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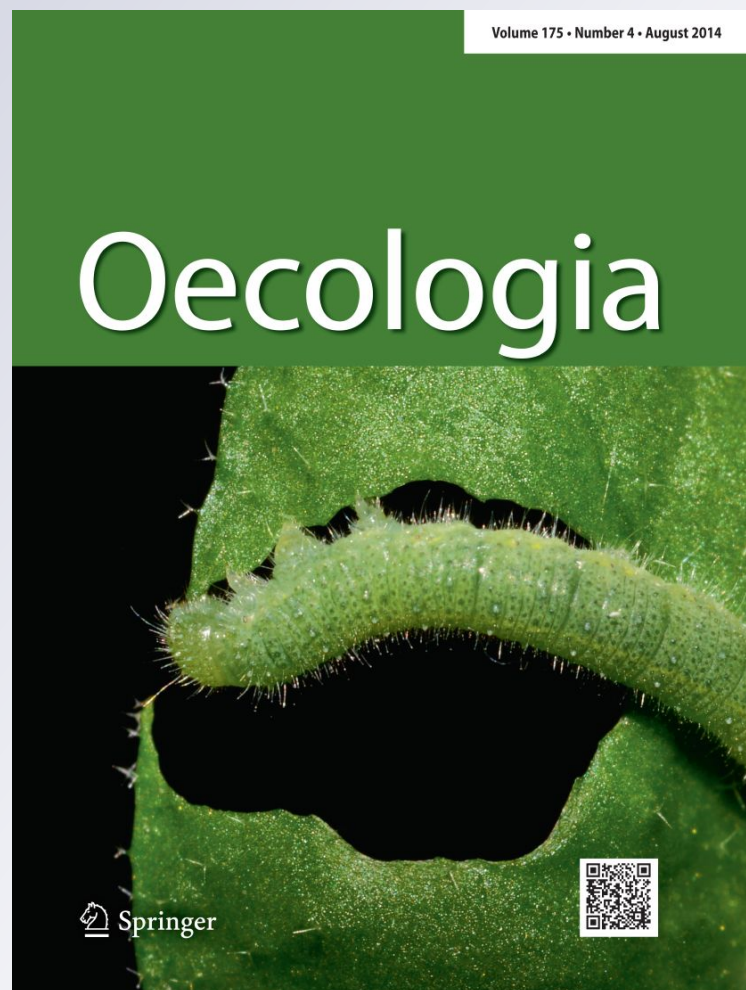
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# Niche opportunities for invasive annual plants in dryland ecosystems are controlled by disturbance, trophic interactions, and rainfall

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## Abstract

Resource availability and biotic interactions control opportunities for the establishment and expansion of invasive species. Studies on biotic resistance to plant invasions have typically focused on competition and occasionally on herbivory, while resource-oriented studies have focused on water or nutrient pulses. Through synthesizing these approaches, we identify conditions that create invasion opportunities. In a nested fully factorial experiment, we examined how chronic alterations in water availability and rodent density influenced the density of invasive species in both the Mojave Desert and the Great Basin Desert after fire. We used structural equation modeling to examine the direct and mediated effects controlling the density of invasives in both deserts. In the first 2 years after our controlled burn in the Great Basin, we observed that fire had a direct effect on increasing the invasive forb *Halogeton glomeratus* as well as a mediated effect through reducing rodent densities and herbivory. 4 years after the burn, the invasive annual grass *Bromus tectorum* was suppressing *Halogeton glomeratus* in mammal exclusion plots. There was a clear transition from years where invasives were controlled by disturbance and trophic interactions to years where resource availability and competition controlled invasive density. Similarly, in the Mojave Desert we observed a strong early influence of trophic processes on invasives, with *Schismus arabicus* benefitted by rodents and *Bromus rubens* negatively influenced by rodents. In the Mojave Desert, post-fire conditions became less important in controlling the abundance of invasives over time, while *Bromus rubens* was consistently benefitted by increases in fall rainfall.

**Keywords** Niche opportunity · Invasive species · Precipitation manipulation · Fire · Rodents

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## Introduction

Critical ecological relationships and ecosystem services provided to humankind are vulnerable to anthropogenic global changes—particularly changes due to plant invasions, altered disturbance regimes, and altered climate (Horn et al. 2015a; Montoya and Raffaelli 2010; St Clair et al. 2016; Vitousek et al. 1997). The success of non-native species introductions into new environments is highly variable, with most introductions failing to establish due to inhospitable environments (e.g., lack of resources, predators), many establishing but never becoming abundant, with a few, catastrophic introductions that fundamentally alter the systems in which they invade (Vila et al. 2010). Stimulated by climate change projections and the obvious influence of aggressive invasive species, numerous studies have looked at how chronically altering the timing and amount of soil resources influences invasive plant species (Eskelinen and Harrison 2014; Suazo et al. 2012; Thomey et al. 2011; Vargas et al. 2012). Substantial evidence also points to the role of biological interactions

in controlling invasion dynamics, including both competitive interactions and direct predation (Levine et al. 2004; Maron and Kauffman 2006; Pearson et al. 2012; St Clair et al. 2016). It is only through addressing multi-trophic interactions in conjunction with abiotic factors that will provide opportunities to predict where invasive species will be able to establish and expand.

