



Rodent competition and fire alter patterns of mound and disk formation of western harvester ants

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Abstract

Consumers exert top-down controls on dryland ecosystem function, but recent increases in fire activity may alter consumer communities in post-fire environments. Native consumers, including ants and rodents, likely have critical roles in defining post-fire plant community assembly and resilience to biological invasions. This study aimed to understand how western harvester ants (*Pogonomyrmex occidentalis*) that form mounds and large vegetation-free disks that significantly influence plant community structure in the Great Basin Desert respond to fire and rodent community abundance. We tested this by installing treatment plots that excluded or allowed rodents and were burned or unburned in a full factorial design. We measured ant disk and mound size and density in each experimental plot. Fire increased ant mound density by 126% compared to unburned plots. Rodent presence decreased mound density by 59%, mound diameter by 13%, and mound height by 166%. We also show an interaction where the adverse effects of rodents on ant disk density were greater in burned than in unburned plots. The results suggest that booms in rodent populations are likely to have suppressive effects on ant mound and disk formation in native shrublands but that harvester ants may be released from rodent competition with the emergence of invasive grass-fire cycles.

Keywords Competition · Granivory · *Pogonomyrmex occidentalis* · Disk space · Resilience

Introduction

In biological communities, consumer-driven processes structure plant community assembly and thus regulate how ecosystems function. Many of these consumers are considered ecosystem engineers who create, modify, or maintain habitats (Jones et al. 1996). Ants affect entire communities by altering soil's physical and chemical properties and changing plant community structure directly through vegetation removal and seed dispersal (Rissing 1986; Soule

and Knapp 1996; MacMahon et al. 2000; Detrain and Tasse 2000; De Almeida et al. 2020). They also affect primary productivity and biodiversity by altering rates of nutrient cycling (Boulton et al. 2003; Wills and Landis 2018). Ants structurally modify landscapes through mound formation and, in some cases, by removing vegetation to form large denuded areas around their mounds, known as disks (Sharp and Barr 1960). Disks change soil nutrients, temperature, and water properties that affect patterns of plant community structure (Carlson and Whitford 1991). Ant disk rims are characterized as having high plant productivity and seed production, compensating for the lack of vegetation in the disk interior (Whitford and DiMarco 1995; Nicolai and Boeken 2012; Gosselin et al. 2016; Uhey et al. 2024). The impacts ants have on biological communities are numerous and can be altered by disturbances, climate extremes, and trophic interactions (Barbosa et al. 2015; St. Clair et al. 2016). Competition between consumers also alters how they influence biological communities (Brown et al. 1979; Davidson et al. 1984; Valone et al. 1994).

Rodents compete with ants for space and food resources and create strong top-down community effects via herbivory,

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Western harvester ants benefit from greater fire activity and lower rodent abundance with significant interactions between them in which fire tends to increase some of the negative impacts of rodents.

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seed dispersal, burrowing, and their impacts on nutrient cycling (Ordóñez and Retana 2004; Ness and Bressmer 2005; Broncano et al. 2008). Experimental exclusion of ants or rodents can increase abundance in the other group due to competition release (Brown et al. 1979). Rodents can negatively impact ants through direct aggression toward mounds in order to access ant seed caches (Wiernasz et al. 2014; Cole et al. 2022). Ants have been shown to limit the dispersion and burrowing activities of rodents (Panteleeva et al. 2016), and both species can limit each other's access to seeds through exploitative competition (Brown et al. 1979; Valone et al. 1994). However, the idea that rodents and ants vigorously compete for seed resources has been disputed; rodents prefer larger seeds, while ants prefer smaller seeds (Connolly et al. 2014; Day et al. 2018; Martyn et al. 2022). Rodent activity can increase the abundance of smaller seed-producing species that ants tend to prefer (Brown et al. 1979; Johnson 2001; Bishop et al. 2020). In the Sonoran Desert, the experimental exclusion of rodents led to declines in ant populations through competition for food resources (Davidson et al. 1984). However, there was little evidence in the Great Basin Desert that rodent exclusion significantly affected ant abundance (Day et al. 2018), suggesting that interactions between rodents and ant consumers are dependent on overlapping resource use in that system and whether resources are limiting. Understanding how ants respond to shifts in rodent population is ecologically relevant because rodent populations fluctuate over time in response to climate variability, shifts in plant community composition, disease cycles, and disturbance (Whitford 1976; Brown and Heske 1990; Shenbrot et al. 2010; Sharp Bowman et al. 2017a). Further research is needed to thoroughly investigate the effects of shifting rodent populations on ant communities across time. Understanding these interactions is particularly challenging due to the increased frequency of human-driven ecological disturbances that may change the nature of the interactions between ants and rodents.

