

Biotic resistance and disturbance: rodent consumers regulate post-fire plant invasions and increase plant community diversity

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Abstract. Biotic resistance and disturbance are fundamental processes influencing plant invasion outcomes; however, the role of consumers in regulating the establishment and spread of plant invaders and how disturbance modifies biotic resistance by consumers is unclear. We document that fire in combination with experimental exclusion of rodent consumers shifted a native desert shrubland to a low-diversity, invasive annual grassland dominated by *Bromus tectorum* (cheatgrass). In contrast, burned plots with rodents present suppressed invasion by cheatgrass and developed into a more diverse forb community. Rodents created strong biotic resistance to the establishment of aggressive plant invaders likely through seed and seedling predation, which had cascading effects on plant competition and plant community diversity. Fire mediated its positive effects on plant invaders through native plant removal and by decreasing the abundance and diversity of the rodent community. The experimental disruption of plant and consumer-mediated biotic resistance of plant invaders using fire and rodent exclusion treatments provides strong evidence that native plants and rodents are important regulators of plant invasion dynamics and plant biodiversity in our study system. While rodents conferred strong resistance to invasion in our study system, fluctuations in rodent populations due to disturbance and climatic events may provide windows of opportunity for exotic plant species to escape biotic resistance by rodent consumers and initiate invasions.

Key words: *Bromus tectorum*; cheatgrass; competition; deserts; fire; Great Basin; halogeton; small mammals.

INTRODUCTION

Rapid global expansion of plant invaders and ecological disturbance due to human activities are among the most significant ecological and societal challenges of the 21st century. Introductions of exotic species into new environments have highly variable outcomes ranging from establishment failure to continental-scale invasions that can have dire economic and ecological consequences (Vila et al. 2010). The establishment and proliferation of exotic species in an ecosystem is largely determined by the interplay between traits of species and conditions in the introduced environment (Williamson and Fitter 1996b, Sol et al. 2012). Exotic species establishment and expansion rates vary between ecosystems, and across space and time, suggesting that a complex set of biotic and abiotic filters are involved. Principal among these factors are resource availability in the introduced environment (resource hypothesis) (Davis et al. 2000) and biological regulation by enemies (biotic resistance hypothesis) (Elton 1958, Levine et al. 2004). The niche-opportunity hypothesis

posits that spatio-temporal fluctuations in resource availability and enemies (e.g., plant competitors and consumers) provide niche opportunities to invaders that create windows of opportunity for exotic species to establish and spread (Shea and Chesson 2002, Allington et al. 2013). This fluctuation-based conceptual model, although largely untested, provides a theoretical framework for understanding and predicting how rapid environmental changes (e.g., wildfire and climate change) and shifts in plant and animal populations may regulate plant invasions under future global change.

Animal consumers can elicit both positive (Orrock et al. 2008, Kalisz et al. 2014) and negative effects (Maron and Vila 2001, Parker and Hay 2005, Pearson et al. 2012) on the establishment of exotic plant species. The majority of research on biotic resistance to plant invasions has focused on plant competition and pathogen-mediated resistance (Levine et al. 2004). Recent seed addition experiments in terrestrial ecosystems demonstrate that top-down regulation by small mammal and ant consumers can suppress the establishment success of exotic plant species (Pearson et al. 2011, 2014a,b, Maron et al. 2012, Connolly et al. 2014) and create population-level biotic resistance against weak plant invaders (Pearson et al. 2012, Allington et al. 2013). However,

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consumer-mediated regulation of the population dynamics and spread of aggressive plant invaders that are ecologically problematic are largely uninvestigated. Although there is emerging evidence that consumers influence invasion outcomes, we know much less about the environmental factors that strengthen consumer-mediated biotic resistance or cause it to break down. In particular, biotic resistance by consumers has not been adequately explored in the context of changing disturbance regimes, particularly fire that is linked to invasion success.

Human activities are rapidly altering earth's disturbance regimes, including global expansion in the size and frequency of wildfires (Bowman et al. 2009). Disturbance often precedes successful plant invasions by releasing exotic species from biotic resistance of native plants and by increasing niche space and plant resource availability (Freeman et al. 2007, Theoharides and Dukes 2007). Fire has been shown to indirectly modify the assembly of native plant communities by shifting the composition or behavior of consumer communities (Zwolak et al. 2010, Horn et al. 2012, Wan et al. 2014), but how fire interacts with consumers to influence plant invasion outcomes and how it modifies competitive interactions between plants is poorly understood.

Competition can be an important driver of state and transition change from native to exotic dominated plant communities (Daehler 2003, Vila and Weiner 2004). However, far fewer studies have examined competition and successional relationships between exotic plant species particularly in the context of disturbance and trophic interactions. Increasingly, community ecology is being studied within a functional trait framework that identifies traits that shape community interactions and confer competitive advantages that underlie patterns of invasion (Drenovsky et al. 2012, Kempel et al. 2013).

Here we report the results of a large field experiment established in a native, semi-arid shrubland to investigate changes in native and invasive plant cover, density and biomass, and plant community diversity in response to factorial combinations of disturbance (fire) and reductions in rodent abundance (experimental and natural). The following questions were addressed: (1) What influence do rodent consumers have in regulating the establishment and proliferation of invasive plant species? (2) How does disturbance modify consumer effects on plant invasions? (3) Do rodent consumer effects on plant invaders have cascading effects on plant competition and plant community diversity?

MATERIALS AND METHODS

Study location and species

The study was conducted in Rush Valley in central Utah, USA (40°05'26.17"N 112°18'18.01"W, elevation: 1650 m). The long-term mean average temperature for Rush Valley is 8.6°C with strong seasonal variation.

Average mean January temperatures are -3.2°C and average mean July temperatures are 22.3°C (Vernon GHCN:COOP, Utah Climate Center). Precipitation is evenly distributed throughout the year with long-term average precipitation being 257 mm/year. Soil at the study site is classified as a silty, mixed mesic Haplic Natrargid, Taylors Flat Loam. The study location at the time the experiment was initiated (2011) had little evidence of grazing and showed no evidence of fire in the last several decades based on a well-developed soil crusts and a climax shrub community.

The most common rodent species at the study site were *Peromyscus maniculatus*, *Dipodomys microps*, and *Perognathus parvus*. Only two native plant species were found in our plots at the beginning of the experiment, *Artemisia tridentata* subsp. *wyomingensis* (Wyoming sagebrush) and *Elymus elymoides*, a common perennial bunch grass. North America is host to several aggressive plant invaders including *Bromus tectorum* an annual invasive grass, and *Halogeton glomeratus* an aggressive annual forb both of which established in our plots. Other exotic annual forbs that established in our study plots were *Ceratocephala testiculata*, *Allysium allysoides*, *Descurainia pinnata* and *Lepidium perfoliatum*. While most of the plant species evaluated in this study were present at the study site when the experiment started, their densities were $<1 \text{ plant m}^{-2}$. Starting the experiment with exotic plant species in an early establishment phase provided an opportunity to characterize ecological drivers and temporal dynamics of plant invasions.