Invasibility of an ecosystem is largely determined by the interplay between non-native species traits and environmental conditions (Sol et al. 2012; Williamson and Fitter 1996). Because non-native species establishment and expansion varies spatially and temporally it has been difficult to build predictive models for non-native species success. However, it is clear that invasions are made possible in most cases by an interaction between available resources and trophic interactions. The “resource” hypothesis posits that the availability of resources in the new environment controls invasion success (Davis et al. 2000) while the “biotic resistance” hypothesis suggests that invasion success is determined by competitive and trophic interactions (Elton 1958; Levine et al. 2004). Many studies have worked to link these two complementary hypotheses by examining the interplay between fluctuations in resources, availability of niches and trophic interactions (Blumenthal 2005; Blumenthal et al. 2009; Blumenthal 2006; Catford et al. 2009; Shea and Chesson 2002). This fluctuation-based concept model provides a compelling theoretical framework for understanding how rapid environmental changes due to human activities (e.g., climate change, disturbance patterns) modify plant resource availability, population dynamics, and plant invasions (IPCC 2014). A better mechanistic understanding of the biological and environmental regulations are critical to developing more accurate forecasts of invasions and management approaches that can be used to mitigate their negative effects (Tingley et al. 2014).

In dryland systems, water is the resource most often limiting plant growth. In the Great Basin and Mojave Deserts available soil moisture from the fall to spring precipitation triggers germination events for both non-native and native species; however, the moisture requirement for non-native annual grasses is typically lower than that of native plants leading to an increased advantage in non-native annual grass establishment (Beatley 1966; Brooks and Berry 2006; Horn et al. 2015a). This advantage promotes invasive grass establishment and growth that accelerate a buildup of litter allowing fire to spread which can degrade the native perennial plant community that shows limited resilience to fire (Horn and St. Clair 2017). Ultimately, after a fire there is a pulse in resource availability and reduced competition from perennial plants (Horn et al. 2015b) and the annual grasses begin to dominate because they can acquire soil resources more readily than native species (Boyd and Davies 2012; Eskelinen and Harrison 2014).

Beyond resource-driven models of invasion, animal consumers can elicit both positive (Jensen and Six 2006; Kalisz et al. 2014; Orrock et al. 2008) and negative effects (Pearson et al. 2012) on the establishment of plant invaders. However, 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 demonstrate that top-down regulation by rodents and ants may modify the establishment success of non-native plant species (Connolly et al. 2014; Pearson et al. 2011, 2012) and create population-level biotic resistance against weak plant invaders (Allington et al. 2013; Pearson et al. 2012). St. Clair et al. (2016) showed that rodents are a key determinant of plant community structure after a major fire, altering the trajectory of succession and determining whether the post-disturbance community is dominated by forbs or winter annual grasses.

Of special concern in invasion biology are the controls over invasive annual grasses in arid land systems because they fuel novel fires in communities without a strong evolutionary history of fire (Abatzoglou and Kolden 2011; Dantonio and Vitousek 1992; Suazo et al. 2012). In the Mojave and Great Basin Deserts, invasions by non-native winter annuals are fueling an increase in fire frequency and substantially altering plant communities and ecosystems structure (Balch et al. 2013; Bowman et al. 2011; Bukowski and Baker 2013; Curtis and Bradley 2015). These fires may serve to release invasive grasses and forbs from competition from natives at the same time that soil resources are higher due to the impacts of fire on both resource and biotic controls over invasions.

Currently, the Mojave Desert is experiencing an unprecedented increase in fire frequency because of the non-native annual grass *Bromus rubens* L. (Brooks and Matchett 2006, Horn and St. Clair 2017). The Great Basin and Columbia Basin have already experienced this shift in fire frequency because of the invasive grass *Bromus tectorum* L. (Chambers et al. 2014; Condon et al. 2011; Mack et al. 2000). Additionally, in both the Mojave Desert and Great Basin, climate change is expected to alter patterns and quantities, as well as form of precipitation adding to the complexity of how non-native plants become established. To understand the combined roles of precipitation, fire, and herbivory on invasive plant success we established an experiment that chronically altered precipitation using passive rainout shelters and water addition plots nested within rodent removal plots with burn treatments in the northeastern Mojave Desert and the central Great Basin (Figure S1). Our primary objective was to determine the direct and consumer-mediated influence of fire on the establishment of aggressive invasive species. Furthermore, we wanted to examine whether changes in precipitation amount could alter competitive and trophic responses to fire. Using theory and empirical observations,

we developed a single a priori model (Grace et al. 2010, 2012) for both the Mojave Desert and the Great Basin that includes trophic interactions, fire, and rainfall as key factors that are hypothesized to affect invader density (Fig. 1). We predicted that (i) fire would negatively affect mammal density and positively affect invasive plant densities (Horn et al. 2012), (ii) precipitation would positively affect the densities of each invasive plant species (Abella et al. 2012; Curtis and Bradley 2015), and (iii) mammal density would negatively affect the densities of both invasive species (Rowe and Terry 2014; St Clair et al. 2016). Because we could not have reciprocal relationships in our SEM, we chose a single directional relationship between our two plant species and made a simplifying assumption that we would observe a symmetrical competitive relationship between the two plant species.

