



Fire, rodent herbivory, and plant competition: implications for invasion and altered fire regimes in the Mojave Desert

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Abstract

Biological invasions are responsive to changing wildfire regimes related to human activities that are altering biological communities. Our objective was to investigate how fire, rodent activity, and competition among plant species modify plant community structure, invasion patterns, and vulnerability to altered fire regimes. We imposed experimental fires, and reduced rodent density using fencing in a full factorial design and quantified competitive interactions among plant species in the northeast Mojave Desert that has experienced dramatic increases in plant invasion and fire in recent years. Vegetation surveys were conducted in the experimental plots to determine plant density, cover, and biomass of herbaceous plants over a 5-year period. Rodent exclusion increased the density, cover, and biomass of *Bromus rubens*, an invasive annual grass, and density of forb species. In contrast, rodent exclusion decreased the density, cover, and biomass of *Schismus* spp. another dominant annual invader. Fire increased *Schismus* spp. and forb species density, cover, and biomass but decreased *B. rubens* density. Negative spatial correlation between *B. rubens* and *Schismus* spp., and forbs indicated interspecific competition among the dominant plant species. Fire reduced rodent community diversity (Shannon's) 2.5-fold, which was correlated with increases in *B. rubens* cover and biomass, and native forb diversity. Fire, high rodent diversity, and competition from the other plant species may decrease fire potential in our study system by reducing the density and biomass of *B. rubens*, which because of its taller growth form tends to ignite and carry fire better than *Schismus* spp. and forbs.

Keywords Annual grasses · Invasive grass–fire cycles · Plant community assembly · Red brome · State change

Introduction

The introduction and spread of exotic species is among the most widespread and problematic human impacts on Earth's ecosystems (Pimentel et al. 2005; Vilà et al. 2010; Vitousek et al. 1997). Plant invasions can trigger state changes in vegetation that result in reductions of biodiversity and loss of ecosystem services (Pimentel et al. 2005). Patterns of plant invasions are influenced by biotic interactions between plant invaders and native organisms via competition and herbivory, which can both enhance and reduce biotic resistance

to invasion (Levine et al. 2004; Pearson et al. 2012). Disturbance can increase the invasibility of an ecosystem by impacting native community composition and structure, leading to reduced biotic resistance to invaders (Davis et al. 2000). For example, disturbance-driven decreases in native plant cover increases space, light, and soil resource availability, which can increase the establishment success of plant invaders (Esque et al. 2010a; Steers and Allen 2012). Disturbance can also modify the composition and abundance of native consumer communities that often exert top-down controls on plant invaders (St. Clair et al. 2016).

Human activities are altering wildfire regimes at a global scale with broad implications for the invasibility of ecosystems (Brooks 1999a; Germino et al. 2016 and references therein; Vitousek et al. 1997). In dryland ecosystems, which cover as much as 40% of the Earth's terrestrial surface (Safriel et al. 2005), there is a close association among disturbance, increased exotic annual grass presence, and increased potential for fire ignition and spread (Gelbard and Belnap 2003; Mack 1981). In deserts of North America, wildfires

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have occurred historically on century time scales; however, with the introduction of exotic annual grasses in the late 1800s sub-decadal fire return intervals are now being observed (Bowman et al. 2011; Germino et al. 2016 and sources therein; Whisenant 1992). Wildfires promote invasion success in deserts of North America by decreasing biotic resistance through removal of native vegetation (St. Clair et al. 2016; Steers and Allen 2012). Removal of intact native plant species by fire provides resource opportunities and competitive release that promotes invasive annual grass establishment (Germino et al. 2016; Horn et al. 2015; Levine et al. 2004). Dominance of invasive grasses after fire can decrease the establishment success of native plant species that alters plant community composition (Brooks et al. 2004; Germino et al. 2016). Fire can also indirectly affect the plant community by modifying the behavior and composition of consumer communities that regulate plant community assembly (Elton 2000; Horn et al. 2012; Levine et al. 2004). Shifts in plant community composition and structure in response to these interactions can alter the fuel characteristics of the plant community that influence the probability and spread of wildfires that promote invasive grass–fire cycles (Brooks et al. 2004; D’Antonio and Vitousek 1992; St. Clair and Bishop 2019).

Rodent herbivory creates top-down control on plant community assembly (Beatley 1976; Inouye et al. 1980; Pearson et al. 2014) and biotic resistance against the establishment of invasive species through seed predation and seedling herbivory (Pearson et al. 2014; St. Clair et al. 2016). Rodents structure plant communities through seed consumption and seed dispersal (Beatley 1969; Price and Joyner 1997). Rodents may therefore facilitate invasion by increasing dispersal of invasive seeds or preferentially consuming native seeds (Beatley 1976; Horn et al. 2017; Price and Joyner 1997). However, post-dispersal establishment of plant invaders may be suppressed by rodent activity (Pearson et al. 2012; St. Clair et al. 2016). Because rodent abundance, richness, and diversity can decrease in response to wildfire (Horn et al. 2012; Ostoja and Schupp 2009), post-fire conditions may create windows of opportunity for plant invaders to be released from rodent suppression (Allington et al. 2013).

Competition is a key driver of plant community structure and biotic resistance against plant invasions (Levine et al. 2004). Intact native plant communities have been shown to reduce the establishment and spread of exotic plant species (Pearson et al. 2012; St. Clair et al. 2016). However, competition within plant communities typically decreases following fire resulting in increased availability of soil resources (Allen et al. 2011; Horn et al. 2017; Shea and Chesson 2002). In arid and semi-arid environments, inter-shrub spaces typically have lower native annual plant abundance, and those that do establish have shorter stature than

those that grow under shrub canopies (Brooks and Chambers 2011; Filazzola et al. 2018) creating resource opportunities in the open spaces between shrubs (Brooks and Chambers 2011; Schafer et al. 2012). This niche opportunity (niche opportunity hypothesis; (Davis et al. 2000)) could allow an exotic plant to move away from a direct competitor and exploit a neighboring but relatively uninhabited area by native plants, filling in the inter-shrub spaces (Shea and Chesson 2002). Plant density and composition in inter-shrub spaces influence the spread and size of wildfires in deserts (St. Clair and Bishop 2019). Since grasses and forbs (exotic and native) have different fuel properties, niche exploitation based on competitive interactions can strongly influence the size and frequency of wildfires in desert ecosystems (D’Antonio and Vitousek 1992; Shea and Chesson 2002).