Experimental design

The study was a full factorial design in five replicated blocks that tested the main and interactive effects of fire and rodent exclusion on native and invasive plant establishment and diversity over a 4-yr period. We randomly assigned all four treatments combinations within each of five experimental blocks that were evenly spread over a 7 ha area. A wire fence was established around the perimeter of the experiment to exclude livestock but there was ample space at the bottom of the fence to allow free access to all native mammals and reptiles. Rodent fences were established using 1.0 m tall welded wire fencing in a 60 m² grid with four 30 m² quadrants in June 2011. The fencing was buried 30 cm below the soil surface and it extended 70 cm aboveground. Two of the 30 m² plots within each block were randomly assigned as rodent exclusion plots that had 20 cm of smooth metal flashing installed on the top of the fence to prevent rodents from climbing over the top of the fences. The other two quadrants were control plots that lacked metal flashing at the fence top and had 12 × 10 cm openings every 4 m in the wire fencing to permit free movement of rodents in and out of the plots.

The burn treatments were conducted September 20, 2011. In each of the five experimental blocks, we randomly selected and independently burned one rodent exclusion

plot and one rodent control plot to create the fire \times rodent exclusion full factorial design. The fires were initiated with drip torches and burn severity was high with >99 percent plant mortality, which is typical of the burn characteristics of mature sagebrush communities in late summer. Because our objective was to track invasion dynamics starting from an early invasion state, there was no fine plant fuel to carry fire through the shrub interspaces. To facilitate the spread of fire between shrubs, we placed 300 g m⁻² of wheat straw in our burn plots according to the methods of (Esque et al. 2010), which is within the range of fine fuel biomass in sagebrush interspaces in Great Basin landscapes invaded by *B. tectorum* (Hulbert 1955). Surveys conducted in *B. tectorum* dominated communities 3 km from our study site, showed an average *B. tectorum* biomass of 462 \pm 20 g m⁻². To test the levels of N inputs from the straw applied to the burn plots, we collected recently senesced *B. tectorum* samples (from the survey mentioned previously) at three separate locations and compared it to three pooled samples of the wheat straw. Samples were analyzed for total N using the combustion method (Campbell 1991). Nitrogen inputs from burned wheat straw were 2.1 \pm 0.12 g m⁻², which was not statistically different from N inputs that would come from burning senesced *B. tectorum* 1.9 \pm 0.12 g m⁻² (*P* value 0.19).

Plant surveys

All experimental plots were surveyed annually (2012–2015) for plant species cover, density and biomass along four parallel transect lines, 26 m in length, spaced >5 m apart with more than a 2 m buffer from the plot boundaries to avoid edge effects. Daubenmire frames (50 \times 25 cm quadrat) were placed at 2 m increment points along each transect line to assess plant density of all species, except *B. tectorum*, where we used tiller counts. Sampling of plants occurred within Daubenmire frames at 4 m increment points along the transect lines. All plants rooted within the frame were harvested at ground level and sorted by species. Plant samples were placed in bags and dried at 60°C for 72 h in drying ovens and weighed on a scale to determine aboveground biomass. Species cover was estimated at each half-meter increment point along each transect line, using the pin drop method (Helm and Mead 2004). Plant community surveys were conducted in early June when vegetation reached peak biomass and just before plants dropped their seeds. *Halogeton glomeratus* was resurveyed in September when it reached peak biomass and just before it released its seeds in the fall. Species abundance, richness, and Shannon diversity index were calculated using the Biodiversity package in R (Kindt and Coe 2005).

Rodent surveys

Rodent surveys were conducted in spring, summer and fall each year using eight Sherman live traps per plot (7.6 \times 8.9 \times 33.0 cm) with bird seed as bait. During each

sampling period, rodents were trapped for three consecutive nights. At first capture, all rodents were identified to species, and general live-trap data (e.g., age, sex, mass to the nearest 0.5 g, and reproductive condition) was recorded. Each new individual was marked with a uniquely numbered ear tag so that we could accurately identify individuals during subsequent sampling periods. The Brigham Young University Animal Care and Use Committee approved the small mammal survey protocols (IACUC#120202).

In decreasing order of abundance, the following rodent species were captured: *Peromyscus maniculatus*, *Dipodomys microps*, *Perognathus parvus*, *Tamias minimus*, *Lemmys curtatus*, and *Onychomys leucogaster*. Rodent abundance was calculated as the minimum number of individuals of each species recorded for each time period (McKelvey and Pearson 2001). Rodent abundance, species richness, and Shannon diversity index were calculated using the Biodiversity package in R (Kindt and Coe 2005).

Statistical analyses

Data exploration was conducted according to the methods of (Zuur et al. 2010) to test that model assumptions were met. Linear mixed models (LMER package in R) were used to test the main and interactive effects of fire and rodent exclusion on the density and cover of each plant species and the whole plant community in 2015. Linear mixed models were also used to test the main and interactive effects of fire, small exclusion and year on biomass and density of *B. tectorum*, *H. glomeratus*, and the plant community. The main effects of fire and year on rodent abundance, richness, and diversity were calculated only from data collected in the rodent control plots. The main and interactive effects of fire and rodent exclusion on plant cover data from 2015 were analyzed using a Logit-transformed linear mixed model (Warton and Hui 2011). Fire, rodent exclusion and year were designated as fixed effects in the linear mixed models and block was included as a random effect. Regression analysis was used to examine the relationships of *B. tectorum* density on the establishment of the other plant species and plant community diversity. To meet equal variance assumptions plant and rodent data were log transformed when appropriate. Statistical analysis was performed using R software (version 3.2.2 R Core Team, Vienna, Austria).

RESULTS

Plant community characteristics

The outcome of fire and rodent exclusion treatments after 4 yr was a strong shift in plant community composition and structure that is visually evident from aerial photographs of the experimental plots (Fig. 1). Unburned plots remained as native perennial shrublands with low exotic plant cover regardless of rodent treatment. Burned, rodent



FIG. 1. Aerial photos of our Rush Valley experiment showing the effects of fire and rodent exclusion on vegetation. Top photo: the burned plots that are darker brown are rodent exclusion plots containing high densities of *B. tectorum*, while the burned plots that are light tan are rodent control plots containing low density of annual forbs. Bottom photo: a more detailed photo of block 2 (lower, right block in upper photo) showing extensive establishment of invasive annuals in the burned, rodent exclusion plot (foreground) producing a distinct green-up due to *B. tectorum* that is absent in the burned, rodent control plot (back of photo), and in the shrub interspaces in the unburned plots on the right and left.

exclusion plots converted to a low-diversity, high-density invasive annual grassland and burned, rodent control plots developed into a more diverse annual forb community.

