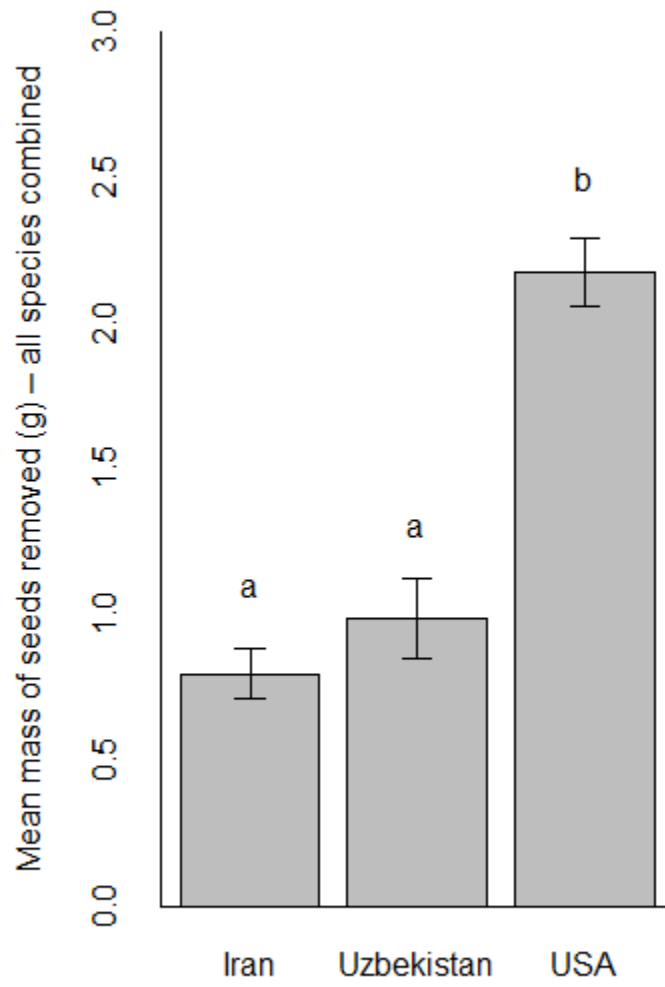
FIGURES

Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.

SUPPLEMENTARY DOCUMENTS

Supplementary documents may be found in the online version of this article in Appendix S1, which consists of three supplementary figures: Fig. S1, Fig. S2, and Fig. S3.
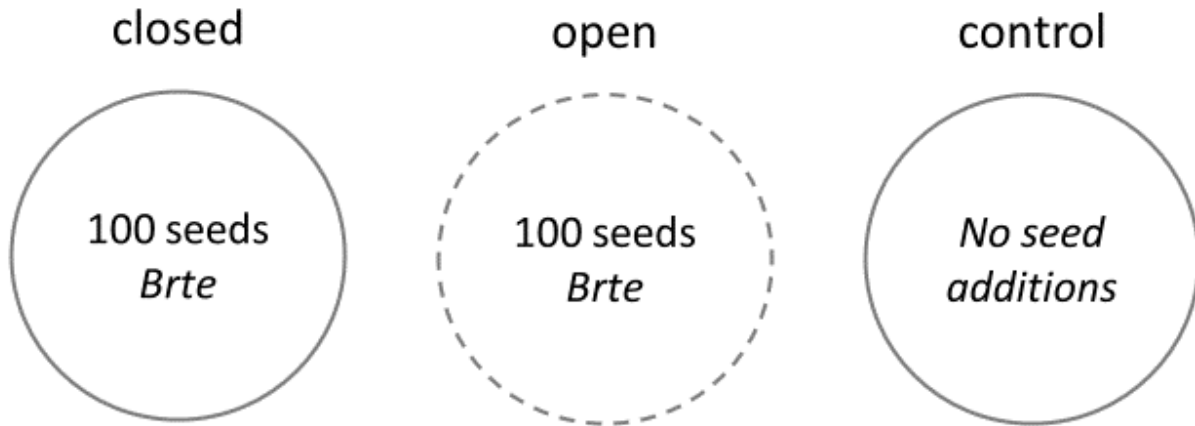
Fig. S1

closed   open   control

100 seeds
Brte

100 seeds
Brte

*No seed
additions*

Fig. S1. Experimental design employed at 7 sampling stations per site (n=4 sites in Iran, n=5 sites in the Great Basin) to determine the region-specific impacts of rodent granivory on cheatgrass (*Bromus tectorum* – "*Brte*") establishment. Each sampling station consisted of three exclosure treatments. In the first treatment, we sowed 100 cheatgrass seeds into a functional "closed" exclosure that excluded rodents. In the second treatment, we sowed 100 cheatgrass seeds into a non-functional "open" exclosure that admitted rodents. For the third treatment, we installed a functional exclosure that excluded rodents but received no cheatgrass seeds. This third treatment served as a "control" to monitor cheatgrass recruitment from seed banks. The difference in establishment between the open cage that received seeds and the closed cage that received seeds reflected the effect of rodent granivory. If cheatgrass has experienced enemy release at the seed stage, rodent granivory should have a significant and negative effect on cheatgrass establishment in Iran but should have no significant effect in the Great Basin.
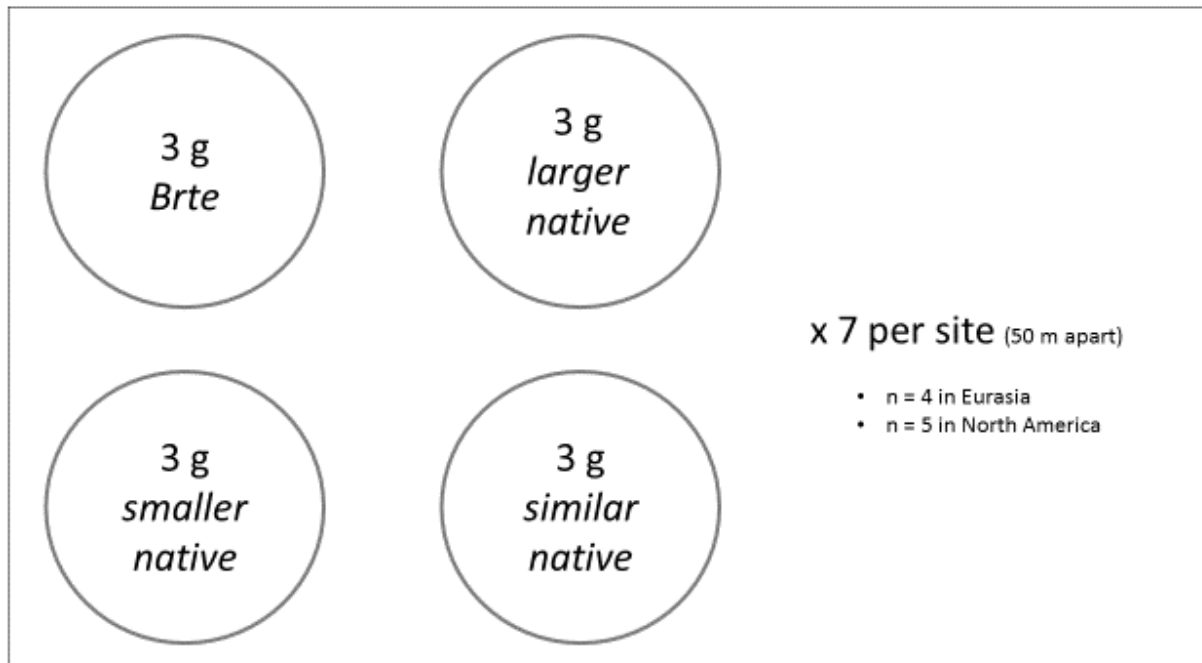
Fig. S2

Fig. S2. Experimental design used to determine region-specific preferences of native rodents with respect to seeds from cheatgrass (*Bromus tectorum*) and other locally-native grasses. Circles represent feeding trays (150 x 25 mm Petri dishes) offered at sampling stations. Each feeding tray contained 3 g of seed from either cheatgrass ("*Brte*") or a locally-common native grass. Seeds from native grasses differed in size relative to cheatgrass. One native had larger seeds ("*larger native*"), one had smaller seeds ("*smaller native*"), and one had similar-sized seeds ("*similar native*") (see Table 2). If patterns of rodent preference follow predictions made by seed size and the enemy release hypothesis, seed size should explain patterns of seed removal only for the native species. Thus, seed size should explain patterns of cheatgrass removal in western Asia but not in North America.

Fig. S3
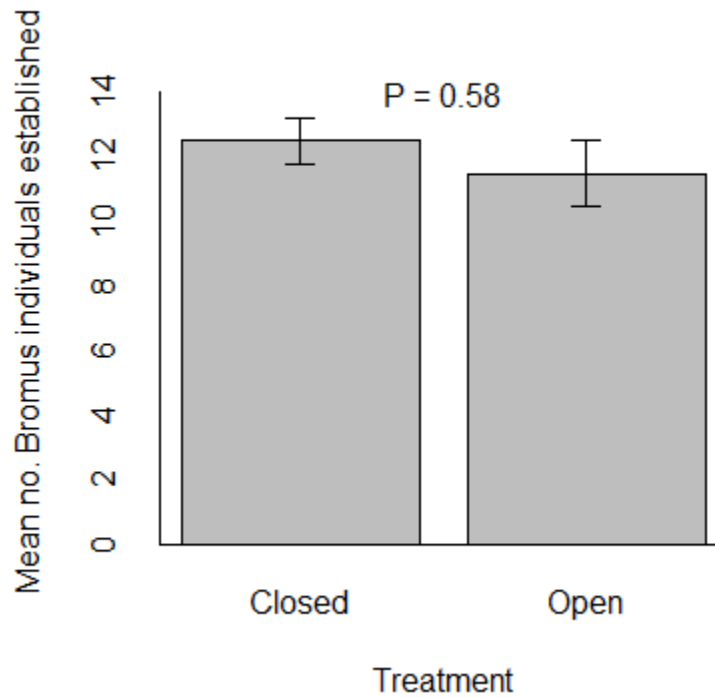
Fig. S3. Mean number of cheatgrass (*Bromus tectorum*) individuals established in cages

protected from rodents that received seeds ("Closed") and cages exposed to rodents that received

seeds ("Open") at our study site located near Vernon, UT, USA (see Table 1 in the main

manuscript for exact location of study site). Error bars show one standard error.

CHAPTER 2

Native granivores limit the establishment of native grasses but not invasive *Bromus tectorum*

Jacob E. Lucero* & Ragan M. Callaway

Division of Biological Sciences, The University of Montana, Missoula, Montana 59812, USA

* jacob.lucero@umontana.edu

SUMMARY

1. Seed predation can structure communities by influencing the population growth, abundance, and distribution of plants. However, granivory does not constrain all species equally because granivores forage selectively. A number of recent studies have shown that native granivores prefer seeds from native plants over seeds from exotic invaders, even when seed traits are otherwise similar. Selective foraging for native seeds could skew seedling establishment towards invaders, potentially facilitating invader dominance. However, few studies have connected such biased granivory to differential patterns of seedling establishment.

2. Cheatgrass (*Bromus tectorum*) invasion in the Great Basin Desert provides an excellent opportunity to examine whether selective foraging for native seeds favours the establishment of an exotic invader. Cheatgrass is native to Eurasia but highly invasive in the Great Basin. Previous work in the Great Basin has shown that cheatgrass seeds disproportionately escape rodent granivory relative to seeds from native grasses. However, whether such selective granivory favours the establishment of cheatgrass over native grasses remains unclear.

3. We used experimental seed additions and exclosure treatments to compare the impacts of rodent granivory on the establishment of less-preferred cheatgrass and four species of more-preferred native grasses at sites distributed across ≈350,000 km^2 of the Great Basin.

4. Rodent granivory reduced the establishment of each species of native grass by at least 74% but had no effect on cheatgrass establishment. These impacts were highly consistent across study sites, and our results were unaffected by seed bank dynamics or germination biases among species.

5. *Synthesis.* Our results suggest that selective foraging for native seeds may favour the establishment of cheatgrass over native grasses, potentially exacerbating one of the most extensive plant invasions in North America.

Key-words: biological invasion, *Bromus tectorum*, community ecology, granivory, Great Basin, invasion ecology, selective predation, small mammals

INTRODUCTION

Seed predation can structure plant communities by imposing seed limitation on plant populations (Brown, Reichman & Davidson 1979; Louda 1989; Hulme 1998; Maron & Crone 2006). Seed limitation caused by granivory can restrict the population growth (Rose, Louda & Rees 2005), abundance (Maron & Kauffman 2006), and distribution (Louda 1982) of plants, which can produce dramatic consequences at the community level (Brown and Heske 1990; Brown & Howe 2000; Paine, Beck & Terborgh 2016). Thus, granivory represents an important "filter" (*sensu* Weiher & Keddy 1999) in the organization of plant communities.

However, granivory does not constrain all species equally. Many seed predators are generalists that have strong preferences for the seeds of some species over others (e.g., Kelrick *et al.* 1986; Pearson, Callaway & Maron 2011; Lucero, Allen & McMillan 2015). These preferences depend on seed traits such as size, caloric value, mineral nutrition, infection by endophytes, and physical/chemical defenses (Kelrick & MacMahon 1985; Kelrick *et al.* 1986, Reader 1993; MacMahon, Mull & Crist 2000). Importantly, preferential granivory can skew the composition of plant communities towards less-preferred species that disproportionally escape predation. For example, Brown & Heske (1990) famously showed that selective foraging by rodents for large seeds promoted the dominance of small-seeded competitors in a desert shrubland.

Furthermore, granivory may not constrain native and exotic plants equally. Many studies indicate that native, generalist granivores prefer seeds from native plants over seeds from invasive plants (Kelrick *et al.* 1986; Orrock, Witter & Reichman 2008; Pearson & Callaway 2008; Ostoja *et al.* 2013; Lucero, Allen & McMillan 2015), even when seed size is similar (Pearson, Callaway & Maron 2011; Connolly, Pearson & Mack 2014; J. E. Lucero *unpublished*

data). Just as selective foraging for large seeds can produce communities dominated by plants with small seeds (Brown & Heske 1990), selective foraging for native seeds could skew the composition of plant communities towards invaders. For example, Pearson, Callaway & Maron (2011) showed that native rodents in the Northern Rockies, USA preferred seeds from native plants over similar-sized seeds from spotted knapweed (*Centaurea stoebe*), an exotic invader native to Eurasia. Importantly, this pattern translated to differential establishment of seedlings in the field; rodent granivory limited the establishment of native plants but not knapweed. Furthermore, Maron *et al.* (2012) examined the impacts of rodent granivory on 20 native and 19 exotic plant species that commonly co-occur in Rocky Mountain grasslands. Using exclosures and experimental seed additions, Maron *et al.* (2012) found that rodents had stronger impacts on large-seeded natives than on large-seeded exotics, indicating that exotics were generally less affected by rodent granivory than natives.