## Materials and methods

### Study locations

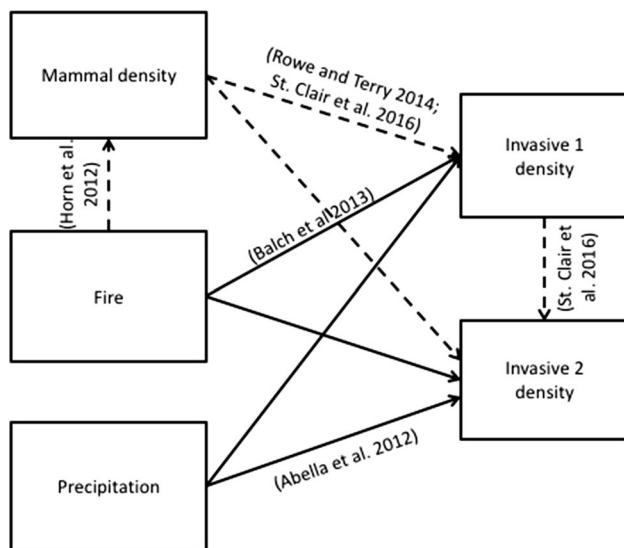
The first study site is located on an upland Mojave Desert site at Lytle Ranch, a property owned by Brigham Young University and partnered with the Nature Conservancy in the Beaver Dam Wash of southwest Utah (37°08'54"N, 114°00'51"W). To our knowledge, the site has not burned since European settlement but has had historic cattle grazing. The soils at the site are a sandy loam (Soil Survey Staff

2014) and desert pavement with the vegetation being typical of a mid-elevation (915 m) Mojave Desert shrub land dominated by *Larrea tridentata* (DC) Colville, *Coleogyne ramosissima* Torr, *Ambrosia dumosa* (A. Gray) Payne, and *Yucca brevifolia* Engelm. Much of the herbaceous intershrub vegetation is dominated by the non-native annuals *Bromus rubens* L., *Schismus arabicus* Nees, and *Erodium cicutarium* (L.) L'Hér. ex Aiton. The mean annual precipitation (1993–2013) of the site is 264 mm with a mean annual temperature of 16 °C (WRCC, Lytle Ranch Station). The kangaroo rat (*Dipodomys merriami*) is the most abundant rodent at the Mojave Desert research site.

The second study site is located in Rush Valley, in central Utah near Vernon, UT, USA (40°05'26.17"N 112°18'18.01"W, elevation: 1650 m). Long-term mean average temperature for Rush Valley is 8.6 °C with strong seasonality. 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<sup>-1</sup>. Soil at the study site is classified as a fine silty, mixed mesic Haplic Natrargid, Taylors Flat Loam. The study location at the time the experiment was initiated had little evidence of grazing with well-developed, intact soil crusts and showed no evidence of fire in the last several decades based on a well-developed, climax-shrub community dominated by Wyoming sagebrush (*Artemisia tridentata wyomingensis*) and bottlebrush squirrel tail (*Elymus elymoides*), a perennial bunchgrass. Two non-native plant species that were present but in low abundances before treatments were cheatgrass (*Bromus tectorum*) and Halogeton (*Halogeton glomeratus*). The most common rodent at our Great Basin research site is the deer mouse (*Peromyscus maniculatus*).

### Experimental design

In 2011, we established the same experimental design at both research sites. Each site has five blocks with a full factorial (2 × 2) design per block for a total of 20 plots to study the relationship between rodents and vegetation recovery post-fire. Each main factor plot was 30 × 30 m surrounded by a wire mesh fence that was buried 0.35 m and is 0.65 m above ground level. Half of the plots (N = 10) had rodents excluded by adding a 0.22-m metal flashing to the top of the wire mesh fence and through trapping in April, July, and October, the other half of the plots (N = 10) have access holes cut into the fence to allow rodent movement into and out of the treatment plots. In June 2011 in the Mojave Desert and September 2011 in the Great Basin, half of the plots were burned as a treatment (N = 10) leaving the other half of the plots unburned (N = 10). In the Mojave Desert, the fire was carried by accumulated annual grass litter, producing



**Fig. 1** Diagram of proposed structural equation model used to evaluate the direct and mediated effects of fire, rodents, and fall precipitation on two key invasive species (*Bromus rubens* and *Schismus arabicus* in the Mojave and *Bromus tectorum* and *Halogeton glomeratus*) in each desert ecosystem. Dashed arrows indicate purported negative interactions and solid arrows indicate purported positive interactions. Citations are for research that supports the hypothesized relationships

a patchy fire that was relatively of low intensity, producing variable mortality for perennial shrubs in the plots. The Great Basin site lacked significant annual grasses; therefore, weed-free straw was used as fuel. The fire was much more intense in the Great Basin than in the Mojave, producing 100% mortality of perennial shrubs and consuming all aboveground biomass. Each treatment was randomly assigned within each block prior to construction of the plots. Within each factorial plot, 2–3 precipitation shelters were constructed and nested within to manipulate the annual rainfall using a modification of the design used by (Yahdjian and Sala 2002). The three treatments present for rainfall manipulation were drought, where we excluded 30% of the annual precipitation ( $N=20$ ), a water addition of 30% of the 20-year long-term average ( $N=20$ ), and a shelter control ( $N=10$ ) for a total of 50 rainfall manipulation shelters at each site. The drought treatment was established based on forecasts of the decreases in soil moisture that would accompany a 2 °C warming in this region. The water-addition experiments were designed to mimic the wet conditions that occur during the wet phase of the Pacific Decadal Oscillation (Wang et al. 2012).

### Precipitation shelter design and construction

Each rain manipulation shelter was 2 × 3 m; the shelters were centered over one *L. tridentata* shrub in the Mojave Desert and over one or two *A. tridentata* shrubs in the Great Basin (Figure S1), in both locations the rain shelter frames were constructed prior to the prescribed fire. During construction of the shelters, a 0.30-m-deep trench was dug and the plot was lined on all four sides with metal flashing to help eliminate lateral water flow. To eliminate external water flowing into the sheltered area, 0.05 m of metal flashing was added to the already buried flashing on the uphill and side hill slopes. The downhill edge did not have the flashing to allow water to move off of the sheltered area to eliminate pooling of water. The sheltered areas for the treatments have an edge buffer of 0.4 × 0.4 m to give a central plot dimension of 1.6 × 2.6 m where all plant sampling occurred to minimize edge effects from the trenching or construction of the shelter. Shelters and their roofs were finished at the end of the spring of 2012 and covered the plots starting from the summer of 2012 to date. The roofs were 1.8 m from ground level sloping to 1.5 m from the ground. The shelters for drought treatments covered 40% of the surface area and empirical measurements indicate that this arrangement excludes approximately 30% of the annual rainfall. The slats in the water addition and control shelters were turned upside down to allow the full amount of the annual rainfall to enter the sheltered area. In the water-addition treatments, we added 30% more water than the long-term monthly average through the use of a gas pump irrigation spraying system.