Total plant cover was significantly greater in burned-rodent exclusion plots (72%) than burned-rodent control plots (47%) or unburned plots (37%) (Table 1). Unburned plots were dominated by native plant cover (31%) with only 5.6% exotic plant cover (Table 1). In contrast, burned plots were dominated by exotic plant cover (67% in burned-rodent excluded plots; 42% in burned-rodent control plots) with very low native plant cover ($\leq 5.2\%$) consisting entirely of *E. elymoides* (Table 1). Invasive plant cover was dominated by *B. tectorum*, and *H. glomeratus*, with the three other exotic species (*C. testiculata*, *A. allysoides*, *L. perfoliatum*) combined contributing $<15\%$ of the total exotic plant cover (Table 1). With the exception of the post-fire loss of the native shrub *A. tridentata*, native vegetation cover showed limited sensitivity to fire and rodent treatments (Table 1). In contrast, exotic species cover responded positively to fire (Table 1). Rodent exclusion dramatically increased *B. tectorum* cover particularly with fire. The cover of the other exotic species was reduced in response to rodent exclusion (Table 1).

Fire and rodent treatments had strong but divergent effects on plant species density. All five exotic species increased in density in burned plots, while fire reduced the density of the native *E. elymoides* (Fig. 2). *Elymus*

elymoides and *D. pinnata* densities were not responsive to rodent treatments. *Bromus tectorum* and *A. allysoides* densities increased exponentially under the combination of fire and rodent exclusion, while *H. glomeratus* and *C. testiculata* densities increased synergistically in burned, rodent control plots (see significant Fire \times Rodent interaction terms) (Fig. 2). Plant species diversity was significantly higher in rodent control plots regardless of burn treatment (Table 1).

Plant invasion dynamics 2012–2015

Changes in vegetation cover, density and biomass over time were overwhelmingly driven by *B. tectorum* and *H. glomeratus*, as evidenced by how closely total plant density and biomass match the time course patterns of those two species (Fig. 3). Density and biomass of *B. tectorum* and *H. glomeratus* remained relatively low in unburned plots over the course of the study but increased rapidly across years in burned plots with patterns of invasion being strongly influenced by rodent effects (Fig. 3C–F). Through 2012, the establishment of all exotic species in our experimental plots was very low (<1 plant m^{-2}). From 2013 to 2015, fire and exclusion of rodents dramatically increased the tiller density and biomass of *B. tectorum* (Fig. 3C). By 2015, the average tiller density (1268 m^{-2}) and biomass (182 g m^{-2}) of

TABLE 1. 2015 plant cover and species diversity data for native and exotic species.

Treatment	df	Native species cover			Exotic species cover				Total cover	Species diversity Shannon's index
		Artr	Elel	Native cover	Brte	Hagl	Other exotic spp.	Invasive cover		
Unburned-present		28 ± 3.0 ^a	3.2 ± 1.3 ^a	31 ± 2.9 ^a	3.8 ± 5.2 ^a	0.9 ± 1.1 ^a	0.8 ± 1.0 ^a	5.6 ± 4.0 ^b	37 ± 3.9 ^a	0.82 ± 0.16 ^a
Unburned-excluded	25 ± 3.0 ^a	4.8 ± 1.3 ^a	31 ± 2.9 ^a	4.9 ± 5.2 ^a	0.3 ± 1.1 ^a	0.2 ± 1.0 ^{ab}	5.6 ± 4.0 ^b	37 ± 3.9 ^a	0.55 ± 0.16 ^{ab}	
Burned-present		0.0 ± 3.0 ^b	4.5 ± 1.3 ^a	4.5 ± 2.9 ^b	23 ± 5.2 ^b	13 ± 1.1 ^b	5.6 ± 1.0 ^c	42 ± 4.0 ^a	47 ± 3.9 ^b	0.78 ± 0.16 ^a
Burned-excluded		0.0 ± 3.0 ^b	5.2 ± 1.3 ^a	5.2 ± 2.9 ^b	63 ± 5.2 ^c	1.9 ± 1.1 ^a	2.4 ± 1.0 ^{bc}	67 ± 4.0 ^a	72 ± 3.9 ^c	0.22 ± 0.16 ^b
Fire	1,12	3274***	1.7	107***	54***	5.8*	16*	155***	20***	1.6
Rodents	1,12	0.06	0.09	0.2	14*	7.7*	3.9	9.8*	6.3*	8.2*
F × R	1,12	0.06	0.01	0.3	13*	0.8	0.03	9.7*	7.2*	1.0

Notes: Means ± SE presented. Statistically significant differences between pairwise comparisons of the four treatment combinations at the 0.05 level are denoted by superscript letters. F-statistics are presented in the bottom three rows to test the main effects and interaction of fire and rodent exclusion treatments. Asterisks indicate level of significance for *P*-values: **P* ≤ 0.05, ***P* ≤ 0.01, ****P* ≤ 0.001. *Artemisia tridentata* (Artr), *E. elymoides* (Elel), *B. tectorum* (Brte), *H. glomeratus* (Hagl).

B. tectorum in burned, rodent exclusion plots was significantly greater than in burned, rodent control plots (by 5.7- and 3.7-fold), unburned, rodent exclusion plots (by 10- and 7.4-fold) and unburned, rodent control plots (by 15- and 24-fold) (Fig. 3C,D). These patterns of *B. tectorum* establishment and growth resulted in strongly significant main effects, and two and three-way interactions of fire, rodent exclusion and year in the statistical models (Appendix S1).

From 2013 to 2015, unburned plots maintained relatively low density and biomass of *H. glomeratus*. In contrast, rodent effects in burned plots created strong fluctuations in *H. glomeratus* density and biomass from 2013 to 2015 (Fig. 3). From 2012 to 2013, *H. glomeratus* density and biomass increased more than 50-fold in burned, rodent exclusion plots and then declined to <15% of their 2013 peak values by 2015 (Fig. 3). *Halogeton glomeratus* density and biomass in burned, rodent control plots remained relatively low through 2013 and then increased more than 100- and 10-fold in 2014 before dropping 60% and 80% in 2015 (Fig. 3). For *H. glomeratus*, the main effects and their two- and three-way interactions were all statistically significant for both biomass and density with the exception of the main effect of rodent exclusion and the fire by rodent interaction term (Appendix S1).

Rodent community responses

Abundance of rodents was 50% lower in burned plots compared to unburned plots across all 4 yr ($F_{1,108} = 50$, $P < 0.0001$). Species richness and diversity were reduced by 38% and 41% in burn plots relative to unburned plots across the 4-yr period ($F_{1,108} = 28$, $P < 0.0001$, $F_{1,108} = 10$, $P = 0.002$) (Fig. 4A).

There were strong fluctuations in rodent abundance over time, with relatively high abundance from June 2011 to October 2012 and a strong peak in April 2012 followed by a precipitous drop that was maintained through April 2014. Rodent abundance began to increase again in the summer of 2014 and maintained relatively high levels through the summer of 2015 (Fig. 4B). These shifts over time resulted in a highly significant time effect ($F_{13,52} = 7.2$, $P < 0.001$).

