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The Responses of Ants and Other Invertebrates to Fire and Rodent Activity in North American Deserts

Joshua David Day

A thesis submitted to the faculty of
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Master of Science

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ABSTRACT

The Responses of Ants and Other Invertebrates to Fire and Rodent Activity in North American Deserts

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Master of Science

Human activities are increasing the size, frequency and severity of disturbance across earth's ecosystems including deserts. Exotic annual grasses have altered fire regimes by increasing the size, frequency, and severity of fires in these systems. Invertebrates make up a large proportion of ecosystem diversity, provide a wide range of ecosystem functions, and are good indicators of ecosystem function and resilience. Ants are particularly good indicators of ecosystem stability. The ability of rodents to modify plant community structure post-fire, could result in rodent communities having important indirect effects on invertebrate communities. In chapter 1 we report changes in ant forager abundance and diversity with fire and rodent treatments over a three year period in the Great Basin. We found that while rodents had significant effects on the plant community in burned plots, this did not affect the ant community. Fire, however played a significant role in determining ant species richness and Shannon's diversity index. Ant richness and diversity were reduced in burned areas compared to unburned areas. Total ant forager abundance was unaffected by fire, however, the abundance of the most common ant species, *Pogonomyrmex occidentalis*, increased in burned areas. The overall abundance of the other species was reduced in burned areas. We saw increases in the densities of *P. occidentalis* mounds in burned areas, but the average size of those discs decreased. The total area occupied by *P. occidentalis* mounds remained equal between burned and unburned plots. In chapter 2 we compare the abundances of different groups of invertebrates, as well as the abundances and diversity of the ant communities, between fire and rodent treatments. We then compared how those responses differed between sites in the Great Basin and Mojave deserts. In this study, we found that the abundances of most invertebrate groups remained unaffected by fire and rodent treatments. In the Great Basin, however, the abundance of flying-foragers was reduced in burned areas. At both locations, ant species richness and Shannon's diversity were reduced in burned areas. Species richness and Shannon's diversity were negatively correlated with invasive plant cover at both sites, and invasive plant cover was positively correlated with fire. The loss of diversity can spell losses in important ecosystem functions, and invasive grass fire cycles threaten to make these losses permanent.

Keywords: Great Basin, Mojave, ants, invertebrates, fire, rodents, cheatgrass, invasive grass, *Pogonomyrmex*

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CHAPTER 1

Fire and Plant Invasion, but not Rodents, Alter Ant Community Abundance and Diversity in a Semi-arid Desert

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ABSTRACT

Human activities are increasing the size, frequency and severity of disturbance across earth's ecosystems including deserts. Ants are important drivers of ecosystem function and are good bioindicators of ecosystem sensitivity to disturbance and change. Rodents also play an important role in ecosystem response to disturbance and often compete with ants for resources. The purpose of our study was to test the main and interactive effects of fire, rodent activity, and time on ant forager abundance, species richness, and diversity, as well as changes in ant mound density and disc area in the Great Basin Desert. We experimentally applied burn and rodent exclusion treatments and used pitfall traps to collect ants each month from April through October from 2014-2016. Over the three-year period, burned areas had lower richness and diversity than unburned areas. Rodent exclusion had minimal effects on the ant community and there was not a significant rodent exclusion interaction with fire. Treatment effects varied by month and year. The western harvester ant, *Pogonomyrmex occidentalis*, was the most abundant ant species, comprising about 70% of the total ants captured. Shifts in ant diversity following fire were driven by positive responses of harvester ants to burned habitat conditions. In contrast, all other ant species when analyzed together had lower forager abundance in burned plots, which drove lower ant diversity in burned plots. Ant forager abundance, richness and diversity increased each year of the study in all plots, however, richness and diversity remained lower in burned areas than in unburned areas each year. Structural equation modeling shows that the effects of fire on ant community diversity are partially mediated through the plant community. While rodents affected the plant community, those effects do not seem to transfer over to the ant community. *Pogonomyrmex occidentalis* mound density was higher in burned areas, but disc area was smaller. Our results suggest that fire has adverse effects on ant community diversity. This could have long-lasting effects on ecosystem function in the face of a changing fire regime in deserts of North America caused by invasive annual plants.

INTRODUCTION

Human activities are increasing the size, frequency and severity of fires across earth's ecosystems (Bowman et al. 2009), which is driving changes in the assembly, succession and trophic interactions of biological communities (St. Clair et al. 2016, Horn and St. Clair 2017). Intermediate levels of disturbance are known to maximize biodiversity, but frequent or novel disturbance can favor a few species and decrease diversity (Hobbs and Huenneke 1992), and increase the establishment and spread of invasive species (Christensen and Burrows 1986). The establishment and spread of invasive grasses is altering fire regimes in North American deserts (Balch et al. 2013), which can have drastic effects on the biodiversity and function of the biological community (St. Clair et al. 2016).

Ants are good indicators of ecosystem sensitivity to disturbance due to short life cycles and their importance as ecosystem engineers (Brown 1997). Ants have a disproportionately large impact on ecosystem function through primary consumption and nutrient cycling (Jones et al. 1994, Hölldobler and Wilson 1990), and they occupy specialized niches across multiple trophic levels (Majer 1983). Ants impact plant community structure through herbivory and by dispersing seeds (Brown et al. 1979). Some species of ants, including *Pogonomyrmex occidentalis*, make large mounds and clear all of the vegetation in a disc around the mound, which can impact vegetation structure at the landscape scale (Sharp and Barr 1960).

Rodents, ants, and the interspecific competition between them can play an important role in desert plant-community assembly (Anderson and MacMahon 2001, Levine et al. 2004). Experimental removal of rodents and ants can cause dramatic shifts in plant community composition and cover (Davidson et al. 1984, St. Clair et al. 2016). Ants and rodents are abundant in deserts and consume and cache large quantities of seeds (Hölldobler and Wilson 1990, Ostoja 2013a, Ostoja 2013b). Ants and rodents have been shown to compete for overlapping food sources in the Chihuahuan Desert (Brown and Davidson 1977, Brown et al. 1979), but little has been done to measure their competitive interactions in the Great Basin Desert.

In desert systems, rodents can have a strong top-down influence on plant community structure that could have important indirect effects on the ant community (Leal and Oliveira 2000). In a previous study at our site, rodent activity dramatically decreased *Bromus tectorum*, or cheatgrass, invasion (St Clair et al. 2016). Where rodents were excluded, invasive grasses dominated the site, but where rodents had access, the plant community was dominated by annual forbs. Rodent-driven shifts in desert plant communities from grass-dominated to forb-dominated communities have been shown to alter small-scale ant species composition (Schooley et al. 2000).

Ant forager abundance and diversity fluctuates strongly across season and year (Hölldobler and Wilson 1990). Ant foraging activity can vary greatly with primary production (Kaspari and Valone 2002), which responds to variation in precipitation, temperature, and humidity (Schumacher and Whitford 1974, Cerda et al. 1997, Mackay and Mackay 1989). Ants are thermophilic, and activity is usually positively correlated with temperature (Hölldobler and

Wilson 1990), but different species have different temperature tolerances due to factors such as body size and desiccation rates. Ant nests are built to create optimal temperature and moisture conditions for certain activities, such as brood rearing and food storage (Hölldobler and Wilson 1990), so nest locations must meet certain requirements. The large mounds and discs of *P. occidentalis* are meant to control temperature and humidity within nests (Cole 1994).