The Mojave Desert was chosen as a study system to examine the interplay of disturbance, herbivory, and competition on ecosystem invasibility because fires are becoming more frequent (Brooks and Matchett 2006), rodents are abundant as a primary consumer, and there are multiple plant invaders influencing fire ecology in the system (Brooks et al. 2016; Brooks and Chambers 2011). The two dominant plant invaders in the Mojave Desert are *Bromus rubens* L. and *Schismus* spp. (*Schismus barbatus* or *Schismus arabicus*), and several studies have examined their role in and response to fire (Brooks and Matchett 2003, 2006; DeFalco et al. 2007; reviewed in Germino et al. 2016). Fewer studies have examined the competitive effects between invasive and native plants in the Mojave Desert in response to fire and little research exists examining the influence of consumers on invasibility of the Mojave Desert through experimental treatments (but see Brooks 1995). In high precipitation years, *B. rubens* and *Schismus* spp. can fill in inter-shrub spaces that typically are left void of enough vegetation to carry fire (Brooks and Matchett 2003). However, when both are present on the landscape, *B. rubens* is found more commonly under shrub canopies, particularly the fire-susceptible shrub *Coleogyne ramosissima* Torr. (Beatley 1966) and dominant shrub *Larrea tridentata*, while *Schismus* spp. fills the inter-shrub spaces (Allen et al. 2011; Brooks and Matchett 2003). However, there is a lack of understanding of how these spatial relationships may be modified by fire or rodent activity and impact competitive relationships and fire potential.

The objective of this study was to experimentally investigate the effects of fire and rodent activity on plant community structure and invasion outcomes in the Mojave Desert. We asked the following questions: (1) What are the effects of fire and rodent exclusion on the establishment and growth of invasive annual grasses and herbaceous forbs, including exotic and native species? (2) Are changes in rodent diversity, richness, and abundance correlated with post-fire plant community characteristics? (3) Is there evidence of competitive interactions between invasive grass species or between

exotic grasses and forb species and are they modified by fire or rodent exclusion across space?

Methods

Study site

The study was conducted at Lytle Research Preserve, Washington Co., UT, USA, in the northeast region of the Mojave Desert (37°08'54"N, 114°00'51"W). No known fires have occurred at the study site in recent decades based on a well-developed perennial shrub community along with personal communication with the preserve manager (Heriberto Madrigal, personal communication). Cattle grazing has not occurred at the site since 1985. The study site is a semi-desert shallow hardpan (blackbrush) with soil classified as a gravelly sandy loam (Soil Survey Staff 2015). It is located at 915 m elevation and mean annual precipitation is 272 mm and mean annual temperature is 16 °C (Western Regional Climate Center 2000). Annual precipitation during the study period was as follows: 228 mm (2012–13), 253 mm (2013–14), 314 mm (2014–15), and 315 mm (2015–16). Precipitation data were collected from the Badger Springs, Ivins Remote Automated Weather Station (RAWS) (Western Regional Climate Center 2000). Vegetation at the study site is dominated by *Larrea tridentata* (DC.) Coville, *Coleogyne ramosissima* Torr., *Ambrosia dumosa* (A. Gray) Payne, and *Yucca brevifolia* Engelm. Common native herbaceous (perennial and annual) plants included *Sphaeralcea ambigua* A. Gray spp. *monticola* Kearney, *Baileya multiradiata* Harv. & A. Gray, *Astragalus nuttaliianus* DC., *Plantago* spp. (*P. patagonica* and *P. ovata*), and *Descurainia pinnata* (Walker) Britton. At the beginning of the study in 2011, shrub interspaces were dominated by non-native annuals, *Bromus rubens* and *Erodium cicutarium*, while *Schismus* spp. was generally absent.

Plot design

The study tests the main effects of fire and rodent exclusion in a full factorial block design replicated five times (St. Clair et al. 2016). Each 60 m × 60 m experimental block was split into four randomly assigned 30 m × 30 m treatment sub-plots with the following treatment combinations: burned–rodents present, burned–rodents excluded, unburned–rodents present, unburned–rodent excluded. Wire mesh fencing was installed around the perimeter of each treatment plot (both rodents present and excluded) with 30 cm buried below ground and 70 cm above ground. Rodent exclusion plots had a 20 cm strip of aluminum flashing placed at the top to keep rodents from climbing over the fences. Rodents present treatment was achieved

by cutting 12 cm × 10 cm opening every 4 m around the fence perimeter to allow rodent entry. The rodent exclusion fences reduced the number of unique individuals trapping session 4.4-fold over the study period. Mean rodent abundance of unique individuals in rodents present plots was 2.76 ± 0.36 individuals per 3-day trapping session, whereas the mean unique individuals in rodent exclusion plots was 0.63 ± 0.15 individuals ($P < 0.001$). The study area was enclosed by barbed wire fencing to exclude livestock, but had an 80 cm gap at the bottom to allow the entry of mammals and reptiles in and out of the study area. The burn treatments in each block were conducted in June 2011 using a drip torch as an ignition source. The study site was already invaded with *B. rubens* when the study began with average densities of 1319 stems m⁻² in the inter-shrub spaces, which carried fire across the plots. The experimental fire decreased native shrub cover by > 80% indicating that burn severity was moderate to high.

Vegetation surveys

Plant density surveys were conducted annually in April–May for the years 2013–2016. Density counts were done using four parallel randomized transect lines, spaced at least 2 m apart with a modified Daubenmire frame (25 cm × 50 cm) placed every 2 m for a total of 12 quadrats per transect line. Transect lines were placed in randomized locations, as well as alternating orientation each year (N–S, E–W). Frame placement on each transect line started at least 2 m from the fence to avoid edge effects. All herbaceous plants rooted within the frame were counted. Because they were so abundant, invasive annual grasses *B. rubens* and *Schismus* spp. were counted in a subframe of 10 cm × 25 cm within the modified Daubenmire frame. Native grasses were largely absent and were not included in the statistical analyses.

Plant canopy cover measurements were done in 2016 using the line-point intercept method (Herrick et al. 2006) along the same four transect lines used for density measurements. A pin was dropped starting at least 2 m from the fence, every 0.5 m for a total of 48 pin drops per transect line. For each pin drop, the topmost plant intersecting the pin was recorded as a canopy layer.