However, the population- and community-level impacts of native-biased granivory are not always clear because few studies have explicitly related biased granivory to its effects on vital rates that affect demography (e.g., establishment; but see Pearson, Callaway & Maron 2011; Connolly, Pearson & Mack 2014). Quantifying demographic consequences is important because even strong selective granivory may not translate to impacts at the population level (Andersen 1989), especially if plants are microsite- rather than seed-limited (Maron & Crone 2006). Also, studies that do link granivore preferences to demographic consequences usually consider limited taxonomic and/or spatial scales. Thus, the extent to which selective foraging for native seeds promotes exotic invasion remains largely unknown.

Cheatgrass (*Bromus tectorum*) invasion in western North America provides an excellent opportunity to more fully examine whether granivory biased towards natives favours the

establishment of an exotic invader. Cheatgrass is native to Eurasia, but has become a particularly problematic invader across much of western North America because of its strong impacts on fire regimes (Balch *et al.* 2013), nutrient cycling (Norton *et al.* 2008), native food webs (Lucero, Allen & McMillan 2015), and native biodiversity (Ostoja & Schupp 2009; Pearson *et al.* 2015). Previous work has shown that cheatgrass in North America experiences biogeographic release (*sensu* Keane & Crawley 2002) from granivorous rodents; rodent granivory reduces cheatgrass establishment by over 60% in Iran (part of the native range) but has no significant impacts in the USA (part of the non-native range) (J. E. Lucero *unpublished data*). In addition, native rodents across much of western North America prefer seeds from native grasses over cheatgrass seeds (Kelrick *et al.* 1986; Lucero, Allen & McMillan 2015), regardless of seed size (Connolly, Pearson & Mack 2014; J. E. Lucero *unpublished data*). This suggests that cheatgrass disproportionately escapes rodent granivory relative to native grasses in North America. However, to our knowledge, only one study has assessed whether disproportionate escape from granivory favours cheatgrass establishment relative to native competitors (Connolly, Pearson & Mack 2014). But this study only considered one species of native grass and was conducted over a relatively limited spatial scale.

Our objective was to explore how disproportionate escape from rodent granivory might affect the establishment of cheatgrass relative to native grasses in the Great Basin, USA. Specifically, we compared the impacts of native rodents on the establishment of cheatgrass and four species of native grasses using experimental seed additions and exclosure treatments at sites distributed across ≈350,000 km^2 of the Great Basin. If granivory biased towards natives favours the establishment of cheatgrass, then rodents should limit the establishment of more-preferred natives to a greater extent than less-preferred cheatgrass.

MATERIALS AND METHODS

We compared rodent impacts on the establishment of cheatgrass vs. native grasses at five, broadly distributed study sites. Native grasses were Idaho fescue (*Festuca idahoensis*; "fescue" hereafter), bottlebrush squirreltail (*Elymus elymoides*; "squirreltail" hereafter), bluebunch wheatgrass *(Pseudoroegneria spicata*; "bluebunch" hereafter), and Indian ricegrass (*Achnatherum hymenoides*; "ricegrass" hereafter). We selected these species because they commonly co-occur with cheatgrass in the Great Basin and because their seed masses form a continuum both above and below that of cheatgrass (see Table S1 in Supporting Information). Previous work has shown that native rodents prefer seeds of all four native species, regardless of size, over cheatgrass seeds (Kelrick *et al.* 1986; Lucero, Allen & McMillan 2015; J. E. Lucero *unpublished data*). We collected cheatgrass seeds by hand during July 2010 in Rush Valley and Skull Valley, UT, USA; and native seeds were field-grown and collected by Granite Seed Co., Lehi, UT, USA. Study sites were located near Jackpot, NV (41°55'28.70"N, 114°43'44.96"W); Elko, NV (41° 3'49.40"N, 115°49'44.02"W); McGill, NV (39°58'26.51"N, 114°40'10.10"W); Baker, NV (39° 1'6.34"N, 114°25'53.44"W); and Vernon, UT (40° 6'54.99"N, 112°32'4.37"W). All sites were located on public land managed by the US Bureau of Land Management and in plant communities dominated by native species with <5% cover by invasive plants. All sites were separated by at least 120 km, which is orders of magnitude further than rodents and most local plants can typically disperse over short time periods (Harper *et al.* 1978; O'Farrell 1978; Jones 1989; Hayssen 1991; Rehmeier *et al.* 2004). Thus, our study sites sampled independent communities, and our experiments have a broad scope of inference in space.

We measured the impacts of rodent granivory at five sampling plots per site, each separated by 50 m. Each sampling plot consisted of six stations. Five of these stations consisted

of paired functional and "dummy" (i.e., non-functional) exclosures, and the sixth consisted of a single, unpaired functional exclosure (a control). Functional exclosures prevented rodent access, and were constructed of 1 cm-mesh hardware cloth assembled into 30 cm (diameter) x 30 cm (height) cylindrical cages with a floor and a roof. Floors and roofs prevented granivores from climbing into or burrowing under the cages. To install cages, we excavated 4 cm of topsoil with a garden hoe and placed cages in the excavated pits. We secured cages into place by pounding 13 cm-long sod staples through cage floors and into the ground with a rubber hammer. We then replaced excavated soil, except for large rocks and plant material. Dummy exclosures were constructed and installed in a similar fashion, except for one 7 x 7 cm hole cut into the sides of cages at ground level to admit rodents. We randomly assigned each pair of functional and dummy exclosures to a single grass species, and sowed each exclosure with 100 seeds from its assigned species (except the control). Seeds were gently patted ≈5 mm into the soil. Burying seeds in this manner made them largely inaccessible to invertebrate and avian granivores because only rodents can locate buried seeds via olfaction (Kamil & Balda 1985), and invertebrates do not dig for buried seeds (MacMahon, Mull & Crist 2000). To monitor recruitment from seed banks, a single functional exclosure was installed as above, but with no experimental seed additions (i.e., the control). This experimental design is depicted in Fig. S1.

Cages and seed additions were installed during August 2014 and left undisturbed until August 2016, when recruits were counted in each cage. After counting, all recruits were left in place to enable long-term monitoring. However, we collected and destroyed all cheatgrass occurring < 2 m from experimental cages. We will continue monitoring for potential cheatgrass recruits outside of cages to prevent the establishment of new cheatgrass populations. This

protocol has successfully prevented cheatgrass invasion following other seed addition experiments in the Great Basin (Lucero, Allen & McMillan 2015).

We quantified rodent impacts by comparing the average number of individuals established in paired functional vs. dummy exclosures. At each sampling station, we defined the absolute impact of rodent granivory (I_a) as the difference in establishment between paired dummy cages that were open to granivores (E_{open}) and functional cages that were closed to granivores (E_{closed}) such that $I_a = E_{open} - E_{closed}$. Absolute impacts are sensitive to *in situ* germination rates, which could vary both within and among species due to microsite heterogeneity and species-specific differences in requirements for breaking seed dormancy (Allen *et al.* 2007; Meyer & Allen 2009). To help mitigate any such germination biases among or within sites, we divided the absolute impact of rodent granivory at each station by the number of individuals established in that station's fully protected cage treatment (E_{closed}). This yielded a relative, germination-specific measure of rodent impacts at each sampling station: $I = \frac{(E_{open} - E_{closed})}{E_{closed}}$. This relative measure can be interpreted as the percent change in establishment caused by rodent granivory. If rodent granivory negatively impacts plant establishment, then I will be nonzero and negative.

We employed linear mixed-effects models using the lme package in R (R Development Core Team 2013) to determine whether the impacts of rodent granivory differed among grass species. We used Tukey contrasts to compare multiple means. Our models treated species as a fixed factor and study site as a random factor. Treating site as a random factor statistically accounted for any biologically-relevant differences (e.g., rodent density, *in situ* germination rates, percent plant cover, elevation, temperature, precipitation, etc.) potentially present among study sites. We excluded from our analyses any stations with damaged or vandalized cages. We

also excluded stations where no seedlings germinated in protected cages (i.e., stations where

$E_{closed} = 0$) because the formula $I = \frac{(E_{closed} - E_{open})}{E_{closed}}$ does not permit division by zero. If

preferential granivory favours the establishment of cheatgrass over natives, then rodents should

have stronger negative impacts on native grasses than on cheatgrass.

RESULTS

Rodent granivory strongly limited the establishment of native grasses but had no

significant effect on cheatgrass (Fig 1). The effect of rodent granivory on plant establishment

was -8.7± 13.4% SE for cheatgrass, -90.5±4.2% for fescue, -74.5±6.65% for squirreltail, -81.4±

5.6% for bluebunch, and -94.5±4.1% for ricegrass. The 95% confidence intervals around these

means (± 26.16% for cheatgrass, ± 8.46% for fescue, ± 13.3% for squirreltail, ± 11.1% for

bluebunch, and ± 8.16% for ricegrass) indicated that rodent impacts were not different from zero

for cheatgrass, but were nonzero and negative for each native grass species. Furthermore, the

impacts of rodent granivory significantly differed between cheatgrass and each native species (P

< 0.001 for each native-cheatgrass pairwise comparison; all Z-values > |5.96|). Rodent impacts

did not differ among native species, regardless of seed size (P > 0.48 for each native-native

pairwise comparison; all Z-values < |1.00|). These results were highly consistent across study

sites. Our analyses revealed no significant effect of site (P = 0.54) and no significant site ×

species interaction (P = 0.54) on establishment.

The impacts of rodent granivory on plant establishment were not determined by seed

bank dynamics. No species recruited appreciably from seed banks (Fig. 2). On average,

cheatgrass, fescue, squirreltail, bluebunch, and ricegrass recruited 0.08 (± 0.06 SE), 0.00 (± 0.06

SE), 0.12 (± 0.06 SE), 0.04 (± 0.04 SE), and 0.00 (± 0.06 SE) individuals per control cage,

respectively. These means did not significantly differ ($P > 0.25$ for all pairwise comparisons; all t-values < 1.32). Furthermore, the 95% confidence intervals around these means (± 0.12 for cheatgrass, ± 0.12 for fescue, ± 0.12 for squirreltail, ± 0.08 for bluebunch, and ± 0.12 for ricegrass) indicated that seed bank recruitment was not different from zero for any species.

We observed a germination bias among plant species (Fig. 3). The average number of individuals established in protected cages with seed additions (i.e., E_{closed}; see Materials and Methods) was 2.28 (± 0.23 SE), 5.08 (± 0.75 SE), 3.30 (± 0.68 SE), 4.77 (± 0.89 SE), and 2.65 $\pm$ (0.63 SE) for cheatgrass, fescue, bluebunch, squirreltail, and ricegrass, respectively. The 95% confidence intervals around these means (± 0.44 for cheatgrass, ± 1.47 for fescue, ± 1.33 for bluebunch, ± 1.74 for squirreltail, and ± 1.24 for ricegrass) indicated that establishment was greater than zero for all species. Fescue and squirreltail exhibited higher germination rates than cheatgrass ($P < 0.05$ for both pairwise comparisons), but all native grasses germinated at equal rates ($P > 0.05$ for all native-native pairwise comparisons).

DISCUSSION

A number of studies have shown that native granivores prefer seeds from native plants over seeds from invaders (e.g., Kelrick *et al.* 1986; Pearson, Callaway & Maron 2011; Lucero, Allen & McMillan 2015), but few have taken the important next step of connecting biased granivory to vital rates that affect plant demography. Thus, the population- and community-level impacts of biased granivory are usually unclear. Previous work in the Great Basin has shown that native rodents distinctly prefer seeds from native grasses over seeds from cheatgrass (Kelrick *et al.* 1986; Lucero, Allen & McMillan 2015; J. E. Lucero *unpublished data*). Here, we relate previously-reported patterns of seed preference to their impacts on plant establishment in

the field. We found that native rodents strongly limited the establishment of more-preferred native grasses but had no effect on the establishment of less-preferred cheatgrass over a large part of the Great Basin (Fig. 1). Our results showed no evidence of context dependence across this spatial gradient. We conclude that disproportionate escape from rodent granivory may consistently favour the establishment of cheatgrass over native grasses, potentially exacerbating one of the most "significant" plant invasions in North America (D'Antonio & Vitousek 1992).

Coupled with previous work, our results relate to the enemy release hypothesis of plant invasion (Maron & Vila 2001; Keane & Crawley 2002). Perhaps the most famous explanation for the success of invasive plants in novel environments is enemy release, which suggests that translocation removes exotic plants from the negative effects of natural enemies in their native communities (Maron & Vila 2001; Keane & Crawley 2002). Specifically, the enemy release hypothesis predicts that 1) native enemies strongly limit populations of invaders in their native range but not their non-native range, and 2) native enemies in recipient communities have stronger impacts on native competitors than on invaders (Keane & Crawley 2002). Previous work in this system has shown that native rodents limited cheatgrass establishment by over 60% in Iran (part of the native range of cheatgrass) but had no effect in the Great Basin. Thus, rodent granivory constrained cheatgrass establishment at home but not abroad (J. E. Lucero *unpublished data*). We extend these results by demonstrating that native rodents in the Great Basin limited the establishment of native competitors but not cheatgrass (Fig. 1). Taken together, these results strongly suggest that cheatgrass in the Great Basin has experienced enemy release (*sensu* Keane & Crawley 2002) at the seed stage, which may contribute to its exceptional invasiveness (Pearson *et al.* 2015) across much of western North America. This finding is unique because empirical studies almost always consider the enemy release hypothesis in terms of *specialist*

herbivores, but not generalists such as our granivores (but see Vermeij *et al.* 2009; Schaffner *et al.* 2011). Also, very few studies have employed experimental exclosures to measure the impacts of natural enemies in both the native and non-native ranges of a focal invader, *sensu* J. E. Lucero *unpublished data* (but see DeWalt, Denslow & Ickes 2004; Williams, Auge & Maron 2010). To our knowledge, cheatgrass is the only invader for which there is biogeographic evidence for enemy release at the seed/seedling stages.

We conducted our experiments at sites distributed across ≈350,000 km^2 of the Great Basin, but our results showed no evidence of context dependence in space (i.e., no significant effect of site and no significant site × species interaction). This suggests that rodent impacts on plant establishment were highly consistent across study sites. Such consistency is rather remarkable given the pervasiveness of context-dependent interactions in biological communities (Lawton 1999). Of course, we do not suggest that our system is free from context dependence, as the foraging behaviour of polyphagous generalists can vary considerably based on the abundance, density, and identity of local food resources (e.g., Pulliam 1974; Charnov 1976; Holt 1977; Barbosa *et al.* 2009; Ostoja et al. 2013). A number of independent studies have shown that native rodents in the Great Basin generally prefer seeds from native plants over cheatgrass seeds (Kelrick *et al.* 1986; Ostoja *et al.* 2013; Lucero, Allen & McMillan 2015; J. E. Lucero *unpublished data*), but theory predicts that selective consumers should become less choosy when preferred resources are scarce (e.g., Pulliam 1974). Thus, normally-selective rodents could more readily consume cheatgrass seeds during periods of resource scarcity. Accordingly, if our study had been conducted at a time and/or place of extreme food limitation (e.g., during an exceptionally dry year or near a large-scale disturbance), we might have obtained different results (e.g., St. Clair *et al.* 2016).