In the Great Basin, a changing fire regime, driven by the spread of invasive grasses (Brooks et al. 2004, D'Antonio and Vitousek 1992), is posing a serious threat to native perennial shrub communities. Modified fire regimes alter habitat conditions, which could have significant bottom-up effects on the abundance and diversity of consumer communities. In the Great Basin, rodents can have strong top-down effects on the development of native plant communities and plant invasions (St Clair et al. 2016) that may modify ant communities indirectly by changing vegetation structure. The object of this study was to determine the effects of fire and rodent exclusion and corresponding shifts in plant community composition on ant-community forager abundance, species richness, and diversity. Our study addressed the following questions: 1) What are the main and interactive effects of fire and rodent exclusion on ant forager abundance, species richness, and diversity? 2) Do the size and density of *P. occidentalis* discs change in response to fire or rodent exclusion? 3) Are fire and rodent effects on ants mediated by changes in the plant community? 4) How does ant forager abundance and diversity change within season and across years?

METHODS

Site Description

The study was conducted in southeast Tooele Co., Utah. Elevation is 1650 m and mean annual temperature is 8.6° C, with an average mean January temperature of 3.2° C and an average mean July temperature of 22.3° C (Vernon GHCN:COOP, Utah Climate Center). The study site is dominated by Wyoming big sagebrush (*Artemesia tridentata wyomingensis*), and at the time of the burn treatments, only one other native plant was present, squirreltail (*Elymus elymoides*), a common perennial bunch grass. At the start of the ant survey work in 2014, several other species of plants were present including: *B. tectorum*, halogeton (*Halogeton glomeratus*) and several other species of annual forbs, *H. glomeratus* and other forbs will be referred to from here on as annual forbs. The most common rodent species at the site were *Peromyscus maniculatus*, *Dipodomys microps*, and *Perognathus parvus*. In the study location, there was little evidence of grazing and no evidence of invasive plant species or fire in the last several decades prior to the start of the experiment in 2011.

Experimental Design

The study area consisted of five 60x60 m replicated experimental blocks, which were each split into four equal 30x30 m plots (Figure 1.1). Each plot was randomly assigned a combination of two treatments, burned or unburned, and rodent access or rodent exclusion, in a full factorial design (St Clair et al. 2016). A barbed-wire fence was placed around the entire perimeter of the research plots to exclude livestock, with enough space at the bottom of the fence to allow free movement of native wildlife. Rodent fences were established on all plots using 1 m tall welded-wire fencing which was buried 30 cm below the soil surface so that it extended 70 cm above the surface. The two plots in each block that were randomly assigned the rodent exclusion treatment had 20 cm of smooth metal flashing attached to the top of the fence to prevent rodents from climbing over the top. The rodent access plots had 12x10 cm openings cut in the bottom of the fence every 4 m to allow rodents free movement in and out of the plots. The burn treatments were conducted September 20, 2011. In each of the five experimental blocks, one rodent exclusion and one rodent access plot were randomly selected and independently burned, completing the full factorial design. The fires were started with drip torches and resulted in >99% plant mortality, wheat straw was also used to facilitate the spread of fire between shrubs (St. Clair et al. 2016).

Plant Cover Measurements

Plant cover was measured with the step point intercept method (Helm and Mead 2004). Four transects were randomly placed in each plot parallel to each other and at least 2 m from any fence or other transect line. A pin was dropped every 50 cm along each transect, starting 2 m from the fence, with 48 pins per transect. For each pin, the topmost plant touching the pin was recorded as canopy, any other plant touching beneath the canopy was recorded as a foliar layer; basal cover was also recorded for each pin. *A. tridentata wyomingensis*, *E. elymoides*, and *B. tectorum*, were each analyzed as separate cover types, annual forbs were all analyzed as a single group. Vegetation surveys were conducted in June of 2015 and 2016.

Ant Trapping Methods

Ants were collected using 7.62 cm diameter pitfall traps (Andersen 1991) filled with approximately 90 ml of propylene glycol. There were four traps placed in each plot, 10 m diagonally from each corner towards the center of the plot (Figure 1.1). In 2014 and 2015, traps were left for 7 days before being collected; in 2016, traps were in place for 72 hrs. during each trapping session. All measurements were standardized to a 3-day period for analysis. Collected ants were stored in 70% isopropyl alcohol. Ants were trapped monthly from April through October for three consecutive years: 2014-2016. Due to an accident in our lab, the data from 2014 lost the monthly distinctions, but treatment designations remained intact.

Ant Identification

Ants were identified using keys from “Ants of Nevada” (Wheeler and Wheeler 1986), and “Identification Guide to the Ant Genera of the World” (Bolton 1994). Collected specimens were also matched against specimens housed in the entomology collection of the Monte L. Bean Life Science Museum (Brigham Young University), where vouchers for each species from this experiment have been placed. Species identifications were verified by John Longino at the University of Utah.

Ant Mound Analysis

Imagery for analysis of *P. occidentalis* mound density and disc area was acquired using a drone with two Sony ILCE-QX1 20.1 MP (Sony Inc.) cameras attached. One camera was modified with a mirrorless NDVI conversion to attain infrared properties (HotPixel LLC). Ant mounds were identified and measured using object based image analysis (OBIA) in eCognition software (Trimble Inc., Sunnyvale, CA, 2016) that incorporates multi-resolution segmentation processes to define multipixel objects using key spatial and spectral features (Flanders et al. 2003). After image analysis of mounds was complete, ground validation of the final analysis was performed to ensure proper identification of the location of each ant mound.

Data Analysis

Repeated measures analysis of variance models were used to test the main and interactive effects of fire, rodent exclusion, month, and year on total forager abundance, species richness and Shannon’s diversity of the ant community in 2014, 2015, and 2016. Total forager abundance, *P. occidentalis* forager abundance, and total forager abundance without *P. occidentalis* data were log transformed and species richness data were square root transformed to meet model assumptions. 2014 and 2015 forager abundance data were standardized to 3 days to match the

2016 data. Statistical analyses were performed using the statistical programs JMP Pro (Version 12.1.0. SAS Institute Inc., Cary, NC, 2015), and R (version 3.2.2 R Core Team, Vienna, Austria). We used structural equation modeling (SEM) with the R package 'piecewiseSEM' (Lefcheck 2015) to estimate the indirect effects of burn and rodent treatments on ant-community forager abundance, richness, and Shannon's diversity mediated through the plant community. Analyses were conducted using combined June ant data from both 2015 and 2016, because our vegetation surveys were conducted in June each year and June represents the peak of both ant forager abundance and Shannon's diversity.

RESULTS

We found 12 species of ants representing 10 genera and 3 subfamilies (Table 1.1). One species, *P. occidentalis*, comprised about 70% of the total ants collected. The next most abundant ant was *Forelius pruinosus*, comprising about 14% of the total. We only trapped one *Stenamma diecki* individual, and only two *Stenamma smithi* individuals. All species, excluding the two *Stenamma* spp., were found in all treatment plots. The *Stenamma* spp. were excluded from the analysis because there were so few individuals. Ants were more abundant in 2016 than in 2015, and were more abundant in 2015 than in 2014 (Table 1.2; Figure 1.2).

Fire Effects

Fire had variable effects on ant forager abundance and Shannon's diversity in our study. The effect of fire on total ant forager abundance averaged over the three-year study period was not statistically significant (Table 1.2). In 2014, burned plots had more than twice as many ants as unburned plots (Table 1.2; Figure 1.2). However, in 2015 and 2016, the burn effect on ant forager abundance was not statistically significant (Figure 1.2). Four of the twelve ant species were more abundant in burned plots than in unburned plots: *P. occidentalis, Myrmecocystus hammetensis, Solenopsis molesta, and Monomorium ergatogyna* (Table 1.1). Seven of the ant species were more abundant in unburned areas compared to burned areas (Table 1.1). The effects of fire on ant richness and Shannon's diversity averaged over the three-year period were statistically significant (Table 1.2). In all three years combined, species richness and Shannon's diversity were higher in unburned plots than in burned plots (Table 1.2; Figure 1.2); average richness and Shannon's diversity also increased each year of our study in all treatment combinations (Table 1.2; Figure 1.2). *Pogonomyrmex occidentalis* foraging abundance was higher in burned plots than in unburned plots in both 2014 and 2015, but not in 2016 (Figure 1.3), and this was statistically significant when averaged over the three-year period (Table 1.2). For all other species, the effects of fire on ant forager abundance varied each year, but was statistically significant when averaged over the three-year period, with forager abundance being higher in unburned compared to burned plots (Table 1.2; Figure 1.3).