Herbaceous plant biomass was collected in April 2016. All living aboveground herbaceous biomass rooted within the 25 cm × 50 cm modified Daubenmire frame used for vegetation density counts was removed by clipping to ground surface. Biomass was collected along the same four randomized transects used for vegetation density measurements starting at the 2 m mark and sampled every 4 m for a total of six sampling frames per transect. All biomass was taken back to the laboratory and dried at 80 °C for 48 h, then weighed to the nearest gram.

Rodent surveys

Rodent surveys were conducted every spring, summer, and fall period for three consecutive nights per trapping session. Eight large Sherman live traps were placed in a circle away from the fence edge in each plot with two control trap circles for each block located at randomized locations outside the treatment plots. Each morning, rodents were collected and assessed for species, gender, age, reproductive status, and weight (to the closest 0.5 g). New individuals were given an ear tag with a unique identifier to track for subsequent nights and trapping sessions. Rodent abundance was calculated as the number of unique individuals per species trapped within a 3-day trapping session. Rodent species in order of abundance were *Dipodomys merriami*, *Peromyscus crinitus*, *Chaetodipus formosus*, *Neotoma lepida*, *Ammospermophilus leucurus*, *Peromyscus boylii*, *Peromyscus maniculatus*, *Peromyscus truei*, and *Onychomys torridus*. The Brigham Young University Animal Care and Use Committee approved the small mammal survey protocols (IACUC#120,202).

Statistical analysis

Plant density, cover, biomass, and plant community richness, and Shannon's diversity index were modeled using linear mixed effects models using the nlme package in R (Pinheiro et al. 2017) with main and interactive fixed effects of fire, rodent, and year with experimental blocks designated as the random effect. To meet homogeneity of variance assumptions a varIdent covariance structure for the fixed effects (fire, rodent, and/or year) was used when needed. R^2_c values are presented to help interpret how much of the model explains the variation in the data with both fixed and random effects included in the model. A simple linear regression was used to analyze the effects of rodent diversity, abundance, and richness on native and total plant diversity and density averaged across treatment blocks.

Piecewise structural equation modeling (pSEM, also known as confirmatory path analysis) (Shipley 2009) was used to model the type (positive or negative) and strength (statistical significance and critical values) that treatments had on plant density between plant species using 'psem' package in R (Lefcheck 2016). We chose pSEM because of the flexibility to have multiple structural equations with different covariance structures as required to meet the assumptions for the linear mixed effects models (Shipley 2009). However, one limitation to using piecewise structural equation models is that they cannot test reciprocal relationships as with traditional SEM. To better understand possible reciprocal relationships between plant species, different pSEM analyses were used with a particular plant species as a predictor vs a response.

To analyze the competitive spatial correlation a simulated permutation Spearman's correlation test ($n=2000$) was used to test the strength of the correlation between *B. rubens* and *Schismus* spp. as measured by densities in each quadrat used for density sampling. This was done for all years combined as well as each year individually across all treatment possibilities and combinations. Each year was included in the analysis because of the unique opportunity for comparing the strength of the competitive interference over time as *Schismus* spp. was not present at the onset of the experiment.

Results

Plant community responses to rodent exclusion

Rodent exclusion increased *B. rubens* density (216 m^{-2} – 294 m^{-2}) ($P=0.001$ Fig. 1, Table 1), cover (11%–17%), and biomass (19 g m^{-2} – 28 g m^{-2}) ($P=0.029$ and $P=0.067$, respectively, Table 2) when averaged across years. Rodent exclusion increased forb density 7% from 156 to 214 m^{-2} ($P=0.0001$, Fig. 1, Table 1), but did not significantly affect forb cover or biomass compared to rodent access plots ($P=0.95$ and $P=0.52$ respectively, Table 2). In contrast, rodent exclusion reduced *Schismus* spp. density (993 m^{-2} – 751 m^{-2}) ($P<0.0001$, Fig. 1, Table 1), cover (30%–22%), and biomass (25 gm^{-2} – 14 gm^{-2}) ($P=0.0001$ and $P=0.015$, respectively, Table 2) 1.2-, 1.5-, and 1.7-fold compared to rodent present plots. Excluding rodents also slightly decreased total herbaceous density ($P=0.068$, Fig. 1, Table 1), but did not affect cover or biomass ($P=0.55$ and $P=0.75$, respectively, Table 2). There was a significant interaction between fire and rodent exclusion on forb density in which the effects of fire were greater in rodent exclusion plots ($P=0.017$, Fig. 1, Table 1). Exotic forbs were 2.5-fold more dense than native forbs, no matter the rodent treatment. Rodent exclusion increased diversity of the plant community 1.4-fold ($P=0.017$, Fig. 2), but had no significant effect on richness of the plant community ($P=0.16$, Fig. 2).

Plant community responses to fire

Forbs and invasive grass species had varying responses to fire in this study. Fire decreased *B. rubens* densities by 9% compared to unburned plots when averaged across the 4-year study period ($P=0.0107$, Fig. 1, Table 1), while fire had no significant effect on *B. rubens* cover and biomass ($P=0.18$ and $P=0.66$, respectively, Table 2). In contrast, *Schismus* spp. densities ($P<0.0001$, Fig. 1, Table 1), cover, and biomass doubled ($P<0.0001$ and $P<0.0001$, respectively, Table 2) in burned plots compared to unburned plots when averaged across the study period. Fire nearly doubled forb density ($P<0.0001$, Fig. 1, Table 1) and cover

Fig. 1 Effects of fire and rodent exclusion on (a) *Bromus rubens*, (b) *Schismus* spp., (c) forb species, and (d) total herbaceous plant density (mean ± SE) over time for the entire study period from 2013 to 2016. F-statistics and levels of significance (P value $\alpha=0.05$) are given in Table 1

($P=0.006$, Table 2) compared to unburned plots. Exotic forbs were threefold more dense than native forbs in burned plots, but only 1.5-fold denser in unburned plots. Similarly, forb biomass increased 2.3-fold in burned plots compared to unburned plots in 2016 ($P=0.002$, Table 2). Fire increased total herbaceous density ($P<0.0001$, Fig. 1, Table 1), cover ($P<0.0001$, Table 2), and biomass (2016 only) 1.5-fold or higher ($P=0.0001$, Table 2). Plant community diversity decreased 1.4-fold in response to fire ($P=0.014$), while fire had no significant effect on plant species richness ($P=0.51$, Fig. 2). Except where stated above, there were no other significant fire and rodent interactions for plant density, cover, biomass, richness, or diversity ($P>0.1$ for all measurements (Tables 1 and 2, Figs. 1 and 2).