Even though cheatgrass seeds escaped the *impacts* of rodent granivory during our study (Fig. 1), they did not necessarily escape consumption. Cheatgrass seeds are often found in the stomach contents of North American rodents (e.g., Flake 1973), and several studies in the Great Basin have shown that rodents remove cheatgrass seeds from experimental seed depots, although native seeds are almost always preferred (e.g., Lucero, Allen & McMillan 2015). Thus, it is plausible that rodents at our study sites consumed cheatgrass seeds to some extent, although we have no data to confirm this. Again, we emphasize that our results speak only to the *impacts* of rodent granivory.

It is surprising that rodent impacts were unrelated to seed size for native species. Pearson, Callaway & Maron (2011) and Connolly, Pearson & Mack (2014) showed that seed size and rodent impacts were positively related for native species in intermountain grasslands; rodents more strongly limited the establishment of large-seeded natives than small-seeded natives because rodents preferred large seeds over small ones (see also Maron et al. 2012). The seeds of native species used in our study varied markedly in size (Table S1), and previous work has shown that native rodents in this system remove seeds from fescue, bluebunch, and ricegrass as predicted by size (J. E. Lucero *unpublished data*). Thus, for native species, we expected rodent impacts and seed size to be positively related *sensu* Pearson, Callaway & Maron (2011) and Connolly, Pearson & Mack (2014). We do not know why seed size accurately predicted removal but not establishment in this system; our results suggest caution when using seed size to predict rodent impacts on plant establishment.

We do not infer that our study species were only seed- and not microsite-limited during our study. Rodent granivory is an important barrier to seedling establishment in many plant communities (Brown, Reichman & Davidson 1979; Louda 1989, Brown & Heske 1990; Hulme

1998) because it can impose seed limitation on plant populations (Maron & Crone 2006). However, seedling establishment can also be highly constrained by suitable microsites (i.e., "safe sites"; Eriksson & Ehrlen 1992). Whether plant populations are generally seed- or microsite-limited has been hotly debated (see review by Eriksson & Ehrlen 1992). The classic experiment used to detect seed vs. microsite limitation involves comparing establishment between paired plots that have and have not received experimental seed additions (Crawley & Ross 1990). If seed addition improves establishment, then plants are seed-limited. If seed addition does not improve establishment, then plants are microsite-limited. Here, average establishment was not different from zero for any species in control cages, which received no seeds (Fig. 2). Conversely, average establishment was significantly greater than zero for all species in protected cages, which did receive seeds (Fig. 3). Thus, seed additions improved plant establishment, and study species were seed-limited within experimental cages (Table S2). However, our data cannot speak to seed vs. safe site limitation outside of experimental cages. Disturbance can alleviate microsite limitation by ameliorating competition among seedlings (Jutila & Grace 2002; Mouquet *et al.* 2004), and all experimental cages were installed in disturbed soil (see Methods). Because no control or protected cage was installed into undisturbed soil, we cannot estimate the effects of disturbance on plant establishment. Therefore, we do not know if adding seeds to undisturbed soil would have improved seedling recruitment, thus precluding tests of seed limitation outside of cages.

Our results were not affected by seed bank dynamics or germination biases among plant species. In nature, all species used in this study can recruit individuals from seed banks (Hassan & West 1986; Humphrey & Schupp 2001). Extensive recruitment from seed banks could have complicated our ability to detect granivore impacts on experimentally-added seeds. However,

recruitment from control cages was no different from zero for any study species (Fig. 2). Thus, patterns of plant establishment in our study were driven by interactions between native rodents and experimentally-added seeds, not seeds from seed banks. Also, our results were not determined by germination bias among species that we observed (Fig. 3). We expressed rodent impacts at each sampling station (*I*) in relative, germination-specific terms: $I = \frac{(E_{open} - E_{closed})}{E_{closed}}$ (see Materials and Methods). Thus, the reported impacts of rodent granivory (Fig. 1) were "corrected" for each species' *in situ* germination rate. Furthermore, establishment from protected cages was greater than zero for all species, including cheatgrass (Fig. 3). This indicates that native rodents had the potential to limit the establishment of all study species but only actually did so for native grasses.

We have shown that rodent granivory differentially impacted native vs. cheatgrass establishment, but the effect of biased granivory on population growth (i.e., λ) remains unclear. Rodent impacts on establishment may well translate to impacts on λ because the transition from seed to seedling (i.e., establishment) is a particularly sensitive demographic transition in the life histories of many plants (e.g., Gross & Mackay 2014; Paine, Beck & Terborgh 2016), including cheatgrass (Griffith 2010). However, we emphasize that plant invasion is ultimately a demographic phenomenon (Chesson 2000), and establishment is only one, albeit important, component of plant demography. To unequivocally show that native-biased granivory promotes cheatgrass invasion, the effects of biased granivory should be related to differential patterns of λ among species. Specifically, granivory should have stronger negative impacts on the λ of natives than on the λ of cheatgrass. Our experimental design is appropriate to detect these effects. We look forward to continued monitoring of experimental plots to evaluate changes in plant abundance (i.e., λ) over time.

AUTHOR'S CONTRIBUTIONS

JEL and RMC conceived the experiments and designed methodology; JEL performed the experiments and collected the data; JEL and RMC analysed the data; JEL led the writing of the manuscript. Both authors contributed critically to the manuscript and gave final approval for publication.

ACKNOWLEDGEMENTS

DATA ACCESSIBILITY

We will archive our data in the Dryad Digital Repository upon acceptance for publication.

REFERENCES

Allen, P.S., Benech-Arnold, R.L., Batlla, D. & Bradford, K.J. (2007) Modeling of seed dormancy. pp. 72-112 In: K.J. Bradford and H. Nonogaki, Eds. Seed Development, Dormancy and Germination. Blackwell Publishing, Oxford, UK.

Andersen, A. N. (1989) How important is seed predation to recruitment in stable populations of long-lived perennials? *Oecologia*, **81**, 310-315.

Balch, J.K., Bradley, B.A., D'Antonio, C.M. & Gomez-Dans, J. (2013) Introduced annual grass

increases regional fire activity across the arid western USA (1980-2009). *Global Change Biology*, **19**, 173-183.

Barbosa, P., Hines, J., Kaplan, I., Martinson, H., Szczepaniec, A. & Szendrei, Z. (2009) Associational resistance and susceptibility: Having right or wrong neighbors. *Annual review of Ecology, Evolution, and Systematics*, **40**, 1-20.

Brown, J.H., Reichman, O.J. & Davidson, D.W. (1979) Granivory in desert ecosystems. *Annual Review of Ecology and Systematics*, **10**, 201-227.

Brown, J.H. & Heske, E.J. (1990) Control of a desert–grassland transition by a keystone rodent guild. *Science*, **250**, 1705-1707.

Howe, H.F. & Brown, J.S. (2000) Early consequences of rodent granivory on synthetic dicot communities. *Ecological Applications*, **10**, 917-924.

Charnov, E.L. (1976) Optimal foraging; the marginal value theorem. *Theoretical Population Biology*, **9**, 129-136.

Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, **31**, 343-366.

Connolly, B.M., Pearson, D.E. & Mack, R.N. (2014) Granivory of invasive, naturalized, and native plants in communities differentially susceptible to invasion. *Ecology,* **95**, 1759-1769.

Crawley, M.J. & Ross, G.J.S. (1990) The population dynamics of plants. *Philosophical Transactions of the Royal Society of London B*, **330**, 125-140.

D'Anotonio, C.M. & Vitousek, P.M. (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics, **23**, 63-87.

DeWalt, S.J., Denslow, J.S. & Ickes, K. (2004) Natural-enemy release facilitates habitat

expansion of the invasive tropical shrub *Clidemia hirta. Ecology*, **85**, 471-483.

Eriksson, O. & Ehrlen, J. (1992) Seed and microsite limitation of recruitment in plant

populations. *Oecologia*, **91**, 360-364.

Flake, L.D. (1973) The food habits of four species of rodents on a short-grass prairie in

Colorado. Journal of Mammalogy, **54**, 636-647.

Griffith, A.B. (2010) Positive effects of native shrubs on *Bromus tectorum* demography.

Ecology, **91**, 141-154.

Gross, C.L. & Mackay, D. (2014) Two decades of demography reveals that seed and seedling

transitions limit population persistence in a translocated shrub. *Annals of Botany*, **114**,

85-96.

Harper, K.T., Freeman, D.C., Ostler, W.K. & Klikoff, L.G. (1978) The flora of Great Basin

mountain ranges: diversity, sources, and dispersal ecology. *The Great Basin Naturalist*

Memoirs, **2**, 81-103.

Hassan, M.A., & West, N.E. (1986) Dynamics of soil seeds pools in burned and unburned

sagebrush semi-deserts. *Ecology*, **67**, 269-272.

Hayssen, V. (1991) *Dipodomys microps*. Mammalian Species, **389**, 1-9.

Holt, R.D. (1977) Predation, apparent competition, and the structure of prey communities.

Theoretical Population Biology, **12**, 197-229.

Hulme, P.E. (1998) Post-dispersal seed predation: consequences for plant demography and

evolution. *Perspectives in Plant Ecology*, **1**, 32-46.

Humphrey, L.D. & Schupp, E.W. (2001) Seed banks of *Bromus tectorum*-dominated

communities in the Great Basin. Western North American Naturalist, **61**, 85-92.

Jones, W.T. (1989) Dispersal distance and the range of nightly movement in Merriam's

kangaroo rats. *Journal of Mammalogy*, **70**, 27-34.

Jutila, H.M. & Grace, J.B. (2002) Effects of disturbance on germination and seedling

establishment in a coastal prairie grassland: a test of the competitive release hypothesis.

Journal of Ecology, **90**, 291-302.

Kamil, A.C. & Balda, R.P. (1985) Cache recovery and spatial memory in Clark's nutcracker

(*Nucifraga colombiana*). Journal of Experimental Psychology: *Animal Behavior*

Processes, **11**, 95-111.

Keane, R.M. & Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis.

Trends in Ecology and Evolution, **17**, 164-170.

Kelrick, M.I & MacMahon, J.A. (1985) Nutritional and physical attributes of seeds of some

common sagebrush-steppe plants: Some implications for ecological theory and

management. *Journal of Range Management*, **38**, 65-69.

Kelrick, M.I., MacMahon, J.A., Parmenter, R.R. & Sisson, D.V. (1986) Native seed preferences

of shrub-steppe rodents, birds and ants: the relationships of seed attributes and seed use.

Oecologia, **68**, 327-337.

Lawton, J.H. (1999) Are there general laws in ecology? *Oikos*, **84**, 177-192.

Louda, S.M. (1982) Distribution ecology: variation in plant recruitment over a gradient in

relation to insect seed predation. *Ecological Monographs*, **52**, 25-41.

Louda, S.M. (1989) Predation in the dynamics of seed regeneration. In Ecology of soil seed

banks (ed. M.A. Leck, Parker, V.T. & Simpson, R.L.), pp. 25-51. Academic Press, San

Diego, CA.

Lucero, J.E., Allen, P.S. & McMillan, B.R. (2015) Increased primary production from an

exotic invader does not subsidize native rodents. *PLoS ONE*, **10**, e 0131564.

MacMahon, J.A., Mull, J.F. & Crist, T.O. (2000) Harvester ants (*Pogonomyrmex* spp.): their

    community and ecosystem influences. *Annual Review of Ecology and Systematics*, **31**,

    265-291.

Maron, J.L. & Crone, E. (2006) Herbivory: effects on plant abundance, distribution and

    population growth. *Proceedings of the Royal Society B*, **273**, 2575-2584.

Maron, J.L. & Kauffman, M. (2006) Habitat-specific consumer impacts on plant population

    dynamics. *Ecology*, **87**, 113-124.

Maron, J.L. & Vila, M. (2001) When do herbivores affect plant invasion? Evidence for the

    natural enemies and biotic resistance hypotheses. *Oikos*, **95**, 361-373.

Maron, J.L., Pearson, D.E., Potter, T. & Ortega, Y. (2012) Seed size and provenance mediate the

    joint effects of disturbance and seed predation on community assembly. *Journal of*

    Ecology, **100**, 1492-1500.

Meyer, S.E. & Allen, P.S. (2009) Predicting seed dormancy loss and germination timing in a

    semiarid environment using hydrothermal time models. *Seed Science Research*, **19**, 225-

    240.

Mouquet, N., Leadley, P., Mériguet, J. & Loreau, M. (2004) Immigration and local competition

    in herbaceous plant communities: a three-year seed-sowing experiment. Oikos, **104**, 77-

    90.

Norton, U., Mosier, A.R., Morgan, J.A., Derner, J.D., Ingram, L.J. & Stahl, P.D. (2008)

    Moisture pulses, trace gas emissions and soil C and N in cheatgrass and native grass-

    dominated sagebrush-steppe in Wyoming, USA. *Soil Biology & Biochemistry*, **40**, 1421-

    1431.

O'Farrell, M.J. (1978) Home range dynamics of rodents in a sagebrush community. *Journal of*

Mammalogy, **59**, 657-668.

Orrock, J.L., Witter, M.S. & Reichman, O.J. (2008) Apparent competition with an exotic plant reduces native plant establishment. *Ecology*, **89**, 1168-1174.

Ostoja, S.M. & Schupp, E.W. (2009) Conversion of sagebrush shrublands to exotic annual grasslands negatively impacts small mammal communities. *Diversity and Distributions*, **15**, 863-870.

Ostoja, S.M., Schupp, E.W., Durham, S. & Klinger, R. (2013) Seed harvesting is influenced by associational effects in mixed seed neighbourhoods, not just by seed density. *Functional Ecology*, **27**, 775-785.

Paine, C.E.T., Beck, H. & Terborgh, J. (2016) How mammalian predation contributes to tropical tree community structure. *Ecology*, **97**, 3326-3336.

Pearson, D.E. & Callaway, R.M. (2008) Weed-control insects reduce native-plant recruitment through second-order apparent competition. *Ecological Applications*, **18**, 1489-1500.

Pearson, D.E., Callaway, R.M. & Maron, J.L. (2011) Biotic resistance via granivory: establishment by invasive, naturalized, and native asters reflects generalist preference. *Ecology*, **92**, 1748-1757.