Rodent Effects

Rodent exclusion had no significant impacts on ant forager abundance, richness, or Shannon's diversity in our study. Rodents had little to no effect on ant species richness or Shannon's diversity in any individual year, or in all years combined (Table 1.2). Rodents had little to no effect on the abundance of *P. occidentalis* foragers or on the combined forager abundance of all other species (Table 1.2). There were no strong interactions between rodent exclusion and fire on total ant forager abundance, richness, or Shannon's diversity in our study (Table 1.2). There was not a significant fire by rodent exclusion interaction on the forager abundance of *P. occidentalis* or other ant species (Table 1.2).

Time Effects

Month and year both had strong effects on the total ant forager abundance and Shannon's diversity. Forager abundance varied by month (Table 1.2), peaking in June and July in all plots (Figure 1.4). Richness and Shannon's diversity also varied by month (Table 1.2), with the highest richness and diversity in May and June of both 2015 and 2016 (Figure 1.4). Forager abundance varied by year (Table 1.2), with average forager abundance increasing in all plots each year of our study (Figure 1.2). Average richness and Shannon's diversity also increased each year of our study in all plots (Table 1.2; Figure 1.2). The fire x month interaction was significant for all variables except total forager abundance (Table 1.2), with the fire effects being strongest during the months of peak activity (Figure 1.4). There were no other significant interactive effects between treatments (Table 1.2).

Structural Equation Modeling

Structural equation modeling suggested that the fire effect on ant diversity is partially mediated through changes in the plant community (Table 1.3; Figure 1.5C). Fire negatively affected *A. tridentata* cover, which had a positive effect on the Shannon's diversity of ants (Table 1.3; Figure 1.5C). The structural equation model did not show significant correlations between plant cover and ant species richness or abundance (Table 1.3; Figure 1.5). While rodents had significant interactions with the plant community, the interactions were not strong and did not seem to carry over to the ants (Tables 1.2 and 1.3; Figure 1.5).

Changes in Ant Mound Density and Disc Area

Average area of individual *P. occidentalis* discs was found to be greater in unburned plots than in burned plots ($F = 6.5$, $p = 0.013$), with average disc area being 11.1 m^2 in unburned plots and 7.1 m² in burned plots (Figure 1.6). There was no significant difference in total *P. occidentalis* disc area per plot between burned and unburned treatments (F = 0.005, p = 0.94) (Figure 1.6). Average *P. occidentalis* mound density was higher in burned plots (3.7 mounds per plot) than in unburned plots (2.4 mounds per plot) (F = 3.8, p = 0.068) (Figure 1.6). Rodent exclusion did not significantly affect mound density or disc area.

DISCUSSION

Wildfires are increasing in desert ecosystems and this study suggests that they can have strong impacts on ant community diversity. Rodents tended to have minimal direct (competitive) or indirect effects (mediated through plant community) on the ant community (Figure 1.2). We observed changes in the size and density of *P. occidentalis* discs (the most common ant species in our study) in response to fire, with average disc size decreasing and density increasing in burned areas. Furthermore, we found that ant forager abundance and Shannon's diversity change dramatically across seasons and years, and that treatment effects varied depending on season and year.

Ant Community Responses to Burn Treatments

Burned plots had higher total ant forager abundance than unburned plots in 2014 (Figure 1.2), and *P. occidentalis* forager abundance was higher in burned plots than unburned plots in 2014 and 2015 (Figure 1.3). In our study, fire led to a loss of native shrub cover and an increase in invasive annual plant densities and total plant cover (St Clair et al. 2016). Newbold and MacMahon (2014) found that desert horned lizards (*Phrynosoma platyrhinos*), an ant specialist, preferred areas of shrub cover with an open understory. Therefore, losses of shrub cover and increases in densities of annual species following fire may reduce ant predation pressure by horned lizards.

Burned plots had higher densities of *P. occidentalis* mounds than unburned plots (Figure 1.6), which is consistent with findings of Holbrook et al. (2016). Additionally, we found that disc size decreased in burned areas relative to unburned areas (Figure 1.6). However, because mound densities increased in burned areas, the total area in each plot occupied by *P. occidentalis* discs remained relatively the same (Figure 1.6). These results are consistent with those of Sneva (1979), who found that mound density increased and disc size decreased with shrub removal. In our system, fire resulted in more mounds and smaller discs. Shade removal by *P. occidentalis* around the mound has been shown to increase the overall foraging time available to them in the year by increasing the temperature of the mound in the early and late parts of the day (Bucy and Breed 2006). In unburned areas, *A. tridentata wyomingensis* are tall and provide a lot of shade, requiring the ants to remove plants in order to increase the amount of sunlight on the mound. Burned areas, however, were dominated by annual plants that are much shorter than *A. tridentata wyomingensis* and perhaps less plant removal is needed to sufficiently reduce the shade. The decrease in disc area in the burned areas likely shrinks foraging territory, allowing colony densities to be higher. Mound size is also correlated with colony age and size (Wiernasz and Cole 1995), with younger and smaller colonies having smaller mounds, so burned areas may also be seeing higher rates of new colony recruitment. Higher plant densities in burned areas may allow those newly established colonies to survive in closer proximity to neighboring colonies.

When *P. occidentalis* numbers are removed from the analysis, we see higher total forager abundance in unburned plots than in burned plots, which is driven mostly by three species: *Forelius pruinosus, Camponotus vicinus,* and *Myrmecocystus testaceus* (Table 1.1). *Forelius pruinosus* interferes with the foraging of *Myrmecocystus* spp. that are several times its size

(Hölldobler 1982). This competition could explain why *M. hammettensis* is more abundant in burned plots where *F. pruinosus* is less abundant. *Myrmecocystus testaceus* likely escapes interference from *F. pruinosus* by foraging at night. The carpenter ant, *C. vicinus*, would be negatively affected by shrub loss from fire as they frequently nest in woody tissue (Chen et al. 2002).

Unburned plots had higher species richness and Shannon's diversity than burned plots in all three years (Figure 1.2). Vegetation structure plays an important role in ant community structure (Bestelmeyer and Schooley 1999, Bestelmeyer 2005, Crist 2009). Plant community and soil type also influence the ant community response to fire (Hoffmann 2003). Ant species richness has been positively correlated with shrub cover (Bestelmeyer 2005, Farji-Brener et al. 2002). This is consistent with the structural equation model showing that Shannon's diversity is positively correlated with shrub cover (Table 1.3; Figure 1.5). Sagebrush removal reduces soil moisture in surface soils (Inouye 2006) and increases soil surface temperature (Chambers and Linnerooth 2001), which could restrict the foraging time of some ant species in the burned areas to cooler parts of the day (Briese and Macauley 1980). *Pogonomyrmex occidentalis* activity increases as soil-surface temperature rises, with activity slowing only during the hottest part of the day in the summer. The loss of shrubs reduces shade, increasing temperatures across the growing season, which also benefits *P. occidentalis* by increasing foraging activity in the earlier and later parts of the year (Bucy and Breed 2006). While some species, such as *P. occidentalis*, may be tolerant of increased soil surface temperature, others may not be as tolerant of the higher soil surface temperature associated with burned plots.