Changes in disturbance regimes can dramatically alter ecosystem structure by modifying consumer-driven processes. Human activities have created novel fire regimes through fuel management, the introduction of non-native plants, and increased ignitions that can result in state changes in vegetation (Westerling et al. 2006; Turner 2010). Increasing fire size and frequency can alter the top-down effects of consumer communities (Burkepile et al. 2016). Reed et al. (2004) demonstrated that burned desert landscapes experienced increased granivory by vertebrates and decreased granivory by invertebrates due to altered habitat conditions (Reed et al. 2004; Holbrook et al. 2016). Fire affects ant activity and the plant community processes they mediate (Day et al. 2018). Ants can affect how vegetation recovers after fire as disk edges promote plant regeneration (Nicolai 2019). Ant response to fire varies by species, with

some increasing in abundance while others decrease (Ostoja et al. 2009; Day et al. 2018), which can result in decreased species richness and diversity but higher total abundance (MontBlanc et al. 2007). These changes are likely driven by indirect effects of fire on the plant community (Holbrook et al. 2016). Harvester ants may be particularly resilient to fire because cleared disk spaces prevent fire from reaching the nest (Zimmer and Parmenter 1998). Western harvester ants (*Pogonomyrmex occidentalis*) are abundant in the Great Basin Desert and have shown positive responses to fire and expansion of annual grasses that are facilitated by fire (Holbrook et al. 2016; Day et al. 2018). Rodent responses to fire vary by functional group; bipedal species tend to increase in abundance due to more open habitat, while quadrupedal species, which are abundant in the Great Basin, are negatively affected by the loss of vegetation cover (Horn et al. 2012; Sharp Bowman et al. 2017a, b). Both rodents and fire are shown to affect ants in desert ecosystems, but further research is necessary to show how these effects interact and vary over time.

The Great Basin Desert is a semi-arid ecosystem where rodents and western harvester ants both play critical ecological roles (Uhey and Hofstetter 2022). Ants and rodents exhibit top-down effects through granivory and herbivory that structure Great Basin plant communities (St. Clair et al. 2016). Rodent populations in the Great Basin naturally fluctuate (Sharp Bowman et al. 2017b); therefore, competition between rodents and ants varies over time. The impacts of ants and rodents on one another are well known, but we know less about how the competition between rodents and ants is affected by fire and the consequent effects on plant communities. Invasive grass-fire cycles have increased fire return frequencies in the Great Basin (D'Antonio and Vitousek 1992; Menakis et al. 2002), exposing ants and rodents to novel disturbance regimes. As a result, the Great Basin Desert is an ideal study system to investigate the interactions between western harvester ants, rodents, and changing wildfire regimes. Understanding these interactions is likely to provide valuable insights into the resilience of desert ecosystems in the face of anthropogenic change.

Our study aims to test the effects of fire and rodent exclusion on harvester ant mound and disk formation and maintenance over time. Evidence suggests that ants and rodents can compete for resources both directly, through acts of aggression, and indirectly through exploitative competition (Brown et al. 1979; Valone et al. 1994; Wiernasz et al. 2014; Day et al. 2018; Cole et al. 2022). Therefore, we predict that rodent exclusion will increase ant mound, disk size, and density. Previous work has shown that ant disks are resilient to fire because of vegetation clearing around the mound (Zimmer and Parmenter 1998) and that harvester ant disk density increases in burned areas that have become dominated

by cheatgrass (Holbrook et al. 2016). Therefore, we predict that fire will positively affect ant mound, disk size, and density. We know relatively little about how fire and rodents might interact to affect harvester ants. We hypothesize that fire will shift vegetation characteristics and food resources, thereby increasing competitive interactions between rodents and ants. Thus, we expect rodents to have a greater negative effect on ants in burned areas than in unburned areas.