All water for the addition shelters comes from groundwater wells near the research plots. The amount of water added to the sheltered areas change every month to follow the long-term monthly averages. Water was applied every 3 weeks and occurred throughout the year in the Mojave Desert and between April and November in the Great Basin because our site is inaccessible between December and April. For each plot we estimated the monthly and annual precipitation based on weather station data near the research plots. Volumetric water sensors (Decagon, Inc.) show that we have been effective in reducing or increasing soil water at 5-cm soil depth based on our treatment conditions.

### Vegetation monitoring

We measured density of all annual grasses beneath each sheltered area using 0.01 m<sup>2</sup> quadrats in the spring 2013–2015. At each location we made 16 measurements corresponding to cardinal directions stratified under the central shrub and in the inter-shrub space (N, NE, E, SE, etc.). At each cardinal direction we placed the 0.01 m<sup>2</sup> quadrat and counted the number of individuals rooted within each quadrat by species. We sampled all 100 shelters.

### Rodent trapping

Rodent trapping was done in April, July, and October each year to ensure that the exclosures were effectively excluding rodents. When rodents were caught in the exclosures they were then removed. Each rodent seasonal sampling occurred over a 3-day period (Horn et al. 2012). Sherman live-traps were baited at dusk and retrieved around dawn. We recorded rodent species, weight, and reproductive status. We ear-tagged the individuals so as to avoid double-counting the recaptures. Data are presented as the minimum number of rodents in a treatment plot.

### Data analysis

All data collected were averaged by rainout shelter for use in the statistical analyses. All data were scaled from their sampling frame size to 1 m<sup>2</sup> for ease of interpreting the data. Species density (individuals/m<sup>2</sup>) was our primary response variable. Burning was considered a binary variable in all models (burned = 1, or unburned = 0). Rodent treatment was included as a continuous variable measured as the annual average of minimum number of rodents present in a plot. Fall precipitation was included as a continuous variable measured as the sum of precipitation during September, October, and November of the preceding year. To evaluate the effectiveness of our small mammal treatments we conducted a Mann–Whitney rank sum test on the minimum number of small mammals in each plot for each year.

We used structural equation modeling (SEM) with the R package ‘piecewiseSEM’ (Lefcheck 2015) to estimate the relative importance of the direct and indirect drivers of invasive species densities. We fit linear mixed effects models using the nlme package in R and included block as a random intercept in each model (Pinheiro et al. 2016). We computed the conditional  $R^2$  ( $R_c^2$ , the proportion of variance explained by both fixed and random effects) using the method of Nakagawa and Schielzeth (2013) and report these for the two invasive species. Analyses were conducted for each year of sampling and the two deserts were analyzed independently. Chi-square test was used to determine how the interactions changed over time. Model fit was assessed using Fisher’s  $C$  statistic, where good-fitting models yield small  $C$  statistics and  $P$  values  $> 0.05$  (Lefcheck 2015). The same a priori model was fit to each ecosystem in each year. The model fit the data well in all cases, but the importance of each relationship changed over time in each ecosystem.

## Results

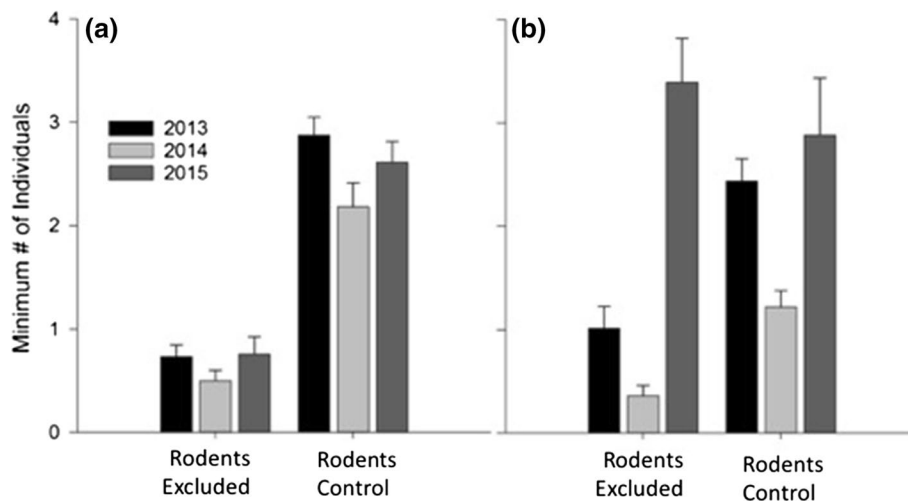
### Mojave Desert

Our rodent exclosures and trapping efforts were effective in reducing the number of rodents in the mammal treatment plots from a minimum number present of 2.56 individuals in the control to 0.66 individuals in the rodent exclusion plots (Fig. 2a, Table S1). Rodent numbers were not impacted by the burn treatments in any of the 3 years (Fig. 3, Table 1). The densities of the dominant, invasive

annuals at the Mojave Desert site (*Bromus rubens*, *Schismus arabicus*) were highly sensitive to the experimental treatments, but the importance and significance of the treatments changed over time.