Ant Community Responses to Rodent Presence

Ants and rodents are known to compete for seed resources in desert systems (Brown and Davidson 1977). Competition and facilitation between ants and rodents has been experimentally demonstrated in deserts (Brown et al. 1979, Davidson et al. 1984, Edelman 2012). Our data show that rodents have no significant competitive or facilitative effects on the ant community (Table 1.2). Between 2012 (first year after fire treatments) and 2015 (second year of ant collection), the burned plots had a 50% reduction in rodent abundance as well as a 38% reduction in species richness and a 41% reduction in Shannon's diversity relative to unburned plots (St Clair et al. 2016). Rodent presence in our plots has led to increased numbers of small-seeded annuals in burned plots (St Clair et al. 2016), a preferred forage for many harvester ants. The combination of burn treatments and rodent exclusion led to a *B. tectorum* dominated plant community. These shifts in plant communities due to rodent exclusion initially led us to hypothesize that the rodents might indirectly affect the ant community through the modification of the plant community, but our data show no such effect (Table 1.3; Figure 1.5). The high levels of plant cover and seed production, combined with the reduction in rodent abundance, may alleviate competition for seed resources. While rodent treatments led to shifts in the types of post-fire plant communities that developed both plant community types were dominated by non-native annuals (St. Clair et al. 2016) and may not lead to strong differences in temperature or food availability to which ants are sensitive (Kaspari et al. 2000).

Changes in Response Across Seasons and Years

Seasonal variation in ant forager activity are well known (Hölldobler and Wilson 1990). Ants are sensitive to fluctuations in abiotic conditions such as temperature and soil moisture (Kaspari et al. 2000, Briese and Macauley 1980, Whitford and Ettershank 1975), as well as to fluctuations in resource availability (Pol et al. 2011) and competition (Fellers 1989). Peak ant forager abundance in early summer (Figure 1.3) is likely due to seed fall. The high spike in richness and Shannon's diversity in May were possibly related to nectar production in the plant community, increasing resource availability for nectivorous species such as *Myrmecocystus* spp. and *F. pruinosus*. Perhaps this is also why we saw higher Shannon's diversity in unburned plots, where there are more perennial plants, like *A. tridentata wyomingensis*, that produce nectar longer, or the shade and cooler temperatures may allow for better nectar storage.

Year to year variation in the ant community is affected by precipitation and primary production (Kaspari and Valone 2002). From 2015 to 2016, our plots saw increases in biomass (St. Clair et al. 2016), which may explain the increase in ant forager abundance in that same time period. Ant colonies are largely sessile, so they are not able to travel long distances in search of resources, making them sensitive to seasonal and annual changes in resource availability. Some species, like harvesters, have the ability to cache large amounts of food, mitigating in part the annual variation in resource availability. Other species that rely heavily on more mobile prey, such as insects, and occupy higher trophic levels, may be more sensitive to annual variation in primary production.

CONCLUSION

Fire and the subsequent loss of shrubs was correlated with reduction in ant richness and Shannon's diversity in our study area. If *B. tectorum* invasion increases the frequency and size of fire, this could prevent shrubs from reestablishing, converting a shrubland into an annual grassland. Based on our findings, this has the potential to reduce ant diversity, which may then reduce the ecosystem services they provide such as seed dispersal (Lengyel et al. 2009), nutrient cycling, and decomposition (Bestelmeyer and Wiens 2003). While total forager abundance and

Shannon's diversity increased each year of our study, the changes in relative abundances in the burned areas may impact the services or the rates of the processes provided by less common ant species. In our study, total forager abundance remained mostly unchanged between treatments, as the reductions in the abundances of foragers of less common species were compensated for by increases in *P. occidentalis* forager abundance (Figure 1.3). Changes in the ant community are known to correlate with changes in other invertebrate communities (Majer 1983), which means that we may not only see reductions in services provided by ants, but a myriad of other organisms. Further research is needed to understand the impact this loss of diversity may have on proper ecosystem functioning. This makes native plant reestablishment a priority in post-fire rehabilitation in sagebrush communities.

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FIGURES

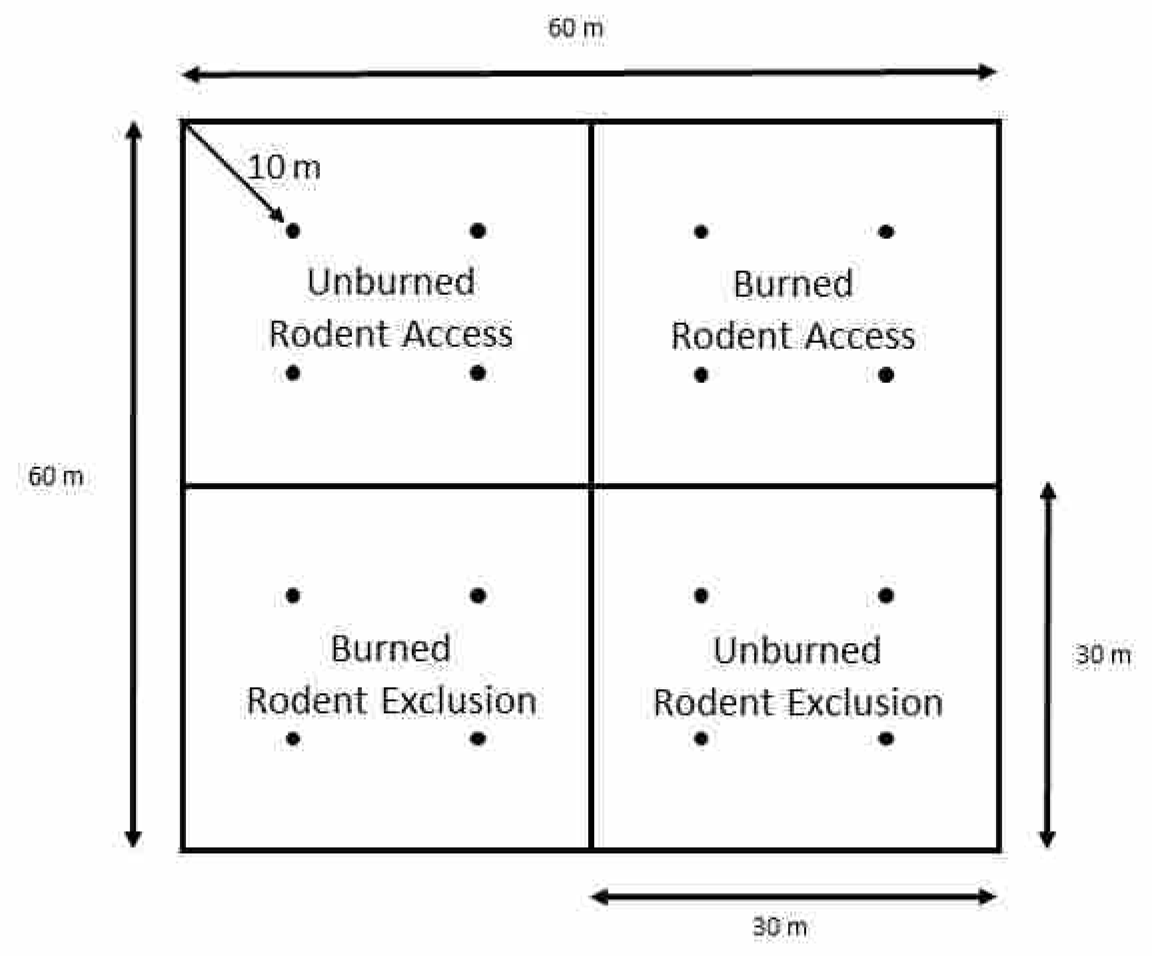

Figure 1.1. Block design showing scale, example of treatment combinations, and pitfall trap placement (•). All treatment combinations were randomized for each experimental block.