Methods

Study area

The study area is in Tooele County, Utah, USA (40.090575, –112.304993), on the eastern side of the Great Basin Desert. The dominant vegetation is Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) and bottlebrush squirreltail (*Elymus elymoides*). The invasive species *Bromus tectorum* and *Halogeton glomeratus* are also found at the site. Common rodent species found at our study site included *Peromyscus maniculatus*, *Dipodomys microps*, and *Perognathus parvus* (Sharp Bowman et al. 2017a). From 2010 to 2022, the mean daily temperature was 9.16 °C, and the site received an average of 261 mm of rain each year (PRISM Climate Group).

Western harvester ants are the most abundant ant species in the area, with nest densities of 3–97 disks per hectare (Uhey and Hofstetter 2022). Western harvester ant mounds are regularly spaced and are at the highest density on sandy loam soils on south-facing slopes (Crist and Wiens 1996). Harvester ants forage on small-seeded annual plants (MacMahon et al. 2000) and, on average, travel ~10 m from the nest to forage (Crist and MacMahon 1991). Harvester ants tend to select native seeds over cheatgrass seeds but have been shown to increase their use of cheatgrass when other seeds are limited (Robertson and Schmasow 2018). Our treatments did not inhibit ant movement outside of the study plots, so they potentially could have foraged beyond the plots' boundaries.

Experimental design

Five 60 m × 60 m treatment blocks within the study area were divided into four treatment combinations per block, so each plot measured 30 m × 30 m (see Fig. 1). Experimental blocks were left approximately 50 m apart from one another. Treatment combinations were randomly assigned. Each block had four treatment combination plots: burned-rodent exclusion, burned-rodent access, unburned-rodent exclusion, and unburned-rodent access. Experimental burns were conducted in September 2011; over 99% of living vegetation was removed by fire. Each plot was fenced using 1 m tall,

welded wire. To prevent rodents from getting into exclusion plots, fences were trenched so that 30 cm extended below the ground to prevent rodents from burrowing, and 70 cm remained above the soil surface. Metal flashing was attached at the top of the fence on exclusion plot treatments to prevent rodents from climbing over the fencing. Rodent access plots were fenced similarly, except there was no flashing, and 12 × 10 cm openings were cut into the fencing every 4 m to allow rodents access into the plot. In rodent exclusion plots, rodents were removed during three trapping events each year to maintain the treatment effect (Fig. 2). From 2011 to 2023, rodent exclusion plots averaged 1.05 individual rodents per trapping event compared to 2.63 in rodent access plots (unpublished data).

The study plots used have been part of ongoing experiments investigating the effects of fire and rodent exclusion on biological communities of dryland ecosystems. Our findings may be due to the indirect effects of treatments that have occurred over time. Potential mechanisms of indirect effects could include increased plant density and biomass after fire (Stanton et al. 2023), changes in invertebrate diversity and abundance due to fire (Day et al. 2019), increased invasion, and decreased rodent abundance in burned plots (Gill et al. 2018; St. Clair and Bishop 2019), and increased invasion and lower plant diversity due to rodent exclusion (St. Clair et al. 2016).