Evidence for plant competition

We observed strong inverse relationships of *B. tectorum* density with plant community diversity ($R^2 = 0.90$, $P < 0.0001$) (Fig. 5), *H. glomeratus* density ($R^2 = 0.58$, $P < 0.0001$) and *C. testiculata* density ($R^2 = 0.49$, $P < 0.0001$). *B. tectorum* density showed weak negative relationships with *D. pinnata* ($R^2 = 0.06$, $P = 0.06$) and *L. perfoliatum* ($R^2 = 0.10$, $P = 0.13$). *Elymus elymoides* demonstrated no significant relationships with *B. tectorum* density, while *A. alyssoides* was positive correlated with *B. tectorum* density ($R^2 = 0.34$, $P < 0.0001$).

A comparison of *H. glomeratus* seedling density in early summer compared to its late summer establishment density provides insight into the potential role of competition in its response to treatment conditions. *Halogeton glomeratus* seedling density (m^{-2}) in burned plots was extremely high in June 2014 and not statistically different between rodent control plots (641 ± 161 and rodent exclusion plots (621 ± 161) ($F = 0.08$, $P = 0.94$). By September, *H. glomeratus* density in burned, rodent control plots had decreased nearly 5-fold but the reduction was more than 20-fold in burned, rodent exclusion plots.

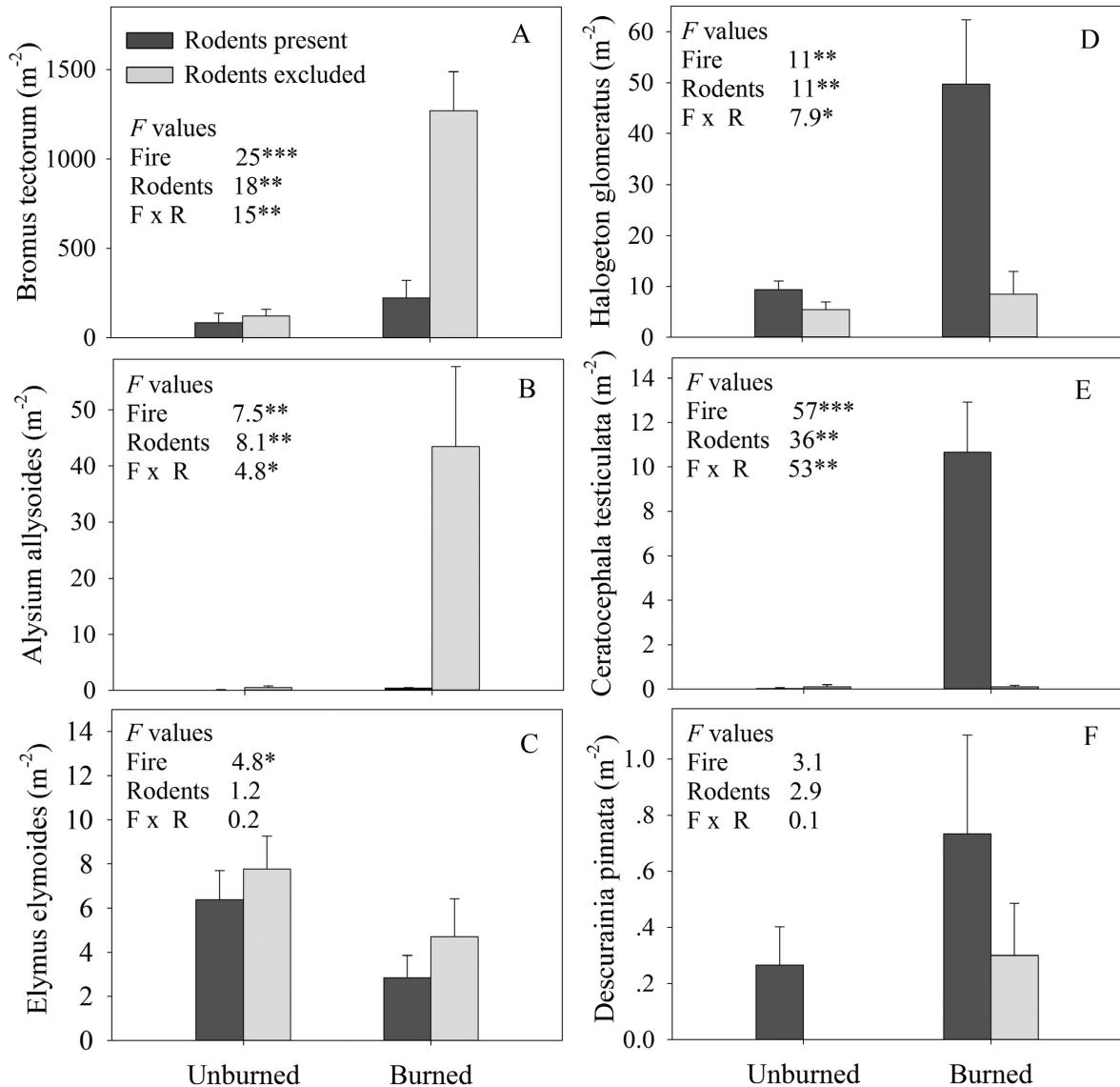


FIG. 2. The main and interactive effects of fire and rodent exclusion on plant species density in 2015. *B. tectorum* densities are tiller densities while all other species are plant densities. *F*-values presented with asterisks indicating level of significance for *P*-values: * $P \leq 0.05$, ** $P \leq 0.001$, *** $P \leq 0.0001$. Mean values presented with ± 1 SE.

DISCUSSION

This study documents that disturbance (fire) in combination with removal of biotic resistance by rodent consumers led to a transformation of the system that produced an annual grass invasion. Although exotic plant introductions are widespread across terrestrial ecosystems, only a small portion of these species successfully establish and become aggressive invaders that devastate ecosystems (Williamson and Fitter 1996a). *Bromus tectorum* is among the most aggressive and ecologically damaging plant invaders on earth (Novak and Mack 2001). Using a community framework that links disturbance and trophic regulation over time, our data provide new insights into the interplay between

environment and biotic interactions in the genesis and proliferation of plant invasions. Specifically: (1) rodent consumers increased plant community diversity and created biotic resistance to the establishment of three plant invaders; (2) fire and rodent exclusion were both required to produce plot-scale invasions of *B. tectorum*; (3) fire appears to facilitate plant invasion indirectly by reducing rodent abundance and diversity; (4) density of *B. tectorum* was inversely related to plant community diversity likely driven by competition; and (5) invasion rates for exotic plants were extremely high, increasing from <1 plant m^{-2} in 2012 to more than 600 plants m^{-2} for *H. glomeratus* in burned plots in June 2014 and more than 1200 *B. tectorum* tillers m^{-2} in burned, rodent