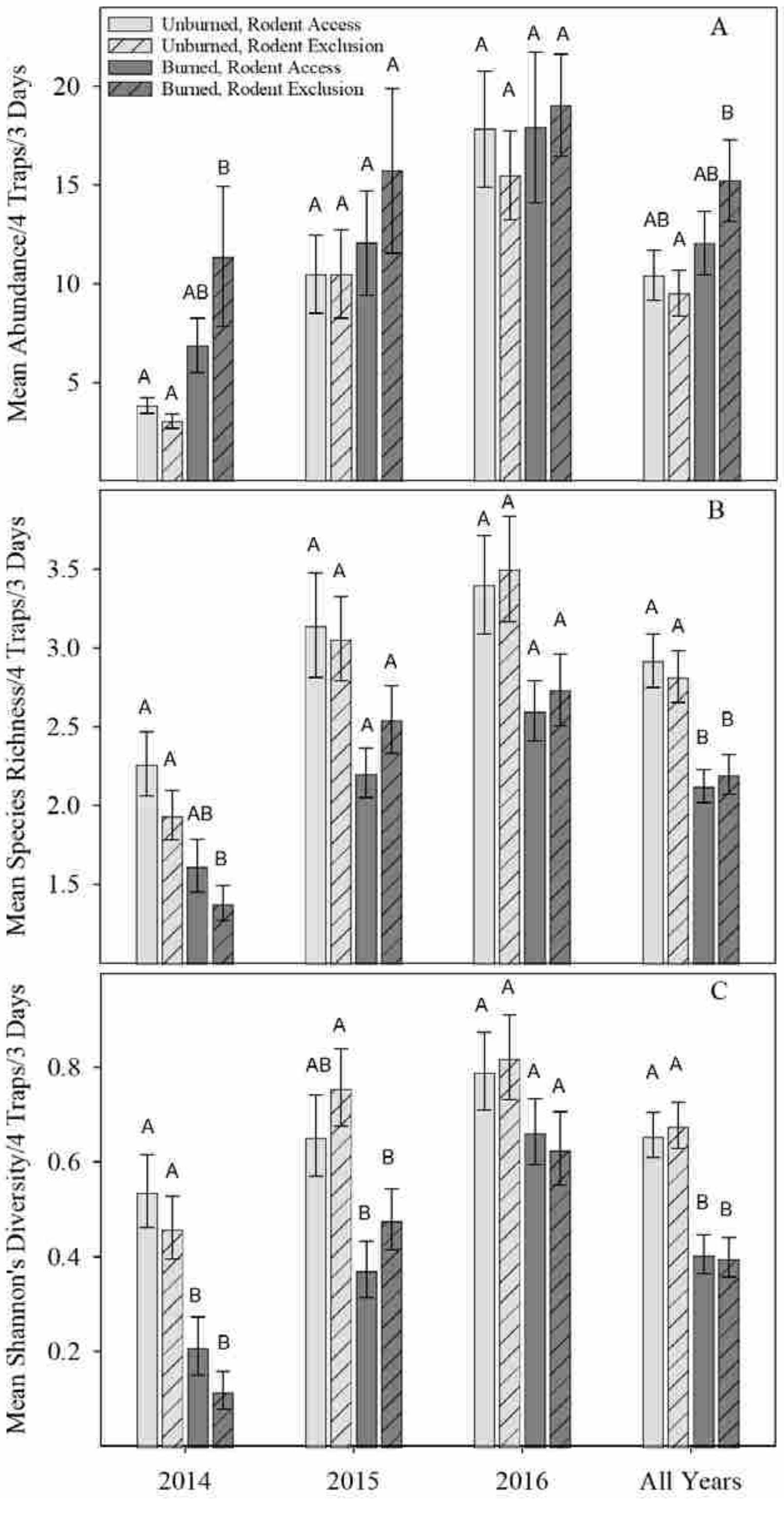

Figure 1.2. Effects of fire and rodent exclusion on ant forager abundance (A), species richness (B), and Shannon's diversity index (C) separated by year. Error bars represent standard error. Pairwise comparisons of means compare means within each individual year, bars not connected by same letter are significantly different.

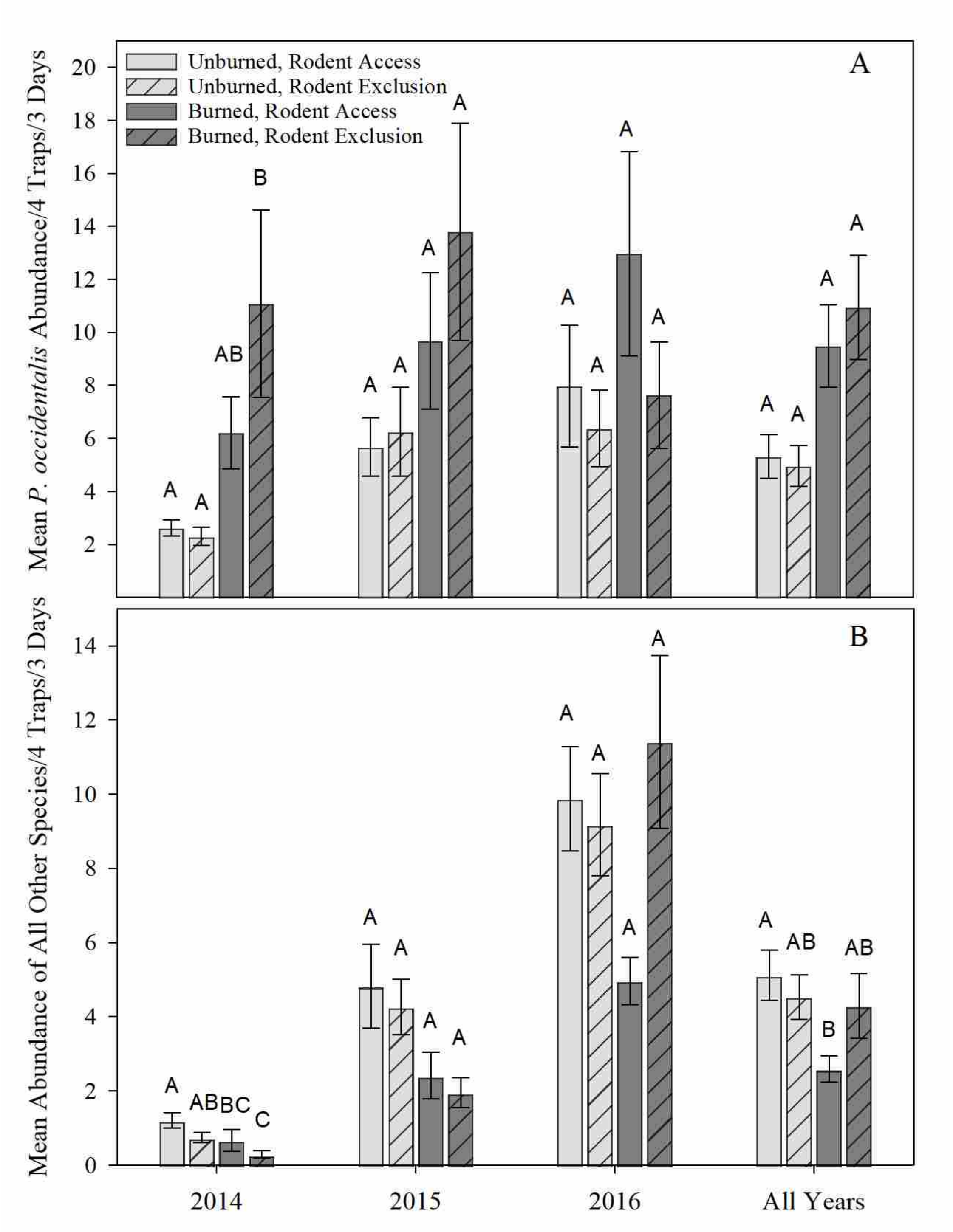

Figure 1.3. Effects of fire and rodent exclusion on the abundance of *P. occidentalis* foragers (A) and the abundance of foragers of all other species (B) separated by year. Pairwise comparisons of means compare means within each individual year, bars not connected by same letter are significantly different. Error bars represent standard error.