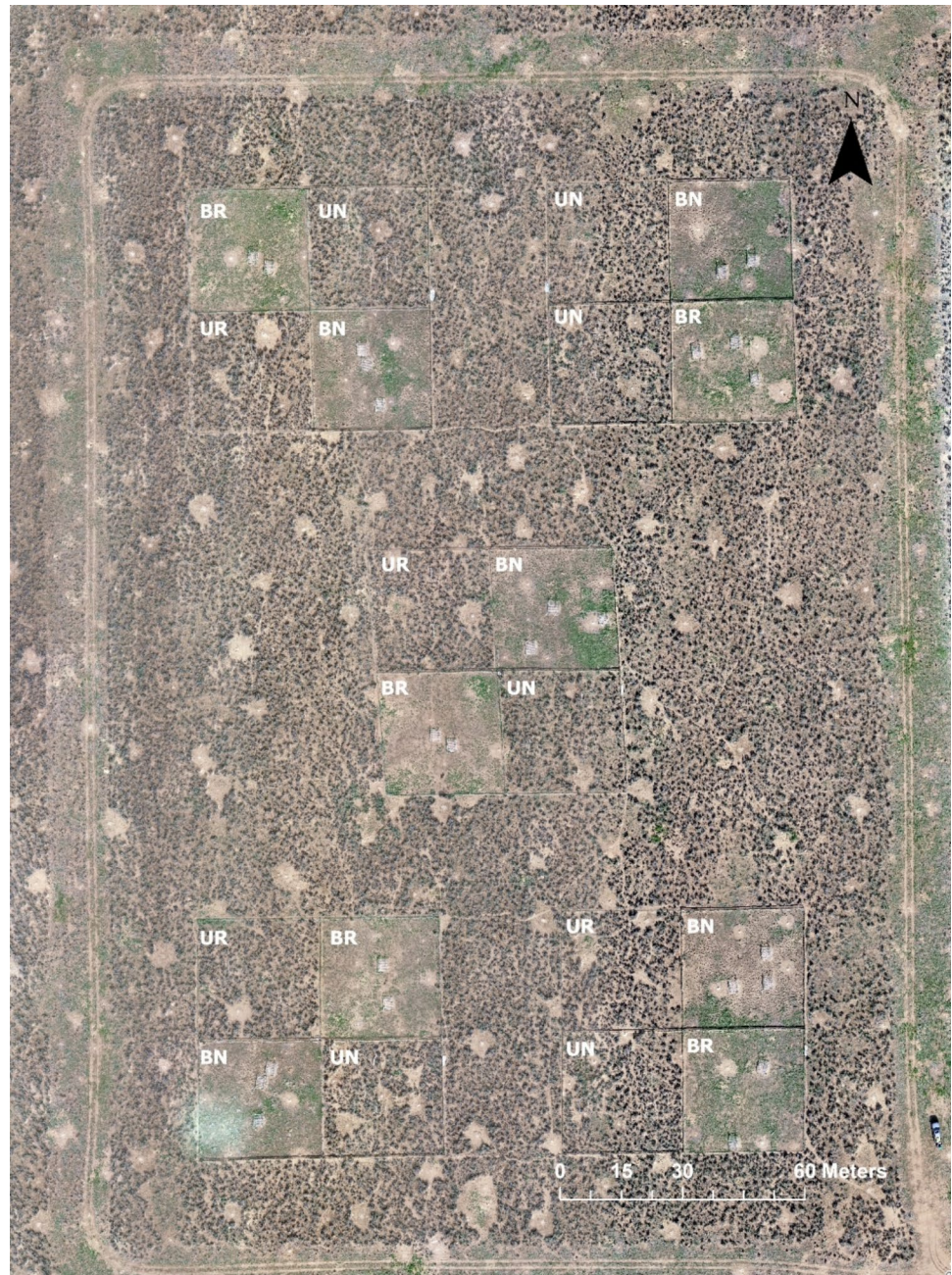
Data collection

We collected data on 17 September 2022, 11 years after the treatments were installed. We measured the size of individual ant disks within each plot and recorded the diameter of the ant disk, the diameter of the ant mound, and the height of the ant mound.