Rodent community responses to fire and rodent exclusion

Burned plots had a 2.5-fold reduction in rodent diversity (Shannon’s diversity index, $P<0.0001$) and a slight decrease in rodent richness ($P=0.064$) compared to unburned plots averaged across the study period (Fig. 3). Fire did not alter rodent abundance ($P=0.16$) in comparison to unburned plots when averaged across time (Fig. 3).

Plant–rodent correlative relationships

Rodent Shannon’s diversity was negatively correlated with forb Shannon’s index of diversity ($R^2=0.68$, $P<0.01$) (Fig. 4) and *B. rubens* cover and biomass ($R^2=0.52$, $P<0.05$ for cover; $R^2=0.59$, $P<0.01$ for biomass). Rodent Shannon’s diversity and abundance were not correlated with *B. rubens* density, *Schismus* spp. density, cover, or biomass ($R^2<0.1$).

Plant competition

There was evidence of competitive interactions between *B. rubens*, *Schismus* spp., and forbs (Figs. 5 and 6). The strength of the negative correlation between the two invasive grasses doubled from 2013 ($\rho=-0.24$, $P<0.0001$), when *Schismus* spp. first started to appear, to 2016 when *Schismus* spp. attained higher densities and percent cover than *B. rubens* ($\rho=-0.43$, $P<0.0001$) (Figs. 1 and 5, Table 1). All treatment combinations had significant negative correlation between the two exotic grasses (Fig. 5).

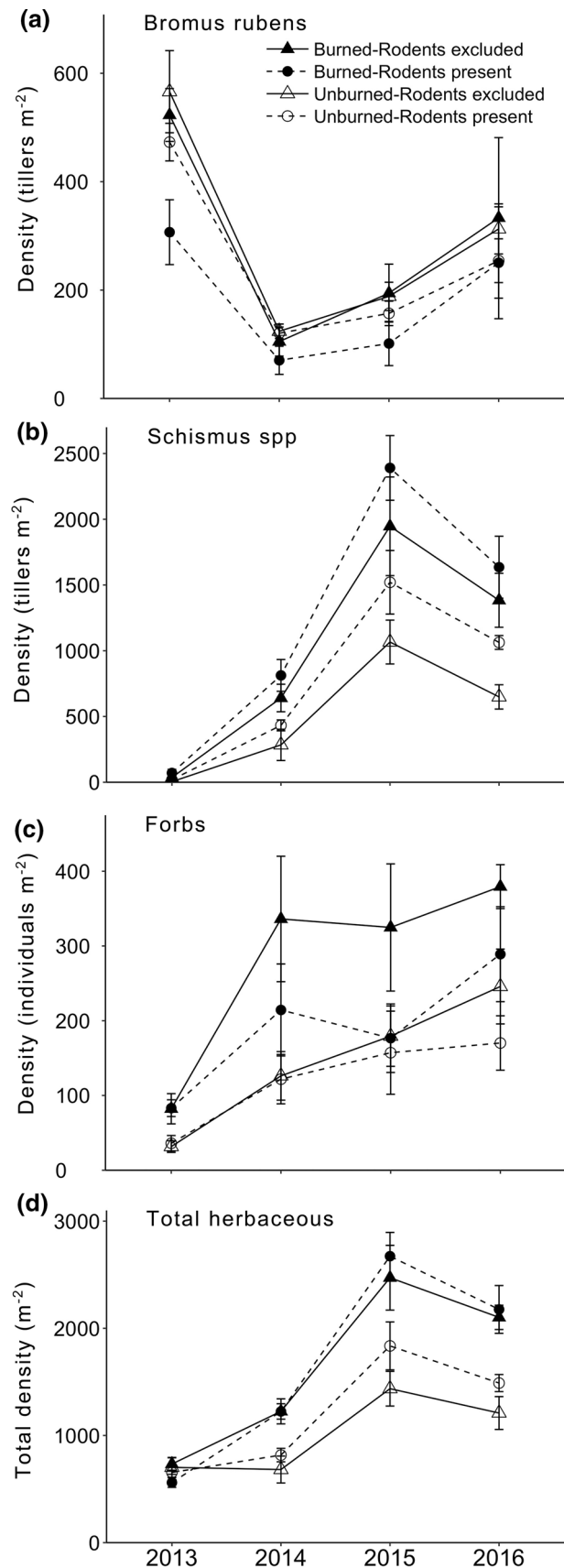


Table 1 Main and interactive effects of fire, rodent exclusion, and year on exotic grass density, forb density, and total herbaceous plant density

Treatment	df	Exotic grass density		Forb density	Total herbaceous density
		<i>Bromus rubens</i>	<i>Schismus</i> spp.		
Fire	1.48	3.53 ⁺	54.87***	54.9***	86.96***
Rodent	1.48	11.67***	34.86***	18.6***	3.47 ⁺
Fire * rodent	1.48	1.95	0.06	6.09*	2.04
Year	3.12	66.4***	44.13***	12.37***	35.46***
Fire * year	3.48	0.77	7.54***	3.23*	13.58***
Rodent * year	3.48	2.5 ⁺	2.82*	2.4 ⁺	2.24 ⁺
F*R*Y	3.48	0.29	0.11	1.5	0.032
R_c^2		0.75	0.81	0.78	0.87

F-statistics presented with P value significance ($\alpha=0.05$) denoted as follows: $0.08 > P > 0.05^+$, $P < 0.05^*$, $P < 0.01^*$, $P < 0.001^{**}$, $P < 0.0001^{***}$. R_c^2 represents the variation explained by the model with both fixed and random effects included

Table 2 Plant biomass and cover response to fire and rodent exclusion for 2016. Means presented \pm SE