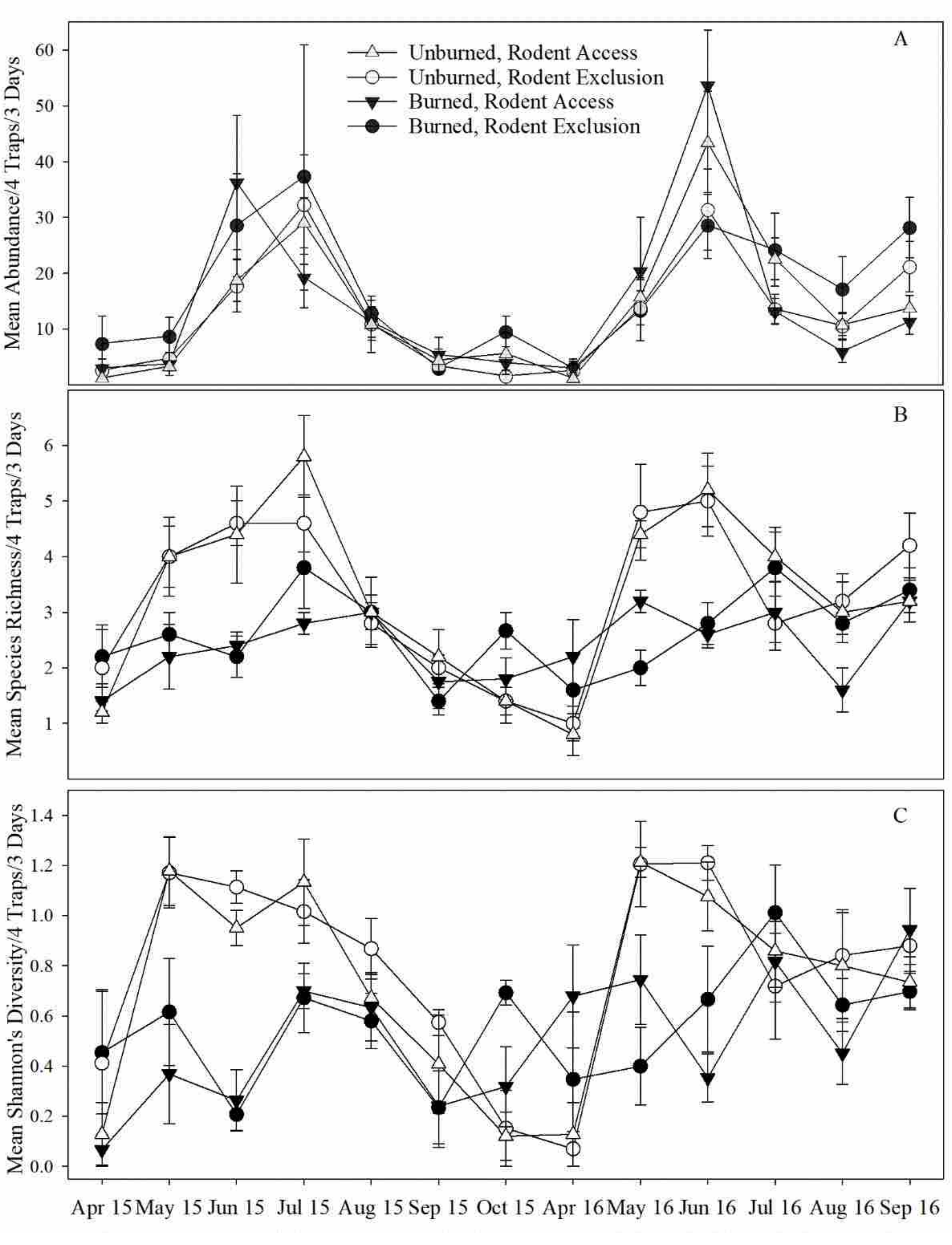

Figure 1.4. Effects of fire and rodent exclusion on ant forager abundance (A), species richness (B), and Shannon's diversity index (C) by month for the 2015 and 2016 seasons. Error bars represent standard error.

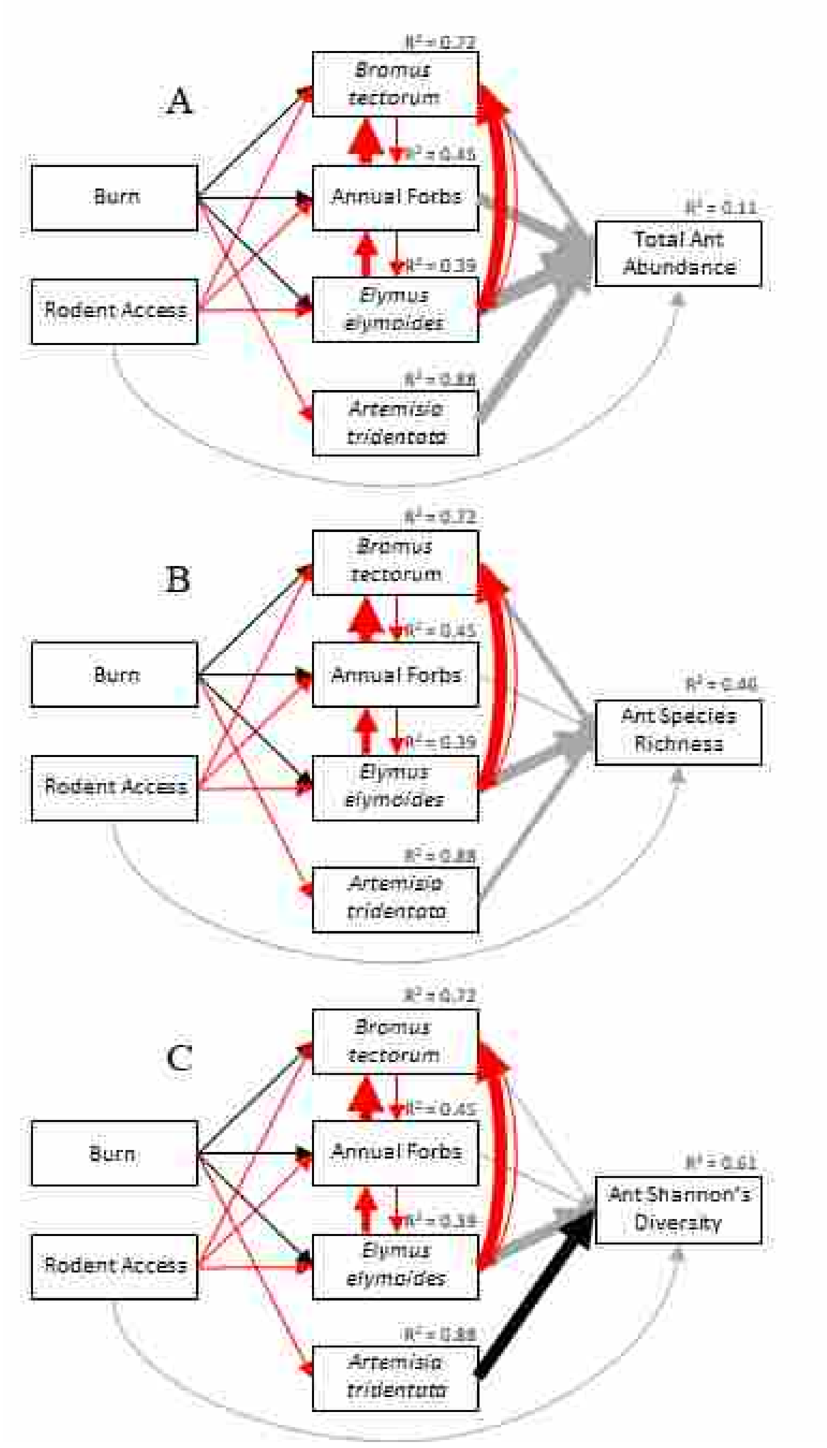

Figure 1.5. Structural equation models, showing relationships between burn treatments, rodent treatments, plant cover types and the abundance (A), species richness (B), and Shannon's diversity (C) of the ant community. R^2 values are shown for each model. Grey lines represent non-significant interactions ($p > 0.05$), black lines represent positive significant interactions ($p \leq 0.05$), and red lines represent negative significant interactions ($p \leq 0.05$). Line widths show the strength of the interaction.