Pearson, D.E., Ortega, Y.K., Ozkan, E., & Hierro J. L. (2015) Quantifying "apparent" impact and distinguishing impact from invasiveness in multispecies plant invasions. *Ecological Applications*, **26**, 162-173.

Pulliam, H.R. (1974) On the theory of optimal diets. *The American Naturalist* **108**, 59-74.

R Development Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reader, R.J. (1993) Control of seedling emergence by ground cover and seed predation in

relation to seed size for some oldfield species. *Journal of Ecology*, **81**, 169-175.

Rehmeier, R.L., Kaufman, G.A. & Kaufman, D.W. (2004) Long distance movements of the deer mouse in tallgrass prairie. *Journal of Mammalogy*, **85**, 562-568.

Rose, K.E., Louda, S.M. & Rees, M. (2005) Demographic and evolutionary impacts of native and invasive insect herbivores on *Cirsium canescens*. Ecology, **86**, 453-465.

Schaffner, U., Ridenour, W.M. Wolf, V.C., Bassett, T., Muller, C., Muller-Scharer, H., Sutherland, S., Lortie C.J. & Callaway, R.M. (2011) Plant invasions, generalist herbivores, and novel defense weapons. *Ecology* **92**, 829-835.

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

Vermeij, M.J.A., Smith, T.B., Dailer, M.L. & Smith, C.M. (2009) Release from native herbivores facilitates the persistence of invasive marine algae: a biogeographical comparison of the relative contribution of nutrients and herbivory to invasion success. *Biological Invasions*, **11**, 1463-1471.

Weiher, E. & Keddy, P. (1999) Assembly rules as general constraints on community composition. Pages 251-271 in E. Weiher and P. Keddy, editors. Ecological assembly rules: perspectives, advances, retreats.

Williams, J.L., Auge, H. & Maron, J.L. (2010) Testing hypotheses for exotic plant success: parallel experiments in the native and introduced ranges. *Ecology*, **91**, 1355-1366.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Table S1 *Seed mass (per seed) of grass species used in our experiments.*

Table S2 *Results of a linear mixed-effects model used to determine whether seed additions improved establishment relative to control cages that received no seed additions.*

Figure S1 *Experimental design used to determine the impacts of rodent granivory on the establishment of grass species used in our experiments.*

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.
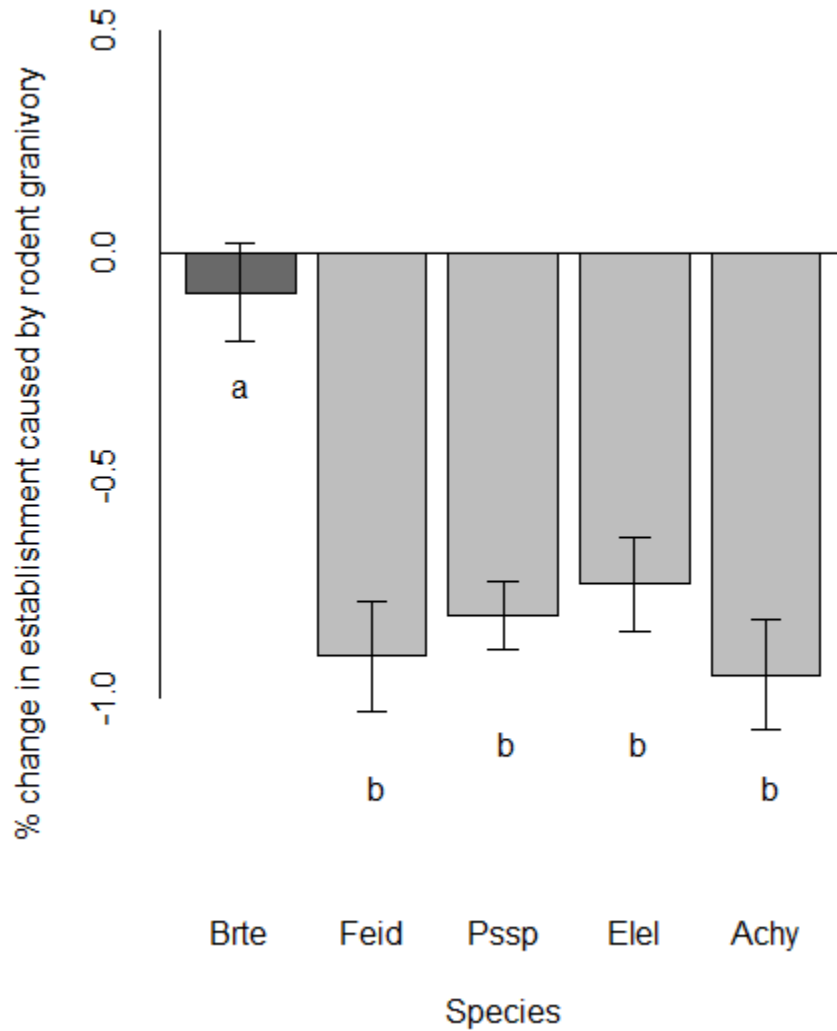
Fig. 1. Mean impact of rodent granivory on the establishment of cheatgrass (*Bromus tectorum,* "Brte"), Idaho fescue (*Festuca idahoensis*, "Feid"), bluebunch wheatgrass (*Pseudoroegneria spicata*, "Pssp"), bottlebrush squirreltail (*Elymus elymoides*, "Elel"), and Indian ricegrass (*Achnatherum hymenoides*, "Achy"). Error bars show one standard error. Means that share letters do not significantly differ (i.e., *P* > 0.05).

Fig. 2. Mean establishment of cheatgrass (*Bromus tectorum,* "Brte"), Idaho fescue (*Festuca idahoensis*, "Feid"), bluebunch wheatgrass (*Pseudoroegneria spicata*, "Pssp"), bottlebrush squirreltail (*Elymus elymoides*, "Elel"), and Indian ricegrass (*Achnatherum hymenoides*, "Achy") from seed banks. Error bars show 95% confidence intervals, and no means differ from each other (*P* > 0.25 for all pairwise comparisons).
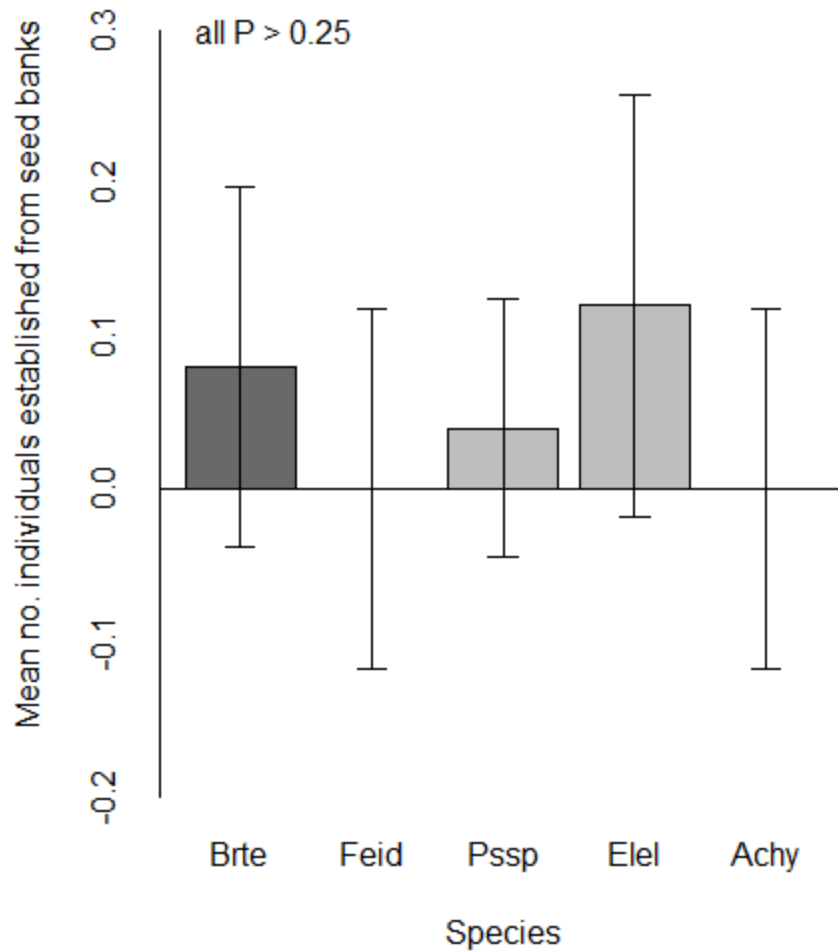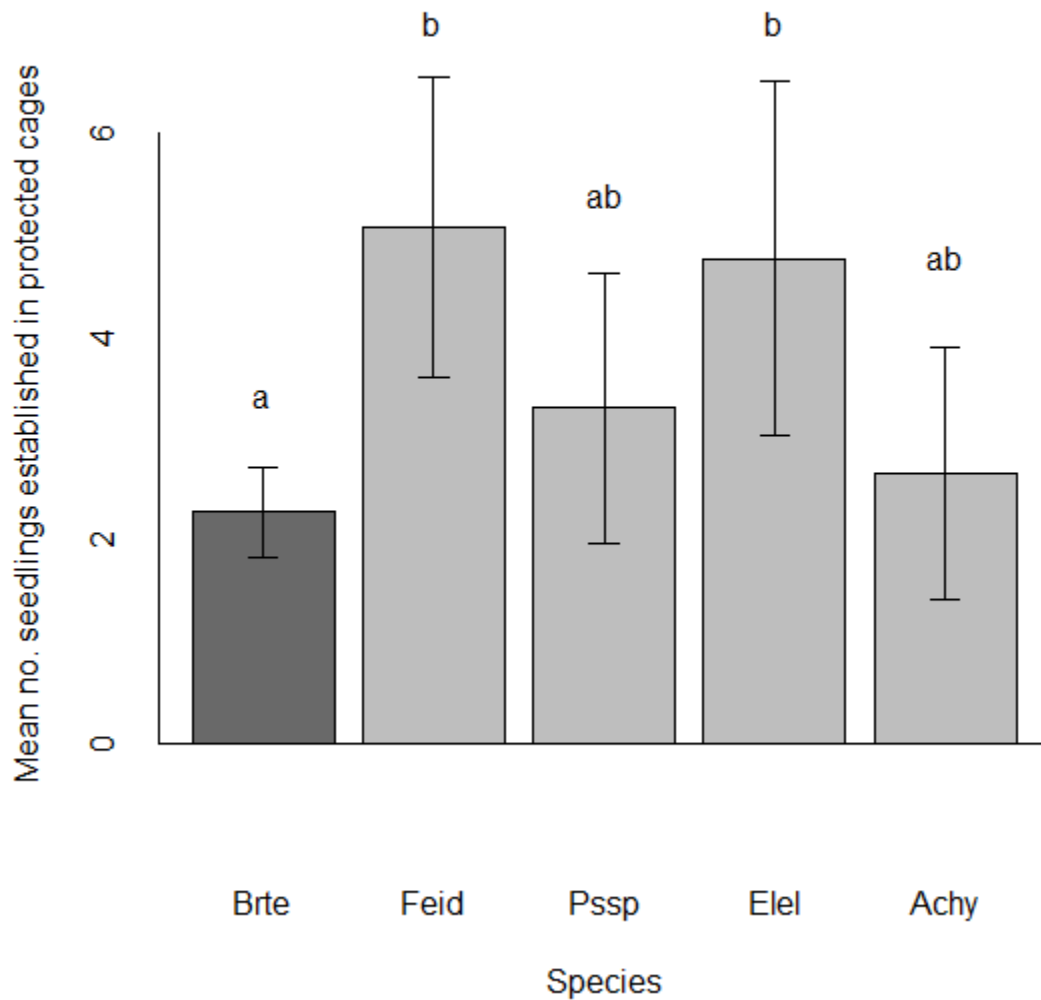
Fig. 3. Mean establishment of cheatgrass (*Bromus tectorum,* "Brte"), Idaho fescue (*Festuca idahoensis,* "Feid"), bluebunch wheatgrass (*Pseudoroegneria spicata,* "Pssp"), bottlebrush squirreltail (*Elymus elymoides,* "Elel"), and Indian ricegrass (*Achnatherum hymenoides,* "Achy") in protected cages that received experimental seed additions (i.e., average E_{closed} for each species; see Materials and Methods). Error bars show 95% confidence intervals. Means that share letters do not significantly differ (i.e., $P > 0.05$).

SUPPORTING INFORMATION

Table S1. Seed mass (per seed) of grass species used in our experiments. Species are labelled
as native (N) or invasive (I).

Species	Seed mass
Festuca idahoensis (N)	1.4 mg
Bromus tectorum (I)	3.1 mg
Pseudoroegneria spicata (N)	3.2 mg
Elymus elymoides (N)	3.5 mg
Achnatherum hymenoides (N)	3.9 mg

Table S2. Results of a linear mixed-effects model (species as a fixed factor and study site as a
random factor) used to determine whether seed additions in protected cages improved
establishment relative to control cages that received no seed additions.