Cover treatment	df	exotic rass cover		Forb cover	Total herbaceous cover
		<i>Bromus rubens</i>	<i>Schismus</i> spp.		
Unburned–present		9.3 \pm 1.6	25.2 \pm 2	4.5 \pm 1.5	39 \pm 4.7
Unburned–excluded		15.3 \pm 3.2	13.4 \pm 1	3.6 \pm 0.9	32.3 \pm 4.6
Burned–present		12.8 \pm 4	35.1 \pm 4.4	6.5 \pm 1.6	54.5 \pm 4.6
Burned–excluded		18.5 \pm 5.6	31.3 \pm 5.2	7.3 \pm 1.1	57.9 \pm 1.1
Fire	1.12	2	14.98**	10.86**	75.64***
Rodent	1.12	6.15*	4.74*	0.003	0.37
F * R	1.12	0.005	1.25	0.62	3.68 ⁺
R_c^2		0.69	0.53	0.59	0.87
Biomass treatment	df	Exotic grass biomass		Forb biomass	Total herbaceous biomass
		<i>Bromus rubens</i>	<i>Schismus</i> spp.		
Unburned–present		18 \pm 4	17 \pm 2	5 \pm 2	40 \pm 8
Unburned–excluded		29 \pm 8	9 \pm 2	5 \pm 1	42 \pm 9
Burned–present		22 \pm 8	34 \pm 8	10 \pm 2	66 \pm 9
Burned–excluded		28 \pm 10	20 \pm 3	14 \pm 3	61 \pm 11
Fire	1.12	0.2	72.2***	15.7**	25.6***
Rodent	1.12	4.1 ⁺	14.6**	0.4	0.11
F * R	1.12	0.6	0.6	1.4	0.8
R_c^2		0.76	0.92	0.68	0.83

F-statistics presented for main and interactive effects of fire and rodent exclusion on exotic grass, forb, and total herbaceous plant cover and biomass for 2016 with p value significance denoted as follows: $0.08 > P > 0.05^+$, $P < 0.05^*$, $P < 0.01^*$, $P < 0.001^{**}$, $P < 0.0001^{***}$. R_c^2 represents the variation explained by the model with both fixed and random effects included

The results from the piecewise structural equation model (pSEM) are displayed in a graphical synthesis of how the experimental treatments affected plant species and potential competitive interactions between plant species (Fig. 6, Table 3). Rodent exclusion positively affected *B. rubens* and forb densities ($P < 0.001$; $P = 0.02$), but negatively affected *Schismus* spp. ($P < 0.01$). The pSEM showed that fire benefitted *Schismus* spp. and forb densities ($P < 0.0001$), but negatively affected *B. rubens* ($P = 0.02$). *Schismus* spp. and

forbs increased with time ($P < 0.001$; $P = 0.04$) and *B. rubens* decreased ($P = 0.02$). Because pSEM is unidirectional with no testing of reciprocal relationships, *B. rubens*, *Schismus* spp., and forbs were each run in a model as the main predictor totaling in three pSEM models. In the first pSEM, *B. rubens* negatively affected *Schismus* spp. ($P = 0.08$) and both *B. rubens* and *Schismus* spp. negatively impacted forb densities ($P = 0.1$; $P < 0.001$) (Fig. 6). The second pSEM model showed *Schismus* spp. negatively affected *B. rubens*

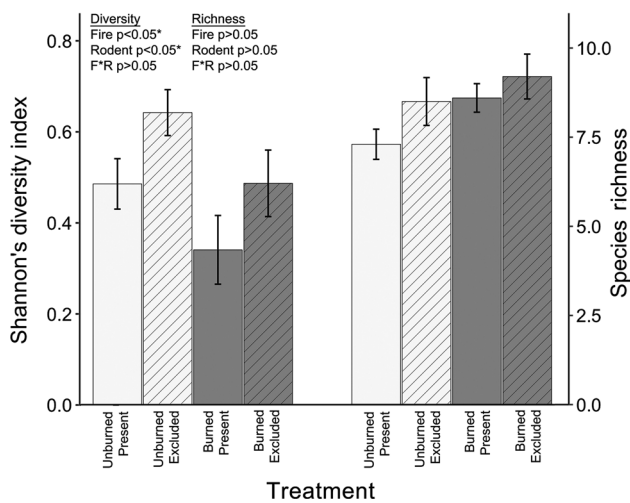


Fig. 2 Effects of rodent exclusion and fire on Shannon’s diversity index (left axis) and species richness (right axis) for the entire herbaceous plant community in 2016. Mean values presented with \pm SE. Levels of significance (P value $\alpha=0.05$) for each treatment and treatment interaction indicated for diversity and richness on the top left of the figure

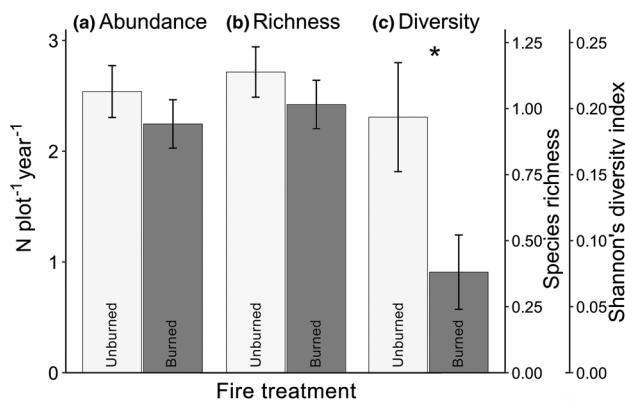


Fig. 3 Effects of fire on (a) rodent abundance (left axis), (b) species richness (primary right axis), and (c) Shannon’s diversity index (secondary right axis) for the study period (2013–2016). Rodent diversity was the only rodent community measurement with significant differences ($P<0.001$) denoted with an asterisk (*). Mean values presented with \pm SE

($P=0.05$) (Fig. 6; Table 3). The third pSEM model forbs negatively impacted *B. rubens* and *Schismus* spp. ($P=0.12$, $P=0.08$) (Fig. 6 and Table 3).