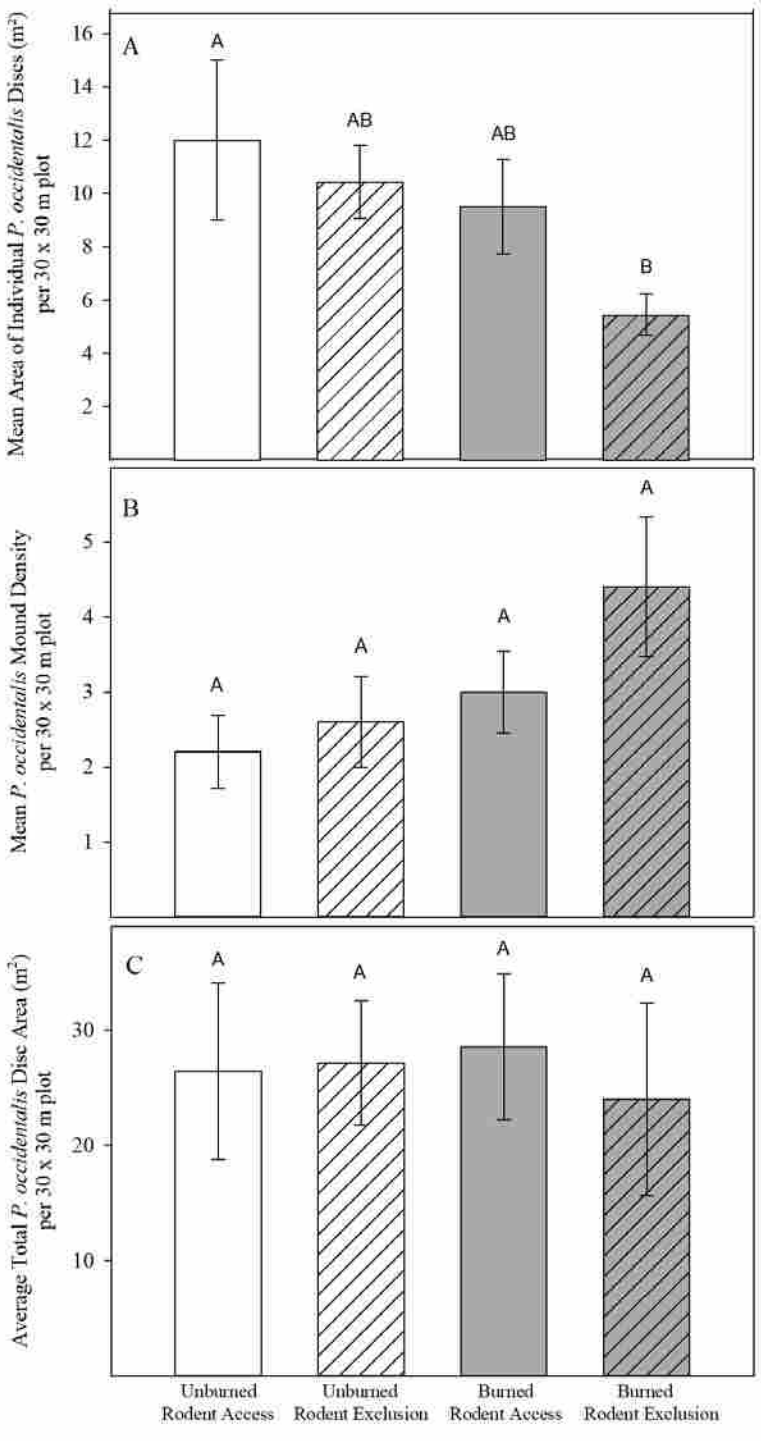

Figure 1.6. Effects of fire and rodent treatment combinations on average *P. occidentalis* disc size (A), the average density of *P. occidentalis* mounds (B), and total area occupied by *P. occidentalis* discs per 30 x 30 m plot (C). Error bars represent standard error. Bars not connected by same letter are significantly different.

TABLES

Table 1.1. Total sum of individuals of each species captured for all three years, with the species separated by subfamily. Numbers are separated by treatment combination: Unburned-Rodent Access (US), Unburned-Rodent Exclusion (UN), Burned-Rodent Access (BS), Burned-Rodent Exclusion (BN).

Subfamily/Species	**US**	**UN**	**Total Unburned**	**BS**	**BN**	**Total Burned**
Dolichoderinae						
Forelius pruinosus	460	322	**782**	221	141	**362**
Myrmicinae						
Temnothorax nevadensis	32	36	**68**	14	21	**35**
Stenamma diecki	0	1	**1**	0	0	**0**
Stenamma smithi	1	0	**1**	0	1	**1**
Pogonomyrmex occidentalis	910	878	**1788**	1649	2170	**3819**
Solenopsis molesta	8	4	**12**	17	22	**39**
Myrmica lobifrons	18	31	**49**	7	18	**25**
Monomorium ergatogyna	24	20	**44**	33	258	**291**
Pheidole jtl-222	14	11	**25**	7	21	**28**
Formicinae						
Myrmecocystus hammettensis	22	15	**37**	54	22	**76**
Myrmecocystus testaceus	22	128	**150**	26	2	**28**
Camponotus vicinus	185	111	**296**	14	9	**23**

Table 1.2. F statistics table for the main effects of fire, rodent exclusion, month, year and their interactions. Asterisks indicate level of significance for p-values: *p ≤ 0.05, **p ≤ 0.001, ***p ≤ 0.0001. (+) and (-) indicate the direction of the effect.

Source of variance	Total Ant Forager Abundance	Species Richness	Shannon's Diversity Index	*P. occidentalis* abundance	All other species' abundance
Fire	2.6	**(-)19.8*** **	**(-)39.4*** **	**(+)11.9** **	**(-)17.9*** **
Rodents	0.02	0.2	0.13	0.01	0.07
Fire x Rodents	0.83	0.26	0.09	0.33	0.26
Month	**81.7*** **	**18.5*** **	**13.62*** **	**55.59*** **	**119.76*** **
Year	**32.5*** **	**26*** **	**29.3*** **	**5.6** **	**107.6*** **
Fire x Month	1.91	**5.9*** **	**14.56*** **	**4.26** **	**10.66** **
Fire x Year	1.6	0.18	2.1	1.3	1.21
Rodents x Month	1.97	0.54	1.72	1.64	0.95
Rodents x Year	0.42	1.01	1.74	0.51	0.94
Fire x Rodents x Month	1.34	1.52	1.02	0.58	1.29
Fire x Rodents x Year	0.32	0.09	0.02	0.13	1.91

Table 1.3. Path estimates, standard error, and p-value for structural equation models. P values <0.05 are bolded for emphasis.