| Species	Mean no. individuals established per control cage	Mean no. individuals established per protected cage	z-value	P-value
Festuca idahoensis	0.00 ($\pm$ 0.06 SE)	5.08 ($\pm$ 0.75 SE)	-6.59	<0.01
Bromus tectorum	0.08 ($\pm$ 0.06 SE)	2.28 ($\pm$ 0.23 SE)	-3.31	0.03
Pseudoroegneria spicata	0.04 ($\pm$ 0.04 SE)	3.30 ($\pm$ 0.68 SE)	-5.23	<0.01
Elymus elymoides	0.12 ($\pm$ 0.06 SE)	4.77 ($\pm$ 0.89 SE)	-7.82	<0.01
Achnatherum hymenoides	0.00 ($\pm$ 0.06 SE)	2.65 ($\pm$ 0.63 SE)	-3.93	<0.01
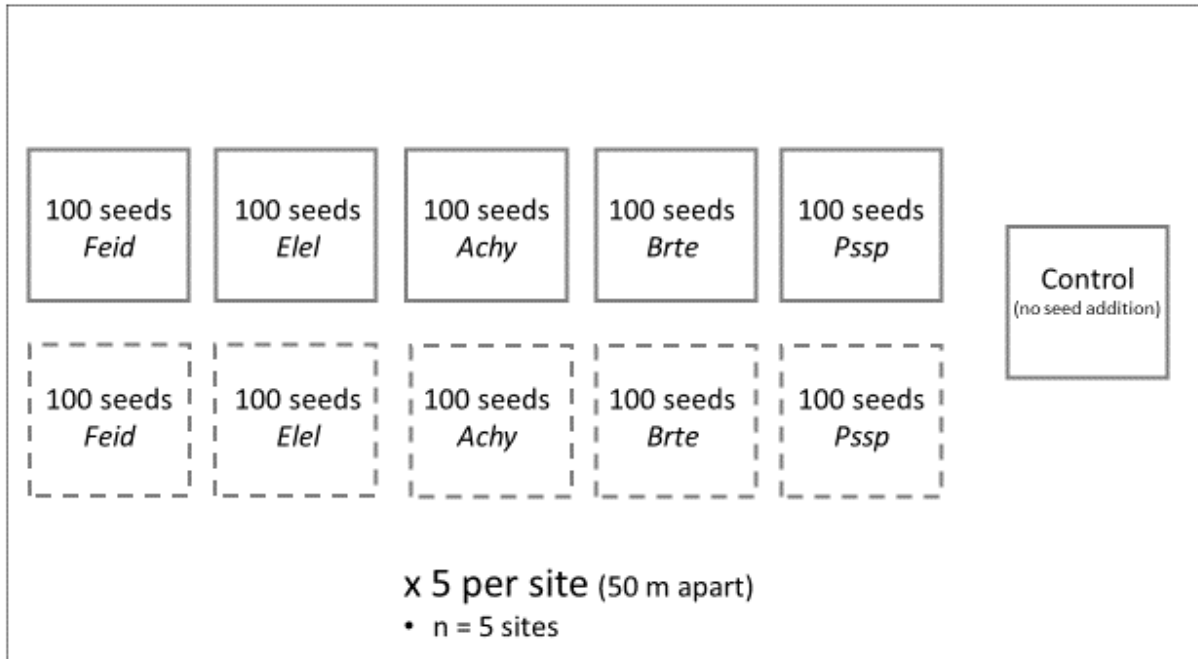
Fig. S1. Experimental design used to determine the impacts of rodent granivory on Idaho fescue (*Festuca idahoensis*, "Feid"), cheatgrass (*Bromus tectorum,* "Brte"), bluebunch wheatgrass (*Pseudoroegneria spicata*, "Pssp"), bottlebrush squirreltail (*Elymus elymoides,* "Elel"), and Indian ricegrass (*Achnatherum hymenoides*, "Achy") in the Great Basin, USA. The seed mass (per seed) and provenance of these species are reported in Table S1. We sowed one hundred seeds of each species into randomly-ordered, paired functional (solid rectangles) and non-functional (dashed rectangles) rodent exclosures. The difference in seedling establishment between paired exclosures reflected the impact of rodent granivory on a particular species. To monitor recruitment from seed banks, we installed a single functional exclosure that received no seed additions ("Control"). This setup was replicated five times per site at five sites that were broadly-distributed across ≈350,000 km^2 the Great Basin.

CHAPTER 3

Granivory from native rodents and competition from an exotic invader strongly and

equally limit the establishment of native grasses

Jacob E. Lucero* and Ragan M. Callaway

Division of Biological Sciences and the Institute on Ecosystems, University of Montana,

Missoula, Montana 59812, USA

* jacob.lucero@umontana.edu

ABSTRACT

Seed predation and resource competition are fundamental biotic filters that affect the assembly of plant communities, yet empirical studies rarely assess their relative importance. Here, we used rodent exclosures and experimental seed additions to compare how rodent granivory and resource competition affected the net establishment of an exotic invader (*Bromus tectorum*) and two native bunchgrasses (*Pseudoroegneria spicata* and *Elymus elymoides*) in the Great Basin Desert, USA. Rodent granivory limited the establishment of both native grasses but not *B. tectorum*. Competition from *B. tectorum* limited the establishment of both native grasses, but neither native grass reciprocated a significant competitive effect on *B. tectorum*. Interestingly, rodent granivory and competition from *B. tectorum* limited the establishment of native grasses to the same extent, indicating that these biotic interactions were equally important barriers to the local establishment of *P. spicata* and *E. elymoides*.

INTRODUCTION

Seed predation and resource competition can determine the identity and abundance of species in plant communities. Seed predation can regulate communities by imposing seed limitation on some plant populations but not others (Hulme 1998, Brown and Heske 1990, Howe and Brown 2000, Maron and Crone 2006), and competition is thought to be a pervasive organizer of plant assemblages (Keddy and Shipley 1989, Shipley and Keddy 1994, Aschehoug and Callaway 2015, Aschehoug et al. 2016). In addition, seed predation and competition along gradients and across ecotones can strongly constrain the abundance and distribution of species (Louda 1982, Gurevitch 1986, Pennings and Callaway 1992, Callaway et al. 1996). Thus, seed predation and competition are fundamental biotic filters (Diamond 1975, Weiher and Keddy 1999, Vellend 2010) that affect the assembly of plant communities.

However, the relative importance (Welden and Slauson 1986, Brooker et al. 2005, Kikvidze et al. 2011) of these fundamental filters is less clear because empirical studies typically consider the effects of seed predation or competition alone (but see Inouye et al. 1980, Louda et al. 1990). Considering the effects of single interactions affords insight into their intensity, but the *importance* of an interaction is tractable only by examining its effects relative to the effects of other interactions in simultaneous, coordinated experiments (Welden and Slauson 1986, Brooker et al. 2005, Kikvidze et al. 2011).

Elucidating the relative importance of seed predation and resource competition may be especially important for managing native species in communities invaded by exotic plants. Biological invasions by exotic plants disrupt native communities at tremendous ecological (Liao et al. 2008, Vila et al. 2011) and economic (Duncan et al. 2004) costs. Interestingly, both seed predation and resource competition could exacerbate exotic invasions by disproportionately

limiting the abundance of native plants. Native granivores in various ecosystems tend to constrain the establishment of native species to a greater extent than they constrain strong invaders (Orrock et al. 2008, Pearson et al. 2011, Maron et al. 2012, Connolly et al. 2014), which may hasten the local extinction of natives (Dangremond et al. 2010). In addition, the superior competitive ability of invasive plants relative to natives is probably the most widely cited explanation for the decline of native species in invaded communities (reviewed by Levine et al. 2003). Although both seed predation and resource competition can strongly limit the abundance of native plants in invaded communities, the relative importance of these interactions is rarely evaluated (but see Inouye et al. 1980, Louda 1990). Understanding which biotic filter limits native abundance the most could help managers prioritize conservation efforts. For example, if seed predation limits the establishment of native plants more than competition from invaders, manipulating plant-granivore interactions may be a better management strategy than culling invaders.

The Great Basin Desert, USA, is an excellent system for evaluating the relative importance of the effects of seed predation from native granivores and competition from invasive plants on the establishment of native species. In the Great Basin, invasive cheatgrass (*Bromus tectorum*; an exotic annual native to Eurasia), native bluebunch wheatgrass (*Pseudoroegneria spicata*; "bluebunch" hereafter), and native bottlebrush squirreltail (*Elymus elymoides*; "squirreltail" hereafter) commonly co-occur, but cheatgrass invasion is displacing native flora and fauna at an alarming rate (Mack et al. 1981, Knapp 1996, Ostoja and Schupp 2009, Hall 2012, Balch et al. 2013, Freeman et al. 2014, Pearson et al. 2016). Seeds from cheatgrass, bluebunch, and squirreltail are all vulnerable to predation by native, granivorous rodents, but rodents prefer seeds from native grasses to cheatgrass seeds (Kelrick et al. 1986, Ostoja et al. 2013, Connolly et

70

al. 2014, Lucero et al. 2015). In addition, cheatgrass, bluebunch, and squirreltail compete

directly for limiting resources, but cheatgrass is a superior competitor and displaces natives,

especially at the seed/seedling stage (Melgoza and Nowak 1991, Humphrey and Schupp 2004,

Vasquez et al. 2008, Parkinson et al. 2013). Thus, both rodent granivory and resource

competition may favor the establishment of cheatgrass over bluebunch and squirreltail.

However, the relative importance of these interactions is unknown.

    We used rodent exclosures and experimental seed additions to compare the effects of rodent

granivory and resource competition on the net establishment of cheatgrass, bluebunch, and

squirreltail across a ≈80,000km^2 portion of the Great Basin. We predicted that 1) rodent

granivory would significantly limit the establishment of bluebunch and squirreltail but not

cheatgrass; and 2) cheatgrass would impose strong competitive effects on bluebunch and

squirreltail, but natives would reciprocate weak competitive effects on cheatgrass. We assessed

the relative importance of rodent granivory and resource competition by comparing the intensity

of their respective effects on seedling establishment, but we had no clear, *a priori* expectations

for which interaction would be stronger.

METHODS

Plant materials and study area

        We evaluated how rodent granivory and resource competition affected the establishment

of cheatgrass, bluebunch, and squirreltail using seed additions and rodent exclosures at seven

study sites distributed across ≈80,000km^2 of the Great Basin. We collected cheatgrass seeds by

hand in July 2010 in Rush Valley and Skull Valley, UT, USA; and bluebunch and squirreltail

seeds were field-grown and collected by Granite Seed Co., Lehi, UT, USA. Study sites were

located near Jackpot, NV (41°55'28.70"N, 114°43'44.96"W); the O'Neil Basin, NV

(41°35'32.69"N, 114°48'36.16"W); Elko, NV (41° 3'49.40"N, 115°49'44.02"W); McGill, NV

(39°58'26.51"N, 114°40'10.10"W); Baker, NV (39° 1'6.34"N, 114°25'53.44"W); Winnemucca,

NV (40°54'47.00"N, 117°23'56.96"W); and Vernon, UT (40° 6'54.99"N, 112°32'4.37"W). All

sites were located on public land managed by the US Bureau of Land Management and in plant

communities dominated by native species (most notably big sagebrush; *Artemisia tridentata*)

with <5% cover by invasive plants. All sites were located in well-delineated drainages and were

separated by at least 35 km, which is farther than granivorous rodents and most plants can

typically disperse over short time periods (Harper et al. 1978, O'Farrell 1978, Jones 1989,

Hayssen 199, Rehmeier et al. 2004). Thus, our study sites sampled independent communities.

Experimental design

Each study site consisted of five subplots, each separated by 50m. Each subplot was

outfitted with nine sampling stations. Eight of these stations received experimental seed

additions, and one station – the control – received no seed additions. This control was used to

monitor seedling establishment from seed banks. Each station was randomly assigned to one of

nine treatments, and each treatment was used only once per subplot. For convenience, we will

hereafter refer to these treatments using the letters a-i). Although each letter corresponds to only

one treatment, we emphasize that the spatial arrangement of these treatments varied randomly

from subplot to subplot. The treatments were: a) 100 bluebunch seeds sown into a functional

rodent exclosure, b) 100 bluebunch seeds sown into a non-functional rodent exclosure, c) 100

squirreltail seeds sown into a functional rodent exclosure, d) 100 squirreltail seeds sown into a

non-functional rodent exclosure, e) 100 cheatgrass seeds sown into a functional rodent exclosure,

f) 100 cheatgrass seeds sown into a non-functional rodent exclosure, g) 50 bluebunch and 50 cheatgrass seeds sown together into a functional rodent exclosure, h) 50 squirreltail and 50 cheatgrass seeds sown together into a non-functional rodent exclosure, and i) a control that received a functional rodent exclosure but no seed additions (Fig. 1). Therefore, total seed density remained constant (100 seeds) across all stations that received seeds, but the frequency of particular focal species fluctuated between 100 seeds in stations a-f) and 50 seeds in stations g-h). Sown seeds were patted ≈5 mm into the soil. Burying seeds in this manner made them largely inaccessible to invertebrate and avian granivores because only rodents can locate buried seeds via olfaction (Kamil and Balda 1985), and invertebrates do not dig for buried seeds (MacMahon et al. 2000).

Functional exclosures prevented rodent access, and were constructed of 1 cm-mesh hardware cloth assembled into 30 cm (diameter) × 30 cm (height) cylindrical cages with a floor and a roof. Floors and roofs prevented rodents from climbing into or burrowing under the cages. To install cages, we excavated 4 cm of topsoil with a garden hoe and placed cages in the excavated pits. We secured cages into place by pounding 13 cm-long sod staples through the cage floors and into the ground with a rubber hammer. We then replaced excavated soil. Dummy exclosures were constructed and installed in a similar fashion, except for one 7 × 7 cm hole cut into the sides of cages at ground level to admit rodents.

Measuring the effects of seed predation and competition

Cages and seed additions were installed in October 2015 and were left undisturbed until August 2016, when established seedlings were counted in each cage. After counting, all seedlings were left in place for long-term monitoring. However, we removed all cheatgrass occurring < 2 m from experimental cages. We will continue monitoring for potential cheatgrass

recruits outside of cages to prevent the establishment of new cheatgrass populations. This protocol has successfully prevented cheatgrass invasion following other seed addition experiments in the Great Basin (Lucero et al. 2015).

We calculated the effects of rodent granivory on focal species by subtracting the number of seedlings established in functional exclosures from the number established in non-functional exclosures. See Table 1 for formulae. In our calculations, reductions in seedling establishment caused by granivory produced negative numbers. Our calculations of granivore effects were not confounded by seed density or frequency because stations a-f) received 100 seeds each. Based on the literature cited in the introduction, we predicted that the mean impact of rodent granivory in monocultures would be non-zero and negative (i.e., statistically significant) for native grasses but would not be different from zero (i.e., statistically insignificant) for cheatgrass.

We assessed the effects of competition reciprocated between native grasses and cheatgrass by comparing the establishment of focal species growing alone in monocultures to the establishment of focal species growing with neighbors in polycultures. We did not examine competitive interactions between bluebunch and squirreltail as these natives were not sown together. Because focal species growing in monocultures were sown at twice the rate as focal species growing in polycultures, we adjusted the number of seedlings established in polycultures using the multiplier φ (defined further below). Table 1 presents formulae for how this was done. In our calculations, competitive interactions produced negative numbers (but facilitative interactions would have produced positive numbers). Based on the literature, we predicted that cheatgrass would impose strong competitive (non-zero and negative) effects on bluebunch and squirreltail, but that bluebunch and squirreltail would reciprocate weak (not significantly different from zero) effects on cheatgrass.

74

To estimate the effects of competition, we used the multiplier φ to correct for the differential frequency of seeds sown into monocultures (stations a-f) vs. polycultures (stations g-h.) The frequency of focal plants sown into monocultures was equal to 1.0 (100 seeds from focal species $X \div 100$ seeds total), but the frequency of focal plants sown into polycultures was equal to 0.5 (50 seeds from focal species $X \div 100$ seeds total). Thus, focal species in polycultures were sown at a 50% lower rate than focal species in monocultures. In order to compare the establishment of focal species between mono- and polycultures, we adjusted the number of seedlings established in polycultures using φ. We defined φ as:

$$\varphi = \frac{1}{\rho}$$

where ρ is the expected percent reduction in seedling establishment given a 50% reduction in sowing rate. For example, a 50% reduction in sowing rate could correspond to a 50% reduction in establishment. If so, $\varphi = 2.0$ because $\frac{1}{0.5} = 2.0$. In this case, a lower sowing rate does not change the per-capita probability of establishment. This could occur if the strength of intraspecific competition among seedlings was relatively low, even at high sowing rates. Alternatively, a 50% reduction in sowing rate could correspond to only a 40% reduction in establishment. If so, $\varphi = 2.5$ because $\frac{1}{0.4} = 2.5$. In this case, a lower sowing rate improves the per-capita probability of seedling establishment. This could occur if decreased sowing rates alleviated per-capita seedling mortality from strong intraspecific competition. Finally, a 50% reduction in sowing rate could correspond to a 60% reduction in establishment. If so, $\varphi = 1.66$ because $\frac{1}{0.6} = 1.66$. Here, a lower sowing rate decreases the per-capita probability of seedling establishment. This could occur if density-mediated Allee effects affected establishment.