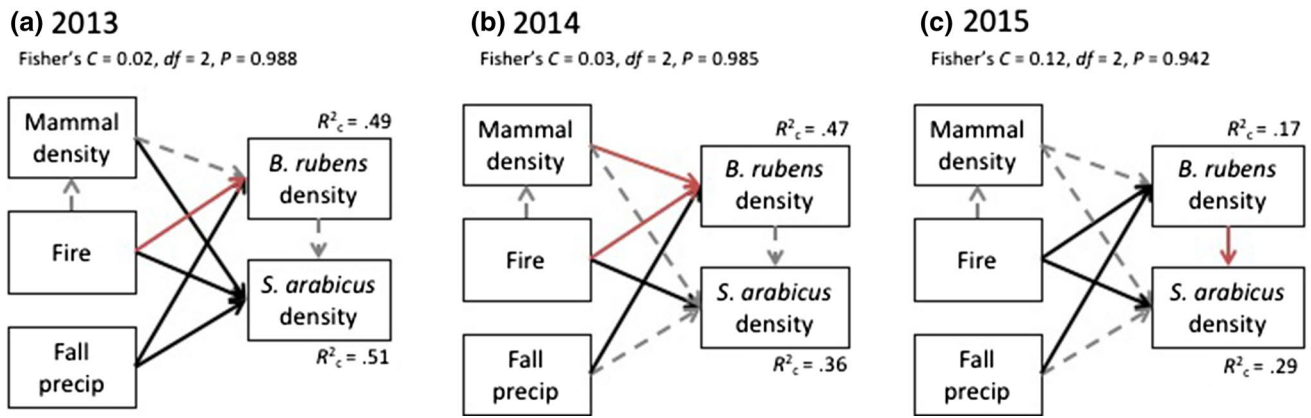
In 2013, 2 years after the burn, *S. arabicus* was most dense in areas that had been burned ( $P < 0.0001$ ; 71 individuals  $m^{-2}$  in burned areas vs 6.8 individuals  $m^{-2}$  in unburned areas), had higher fall precipitation ( $P = 0.023$ ), and that had higher rodent density ( $P = 0.074$ , 46 individuals  $m^{-2}$  in rodent control plots versus 32 individuals  $m^{-2}$  in rodent removal plots; Fig. 3a, S2). In contrast, *B. rubens* was most abundant in unburned plots ( $P = 0.021$ ; 1176 individuals  $m^{-2}$  versus 882 individuals  $m^{-2}$  in burned plots), and was positively impacted by fall rainfall ( $P = 0.009$ ). In 2013, rodents were not a predictor of *B. rubens* density.

In 2014, *S. arabicus* substantially increased in density and continued to benefit 3 years after the burn ( $P = 0.0021$ ; 1253 individuals  $m^{-2}$  in burned plots versus 593 individuals  $m^{-2}$  in unburned plots; Fig. 3b, S2). The magnitude and significance of the rodent benefit decreased compared to 2013, and the precipitation effect disappeared (Fig. 3a, b). *Bromus rubens* density declined from 2013 to 2014 and continued to be found at lower densities in burned plots ( $P = 0.0079$ ; 88 individuals  $m^{-2}$  compared to 196 individuals  $m^{-2}$ ) with rodents also reducing *B. rubens* density ( $P = 0.0069$ ; 100 individuals  $m^{-2}$  in rodent control plots versus 181 individuals  $m^{-2}$  in rodent exclusion plots). As a result, rodents indirectly influenced competition between the two annual grasses, promoting *S. arabicus* and suppressing *B. rubens*. The one factor that did favor *B. rubens* while



**Fig. 2** Median small mammal density in response to experimental removal of rodents in **a** Mojave Desert research site and **b** Great Basin Desert research site. Treatment plots are 30- × 30-m surrounded by a wire mesh fence that was buried 0.35 m and is 0.65 m above ground level. Rodent exclusion plots ( $N=10$ ) had rodents

excluded by adding a 0.22-m metal flashing to the top of the wire mesh fence and through trapping in April, July, and October, while control plots ( $N=10$ ) have access holes cut into the fence to allow rodent movement into and out of the treatment plots



**Fig. 3** Direct and indirect effects of trophic interactions, disturbance, and rainfall on the density of *Bromus rubens* and *Schismus arabicus* in the northeastern Mojave Desert for **a** 2, **b** 3, and **c** 4 years after

the controlled burn (2013, 2014, and 2015, respectively). Black solid lines are positive relationships and solid red lines are negative relationships ( $P < 0.05$ ). Dashed pathways are not significant

**Table 1** Path estimates, standard error, and  $P$  value for structural equation models for the 3 years of the experiment. Predictors include minimum number of rodents in the treatment plots (Min. Mammals),

Burn treatment, sum of precipitation in September, October, and November (Fall Precip), and *Bromus tectorum* density or cover (Brte)