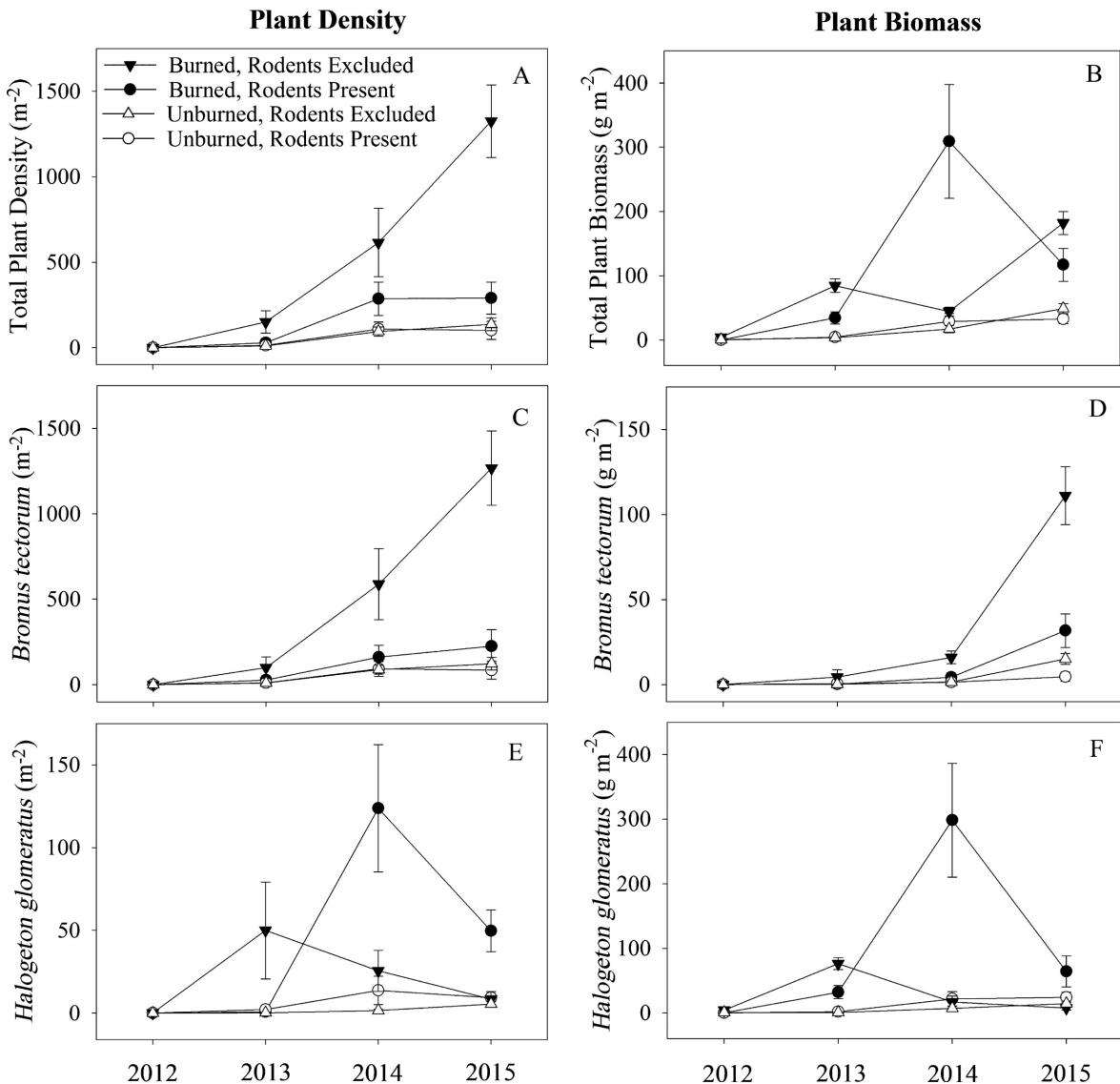


FIG. 3. Time course trends (2012–2015) of density and biomass of *B. tectorum*, *H. glomeratus* and the whole plant community in response to fire and rodent treatments. Mean values presented with ± 1 SE.

exclusion plots by 2015 (Fig. 3). This explosive population growth potential has contributed to the rapid spread of *B. tectorum* around the world and *H. glomeratus* across parts of western North America since their introductions in the late 19th and early 20th century (Williams 1980, Novak and Mack 2001).

Rodent effects

Previous studies have shown rodent suppression of the establishment of weak plant invaders (Inouye et al. 1980, Pearson et al. 2012) and rodent effects on seed fate and establishment of exotics in seeding experiments (Maron et al. 2012, Connolly et al. 2014). This is the first study we are aware that experimentally links the reduction of rodent

consumers with the establishment and proliferation of populations of aggressive invaders. Effects of rodent on plant invaders in our study were strong enough to completely shift the composition and structure of the plant community (Table 1, Figs. 1–3). Plant diversity was significantly greater in the presence of rodents (Table 1). This appears to be an indirect effect due to biotic resistance of *B. tectorum* by rodents (Fig. 3C,D) releasing the other plant species from competitive exclusion by *B. tectorum* (Fig. 5). Top-down control of native plant community assembly by rodents has previously been observed in deserts (Brown and Heske 1990), and our data demonstrate that these effects extend to plant invasions.

There are multiple mechanisms by which rodents may exert top-down control on plant communities. Rodents