Discussion

This study provides evidence that top-down effects of consumers on plants, competition among plants, and their response to fire (Chambers et al. 2007; Melgoza et al. 1990;

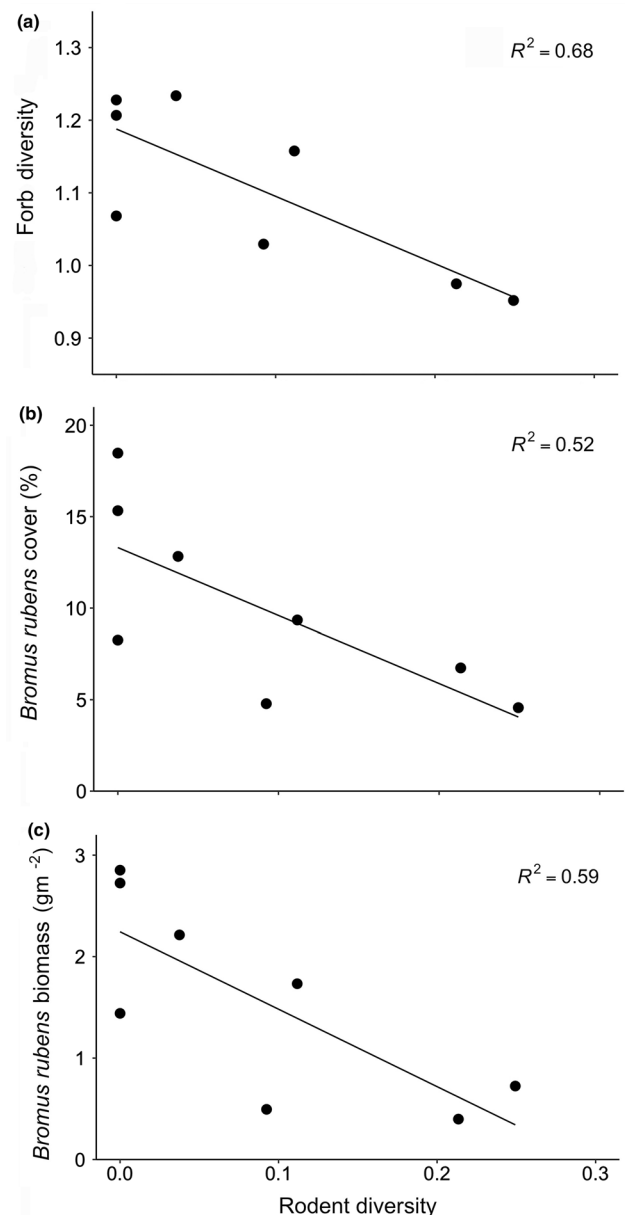


Fig. 4 Negative linear relationship between rodent Shannon’s diversity in rodent present plots and (c) herbaceous forb Shannon’s diversity, (b) *Bromus rubens* cover, and (c) *B. rubens* biomass from 2013 to 2016

St. Clair et al. 2016) influence patterns of invasion and susceptibility to invasive grass–fire cycles in arid ecosystems (Brooks et al. 2004; Gill et al. 2018). Plants, particularly invasive species, often respond positively to post-fire conditions (Brooks et al. 2004; St. Clair and Bishop 2019), which is consistent with the twofold increase in *Schismus* spp. and forb species (which include exotic annuals) in this study (Figs. 1 and 6, Table 2). Rodents have been shown to have both positive and negative effects on plant establishment (Maron et al. 2012; Orrock et al. 2008), which was consistent

Fig. 5 Correlation of *B. rubens* and *Schismus* spp. density over time in each experimental treatment plot. Spearman's rho presented in middle right from the simulated permutation correlation tests ($n=2000$) for all possible treatment combinations averaged over the study period. Asterisks (***) denote $P < 0.0001$

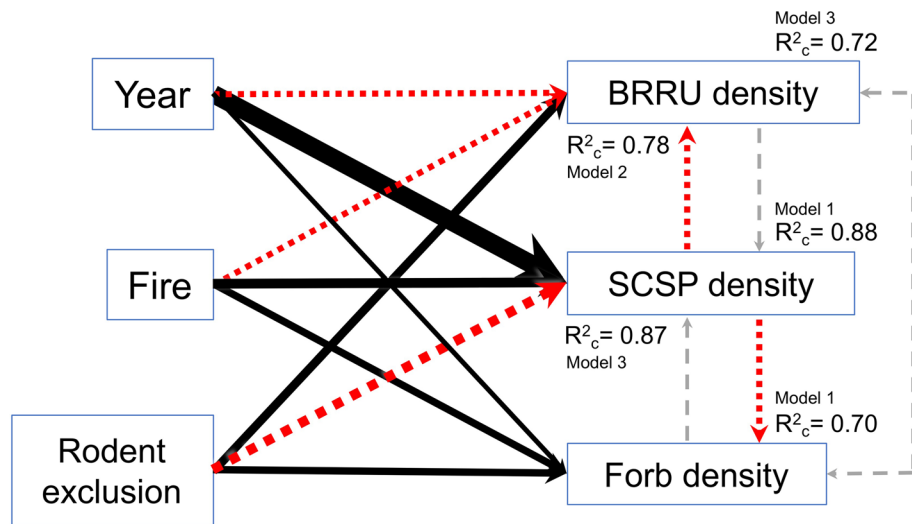
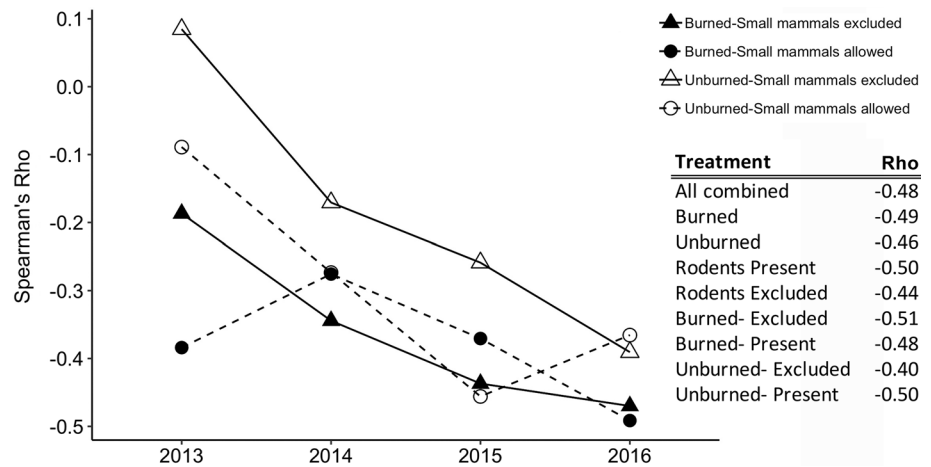