In summary, $\varphi = 2$ when a reduced sowing rate has no effect upon the per-capita probability of establishment, $\varphi > 2$ when a reduced sowing rate has a positive effect upon the per-capita probability of establishment, and $\varphi < 2$ when a reduced sowing rate has a negative effect upon the per-capita probability of establishment. Previous work has shown that cheatgrass, bluebunch, and squirreltail in the Great Basin are seed-limited (i.e., seed addition results in increased establishment) at sowing rates equal to the 100% sowing rate experienced by focal plants in monocultures (JE Lucero *unpublished data*). Therefore, seed limitation is also likely at the lower sowing rate experienced by focal plants in polycultures. In addition, we are aware of no evidence suggesting that the establishment of cheatgrass, bluebunch, or squirreltail experiences positive density-dependence under field conditions. Thus, we believe that the most accurate value of φ is likely to be ≥ 2.0. However, because we cannot be certain of the true value of φ, we used a range of values for φ that formed a continuum above and below 2.0 ($\varphi =$ 2.5, 2.0, 1.5). The multiplier φ was not used to calculate the impacts of rodent granivory in monocultures.

Statistical analysis

We employed three linear mixed-effects models (one each for $\varphi = 2.5$, 2.0, and 1.5) using the lme package in R (R Development Core Team 2013) to compare the effects of rodent granivory and resource competition experienced by each species (we reemphasize that the value of φ did not influence our calculations of granivore effects; see above). All models used Tukey contrasts to compare multiple means, and all models treated species as a fixed factor and study site as a random factor. Treating site as a random factor accounted for any biologically relevant differences (e.g., rodent density, *in situ* germination rates, percent plant cover, elevation, temperature, precipitation, etc.) potentially present among study sites.

76

RESULTS

Effects of seed predation and competition

Rodents significantly limited the establishment of bluebunch and squirreltail, but not

cheatgrass (Figs. 2-3). Per 707 cm^2 sampling station, bluebunch recruited 8.64 ± 1.84

individuals in the absence of granivores but only 3.28 ± 1.80 individuals in the presence of

granivores (*Z* value = -5.82, *P* < 0.001); and squirreltail recruited 6.07 ± 1.80 individuals in the

absence of granivores but only 1.46 ± 1.80 individuals in the presence of granivores (± 95 % CI)

(*Z*-value = -5.01, *P* < 0.001). Thus, rodent granivory reduced bluebunch and squirreltail

establishment by 62.01% and 71.00%, respectively. However, rodent granivory caused no

significant change in cheatgrass establishment. Cheatgrass recruited 9.21 ± 1.80 individuals in

the absence of granivores and 9.67 ± 1.80 individuals in the presence of granivores (± 95 % CI)

(*Z*-value = 0.51, *P* = 0.99). *P*-values for all pairwise comparisons of granivore effects are shown

in Supplementary Table 1.

Cheatgrass imposed strong competitive effects on both bluebunch and squirreltail, but the

competitive effects of native grasses on cheatgrass were insignificant (Figs. 2-3). Per 707 cm^2

sampling station and for $\varphi = 2.0$, cheatgrass competition reduced bluebunch establishment from

8.64 ± 1.84 to 2.35 ± 1.80 individuals (± 95 % CI) (*Z*-value = -6.83, *P* < 0.001); and cheatgrass

competition reduced squirreltail establishment from 6.07 ± 1.80 to 2.03 ± 1.82 individuals (± 95

% CI) (*Z*-value = -4.34, *P* < 0.001). Thus, for $\varphi = 2.0$, cheatgrass competition reduced

bluebunch and squirreltail establishment by 72.80% and 66.56%, respectively. Conversely,

neither native species imposed a significant competitive effect on cheatgrass. For $\varphi = 2.0$,

competition from bluebunch "reduced" cheatgrass establishment from 9.21 ± 1.80 to 9.17 ± 1.80

individuals (± 95 % CI) (*Z*-value = -0.04, *P* = 1.00), and competition from squirreltail "reduced"

cheatgrass establishment from 9.21 ± 1.80 to 9.11 ± 1.82 individuals (± 95 % CI) (*Z*-value = -0.11, *P* = 1.00). *P*-values for all pairwise comparisons of competitive effects are shown in Supplementary Table 1.

Altering the value of φ ($\varphi = 1.5$, $\varphi = 2.0$, $\varphi = 2.5$) slightly affected the magnitude of competitive effects, but did not change whether these effects differed significantly from zero (Table 2) or from each other (Supp. Table 1). Thus, moderate (± 25%) changes of the value of φ did not qualitatively affect our results.

Seed bank dynamics

The effects of seed predation and resource competition were not determined by recruitment from seed banks. No species recruited significantly from the seed bank (Fig. 4). On average, cheatgrass, bluebunch, and squirreltail recruited 0.08 ± 0.12, 0.04 ± 0.08, and 0.11 ± 0.12 individuals per control cage, respectively (± 95% CI), and seed bank recruitment was not different than zero for any species. These means did not significantly differ from each other (*P* > 0.25 for all pairwise comparisons).

DISCUSSION

Our most interesting result was that rodent granivory limited the establishment of native grasses to the same extent as resource competition from cheatgrass (Figs. 2-3). This suggests that these biotic filters presented equally important (*sensu* Welden and Slauson 1986, Brooker et al. 2005, Kikvidze et al. 2011) barriers to the local establishment of bluebunch and squirreltail at the temporal and spatial scale of our experiment. Many studies have shown that cheatgrass is a strong competitor against native species (Melgoza and Nowak 1991, Humphrey and Schupp

2004, Vasquez et al. 2008, Parkinson et al. 2013), and others have documented the potential for rodent granivory to limit native establishment (Orrock et al. 2009, Pearson et al. 2011, Maron et al. 2012), but to our knowledge, this is the first study to show that these filters can be equally important.

This main result has practical implications. The conservation and restoration of native species in wildlands infested by invasive plants is a high priority for many land managers (e.g., Rowe 2010). One common practice for increasing the abundance of native plants and expanding native communities is restoration seeding, in which seeds of desirable natives are sown into degraded habitats (Whisenant 1999). One of the most expensive steps in restoration seeding is procuring seeds (Frischie and Rowe 2012). Accordingly, land managers try to maximize the establishment of seeded species. However, granivory (Orrock et al. 2009) and competition from invaders (Davies 2010) can hamper these efforts, which may undermine the effectiveness of restoration seeding. Land managers can ameliorate the effects of granivory by increasing seeding density (Orrock et al. 2009) or by treating target seeds with chemicals like capsaicin that reduce palatability (Hemsath 2007). Competition from invaders can be moderated by mowing, burning, tilling, or applying herbicides before seeding (Fritschie and Rowe 2010). Although these practices may be costly (especially increasing seeding density), our results (Figs. 2-3) suggest that land managers in the Great Basin may need to place equal emphasis on mitigating the effects of rodent granivory and cheatgrass competition in order to maximize the establishment of native bunchgrasses during restoration.

Our finding that rodent granivory limited the establishment of native grasses but not cheatgrass corresponds with a number of recent studies. Reports from Mediterranean (Orrock et al. 2008), coastal (Dangremond et al. 2010), intermountain, (Pearson et al. 2011) and Palouse

79

grasslands (Connolly et al. 2014) demonstrate that native rodents can limit the establishment of native species to a greater extent than strong invaders. However, very few studies have evaluated the long-term, demographic consequences of this pattern (but see Dangremond et al. 2010). Thus, it remains generally unclear whether selective granivory for native species actually influences the trajectory of plant invasions.

Several studies have shown that native rodents in the Great Basin selectively forage for native seeds over cheatgrass seeds (Kelrick et al. 1986, Ostoja et al. 2013, Lucero et al. 2015), but the reasons why remain unclear. Kelrick and MacMahon (1985) showed that cheatgrass seeds are lower in soluble carbohydrates than seeds from similarly sized natives, indicating poor nutritional quality. Other studies have invoked the mechanical structure of cheatgrass seeds, positing that persistent awns may increase handling time (Kelrick et al. 1986, Ceradini and Chalfoun 2017). Furthermore, native rodents in the Great Basin may be underequipped to exploit cheatgrass seeds if they contain phytochemicals that are biogeographically novel (i.e. "novel weapons"; Callaway and Aschehoug 2000, Cappucino and Carpenter 2005). These alternatives are not mutually exclusive and remain mostly unexplored (but see Kelrick and MacMahon 1985).

Importantly, cheatgrass in the Great Basin does not always escape the negative effects of rodent granivory. Recently, St. Clair et al. (2016) showed that rodents inhibited the establishment of cheatgrass in the wake of small-scale disturbances from fire, resulting in meaningful biotic resistance (we found no evidence for such biotic resistance here; Figs. 2-3). What can explain the divergent results reported by St. Clair et al. (2016) vs. those presented here (Figs. 2-3)? We suggest that rodent impacts on cheatgrass establishment may depend on the relative availability of more-preferred seeds from native species. As mentioned, rodents in the

80

Great Basin generally prefer seeds from native plants to seeds from cheatgrass (Kelrick et al. 1986, Ostoja et al. 2013, Lucero et al. 2015). However, selective consumers become less choosy when preferred resources are scarce (Pulliam 1974). For example, Krebs et al. (1977) showed that great tits (*Parus major*) increased consumption of inferior prey as the frequency of preferred prey decreased. Similarly, native rodents in the Great Basin may suppress less-preferred cheatgrass only when more-preferred native species are locally rare. The disturbance treatments imposed by St. Clair et al. (2016) virtually eliminated native species from study plots, potentially leaving local rodents with few foraging alternatives to cheatgrass. In contrast, we conducted our experiments in habitats dominated by native species where preferred resources from natives may have been relatively abundant. Hence, the divergent outcomes reported in our study (Figs. 2-3) vs. that of St. Clair et al. (2016) could result from large differences in the local availability of more-preferred seeds from native species. Accordingly, we recognize that our experiments may have produced different results had they been conducted at a time and/or place in which native seeds were extremely limited (e.g., during an exceptionally dry year or near a large-scale disturbance).

In polycultures, cheatgrass imposed significant competitive impacts on native grasses that were not reciprocated. This result coincides with many experimental accounts. Competition experiments often reveal strong negative effects of invaders on the growth, reproduction, and resource allocation of natives (reviewed by Levine et al. 2003), but natives rarely reciprocate such strong effects on invaders. This competitive asymmetry is well-documented with respect to cheatgrass vs. native plants in the Great Basin (Melgoza and Nowak 1991, Vasquez et al. 2008, Parkinson et al. 2013), especially at the seed/seedling stage (Humphrey and Schupp 2004). In

general, the competitive superiority of invasive plants relative to natives is probably the most widely invoked explanation for the local extirpation of natives by invaders (Levine et al. 2003).

Our calculations of the effects of competition were robust to moderate ($\pm$ 25%) perturbations of the value of φ. Altering the value of φ did not change whether or not the magnitude of competitive interactions differed significantly from zero (Table 2) or from each other (Supp. Table 1). In other words, if a competitive effect was significant (non-zero) when φ = 2, it remained significant when φ = 1.5 and φ = 2.5. Similarly, if competitive effects significantly differed from each other when φ = 2, they remained different when φ = 1.5 and φ = 2.5 (Supp. Table 1).

Associational effects could dampen the strong impacts of rodent granivory and cheatgrass competition reported here. Associational effects arise when consumer effects on focal plants depend upon the presence or identity of neighboring plants (see reviews by Barbosa et al. 2009, Underwood et al. 2014). For example, proximity to palatable neighbors may increase predation risk for focal plants (e.g., White and Whitham 2000, Palmer et al. 2003, Rand 2003, Orrock et al. 2015), resulting in "associational susceptibility." Alternatively, proximity to unpalatable neighbors might decrease predation risk for focal plants (e.g., Atsatt and O'Dowd 1976, Callaway et al. 2005, Baraza et al. 2006, Atwater et al. 2011, Axelsson and Stenberg 2014), resulting in "associational resistance." Because seeds from cheatgrass, bluebunch, and squirreltail are all vulnerable to rodent granivory, rodents could potentially mediate associational effects among these grasses at the seed stage (Ostoja et al. 2013). A recent meta-analysis has shown that when mammalian herbivores (like rodents) mediate associational effects between differentially palatable plants (like cheatgrass, bluebunch, and squirreltail), palatable plants often experience associational resistance (a positive [+] effect), but unpalatable plants experience no

significant associational effects (a neutral [0] effect) (Fig. 3b in Barbosa et al. 2009). If this general trend applies to interactions in this system, proximity to unpalatable cheatgrass should result in associational resistance for both bluebunch and squirreltail, but these natives should reciprocate no associational effects upon cheatgrass. The resulting indirect commensalism [+/0] (Dethier and Duggins 1984, Menge 1995) could at least partially counteract the negative impacts of granivory and resource competition experienced by bluebunch and squirreltail in the absence of associational effects (Figs. 2-3).

There are several important caveats to consider for our experiments. For one, our calculations of competitive effects are estimates and not direct measures because of the parameterization of φ. However, our use of φ accounted for the differential frequency of focal plants sown into experimental treatments in a novel and relatively simple way, and our results coincide well with the literature. Also, our calculations of competitive effects only considered the impacts of moderate ($\pm 25\%$) perturbations of the value of φ. Although moderate perturbations did not qualitatively affect our results (Table 2, Supp. Table 1), more dramatic perturbations might. In addition, we do not know how the effects of resource competition and rodent granivory interact because we employed no experimental treatments in which competition and granivory could affect seedling establishment simultaneously. Finally, we showed that rodent granivory and cheatgrass competition were equally important barriers to the establishment of native grasses, but we acknowledge that there are many other abiotic and biotic processes that could be just as or more important. For example, drought (Brown et al. 1979), disturbance (Stylinski and Allen 1999), and pathogens (Beckstead et al. 2010) can all limit the establishment, growth, and fitness of each species we tested. Evaluating the relative importance of any biotic or abiotic filter (Diamond 1975, Weiher and Keddy 1999) can be challenging because it requires

simultaneous, coordinated experiments, but such studies can lend valuable insight into the

processes that drive community-level patterns (Welden and Slauson 1986, Brooker et al. 2005,

Kikvidze et al. 2011).