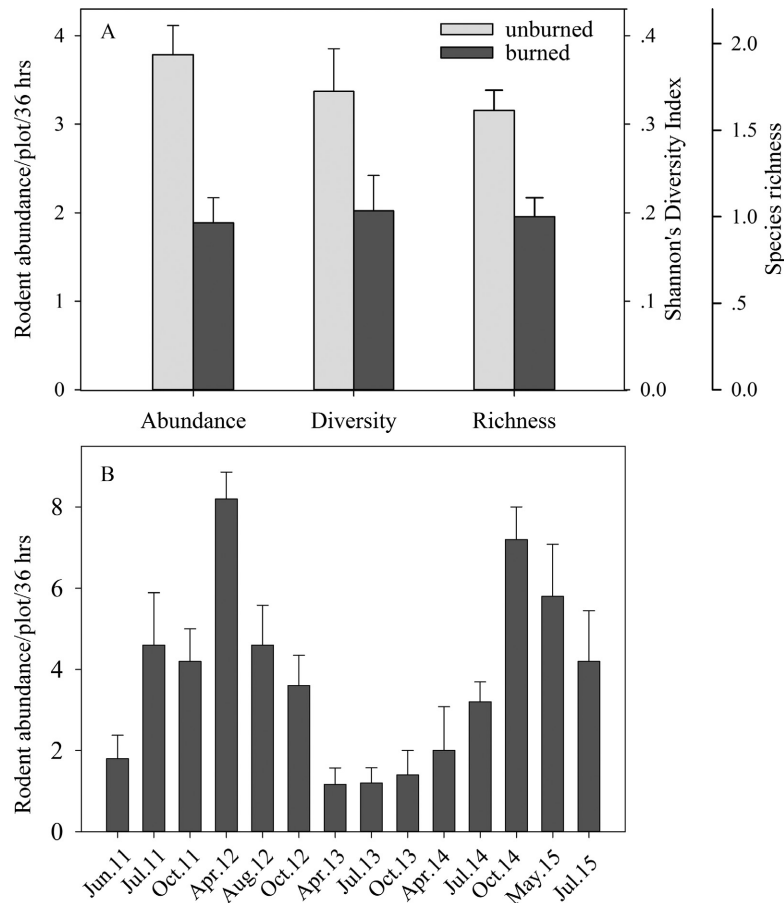


FIG. 4. (A) The effects of fire on the abundance, species richness and diversity of the rodent community in rodent control plots averaged across all survey periods from 2011 to 2015. Fire effects on abundance, diversity and richness were all strongly significant $P < 0.0001$; (B) Fluctuations in rodent abundance during the spring, summer and fall periods from June 2011 to July 2015 in rodent control plots. Mean values presented with ± 1 SE.

have been shown to consume *B. tectorum* seedlings in controlled experiments (Pyke 1986). Seed addition experiments demonstrated that rodents can reduce exotic plant establishment through seed predation (Maron et al. 2012, Connolly et al. 2014). Species comparison studies suggest that rodents can have differential preference for native and exotic seeds (Maron et al. 2012, Connolly et al. 2014). Rodents had relatively low preference for *B. tectorum* and *H. glomeratus* seed in two studies (Becker and Balph 1976, Kelrick et al. 1986). However, a recent study showed that *B. tectorum* seeds dominated the cheek pouch contents of the Great Basin Pocket Mouse in three habitat types across 48 study sites in the northern Great Basin (Richardson et al. 2013). Studies in the Great Basin and Mojave Deserts have also demonstrated that invasive brome grasses can be important food sources for rodents (Beatley 1969). Rodents created high seedling mortality rates and had strong preference for *B. tectorum* seed in our experimental plots (Bowman 2015), suggesting that seedling herbivory and seed predation were the primary mechanisms by which rodents created biotic resistance to the aggressive plant invaders in our study.

Rodent populations fluctuate strongly across space and time including periods in which they crash (Brown and Heske 1990, Hoset et al. 2014). Rodent abundance in this study was high between 2011–2012 and 2014–2015 with a noticeable crash in 2013 (Fig. 4B). The reduction in rodent population in 2013 was a regional phenomenon (also observed in the Mojave Desert) and may have been a lag response to the 2012 drought. These periods of reduction in rodent populations may function very similarly to our rodent exclusion treatments in creating windows of opportunity for exotic plants to establish and proliferate with relaxed top-down controls by consumers (Allington et al. 2013). There is evidence for this in June 2014 where we observed over 600 *H. glomeratus* seedlings m^{-2} in both burned, rodent exclusion plots and burned, rodent control plots in contrast to the previous year where there was strong suppression of *H. glomeratus* by rodents (Fig 3E,F). This suggests that the low native abundance of rodents from April 2013 to April 2014 was not sufficient to control *H. glomeratus* establishment in the rodent control plots. Interestingly, with the recovery of rodent abundance in 2014–2015, there was a sharp

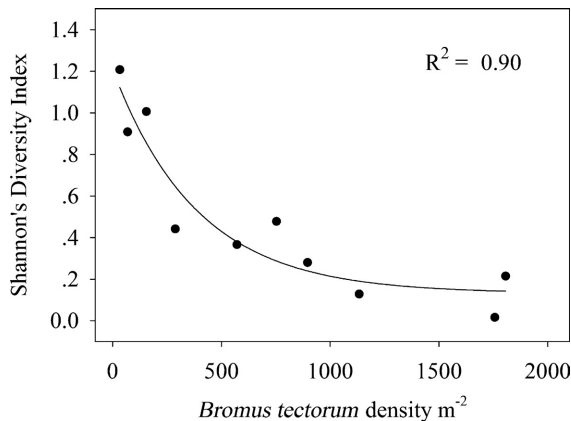


FIG. 5. Relationship between *B. tectorum* density and plant community diversity in burned plots in the summer of 2015. The significance of the relationship is $P < 0.0001$.

decline in *H. glomeratus* density and biomass in 2015 (Fig. 3E,F).

In addition to environmental reductions of rodent population, plant invaders may have traits that reinforce their invasion success by reducing rodent abundance or activity. *Halogeton glomeratus* and *C. testiculata* have been shown to have poisonous effects on livestock (Nachman and Olsen 1983, James 1999) raising the question of their potential toxicity effects on rodents. Also, rodent abundance and richness decrease with high *B. tectorum* cover (Ostoja et al. 2013, Freeman et al. 2014), suggesting that increasing *B. tectorum* cover could have positive feedbacks on its own invasion success by antagonizing top-down controls by rodents through habitat modification.

Direct and indirect effects of fire

Disturbance often facilitates exotic plant establishment, and fire in particular has been linked to large-scale plant invasions (Mack et al. 2000). The low exotic plant densities early in the study and then the rapid transformation of the system following fire (Figs. 2 and 3) suggests that exotics plants and their propagules were already present and the system was resisting invasion due to biotic resistance created by the native shrub community, intact soil crusts and rodent consumers. The experimental disruption of plant and consumer biotic resistance with fire and rodent exclusion followed by the dramatic proliferation of exotic species provides strong evidence that native plants and rodents are key regulators of plant invasion dynamics in our study system. The positive effects of fire on exotic species establishment in this study (Fig. 2) and its neutral to negative effects on the native species (*A. tridentata*, *E. elymoides*) indicate that exotic species were more opportunistic in their post-fire establishment. Fire likely promoted exotic plant establishment through competitive release from the native shrub community, soil disturbance and increased soil N availability (Allen et al. 2011).

Although it is clear that fire can have direct positive effects on plant invaders through removal of native plant species, our data for the first time suggest that fire may also indirectly facilitate plant invasions by relaxing consumer-mediated biotic resistance via reductions in rodent abundance, richness and diversity (Fig. 4A). The antagonistic effects of fire on rodents in this study are consistent with other studies demonstrating losses of mice abundance in post-fire desert environments (Horn et al. 2012). Quadrupedal rodent species (e.g., *Peromyscus* sp., *Perognathus* sp.) prefer foraging under and near shrubs (Ostoja and Schupp 2009, Horn et al. 2012) suggesting that the negative effects of fire on rodent abundance and diversity observed in our study are most likely mediated by reductions in shrub cover (Horn et al. 2012, Freeman et al. 2014). This suggests that post-fire recovery of shrub cover may be necessary to reassemble and restore the function of the rodent community in burned landscapes. High exotic grass cover in post-disturbance landscapes does not compensate for loss of native shrub cover and instead contributes to the loss of abundance and diversity of the rodent community (Ostoja and Schupp 2009, Freeman et al. 2014). Finally, wildfire characteristics are highly variable. Additional research is needed to identify how wildfire extent, severity and frequency affects rodent communities and their capacity to confer biotic resistance to plant invaders in post-fire landscapes.