Predictor	Response	2013			2014			2015		
		Estimate	SE	$P$ value	Estimate	SE	$P$ value	Estimate	SE	$P$ value
<b>Great Basin</b>										
Min. mammals	Brte	-36.28	17.63	0.0459	-85.702	117.090	0.468	12.306	26.417	0.644
Burn	Brte	28.26	44.199	0.5259	505.114	178.248	0.007	281.417	124.814	0.029
Fall precip	Brte	0.538	0.888	0.5476	5.571	3.835	0.154	2.363	1.305	0.077
Burn	Hagl	78.56	32.92	0.0217	568.647	173.967	0.002	-8.993	24.809	0.719
Min. mammals	Hagl	-29.05	13.66	0.0395	40.602	108.016	0.709	-7.076	4.992	0.164
Fall precip	Hagl	0.176	0.66	0.7913	5.641	3.520	0.117	-0.339	0.254	0.190
Brte	Hagl	0.011	0.109	0.9205	-0.025	0.136	0.855	-0.057	0.028	0.047
Burn	Min. mammals	-1.04	0.334	0.0033	-0.573	0.206	0.008	-4.373	0.264	0.000
<b>Mojave Desert</b>										
Min. mammals	Brru	-74.738	54.319	0.176	-55.077	19.387	0.007	0.676	2.654	0.800
Burn	Brru	-319.409	134.012	0.022	-119.250	42.765	0.008	12.519	6.663	0.067
Fall precip	Brru	15.376	5.581	0.009	4.274	1.021	0.000	0.318	0.146	0.035
Burn	Scar	63.266	12.283	0.000	581.719	177.215	0.002	131.622	39.935	0.002
Min. mammals	Scar	8.726	4.758	0.074	2.511	79.899	0.975	24.884	15.502	0.116
Fall precip	Scar	1.231	0.520	0.023	5.278	4.595	0.257	-1.052	0.885	0.241
Brru	Scar	-0.013	0.012	0.296	-0.740	0.561	0.194	-1.586	0.857	0.071
Burn	Min. mammals	-0.347	0.366	0.349	-0.213	0.318	0.506	-0.413	0.344	0.236

having no impact on *S. arabicus* in 2014 was fall precipitation ( $P = 0.0001$ ).

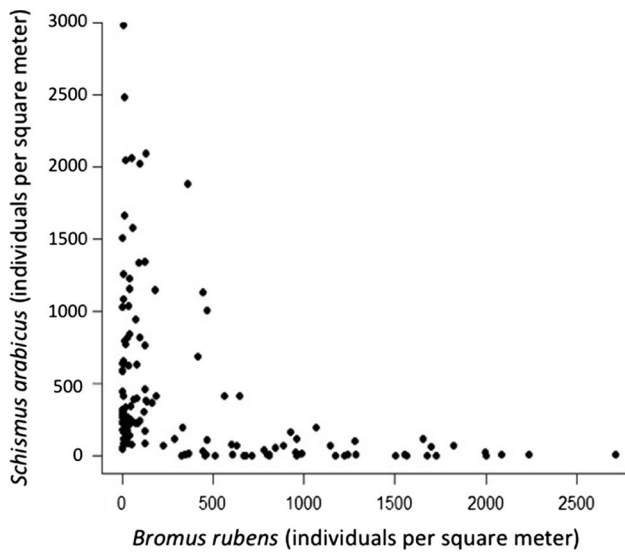
In 2015, the trophic effects disappeared, with rodent density having no correlation with density of either annual grass species. The fire effect continued to be a strong, positive predictor of *S. arabicus* density, with nearly a 50% increase in density in burned plots ( $P = 0.002$ ; 309 individuals  $m^{-2}$  compared to 207 individuals  $m^{-2}$  in unburned plots, Figure S2). There was also a weak positive effect of fire on *B.*

*rubens* as well ( $P = 0.067$ ). *Bromus rubens* continued to benefit from fall precipitation ( $P = 0.0347$ ; Fig. 2c). For the first time, there was a weak direct negative interaction between *B. rubens* and *S. arabicus* ( $P = 0.071$ , Figs. 2c, 4).

**Great Basin Desert**

Our rodent exclosures and trapping were particularly effective at reducing rodent density in the first 2 years of our





**Fig. 4** Relationship between *Bromus rubens* and *Schismus arabicus* density (individuals m<sup>-2</sup>) in the northeastern Mojave Desert

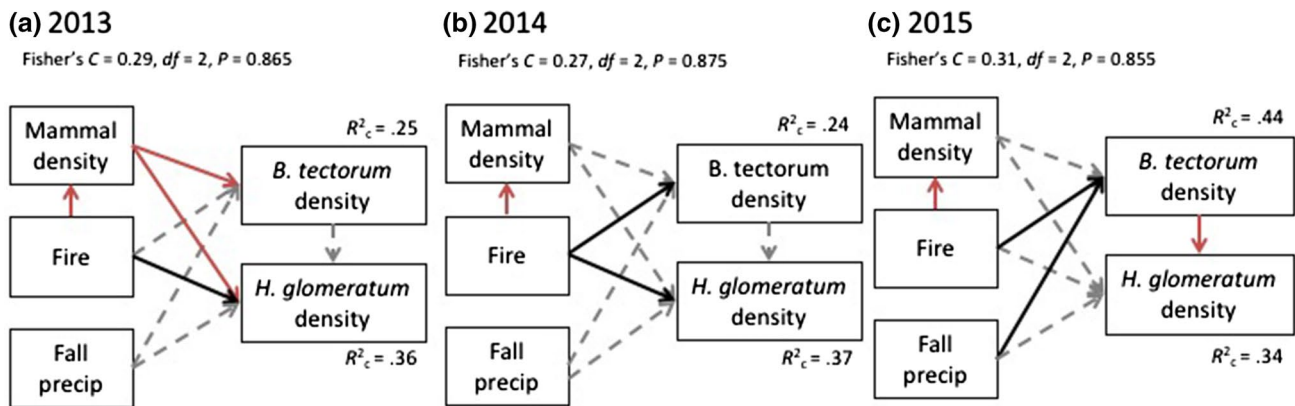
experiment (Fig. 2b,  $P < 0.001$ , Table S1). As is typical of these desert rodent communities there was substantial between year variability in rodent density. In 2015, there were no significant differences in rodent density, perhaps due to a large snowfall event that may have allowed rodents to re-invade the exclusion plots ( $P = 0.274$ ). In all 3 years of the experiment, the burn treatment significantly reduced the abundance of rodents (Fig. 5a–c).