Data analysis

We included the mean number of ant mounds per plot, ant mound height, ant mound diameter, and ant disk diameter as response variables in our statistical models. Independent variables included experimental burn and rodent exclusion. We chose different statistical models for different dependent variables based on the distribution of the data. We evaluated mound height and diameter using both ANOVA and a non-parametric Scheirer Ray Hare test, as a Shapiro–Wilk test did not indicate a clear normal distribution. ANOVA is robust against non-normality with sufficient sample sizes (Glass et al. 1972), but to ensure there were no false positives, we first reported findings on the Scheirer Ray Hare test, and then if an interaction effect was shown, we used ANOVA to perform a post hoc Tukey test to evaluate which plots were different from each other. We only used two-way ANOVAs for ant disk density and diameter as the distributions were normal and all assumptions were met. Again,

Fig. 1 Aerial image of the experimental design at the study site in 2022 with harvester ant disks being a dominant feature throughout the landscape. B: burned, U: unburned, R: rodents present, N: rodents excluded



interactive effects were investigated using a post hoc Tukey test. All statistical tests used the experimental block as a random effect. All statistical analyses were performed in program R (R CoreTeam 2020).

Results

Mound density

Rodent exclusion and fire both significantly influenced ant mound density. Rodent presence decreased ant mound

density by 59% compared to rodent exclusion plots ($P < 0.05$) (see Fig. 3A). Fire increased mound density by 126% compared to unburned plots ($P < 0.05$) (see Fig. 3A). The effects of rodents on mound density varied by burn status ($P = 0.07$). Rodent presence decreased mound density more in burned plots than in unburned plots (post hoc Tukey test $P < 0.05$) (see Fig. 3A).

Mound and disk dimensions

Rodent presence and fire affected mound and disk dimensions, but the effects were different. Rodent presence

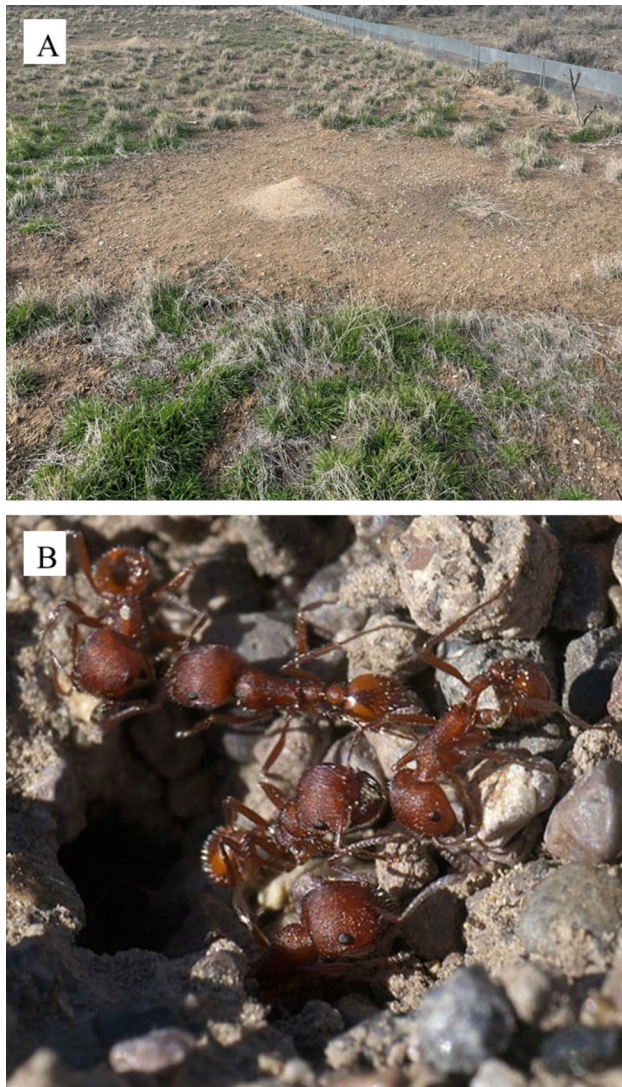


Fig. 2 **A** Photograph of a western harvester ant mound and disk within the study plot, with rodent exclusion fencing visible in the background. **B** Western harvester ants at a mound entrance