Competition and functional traits

Successful plant invaders are able to outcompete other plant species for available space and resources. Many studies have shown that successful invaders are more competitive for resources than the native plants they displace (Daehler 2003, Vila and Weiner 2004). Far fewer studies have explored competition and succession dynamics between invading exotic plant species. In this study, there was evidence of coexistence of *B. tectorum* and *H. glomeratus* during the first 2 yr of the study based on rapid population growth of both species (Fig. 3). However, by 2014 exponential increases in their population numbers resulted in both species reaching densities near 600 plants m^{-2} in burned, rodent exclusion plots creating a much more competitive environment. Comparing our June and September 2014 plant survey data, there was high *H. glomeratus* seedling mortality over the summer of 2014 in burned plots that was 15-fold greater in rodent exclusion plots (with high *B. tectorum* densities) than rodent control plots. This seasonal mortality pattern and dramatic decreases of *H. glomeratus* density in burned, rodent exclusion plots from 2013 to 2015 as *B. tectorum* density was rapidly increasing (Fig. 3C,E) suggest competitive exclusion of *H. glomeratus* by *B. tectorum*. The strong inverse relationship between *B. tectorum* with plant biodiversity (Fig. 5) and

densities of *H. glomeratus* and *C. testiculata* further support the interpretation of competitive exclusion of other species by *B. tectorum*.

Although all of the exotic species surveyed in this study are annual plants, their differential success appears to be driven by contrasting life history strategies. As winter annuals, *B. tectorum* and *A. alyssoides* often germinate in the fall, allowing them to develop vegetatively during periods of more optimal soil moisture. As they mature at the end of spring, they reach maximum water usage just as *H. glomeratus* and *C. testiculata*, both summer annuals, are beginning their early, water-sensitive seedling growth stage. This is consistent with a study showing low survival of native plant species growing in competition with *B. tectorum* due to poor water relations (Melgoza et al. 1990). *Alyssum Alyssoides*' positive correlation with *B. tectorum* density may be due to similar sensitivities to rodent pressure and its parallel development with *B. tectorum* as a winter annual allowing coexistence due to higher soil moisture availability during the winter-spring growth period. The strong regulation of *B. tectorum* by rodents (Fig. 3C) and its subsequent competitive effects on the rest of the plant community (Fig. 5) suggest that consumer-mediated biotic resistance can have cascading effects on competitive interactions among plants and plant community diversity.

Implications for plant invasion-fire regimes and interactions with climate change

Annual invasive grasses including *B. tectorum* possess a suite of functional traits that facilitate reproduction and growth in post-fire environment that is linked to greater fire frequency (Brooks et al. 2004, Horn et al. 2015). This positive feedback loop can lead to invasive grass-fire regimes that reinforce state and transition changes with significant ecological and economic consequences (D'Antonio and Vitousek 1992). It has been estimated that fire return intervals in the Great Basin that occurred on multi-century time scales in native shrublands can now have a periodicity of a decade or less due to *B. tectorum* invasion (Balch et al. 2013, Bukowski and Baker 2013).

Plant invasions are strongly regulated by a complex interplay between abiotic environmental conditions and bottom-up and top-down feedbacks within biological communities (Levine et al. 2004). Currently, we have a good understanding of the direct effects of climate and disturbance on plant invasions and an emerging understanding of the role of biological interactions in controlling or releasing plant invaders. Within our study system, consumer-mediated biotic resistance appears to be a key control point that integrates climate variability, disturbance, and plant-plant interactions in determining plant community assembly and invasion dynamics. Although rodents suppressed invasion in our study system, fluctuations in rodent populations due to reproduction cycles, disturbance, and extreme climatic events

may provide windows of opportunity for plant invaders to escape consumer-mediated biotic resistance and initiate the invasion process. Consistent with the niche-opportunity hypothesis (Shea and Chesson 2002), our data suggest that invasive grass-fire regimes will be reinforced with reductions in rodents linked to environmental perturbations (wildfire, extreme climate events) that are forecasted to be more frequent with future climate change and human activity.

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LITERATURE CITED

- Allen, E. B., R. J. Steers, and S. J. Dickens. 2011. Impacts of fire and invasive species on desert soil ecology. *Rangeland Ecology and Management* 64:450–462.
- Allington, G. R. H., D. N. Koons, S. K. M. Ernest, M. R. Schutzenhofer, and T. J. Valone. 2013. Niche opportunities and invasion dynamics in a desert annual community. *Ecology Letters* 16:158–166.
- 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.
- Beatley, J. C. 1969. Dependence of desert rodents on winter annuals and precipitation. *Ecology* 50:721–724.
- Becker, E., and D. Balph 1976. Plant food preferences of two sympatric rodents and their potential impact on a Great Basin shrub community In: US/IBP Desert Biome Research Memorandum 76-21: Reports of 1975 progress.
- Bowman, T. 2015. The cascading effects of invasive grasses in North American deserts: the interactions of fire, plants and small mammals. Brigham Young University Provo, Utah.
- Bowman, D., et al. 2009. Fire in the earth system. *Science* 324:481–484.
- Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, et al. 2004. Effects of invasive alien plants on fire regimes. *BioScience* 54: 677–688.
- Brown, J. H., and E. J. Heske. 1990. Control of a desert-grassland transition by a keystone rodent guild. *Science* 250:1705–1707.
- Bukowski, B. E., and W. L. Baker. 2013. Historical fire regimes, reconstructed from land-survey data, led to complexity and fluctuation in sagebrush landscapes. *Ecological Applications* 23:546–564.
- Campbell, C. R. 1991. Determination of total nitrogen in plant tissue by combustion. In: *Plant analysis reference procedures for the southern region of the United States*. Southern cooperative series bulletin 368. (ed. Plank, CO). University of Georgia Athens, pp. 21–23.