Fig. 6 Direct and indirect effects of rodent exclusion, fire, and plant species on density of *Bromus rubens* (BRRU), *Schismus* spp. (SCSP), and forb plant species. Black solid lines indicate positive significant ($P < 0.05$) relationships, red short-dashed lines indicate negative significant relationships, gray long-dashed lines indicate non-signifi-

cant ($0.15 < P > 0.05$) negative relationship. Line widths indicate the strength of the relationship as determined by the critical value. R^2 values are given for each unidirectional response for each model. Color version of this figure is available online

in our data as the two dominant invasive grasses had opposite responses to rodent treatments (Fig. 6). This is likely due to variation in their functional traits and competitive interactions (Bowman et al. 2017; Cubera et al. 2009; Steers and Allen 2012). Shifts in the rodent communities altered plant community structure and invasibility of the study system (Figs. 4 and 5), which is consistent with a comparable study in the Great Basin Desert (St. Clair et al. 2016). Our results also suggest that invasive grasses had strong competitive interactions in our study system (Figs. 5 and 6), along with forbs, that may dictate fine fuel composition under shrub canopies and in inter-shrub spaces (Brooks 1999a; Shea and Chesson 2002). While fine fuel composition thresholds in areas such as the Mojave and Sonoran deserts have not been

strongly defined (Rao and Allen 2010 and sources therein), understanding how fine fuel composition may change due to competition and consumer activity may dictate future state changes within arid ecosystems experiencing more frequent wildfires.

Effects of rodents on invasive and herbaceous plant communities

Rodent exclusion positively affected both *B. rubens* and forb species in our study (Figs. 1 and 6, Table 1 and 2) (St. Clair et al. 2016). Seed predation is a primary mechanism by which rodents influence plant community assembly (Brown and Heske 1990). Rodent consumers have been shown to

Table 3 Path estimates, standard error, and *P* value for piecewise structure equation models (pSEM)

Predictor	Response	Estimate	SE	<i>P</i> value
SEM model 1				
Rodent	<i>Bromus rubens</i>	41	14.2	<0.001
Rodent	<i>Schismus</i> spp.	−210	72.7	<0.01
Rodent	Forbs	10	4.1	0.02
Fire	<i>Bromus rubens</i>	−34	17.2	0.02
Fire	<i>Schismus</i> spp.	461	78	<0.0001
Fire	Forbs	36	5	<0.0001
Year	<i>Bromus rubens</i>	−47	14.2	0.02
Year	<i>Schismus</i> spp.	377	82	<0.001
Year	forbs	9.3	1.9	0.04
<i>Bromus rubens</i>	<i>Schismus</i> spp.	−0.6	0.35	0.08
<i>Bromus rubens</i>	Forbs	−0.04	0.02	0.1
<i>Schismus</i> spp.	Forbs	−0.1	0.004	<0.001
Fischer's goodness of fit=0 with <i>P</i> value=1, 0 <i>df</i>				
SEM model 2				
<i>Schismus</i> spp.	<i>Bromus rubens</i>	−1.4	0.02	0.05
Fischer's goodness of fit=0 with <i>P</i> value=1, 0 <i>df</i>				
SEM model 3				
Forbs	<i>Bromus rubens</i>	−0.05	0.003	0.12
Forbs	<i>Schismus</i> spp.	−0.16	0.01	0.08
Fischer's goodness of fit=0 with <i>P</i> value=1, 0 <i>df</i>				

Predictors are rodent exclusion, the presence of fire, year, and each of the main plant species (*Bromus rubens*, *Schismus* spp., and forbs). The main differences between each pSEM model were the switch of plant species predictors and the plant species as a response. Fischer's goodness of fit with accompanying *P* value is stated on the last row for each SEM model

prefer larger seeds over small seeds (Brooks 1999b; Maron et al. 2012). The positive effect of rodent exclusion on *B. rubens* may be due it having a larger seed than most of the other species. The increase in forbs in rodent exclusion plots is consistent with other studies that suggest most native forbs, albeit small seeded species in our study, are most likely preferred by small mammals over exotic plant species (Bowman et al. 2017; Maron et al. 2012). Seedling herbivory is another mechanism by which rodents exert top-down control on plant community assembly (Bowman et al. 2017). Forb seedlings are typically preferred by rodents due to their increased forage quality compared to grasses (Bowman et al. 2017; Cubera et al. 2009), but seedling size is also a contributing factor (Pérez-Harguindeguy et al. 2003). Given that *B. rubens* seedlings may be larger or more abundant due to earlier germination than most natives, rodents may exert higher pressure on *B. rubens* seedlings at certain times of the year (Beatley 1969; Veech 2001). Excluding rodents increased total plant Shannon's diversity (Fig. 2) (Keane and Crawley 2002), but did not change plant species richness, suggesting that the rodent community may have

more of a generalist strategy rather than targeting specific native plants (Keane and Crawley 2002).

Rodents had positive impacts on *Schismus* spp. (Figure 1, Table 1 and 2). *Schismus* spp. has miniscule seeds that have been documented to fall into small soil cracks thereby avoiding seed predation by rodents (Guterman 1994). The positive effect of rodents on *Schismus* spp. are also likely indirectly driven by reduced competitive pressure by *B. rubens* and forbs, as they experience greater top-down control by rodents (Figs. 1 and 6) potentially due to greater seed predation (Orrock et al. 2008; Shea and Chesson 2002). Rodent consumers have been shown to influence invasions indirectly by reducing competition from native species (Allington et al. 2013; Orrock et al. 2008; Shea and Chesson 2002; Veech 2001).

Effects of fire on invasion and the herbaceous plant community

Fire decreased *B. rubens* density with little to no effect on cover and biomass (Fig. 1, Table 2). Shortly after fire, *B. rubens* has been known to decrease in abundance most likely due to high seed mortality because of the lethal temperatures from the fire (Brooks 2002; Esque et al. 2010b). Fire increased the density, cover, and biomass of *Schismus* spp. and forbs over time (Fig. 1, Table 2), perhaps due to reduced competition and increasing soil resource availability (Figs. 1 and 6) (Chambers et al. 2007; Melgoza et al. 1990; Shea and Chesson 2002). Increased soil nutrients in post-fire environments (Allen et al. 2011; Horn et al. 2017) can lead to increased density, biomass, and cover in annual plants which is consistent with the responses of *Schismus* spp. and forbs in our study (Figs. 1 and 6; Table 2) (Allen et al. 2011; Steers and Allen 2012). *Schismus* spp.'s positive response to fire (Fig. 1) appears to have reduced the abundance (Fig. 6) and Shannon's diversity of forbs (Brooks 2000; Steers and Allen 2012). Due to its distinctive phenology, early season invaders such as *Schismus* spp. may be superior competitors in a burned environment by capitalizing on the post-fire nitrogen pulse and water earlier than most native plants (Fig. 6) (Brooks et al. 2004; Esque et al. 2010a; Melgoza et al. 1990). This may explain why Shannon's diversity of herbaceous plants was lowest in burned plots (Fig. 2), where *Schismus* densities were highest (Fig. 1) along with observed increases in *Erodium cicutarium* (exotic forb) in burned plots.