decreased mound diameter by 13% compared to plots with rodents absent ($P < 0.05$) (see Fig. 3B). However, rodent presence had no effect on disk diameter ($P = 0.15$) (see Fig. 3C). The effect of fire on mound diameter was not significant ($P = 0.25$) (see Fig. 3B). However, disk diameter decreased by 32% in burned plots compared to unburned plots ($P < 0.05$) (see Fig. 3C). The rodent by fire interaction was not significant for mound ($P = 0.69$) or disk diameter ($P = 0.68$) (see Fig. 3B, C). Ant mound height decreased by 166% in rodent access plots compared to rodent exclusion plots ($P < 0.05$) (see Fig. 3D). Fire did not significantly alter mound height ($P = 0.37$) (see Fig. 3D). There was evidence of an interactive effect between fire and rodents ($P = 0.07$), in which the negative effect of rodent presence on mound height was greater in

unburned plots than in burned plots (post hoc Tukey test $P < 0.05$) (see Fig. 3D).

Discussion

Study results indicate that changing fire regimes and fluctuating rodent populations have contrasting effects on western harvester ants in the Great Basin Desert (see Fig. 3). Our predictions were generally supported in that fire had a positive effect on ant mound and disk characteristics, while rodents had a negative impact with ant responses to rodents being dependent on whether the plot was burned or not. Rodent presence decreased ant mound size and disk density (see Fig. 3). Fire increased ant disk density, while disk size decreased in burned areas (see Fig. 3). The effects of rodents on ant disk density may be greater in burned than unburned areas (see Fig. 3). These results suggest that western harvester ants demonstrate resilience to changing fire regimes and are sensitive to shifts in rodent abundance in desert ecosystems.

Fire effects on ants

Fire did not affect mound height but strongly increased the number of disks formed in our experimental plots (see Fig. 3). Fire may increase disk density by reducing forbs, bunch grasses, and shrub cover and opening more space for ants to establish their vegetation-free disks (Sneva 1979). Furthermore, the reduction of native plant cover facilitates the establishment of *Bromus tectorum* (cheatgrass) in our study system (D'Antonio and Vitousek 1992). Within our study, burned-rodent exclusion plots were entirely dominated by cheatgrass (St. Clair et al. 2016), which has been associated with increased disk density of harvester ants (Ostoja et al. 2009; Gosselin et al. 2016). Cheatgrass may be used as a food source by harvester ants (Holbrook et al. 2016) and is relatively easy to remove to clear disk space compared to woody vegetation.

While disk density increased significantly in burned areas, fire resulted in modest decreases in disk size (see Fig. 3). The reduction of ant disk size in post-fire environments may be partially driven by an increase in the prevalence of invasive annual grasses (Sneva 1979; St. Clair et al. 2016; Day et al. 2018). Ants maximize activity by clearing vegetation to increase solar radiation and temperature. Fire-driven conversion of native shrubs to cheatgrass reduces shade, requiring less vegetation removal by ants to maintain optimal soil temperatures (Bucy and Breed 2006). As a result, ants may reduce denuded areas while still maintaining optimal soil temperatures (Clark and Comanor 1975).