REFERENCES

Aschehoug ET, Callaway RM. 2015. Diversity increases indirect interactions, attenuates the
        intensity of competition, and promotes coexistence. The American Naturalist 186: 452-
        459.

Aschehoug ET, Brooker R, Atwater DZ, Maron JL, Callaway RM. 2016. The mechanisms and
        consequences of interspecific competition among plants. The Annual Review of
        Ecology, Evolution, and Systematics 47:263-281.

Atsatt PR, O'Dowd DJ. 1976. Plant defense guilds. Science 193: 24-29.

Atwater DZ, Bauer CM, Callaway RM. 2011. Indirect positive effects ameliorate strong
        negative effects of *Euphorbia esula* on a native plant. Plant Ecology 212: 1655-1662.

Axelsson EP, Stenberg JA. 2014. Associational resistance mediates interacting effects of

herbivores and competitors on fireweed performance. Basic and Applied Ecology 15:
10-17.

Balch JK, Bradley BA, D'Antonio C, Gomez-Dans J. 2013. Introduced annual grass increases
regional fire activity across the arid western USA (1980-2009). Global Change Biology
19: 173-183.

Baraza E, Zamora R, Hodar JA. 2006. Conditional outcomes in plant-herbivore interactions:
neighbours matter. Oikos 113: 148-56.

Barbosa P, Hines J, Kaplan I, Martinson H, Szczepaniec A, Szendrei Z. 2009. Associational
resistance and associational susceptibility: Having right or wrong neighbors. Annual
Reviews in Ecology and Systematics 40: 1-20.

Beckstead J, Meyer SE, Connolly BM, Huck MB, Street LE. 2010. Cheatgrass facilitates
spillover of a seed bank pathogen onto native grass species. Journal of Ecology 98: 168-
177.

Brooker R, Kikvidze Z, Pugnaire FI, Callaway RM, Choler P, Lortie CJ, Michalet R. 2005. The
importance of importance. Oikos 109: 63-70.

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

Brown JH, Reichman OJ, Davidson DW. 1979. Granivory in desert ecosystems. The Annual
Review of Ecology and Systematics 10: 201-227.

Callaway, R.M. and E.T. Aschehoug. 2000. Invasive plants versus their new and old neighbors:
a mechanism for exotic invasion. Science 290:521-523.

Callaway RM, DeLucia EH, Moore D, Nowak R, Schlesinger WH. 1996. Competition and

facilitation: Contrasting effects of *Artemisia tridentata* on desert vs. montane pines. Ecology 77: 2130-2141.

Callaway RM, Kikodze D, Chiboshvilli M, Khetsuriani L. 2005. Unpalatable plants protect neighbors from grazing and increase plant community diversity. Ecology 86: 1856-1862.

Cappuccino N, Carpenter D. 2005. Invasive exotic plants suffer less herbivory than non-invasive exotic plants. Biology Letters 1: 435-438.

Ceradini JP, Chalfoun AD. 2017. Species traits help predict small mammal responses to habitat homogenization by an invasive grass. Ecological Applications 0:1-15.

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

Dangremond EM, Pardini EA, Knight TM. 2010. Apparent competition with an invasive plant hastens the extinction of an endangered lupine. Ecology 91: 2261-2271.

Davies KW. 2010. Revegetation of medusahead-invaded sagebrush steppe. Rangeland Ecology and Management 63: 564-571.

Dethier MN, Duggins DO. 1984. An "indirect commensalism" between marine herbivores and the importance of competitive hierarchies. The American Naturalist 124: 205-219.

Diamond JM. 1975. Assembly of species communities. Pages 342–444 in M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Harvard University Press, Cambridge, Massachusetts, USA.

Duncan CA, Jachetta JJ, Brown ML, Carrithers VF, Clark JK, DiTomaso JM, Lym RG, McDaniel KC, Renz MJ, Rice P. 2004. Assessing the economic, environmental, and societal losses from invasive plants on rangeland and wildlands. Weed Technology 18: 1411-1416.

Freeman ED, Sharp T, Larsen RT, Knoght RN, Slater SJ, McMillan BR. 2014. Negative effects of an exotic grass invasion on small-mammal communities. PLoS ONE 9: e108843.

Frischie SL, Rowe HL. 2012. Replicating life cycle of early-maturing species in the timing of restoration seeding improves establishment and community diversity. Restoration Ecology 20: 188-193.

Gurevitch J. 1986. Competition and the local distribution of the grass *Stipa neomexicana*. Ecology 67: 46-57.

Hall LK. 2012. Effect of cheatgrass on abundance of the North American deermouse (*Peromyscus maniculatus*). The Southwestern Naturalist 57: 166-169.

Harper KT, Freeman DC, Ostler WK, Klikoff LG. 1978. The flora of Great Basin mountain ranges: diversity, sources, and dispersal ecology. The Great Basin Naturalist Memoirs 2: 81-103.

Hayssen V. 1991. *Dipodomys microps*. Mammalian Species 389: 1-9.

Hemsath CM. 2007. Quantifying granivory in a reconstructed prairie: effects of season, species, seed predators, sacrificial food, and the chemical deterrent capsaicin. Electronic Theses and Dissertations 142.

Howe HF, Brown JS. 2000. Early consequences of rodent granivory on synthetic dicot communities. Ecological Applications 10: 917-924.

Humphrey LD, Schupp EW. 2004. Seed banks of *Bromus tectorum*-dominated communities in the Great Basin. Western North American Naturalist. 61: 85-92.

Inouye RS, Byers GS, Brown JH. 1980. Effects of predation and competition on survivorship, fecundity, and community structure of desert annuals. Ecology 61: 1344-1351.

Jones WT. 1989. Dispersal distance and the range of nightly movement in Merriam's kangaroo

rats. Journal of Mammalogy 70: 27-34.

Kamil AC, Balda RP. 1985. Cache recovery and spatial memory in Clark's nutcracker (*Nucifraga colombiana*). Journal of Experimental Psychology: Animal Behavior Processes 11: 95-111.

Keddy PA, Shipley B. 1989. Competitive hierarchies in herbaceous plant communities. Oikos 54: 234-241.

Kelrick MI, MacMahon JA. 1985. Nutritional and physical attributes of seeds of some common sage-steppe plants: Some implications for ecological theory and management. Journal of Range Management 38: 65-69.

Kelrick MI, MacMahon JA, Parmenter RR, Sisson DV. 1986. Native seed preferences of shrub-steppe rodents, birds and ants: the relationships of seed attributes and seed use. Oecologia 68: 327-337.

Kikvidze Z, Suzuki M, Brooker R. 2011. Importance versus intensity of ecological effects: why context matters. Trends in Ecology and Evolution 26: 383-388.

Knapp PA. 1996. Cheatgrass (*Bromus tectorum L*) dominance in the Great Basin Desert: history, persistence, and influences to human activities. Global Environmental Change 6: 37-52.

Krebs JR, Erichsen JT, Webber MI, Charnov EL. 1977. Optimal prey selection in the great tit (*Parus major*). Animal Behaviour 25: 30-38.

Levine JM, Vila M, D'Antonio CM, Dukes JS, Grigulis K, Lavorel S. Mechanisms underlying the impacts of exotic plant invasions. Proceedings of the Royal Society of London B 270: 775-781.

Liao C, Peng R, Luo Y, Zhou X, Wu X, Fang C, Chen J, Li B. 2008. Altered ecosystem carbon

and nitrogen cycles by plant invasion: a meta-analysis. New Phytologist 177: 706-714.

Louda SM. 1982. Distribution ecology: variation in plant recruitment over a gradient in relation to insect seed predation. Ecological Monographs 52: 25-41.

Louda SM, Povtin MA, Collinge SK. Predispersal seed predation, postdispersal seed predation and competition in the recruitment of seedlings of a native thistle in sandhills prairie. American Midland Naturalist 124: 105-113.

Lucero JE, Allen PS, McMillan BR. 2015. Increased primary production from an exotic invader does not subsidize native rodents. PLoS ONE 10: e 0131564.

Mack RN. 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. Agro-Ecosystems 7:145-165.

MacMahon JA, Mull JF, Crist TO. 2000. Harvester ants (*Pogonomyrmex* spp.): their community and ecosystem influences. Annual Review of Ecology and Systematics: 31 265-291.

Maron JL, Crone E. 2006. Herbivory: effects on plant abundance, distribution and population growth. Proceedings of the Royal Society B 273: 2575-2584.

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

Melgoza G, Nowak RS. 1981. Competition between cheatgrass and two native species after fire: Implications from observations and measurements of root distribution. Journal of Range Management 44: 27-33.

Menge BA. 1995. Indirect effects in marine rocky intertidal interaction webs: Patterns and importance. Ecological Monographs 65: 21-74.

O'Farrell MJ. 1978. Home range dynamics of rodents in a sagebrush community. Journal of
Mammalogy 59: 657-668.

Orrock JL, Witter MS, Reichman OJ. 2008. Apparent competition with an exotic plant reduces
native plant establishment. Ecology 89: 1168–1174.

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.

Orrock JL, Dutra HO, Marquis RJ, Barber N. 2015. Apparent competition and native
consumers exacerbate the strong competitive effect of an exotic plant species. Ecology
96: 1052-1061.

Ostoja SM, Schupp EW. 2009. Conversion of sagebrush shrublands to exotic annual grasslands
negatively impacts small mammal communities. Diversity and Distributions 15: 863-
870.

Ostoja SM, Schupp EW, Durham S, Klinger R. 2013. Seed harvesting is influenced by
associational effects in mixed seed neighbourhoods, not just by seed density. Functional
Ecology 27: 775-785.

Palmer SCF, Hester AJ, Elston DA, Gordon IJ, Hartley SE. 2003. The perils of having tasty
neighbors: grazing impacts of large herbivores at vegetation boundaries. Ecology 84:
2877-2890.

Parkinson H, Zabinski C, Shaw N. 2013. Impact of native grasses and cheatgrass (*Bromus
tectorum*) on Great Basin forb and seedling growth. Rangeland Ecology and
Management 66: 174-180.

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, Ortega YK, Ozkan E, Hierro JL. 2015. Quantifying "apparent" impact and
distinguishing impact from invasiveness in multispecies plant invasions. Ecological
Applications 26: 162-173.

Pennings SC, Callaway RM. 1992. Salt marsh plant zonation: the relative importance of
competition and physical factors. Ecology 73: 681-690.

R Development Core Team. 2013. R: a language and environment for statistical computing. R
Foundation for Statistical Computing, Vienna, Austria.

Rand TA. 2003. Herbivore-mediated apparent competition between two salt marsh forbs.
Ecology 84: 1517-1526.

Rehmeier RL, Kaufman GA, Kaufman DW. 2004. Long distance movements of the deer mouse
in tallgrass prairie. Journal of Mammalogy 85: 562-568.

Shipley B, Keddy PA. 1994. Evaluating the evidence for competitive hierarchies in plant
communities. Oikos 69: 340-345.

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

Underwood N, Inouye BD, Hamback PA. 2014. A conceptual framework for associational
effects: when do neighbors matter and how would we know? The Quarterly Review of
Biology 89: 1-19.

Vasquez E, Sheley R, Svejcar T. 2008. Nitrogen enhances the competitive ability of cheatgrass

(*Bromus tectorum*) relative to native grasses. Invasive Plant Science and Management 1: 287-295.

Vellend M. 2010. Conceptual synthesis in community ecology. The Quarterly Review of Biology 85: 183-206.

Vila M, Espinar JL, Hejda M, Hulme PE, Jarosik V, Maron JL, Pergl J, Schaffner U, Sun Y, Pysek P. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecology Letters 14: 702-708.

Weiher E, Keddy, PA. 1999. Assembly rules as general constraints on community composition. Pages 251-271 in E. Weiher and P. Keddy, editors. Ecological assembly rules: perspectives, advances, retreats. Cambridge University Press, Cambridge, UK.

Welden CW, Slauson WL. 1986. The intensity of competition versus its importance: an overlooked distinction and some implications. The Quarterly Review of Biology 61: 23-44.

Whisenant SG. 1999. Repairing damaged wildlands: a process-oriented, landscape-scale approach. Cambridge University Press, Cambridge, UK.

White JA, Whitham TG. 2000. Associational susceptibility of cottonwood to a box elder herbivore. Ecology 81: 1795-1803.

TABLES

Table 1. Description of calculations for the effects of rodent granivory ("P") and plant-plant competition ("C") on the net establishment of cheatgrass ("ch"), bluebunch wheatgrass ("bb"), and bottlebrush squirreltail ("sq") in the Great Basin Desert, USA. Abbreviations in the "Biotic interaction" column are also used in Table 2, Figs. 2-3, and in Supp. Table 1. Letters a-i) in the "Formula for quantification" column correspond to the sampling stations depicted in Fig. 1. The multiplier φ was used to correct for the differential frequency of focal plants sown into stations a-f) vs. stations g-h) (see Methods).

Biotic interaction	Description of biotic interaction	Formula for quantification (see Fig. 1)
P $_{(ch)}$	Effect of predation on ch when ch occurs alone	$(f - e)$
P $_{(bb)}$	Effect of predation on bb when bb occurs alone	$(b - a)$
P $_{(sq)}$	Effect of predation on sq when sq occurs alone	$(d - c)$
C $_{(ch \to bb)}$	Competitive effect of ch on bb	$(\varphi \cdot g_{bb} - a)$
C $_{(bb \to ch)}$	Competitive effect of bb on ch	$(\varphi \cdot g_{ch} - e)$
C $_{(ch \to sq)}$	Competitive effect of ch on sq	$(\varphi \cdot h_{sq} - c)$
C $_{(sq \to ch)}$	Competitive effect of sq on ch	$(\varphi \cdot h_{ch} - e)$

Table 2. Mean effects (± 95% CI) of resource competition ("C") on the establishment of cheatgrass ("ch"), bluebunch wheatgrass ("bb"), and bottlebrush squirreltail ("sq") in the Great Basin Desert, USA, given φ = 1.5, 2.0, and 2.5 (see Methods for definition of φ). Abbreviations used in the "Competitive interaction" column are defined in Table 1. Effects with $P \leq 0.05$ are shown in bold.