- 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.
- Daehler, C. C. 2003. Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. *Annual Review of Ecology Evolution and Systematics* 34:183–211.
- D'Antonio, 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.
- Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* 88:528–534.
- Drenovsky, R. E., B. J. Grewell, C. M. D'Antonio, J. L. Funk, J. J. James, N. Molinari, et al. 2012. A functional trait perspective on plant invasion. *Annals of Botany* 110:141–153.
- Elton, C. 1958. *The ecology of invasions by animals and plants*. Methuen, London, UK. 20.
- Esque, T. C., J. P. Kaye, S. E. Eckert, L. A. DeFalco, and C. R. Tracy. 2010. Short-term soil inorganic N pulse after experimental fire alters invasive and native annual plant production in a Mojave Desert shrubland. *Oecologia* 164:253–263.
- Freeman, J. P., T. J. Stohlgren, M. E. Hunter, P. N. Omi, E. J. Martinson, G. W. Chong, et al. 2007. Rapid assessment of postfire plant invasions in coniferous forests of the western united states. *Ecological Applications* 17:1656–1665.
- Freeman, E. D., T. R. Sharp, R. T. Larsen, R. N. Knight, S. J. Slater, and B. R. McMillan. 2014. Negative effects of an exotic grass invasion on small-mammal communities. *PLoS ONE* 9:1–7.
- Helm, D. J., and B. R. Mead. 2004. Reproducibility of vegetation cover estimates in south-central Alaska forests. *Journal of Vegetation Science* 15:33–40.
- Horn, K. J., B. R. McMillan, and S. B. St. Clair. 2012. Expansive fire in Mojave Desert shrubland reduces abundance and species diversity of small mammals. *Journal of Arid Environments* 77:54–58.
- Horn, K. J., R. Nettles, and S. B. St. Clair. 2015. Germination response to temperature and moisture to predict distributions of the invasive grass red brome and wildfire. *Biological Invasions* 17:1849–1857.
- Hoset, K. S., K. Kyro, T. Oksanen, L. Oksanen, and J. Olofsson. 2014. Spatial variation in vegetation damage relative to primary productivity, small rodent abundance and predation. *Ecography* 37:894–901.
- Hulbert, L. C. 1955. Ecological studies of *Bromus tectorum* and other annual Brome grasses. *Ecological Monographs* 25:181–213.
- Inouye, R. S., G. S. Byers, and J. H. Brown. 1980. Effects of predation and competition on survivorship, fecundity, and community structure of desert annuals. *Ecology* 61:1344–1351.
- James, L. F. 1999. Halogeton poisoning in livestock. *Journal of Natural Toxins* 8:395–403.
- Kalish, S., R. B. Spigler, and C. C. Horvitz. 2014. In a long-term experimental demography study, excluding ungulates reversed invader's explosive population growth rate and restored natives. *Proceedings of the National Academy of Sciences of the United States of America* 111:4501–4506.
- 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.
- Kempel, A., R. Chrobok, M. Fischer, R. P. Rohr, and M. van Kleunen. 2013. Determinants of plant establishment success in a multispecies introduction experiment with native and alien species. *Proceedings of the National Academy of Sciences of the United States of America* 110:12727–12732.
- Kindt, R., and R. Coe. 2005. *Tree diversity analysis. A manual and software for comon statistical methods for ecological and biodiversity studies*. World Agroforestry Centre (ICRAF), Nairobi.
- Levine, J. M., P. B. Adler, and S. G. Yelenik. 2004. A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters* 7:975–989.
- Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10:689–710.
- 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., D. E. Pearson, T. Potter, and Y. K. Ortega. 2012. Seed size and provenance mediate the joint effects of disturbance and seed predation on community assembly. *Journal of Ecology* 100:1492–1500.
- McKelvey, K. S., and D. E. Pearson. 2001. Population estimation with sparse data: the role of estimators vs. indices revisited. *Canadian Journal of Zoology* 79:1754–1765.
- Melgoza, G., R. S. Nowak, and R. J. Tausch. 1990. Soil water exploitation after fire – competition between *Bromus tectorum* (cheatgrass) and 2 native species. *Oecologia* 83:7–13.
- Nachman, R. J., and J. D. Olsen. 1983. Ranunculin - a toxic constituent of the poisonous range plant Bur Buttercup (*Ceratosephalus testiculatus*). *Journal of Agricultural and Food Chemistry* 31:1358–1360.
- Novak, S. J., and R. N. Mack. 2001. Tracing plant introduction and spread: genetic evidence from *Bromus tectorum* (Cheatgrass). *BioScience* 51:114–122.
- 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.
- Ostojia, S. M., and E. W. Schupp. 2009. Conversion of sagebrush shrubland to exotic annual grasslands negatively impacts small mammal communities. *Diversity and Distributions* 15:863–870.
- Ostojia, 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.
- Parker, J. D., and M. E. Hay. 2005. Biotic resistance to plant invasions? Native herbivores prefer non-native plants. *Ecology Letters* 8:959–967.
- 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. E., T. Potter, and J. L. Maron. 2012. Biotic resistance: exclusion of native rodent consumers releases populations of a weak invader. *Journal of Ecology* 100:1383–1390.
- Pearson, D. E., J. L. Hierro, M. Chiuffo, and D. Villarreal. 2014a. Rodent seed predation as a biotic filter influencing exotic plant abundance and distribution. *Biological Invasions* 16:1185–1196.
- Pearson, D. E., N. S. Icasatti, J. L. Hierro, and B. J. Bird. 2014b. Are local filters blind to provenance? ant seed predation suppresses exotic plants more than natives. *PLoS ONE* 9:1–11.
- Pyke, D. A. 1986. Demographic responses of *Bromus tectorum* and seedlings of *Agropyron spicatum* to grazing by small mammals – occurrence and severity of grazing. *Journal of Ecology* 74:739–754.

- Richardson, K., S. West, and R. Gitzen. 2013. Cheatgrass (*Bromus tectorum*) dominates the pouch contents of the Great Basin pocket mouse. *Western North American Naturalist* 58:158–167.
- Shea, K., and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution* 17:170–176.
- Sol, D., J. Maspons, M. Vall-Llosera, I. Bartomeus, G. E. Garcia-Pena, J. Pinol, et al. 2012. Unraveling the life history of successful invaders. *Science* 337:580–583.
- Theoharides, K. A., and J. S. Dukes. 2007. Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytologist* 176:256–273.
- Vila, M., and J. Weiner. 2004. Are invasive plant species better competitors than native plant species? evidence from pairwise experiments. *Oikos* 105:229–238.
- Vila, M., C. Basnou, P. Pysek, M. Josefsson, P. Genovesi, S. Gollasch, et al. 2010. How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Frontiers in Ecology and the Environment* 8:135–144.
- Wan, H. Y., A. C. Rhodes, and S. B. St. Clair. 2014. Fire severity alters plant regeneration patterns and defense against herbivores in mixed aspen forests. *Oikos* 123:1479–1488.
- Warton, D. I., and F. K. C. Hui. 2011. The arcsine is asinine: the analysis of proportions in ecology. *Ecology* 92:3–10.
- Williams, M. 1980. Purposefully introduced plants that have become noxious or poisonous weeds. *Weed Science* 28:300–305.
- Williamson, M., and A. Fitter. 1996a. The varying success of invaders. *Ecology* 77:1661–1666.
- Williamson, M. H., and A. Fitter. 1996b. The characters of successful invaders. *Biological Conservation* 78:163–170.
- Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1:3–14.
- Zwolak, R., D. E. Pearson, Y. K. Ortega, and E. E. Crone. 2010. Fire and mice: seed predation moderates fire's influence on conifer recruitment. *Ecology* 91:1124–1131.

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