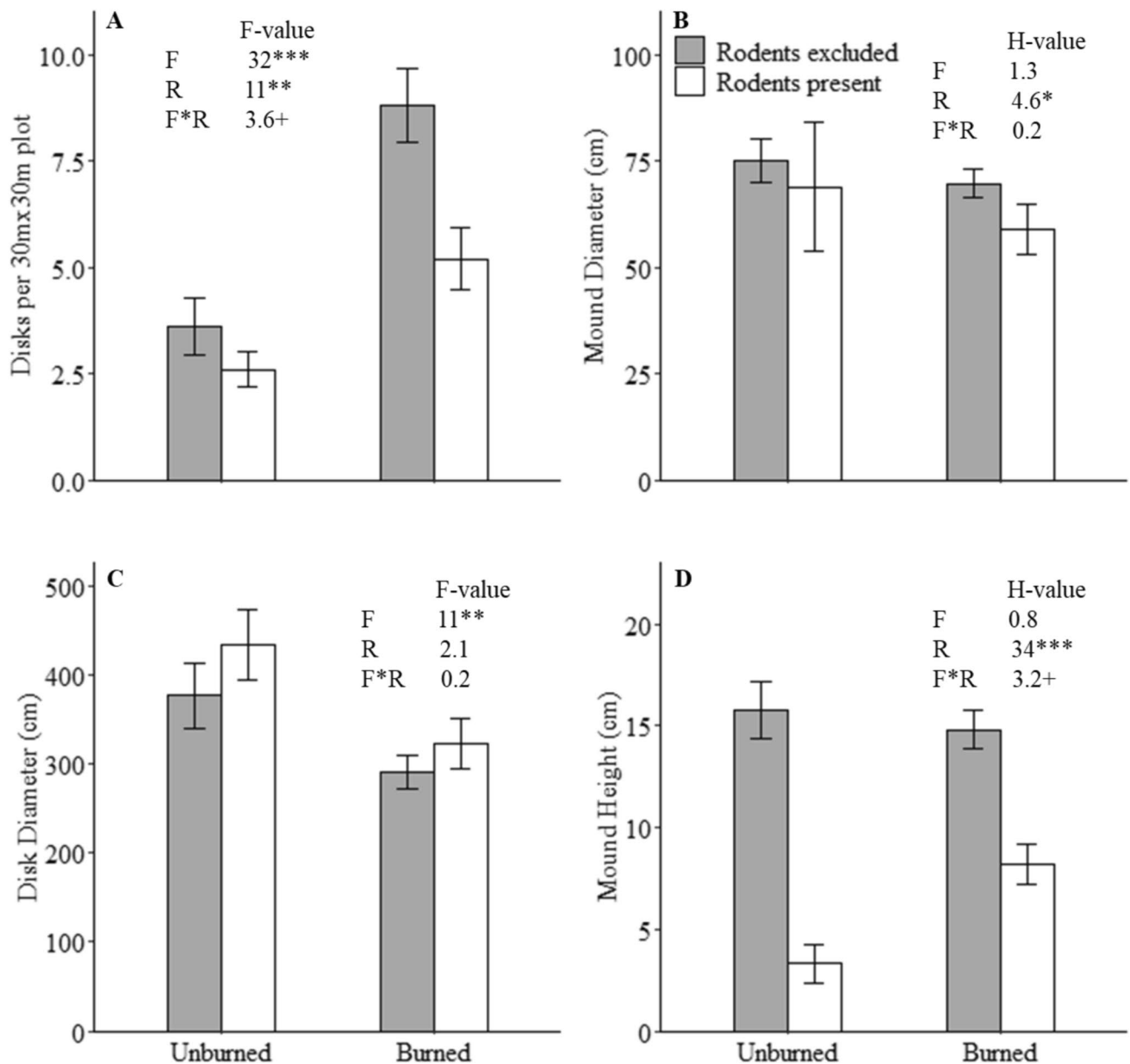


Fig. 3 Effects of fire and rodent exclusion on ant mount and disk characteristics. **A** Ant disk density measured as the number of ant disks per 30 m x 30 m plot (cm), **B** mound diameter (cm), **C** ant disk diameter (cm), and **D** mound height (cm). Mean values are presented with \pm SE. Significance indicated with + ($P < 0.1$), * ($P < 0.05$),

** ($P < 0.01$), *** ($P < 0.001$). Burned, rodents excluded: $n = 44$; burned, rodents present: $n = 26$; unburned, rodents excluded: $n = 18$; unburned, rodents present: $n = 13$. Degrees of freedom for all statistical tests were 1. Panels **B**, **D** present H -statistics rather than F -statistics as produced by the Scheirer Ray Hare test