In 2013, we observed that the burn had both direct and indirect positive effects on *H. glomeratus*. Fire was a major influence on *H. glomeratus* density ( $P = 0.0217$ , with burned plots having 110 individuals m<sup>-2</sup> while unburned

plots only had 0.75 individuals m<sup>-2</sup>, Figure S3). This was a consequence of both the direct effect of the burn and the mediation that occurred because the burn reduced mammal densities and *H. glomeratus* were negatively impacted by the presence of mammals (Fig. 5a). This indirect positive effect of fire mediated through rodents was also detected for *B. tectorum* (Fig. 5a). Mammals had a negative impact on *B. tectorum* densities in the first year ( $P = 0.0459$ ), reducing their density from 74 individuals m<sup>-2</sup> in the rodent control plots to 8.7 individuals m<sup>-2</sup> in the rodent removal plots.

In 2014, we no longer observed a mediated effect of the burn on invasives because rodents did not have a significant impact on either *B. tectorum* or *H. glomeratus* densities (Fig. 5b). However, the burn did continue to promote both invasives (Figure S3). There was a particularly notable increase in *B. tectorum* densities, with burned plots having 628 individuals m<sup>-2</sup> and unburned plots having 74 individuals m<sup>-2</sup> ( $P = 0.007$ ). For *H. glomeratus*, there were 532 individuals m<sup>-2</sup> in burned plots and only 1.25 individuals m<sup>-2</sup> in unburned plots ( $P = 0.0022$ ).

Fall precipitation became an important factor for either invasive for the first time in 2015, with increases in the amount of fall precipitation weakly promoting *B. tectorum* ( $P = 0.077$ ) while having no impact on the summer annual *H. glomeratus* (Fig. 5c). The burn continued to benefit *B. tectorum* ( $P = 0.0294$ ), although absolute densities decreased between 2014 and 2015. In 2015, densities of *B. tectorum* were 247 individuals m<sup>-2</sup> in burned plots and 19 individuals m<sup>-2</sup> in unburned plots. *Halogeton glomeratus* was no longer benefitted by fire in 2015, in part because we observed a strong competitive effect between *B. tectorum* and *H. glomeratus* ( $P = 0.0467$ ).



**Fig. 5** Direct and indirect effects of trophic interactions, disturbance, and rainfall on the density of *Bromus tectorum* and *Halogeton glomeratus* in the central Great Basin for a 2, b 3, and c 4 years after the controlled burn (2013, 2014, and 2015, respectively). Black solid

lines are significant positive pathways and solid red lines are significant negative pathways ( $P < 0.05$ ). Dashed pathways are not significant

## Discussion

Plant invasions, climate change, and changing fire regimes are global-scale phenomena and are occurring at unprecedented rates with far-reaching ecological and economic consequences for human societies (D'Antonio and Vitousek 1992; Vitousek et al. 1997). The direct cost of wildfires in the USA now averages \$1.5 billion annually with rehabilitation and indirect costs estimated to be significantly higher (WFLC 2009). Plant invasions in the USA are estimated to cost more than \$120 billion annually and over 40% of species on the threatened and endangered list are at risk because of invasions (Pimentel et al. 2000). This context motivated our three objectives so that we can identify interactions between biotic and abiotic controls over plant invasions in desert ecosystems. Fire in desert shrub lands clearly is important as they create niche opportunities for plant invasion (Shea and Chesson 2002), but here we show that these opportunities are modified by resource variability and trophic interactions.

Our first objective was to determine whether rodent herbivory directly reduced the density of aggressive invasive species and to what extent the influence of fire was mediated through changes in rodent communities. For both the Mojave Desert and Great Basin, we saw that rodents directly influenced the density of invasive plant species, particularly in the first years after the burn. However, by the fourth year after the fire, the rodent top-down effect was no longer significant. We only saw evidence of mediation at one site in 1 year—in the Great Basin in the second year after the burn. During this early establishment phase, reductions in rodent densities accompanying a fire can create opportunities for invaders to establish. In 2013, we saw that *Halogeton glomeratus* was both directly benefitted by the burn, likely due to the reduction of competition from native plants and the destabilization of biological soil crusts (Dettweiler-Robinson et al. 2013), and also benefitted because the fire reduced rodent density allowing seedlings to escape herbivory (Bowman 2015). Of particular note is that the effect of the fire on rodent numbers persisted in the Great Basin for all of the years that we monitored but that the rodent suppression of invasion was not apparent in these plots after the second year. In the Mojave Desert, we failed to detect any fire effects on rodent densities; therefore, we never had a mediated effect of rodents. One potential mechanism that could explain the differences between deserts is the ecology of the dominant rodents. The Great Basin is dominated by *Peromyscus maniculatus*, which is most often found in areas with high vegetation cover and is likely quite sensitive to fire, whereas *Dipodomys merriami* is the dominant rodent at our Mojave Desert site, and it prefers open habitat similar to that produced by our experimental fires (Horn et al. 2012, 2015b).