The effects of fire on plant and rodent community diversity

Fire decreased Shannon's diversity of the herbaceous plant community, but not plant species richness in our study (Fig. 2). Disturbance initially can decrease diversity by

removing individual plants and altering herbivore behavior (Grime 1973; Horn et al. 2012). But as succession continues, diversity can increase until competitive effects are manifested (Catford et al. 2012; Shea et al. 2004). Native plant diversity has shown positive responses after fire in the Mojave, particularly with long disturbance-free time periods (Vamstad and Rotenberry 2010). However, increasing the frequency of disturbance likely favors the fast, early successional invasive grass species where niche pre-emption or environment transformation can decrease local diversity long term (Catford et al. 2012). Species such as *Schismus* spp. or *B. rubens* have faster growth and higher propagule production, which means that they can pre-empt native species inhabiting microsites and niche space (niche pre-emption) (Catford et al. 2012). Also, transforming native shrubland by decreasing shrub cover (> 80% in this study) and density into invasive grassland will promote fire and establish an alternate transient state (Brooks et al. 2004; Fukami and Nakajima 2011), preventing the community from attaining greater biodiversity in the future (Catford et al. 2012).

Fire decreased rodent Shannon's diversity as also observed by Horn et al. (2012), but not species richness or abundance (Fig. 3). This was likely because *Dipodomys merriami*, a rodent species that spends more time in open spaces, compensated for the losses of quadrupedal species which prefer shrub cover and emigrated from burned areas (Horn et al. 2012; Ostoja and Schupp 2009). The loss of shrub cover (> 80%) due to the experimental fires increased open canopy space and increased inter-shrub space (Bishop, unpublished data) perhaps providing residual soil nutrients for plant growth (Horn et al. 2017). Exotic grasses such as *Schismus* spp. and *B. rubens* re-establish plant cover after fire (Brooks et al. 2004; St. Clair et al. 2016), but do not provide the same cover structure as native shrubs (Freeman et al. 2014; St. Clair et al. 2016). This interpretation is supported by our data showing rodent Shannon's diversity was negatively correlated with forb Shannon's diversity and *B. rubens* growth (Fig. 4).

The role of competition in structuring an invasive annual grass community

Competitive exclusion by exotic plant species can reduce native plant establishment in both unburned and burned environments (Brooks 2000). *Bromus rubens* and *Schismus* spp. negatively affected the establishment of forbs (Fig. 6) (Brooks 2000; DeFalco et al. 2007). In one study, however, higher precipitation increased cover and biomass of a native forb even in the presence of invasive grasses, which may indicate some native species have competitive abilities toward exotic grasses dependent on temporal availability of resources (Rao and Allen 2010). There was evidence of

strong competition between *Schismus* spp. and *B. rubens* in our study (Figs. 5 and 6). One mechanism by which two strong competitors can maintain co-existence on the same landscape is through spatial niche differentiation (Davis et al. 2000; Shea and Chesson 2002). Open shrub interspaces are a common characteristic of vegetation patterns in hyper-arid deserts. At the beginning of our experiment, *B. rubens* was commonly found throughout the plots and was one of the few species inhabiting this open space. When *Schismus* spp. appeared, possible direct plant–plant competition may have led to a reduction of *B. rubens* over time (Fig. 1). An indication that *Schismus* spp. is driving niche differentiation is seen in the strengthening of the negative spatial correlation as *Schismus* spp. enters and increases in the experimental plots over time (Fig. 5), with *B. rubens* increasing under native shrubs (Horn et al. 2017; Price and Joyner 1997), and *Schismus* spp. becoming dominant in the inter-shrub space (Pucheta et al. 2011) (Bishop, personal observation).

Conclusion

The activity of rodent communities may be a critical mitigating factor in establishment of the invasive grass–fire cycle in the Mojave Desert (Fig. 6). The loss of diversity in the rodent community due to fires (Fig. 3) may provide a window of opportunity for *B. rubens* to increase propagule pressure (Fig. 4) and overcome predation control from rodents and facilitate invasion. This positive feedback between rodent herbivory in post-fire environments and *B. rubens* growth may increase the size and frequency of wildfires in the Mojave Desert by providing more flammable and continuous fine fuels (Fig. 4) (Brooks and Matchett 2006; St. Clair and Bishop 2019; Steers and Allen 2012). In the Great Basin, St. Clair and Bishop (2019) showed that reduction in rodent activity in a post-fire environment created areas with high *Bromus tectorum* (cheatgrass) propagule pressure that led to more severe secondary fires. However, our data also suggest that if rodent consumer activity is high, the differential effects of rodent herbivory between *B. rubens* and *Schismus* spp. could cause *Schismus* spp. to become a dominant fuel in the inter-shrub space. *Schismus* spp. has shorter stature and does not carry fire as well as *B. rubens* (Brooks 1999a); therefore, fire ignition and spread may be less severe when *Schismus* spp. abundance increases. How invasive grasses compete with native and exotic forbs is also important in understanding the ecological underpinnings of invasive grass–fire cycles and state changes in arid ecosystems. As forbs have less favorable fuel properties for spreading fire, years with higher precipitation or low herbivory that favor forbs may lead to a forb-dominated community with lower fire risk (Brooks 2000; Schutzenhofer and Valone 2006). In summary, our data indicate that shifts

in plant community composition in response to fire, rodent activity, and competitive interactions among plant species can influence the fuel structure of the vegetation that determines vulnerability to invasive grass–fire cycles.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Research involving human and/or animal participants This article does not contain any studies with human participants. Small mammal survey protocols were approved by the Brigham Young University Animal Care and Use Committee (IACUC#120202).

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