Rodent effects on ants

Rodent exclusion increased ant disk density, mound height, and mound diameter (see Fig. 3). Previous research has provided varied results surrounding the interactions between ants and rodents in desert ecosystems. Rodents and ants compete for seed resources in desert communities (Brown et al. 1979; Valone et al. 1994), which could explain the negative effects of rodents on measures of ant

disks and mounds in our study (see Fig. 3). Competition with rodents may be limiting ant population size, resulting in decreased ant disk density and mound height. These results are in contrast with previous studies, showing that rodents had minimal effects on harvester ants in the Great Basin early on in our study system (Day et al. 2018). Rodent populations fluctuate dramatically, so the effects of rodents on ants likely vary across space and time. In contrast, rodent exclusion can shift vegetation dominance

from ant-preferred forage to rodent-preferred forage, increasing their competitive interaction (Davidson et al. 1984; Samson et al. 1992). Our results differ from those of Davidson et al. (1984) in the Sonoran Desert in that we saw long-term positive effects of rodent exclusion on western harvester ants. Similar to the effects of fire, rodent exclusion increased cheatgrass cover in our experimental plots (St. Clair et al. 2016), which has been positively correlated with increased harvester ant activity (Ostoja et al. 2009; Holbrook et al. 2016).

The impacts of rodents on ants may be altered through human influences on desert ecosystems. The effects of rodents on ant disk density were greater in burned areas than in unburned areas (see Fig. 3). Fire frequency and severity have been increasing in the Western United States, coupled with the invasion of non-native grasses has led to dramatic changes in ecosystem composition (D'Antonio and Vitousek 1992; Abatzoglou and Kolden 2011; Steers and Allen 2011), which could lead to higher levels of competition between ants and rodents. Ant nests can contain substantial seed caches, which may lead to rodents targeting seed caches as food resources become more limiting in post-fire environments (Clark and Comanor 1975; Wiernasz et al. 2014; Cole et al. 2022). Rodents typically prefer larger seeds, while ants mainly predate on smaller seeds (Davidson et al. 1984; Martyn et al. 2022), but when the vegetation community is reduced to one dominant species, competition between ants and rodents can increase (Brown et al. 1979). Ant disk rims promote the regrowth of vegetation after fires, which may result in amplified competition for limited resources along the rims of the ant disk (Nicolai 2019). The underlying cause of the interactive effect of fire and rodents is likely increased competition caused by the transition of vegetation states after fire (Brown et al. 1979; Holbrook et al. 2016), along with decreased rodent abundance in burned areas (Sharp Bowman et al. 2017b).

Conclusion and synthesis

Harvester ants are a keystone species in western US deserts (Gosselin et al. 2016) and are likely to be responsive to dramatic anthropogenic changes occurring in arid ecosystems. In the Great Basin Desert, changing fire regimes are threatening biodiversity by facilitating transitions from diverse shrub and perennial grassland communities to cheatgrass-dominated systems (D'Antonio and Vitousek 1992). Rodents provide resistance to these state transitions and thus are critical for maintaining biodiversity in these regions (St. Clair et al. 2016). Harvester ants' positive response to fire (see Fig. 3) suggests that they may be relatively resilient to shifting fire regimes and may even benefit from post-fire grass invasions. The negative impacts of rodents on ants (see Fig. 3) demonstrate the complex interplay within the

biological community where fire facilitates invasion but positively impacts ants, while rodents prevent invasion and yet negatively impact ants. In summary, changes in fire regimes positively impact ants and increase their effects on desert communities, while increasing rodent populations will decrease the effects of ants in the Great Basin Desert.

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Author contribution statement SBS, RP, and TBBB conceived and designed the experiments. RP collected and analyzed the data. RP and SBS wrote the manuscript; TBBB edited the manuscript.

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Data availability The datasets used during the current study are available from the corresponding author upon reasonable request.

Code availability Not applicable.

Declarations

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

Consent to participate Not applicable.

Consent for publication Not applicable.

Ethical approval All capture and handling methods were approved by the Institutional Animal Care and Use Committee (IACUC) of Brigham Young University (Protocol Numbers 090302 and 120202). All applicable institutional and/or national guidelines for the care and use of animals were followed.

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