There are a number of studies that have shown that rodents can alter plant community assembly, but these studies were not conducted with an emphasis on post-disturbance landscapes. Brown and Heske (1990) found strong rodent control over species-specific plant establishment that varied depending on rodent presence and herbivore species composition. More recently, Allington et al. (2013) found that a decline in rodent granivory combined with ideal weather conditions to produce an irruption in the invader *Erodium cicutarium*. We found that rodent herbivory reduced the density of *B. rubens* while at the same time promoting *Schismus arabicus*, serving as a strong trophic influence on competition between these two invasive grasses. In the Great Basin, there was a lag in the establishment of *B. tectorum* and expansion after the fire. However, *B. tectorum* increased dramatically in only a single treatment condition—post-fire landscapes on the rodent removal plots—while post-fire landscapes with rodents present had much lower densities. In addition, *H. glomeratus*, after an initial establishment in burned, rodent removal plots (St. Clair et al. 2016), ultimately was only found in high density and cover in those plots that had both been burned and where rodents were present. For all of the species we examined, fire created a context in which competitive and top-down biological interactions determined density of critical invasive species. Shea and Chesson (2002) present a model where disturbances are key to increasing opportunities for invasions—as we clearly see with fire in the two desert ecosystems of this study—but that those niche opportunities may be further modified by resource variability, including fall precipitation in our case, and trophic interactions such as competition or rodent herbivory.

Our second objective was to see if increases in soil resources, particularly soil moisture, could swamp biotic resistance to allow invasives to escape consumer controls. We found that there were both temporal and species-specific responses to changes in rainfall. In the Great Basin, it was not until the final year of the experiment that we observed an increase in plant density with increases in water availability, and even then it was only observed in *Bromus tectorum* and not with *Halogeton glomeratus*. In that final year, we did not see a significant rodent effect on either species. As a result, it is inconclusive whether resource abundance can overcome rodent control on annual invasive establishment. In the Mojave Desert in 2013 and 2014, the burn and the presence of rodents reduced *Bromus rubens* abundance by more than 50% (Figure S2). However, our precipitation treatments promoted the establishment of *B. rubens*. When rodents were excluded, precipitation additions more than doubled the density of *B. rubens* compared to drought. In the presence of rodents, this increase was a more modest 42%. *Bromus rubens* density in the water addition

treatments with mammals present were over 100 individuals  $m^{-2}$  lower than the control treatments with mammals excluded, indicating that a 30% increase in precipitation was not sufficient to offset the impacts of rodents. Our results are similar to Allington et al. (2013), who applied a niche-opportunity framework to show that the interaction between resource availability and trophic dynamics best explains invasive species density and cover. The ideal time to see expansions in invasive annuals was during seasons when rodent numbers were suppressed and there was high resource availability both due to disturbance and climate variability.

Our third objective was to determine if there are predictable and consistent changes in the relative role of resources and trophic interactions in years following fire when comparing the Mojave desert and the Great Basin desert? We observed that fire is a consistent and large determinant of the density of invasive species. While trophic controls, competition and resource alteration all influenced the abundance of invaders, the most consistent driver of invasive species success is disturbance. In both systems, we saw that rodents played an important role early in determining invader density, serving to reduce densities of three of our four target species. In both systems, the rodent effect occurred early in the study and was no longer significant in the final year of the study. The one species that was benefitted by the presence of rodents was *S. arabicus*, likely through the suppression of competitors like *B. rubens*. Finally, there are species that are able to capitalize on increases in resources and possess traits that may allow them to respond to a changing resource environment, so long as there are open spaces caused by disturbance and biotic resistance is low. In the Great Basin, *B. tectorum* was the only species to respond to changes in soil water availability, while *H. glomeratus* density was insensitive to experimental changes in soil water. This may be a consequence of the different life history strategies between these two species, with *B. tectorum* germinating in the fall, persisting through the winter, and flowering and setting seed by early summer. In contrast *H. glomeratus* germinates in the spring and persists through the summer, flowering and setting seed in late summer. In the Mojave Desert, we saw that in the initial establishment phase, both *B. rubens* and *S. arabicus* responded to increases in soil moisture but only *B. rubens* continued to be positively impacted by increases in soil moisture over the entire course of the experiment. Kempel et al. (2013) showed that traits controlling establishment success among invasives shifted with time after disturbance, with initial success determined by propagule pressure while traits relating to biotic interaction such as those allowing for escape from predation or increased competitive traits become more important over time.

## Conclusions

This work furthers our understanding of how seed predation or seedling herbivory by rodents can alter patterns of non-native plant establishment and community assembly (Bowman 2015; Connolly et al. 2014; Maron et al. 2012; Reader 1993). This experimental approach demonstrated invasive annuals were potentially sensitive to alterations in soil resources; these responses tended to be strongly mediated by competitive interactions or patterns of granivory and herbivory (Bowman 2015). Four years after our experimental fire, very little of the ultimate plant community was explained by inter-annual differences in rainfall or intra-annual differences in water treatments. Rather, *Schismus arabicus* ultimately dominated the Mojave Desert plots that had been burned because it competitively displaced *B. rubens*. However, *B. rubens* was able to remain a significant part of the community when rodents were excluded. In the Great Basin, increases in fall rainfall did increase *B. tectorum* cover, but only when rodents were excluded. However, at a large scale, rodents were critical in determining whether *B. tectorum* dominated the post-fire landscape or *H. glomeratus* was the dominant. Understanding seed or seedling preference including a focus on seed traits (e.g., seed mass, architecture) or palatability (e.g., oxalate concentrations, secondary compounds and nutrient content) as well as rodent densities and community composition will be critical in forecasting invasion success in disturbed landscapes.

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**Author contribution statement** RAG and SBS conceived and designed the experiments. RAG, RCO, TBB, and SBS performed the experiments, RAG, AR, and DCL analyzed the data. RAG and RCO wrote the manuscript; other authors provided editorial advice.

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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