Competitive interaction	Mean impact of biotic interaction		
	φ = 1.5	φ = 2	φ = 2.5
C $_{(ch \rightarrow bb)}$	**-6.92 (2.52)**	**-6.29 (1.82)**	**-5.65 (2.32)**
C $_{(bb \rightarrow ch)}$	-0.37 (0.67)	-0.04 (1.80)	0.31 (0.82)
C $_{(ch \rightarrow sq)}$	**-4.67 (2.09)**	**-4.03 (1.82)**	**-3.61 (2.15)**
C $_{(sq \rightarrow ch)}$	-0.48 (0.78)	-0.10 (1.82)	0.13 (0.98)

LIST OF FIGURES

Fig. 1. Experimental design used to assess the relative importance of rodent granivory vs. resource competition as barriers to the establishment of cheatgrass ("ch"), bluebunch wheatgrass ("bb"), and bottlebrush squirreltail ("sq") in the Great Basin Desert. Stations a-i) collectively comprised one subplot, five subplots comprised a study site, and we employed seven study sites (n=7). The spatial arrangement of stations a-i) varied randomly from subplot to subplot. Solid circles represent functional exclosures that excluded rodents, and dashed circles represent "dummy" exclosures that admitted rodents. Numbers within circles show the number of seeds sown from each species. Station i) was a control that received no seed additions and was used to monitor establishment from seed banks (see Fig. 4).

Fig. 2. Mean effects (±95% CI) of rodent granivory ("P") and resource competition ("C") on the establishment of cheatgrass ("ch"), bluebunch wheatgrass ("bb") and bottlebrush squirreltail ("sq") in the Great Basin Desert, given $\varphi = 2.0$ (φ defined in Methods). The effect of a biotic interaction is defined as the difference in the number of seedlings established in the interaction's presence vs. absence (see Methods). Abbreviations for biotic interactions are defined in Table 1. Moderate (± 25%) perturbations to the value of φ did not change whether these effects differed significantly from zero (Table 2), or from each other (Supp. Table 1).

Fig. 3. Interaction webs that show the effects of biotic interactions between a) granivorous rodents ("P"), bluebunch wheatgrass ("bb"), and cheatgrass ("ch"); and b) granivorous rodents, bottlebrush squirreltail ("sq"), and cheatgrass on the establishment of seedlings in the Great Basin Desert, for $\varphi = 2.0$ (φ defined in Methods). Arrows indicate the direction of biotic interactions and are labelled with the interaction's mean effect (± 95% CI) on seedling establishment. Abbreviations for biotic interactions are defined in Table 1. Interactions with

95

effects that differed significantly from zero appear in black, and interactions with effects that did not differ significantly from zero appear in grey. Moderate ($\pm$ 25%) perturbations to the value of φ did not change whether the effects of biotic interactions differed significantly from zero (Table 2) or from each other (Supp. Table 1).

Fig. 4. Mean establishment of cheatgrass ("ch"), bluebunch wheatgrass ("bb"), and bottlebrush squirreltail ("sq") from seed banks ($\pm$ 95% CI).

Fig. 1

a — 100 bb

c — 100 sq

e — 100 ch

g — 50 bb / 50 ch

i — Control

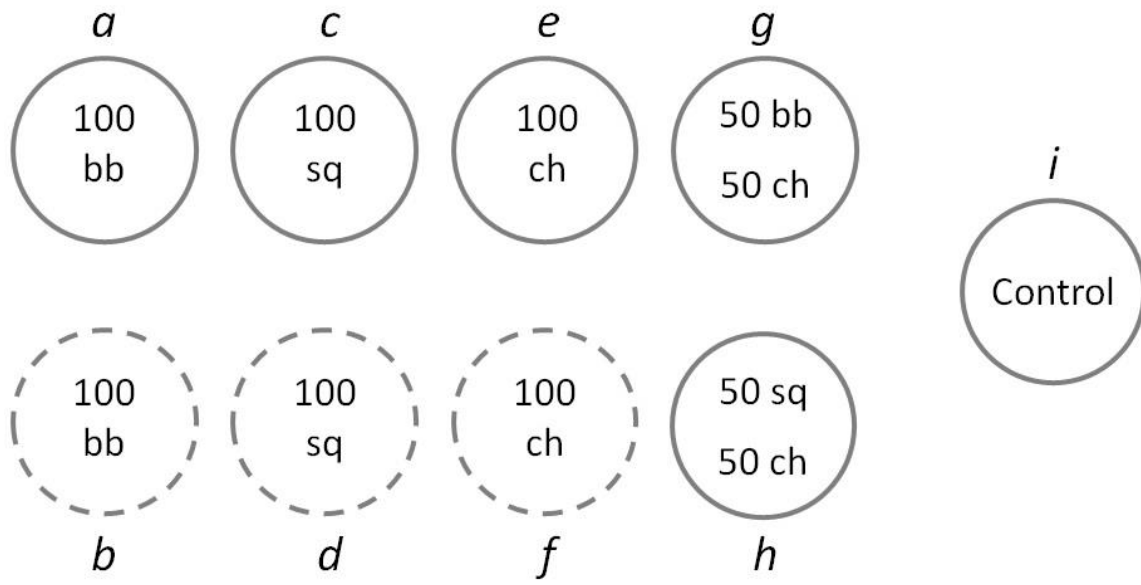*b* — 100 bb

d — 100 sq
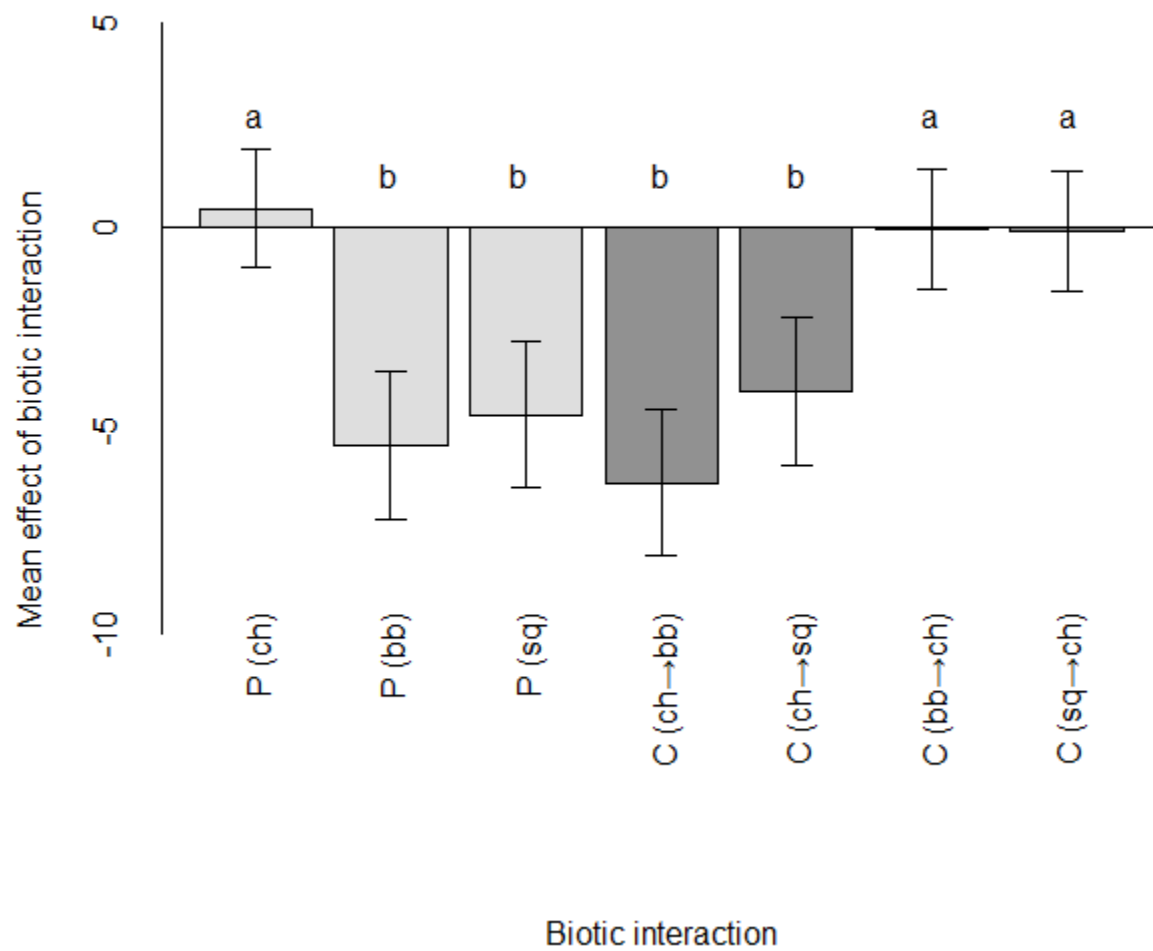
f — 100 ch

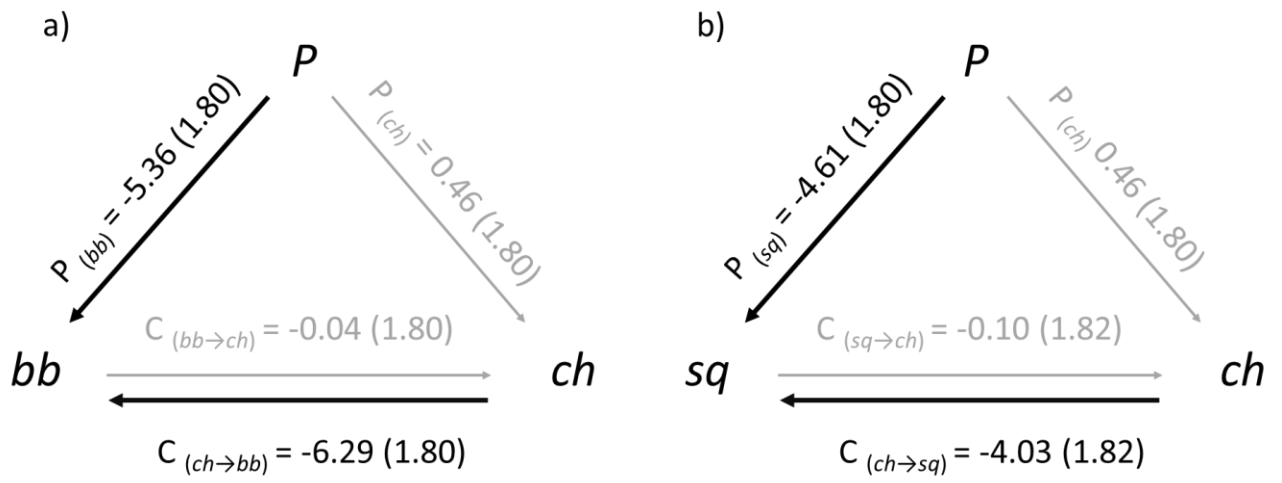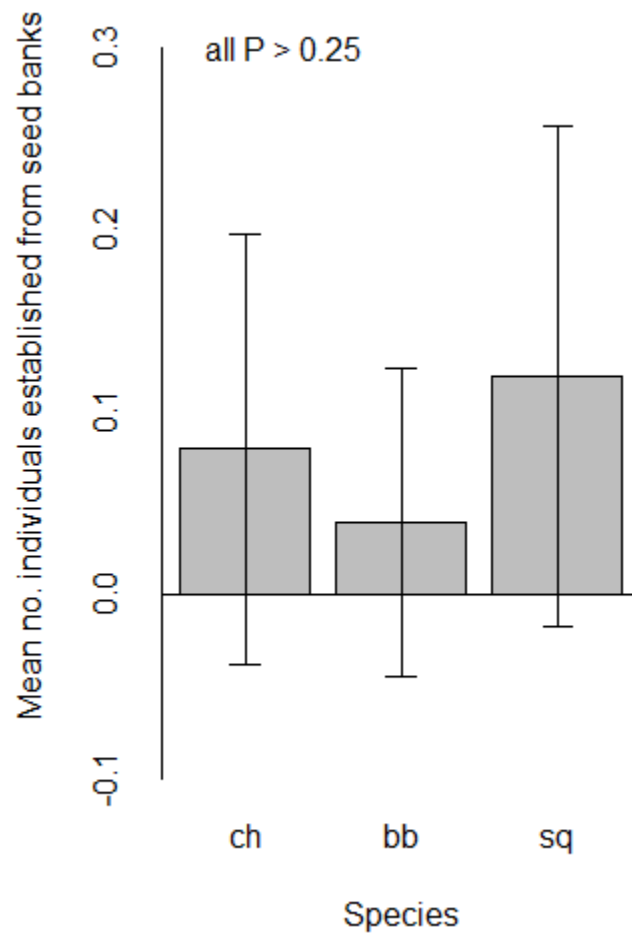*h* — 50 sq / 50 ch

Fig. 2

Fig. 3.

Fig. 4

SUPPLEMENTARY MATERIALS

Supp. Table 1. *P*- values for pairwise comparisons of the effects of rodent granivory ("P") and competition ("C") on the establishment of cheatgrass ("ch"), bluebunch wheatgrass ("bb"), and bottlebrush squirreltail ("sq") in the Great Basin Desert, given $\varphi = 1.5$, 2.0, and 2.5 (see Methods for definition of φ). Table 1 defines abbreviations in the "Pairwise comparison" column. *P*-values were obtained with linear mixed-effects models that treated species as a fixed factor and study site as a random factor. *P*-values ≤ 0.05 are shown in bold.

Pairwise comparison	$\varphi = 1.5$	$\varphi = 2$	$\varphi = 2.5$
C (ch→bb) - C (bb→ch)	**<0.01**	**<0.01**	**<0.01**
C (ch→sq) - C (bb→ch)	**<0.01**	**<0.01**	**<0.01**
C (ch→sq) - C (ch→bb)	0.35	0.43	0.52
C (sq→ch) - C (bb→ch)	1.00	1.00	1.00
C (sq→ch) - C (ch→bb)	**<0.01**	**<0.01**	**<0.01**
C (sq→ch) - C (ch→sq)	**<0.01**	**<0.01**	**<0.01**
P (bb) - C (bb→ch)	**<0.01**	**<0.01**	**<0.01**
P (bb) - C (ch→bb)	0.77	0.98	1.00
P (bb) - C (ch→sq)	1.00	0.92	0.70
P (bb) - C (sq→ch)	**<0.01**	**<0.01**	**<0.01**
P (ch) - C (bb→ch)	0.99	1.00	1.00
P (ch) - C (ch→bb)	**<0.01**	**<0.01**	**<0.01**
P (ch) - C (ch→sq)	**<0.01**	**<0.01**	**<0.01**
P (ch) - C (sq→ch)	0.98	1.00	1.00
P (ch) - P (bb)	**<0.01**	**<0.01**	**<0.01**
P (sq) - C (bb→ch)	**<0.01**	**<0.01**	**<0.01**
P (sq) - C (ch→bb)	0.32	0.71	0.96
P (sq) - C (ch→sq)	1.00	1.00	0.97
P (sq) - C (sq→ch)	**<0.01**	**<0.01**	**<0.01**
P (sq) - P (bb)	0.99	0.99	0.99
P (sq) - P (ch)	**<0.01**	**<0.01**	**<0.01**