Predictor	Response	Estimate	Std. error	p.value
Burn	*B. tectorum*	0.454	0.032	**0.000**
Rodent access	*B. tectorum*	-0.192	0.032	**0.000**
Annual Forbs	*B. tectorum*	-1.023	0.185	**0.000**
E. elymoides	*B. tectorum*	-1.674	0.561	**0.006**
Burn	Annual Forbs	0.229	0.039	**0.000**
Rodent access	Annual Forbs	-0.078	0.028	**0.008**
B. tectorum	Annual Forbs	-0.449	0.081	**0.000**
E. elymoides	Annual Forbs	-0.837	0.383	**0.037**
Burn	*E. elymoides*	0.055	0.020	**0.011**
Rodent access	*E. elymoides*	-0.036	0.011	**0.002**
B. tectorum	*E. elymoides*	-0.123	0.040	**0.005**
Annual Forbs	*E. elymoides*	-0.133	0.063	**0.044**
Burn	*A. tridentata*	-0.208	0.012	**0.000**
Rodent access	Ant Shannon's Diversity	-0.193	0.140	0.177
B. tectorum	Ant Shannon's Diversity	-0.449	0.502	0.379
Annual Forbs	Ant Shannon's Diversity	0.257	0.784	0.745
E. elymoides	Ant Shannon's Diversity	2.220	2.044	0.286
A. tridentata	Ant Shannon's Diversity	2.247	1.137	**0.057**
Rodent access	Ant Species Richness	-0.098	0.132	0.462
B. tectorum	Ant Species Richness	-0.665	0.474	0.171
Annual Forbs	Ant Species Richness	-0.428	0.739	0.567
E. elymoides	Ant Species Richness	1.321	1.898	0.492
A. tridentata	Ant Species Richness	0.773	1.074	0.477
Rodent access	Total Ant forager abundance	-0.054	0.355	0.880
B. tectorum	Total Ant forager abundance	-0.789	1.276	0.541
Annual Forbs	Total Ant forager abundance	-1.312	1.992	0.515
E. elymoides	Total Ant forager abundance	-9.022	5.114	0.088
A. tridentata	Total Ant forager abundance	-2.797	2.896	0.342

CHAPTER 2

Comparison of Invertebrate Responses to Fire and Rodent Activity Between the Mojave and Great Basin Deserts

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ABSTRACT

Exotic annual grasses have altered fire regimes by increasing the size, frequency, and severity of fires in desert ecosystems. Invertebrates make up a large proportion of desert ecosystem diversity and are good indicators of desert ecosystem function and resilience. The recent increase in the frequency and size of desert wildfires brings into question the direct and indirect impacts of fire on desert invertebrate communities. The ability of rodents to modify plant community structure post-fire, could result in rodent communities having important indirect effects on invertebrate communities. The Great Basin and the Mojave Desert share a border but have very different climates and biotic communities. Despite these differences, both are facing a similar threat of changing fire regimes caused by invasive annual grasses. The purpose of our study was to examine the influence of fire and rodent exclusion on invertebrate community abundance and diversity in the Great Basin and Mojave Deserts and whether they were related to changes in the plant community. We experimentally applied burn and rodent exclusion treatments at sites in both the Mojave and Great Basin deserts. We used pitfall traps to collect invertebrates each month from April through September in 2016. Invertebrates were identified to family and ants were identified to species. We measured changes in the abundances of invertebrate groups, as well as in the abundance, richness, and diversity of the ant community in response to fire and rodent treatments. Rodent exclusion had very little effect on invertebrate abundance or on ant forager abundance, richness or diversity. Fire had little effect on invertebrate abundance, though fire had a significant negative effect on flying-forager abundance at our Great Basin site. Fire reduced ant species richness and Shannon's diversity at both sites. Structural equation models suggest that fire positively influences invasive plant cover, which in turn reduces ant species richness and Shannon's diversity. These effects show that fire and plant invasion may significantly alter ecosystem function by reducing biodiversity, this loss in ecosystem function may become permanent in the face of an altered fire regime caused by invasive annual grasses.

INTRODUCTION

Disturbance and exotic plant invasion are an increasing threat to global biodiversity (Brooks et al. 2004, D'Antonio and Vitousek 1992). Changes in disturbance regimes due to human activities can have negative impacts on ecosystem biodiversity (Hobbs and Huenneke 1992). Historically, fire has played a minor role in plant community succession in North American deserts. However, exotic annual grasses have altered fire regimes by increasing the size, frequency, and severity of fires in these systems (Brooks et al. 2004, Brooks and Matchett 2006), which could have long-term effects on the stability and biodiversity of these systems.

Invertebrates make up a large proportion of ecosystem diversity (May 1988) and provide a wide range of ecosystem functions. Invertebrates often have specialized relationships with plants, vertebrates, and microbes. Invertebrates are critical to food webs in serving as prey for many vertebrate species and have important interactions with plants through herbivory, seed dispersal and pollination. Many invertebrates have small home ranges, making them less able to escape unfavorable changes in their environment. These qualities make invertebrates good indicators of ecosystem function and resilience (Andersen 1990, Lavelle et al. 2006, Majer 1983). Ants (Hymenoptera: Formicidae) are particularly good indicators of ecosystem stability

(Andersen 1997) because they are among the most abundant and diverse group of invertebrates, and occupy a variety of specialized niches across multiple trophic levels (Majer 1983).

The recent increase in the frequency and size of desert wildfires (Brooks et. al 2004) brings into question the direct and indirect impacts of fire on desert insect communities. Direct fire mortality is influenced by the degree of exposure and the mobility of the species or life stage (Swengel 2001). Rice (1932) and Morris (1971) show that mortality can often continue to occur post-fire from starvation and exposure while others report shifts in insect abundance and diversity after repeat burns (Wright and Samways 1998, 1999). Flying insects and other highly mobile insects are often the first to recolonize into burned landscapes (Swengel 2001). Grasshoppers have been shown to increase in abundance in burned areas (Lamotte 1975), however, grasshopper richness is usually lower in frequently burned areas (Evans 1984, 1988). Evans (1984, 1988) found that forb-feeding grasshopper richness declined in more frequently burned areas because of fewer forbs in those areas, and grass-feeding grasshoppers increased because of relatively higher grass cover in burned areas. Insect species that require a specific plant community structure that does not re-occur in the first few years after fire can lose resource availability for generations, and, if fires are too frequent, this can dramatically reduce their population size (Wright and Samways 1998, 1999). Fire tends to favor some ant species (Holbrook et al. 2016), while reducing overall ant species richness (Ostoja et al. 2009). In many cases, fire decreases the diversity of the entire insect community (Swengel 2001).

The ability of rodents to modify plant community structure, and their sensitivity to fire, could result in rodent communities having important effects on invertebrate communities in post-fire environments. Many rodent species include insects as part of their diet, and small mammal insectivory has been shown to have strong effects on grassland invertebrate communities (Churchfield et al. 1991). The effects of rodents on plant community structure via granivory and folivory (Sharp-Bowman et al. 2017a, Sharp-Bowman et al. 2017b) are also likely to have indirect effects on the abundance and diversity of insect communities. A previous study at our Great Basin site determined that rodents can suppress cheatgrass invasion (St. Clair et al. 2016); rodent exclusion produced a plant community dominated by invasive grasses, and where rodents had access, the plant community was a much more diverse annual forb community. In both burned treatments (with and without rodents), plant diversity was reduced compared to unburned plots, but burned plots with rodent access had higher plant diversity than burned plots without rodents; these changes in plant habitat could have bottom up influences on invertebrate diversity. Bannertail kangaroo rats have been known to alter ant community composition (Schooley et al. 2000) via changes in plant community structure through mound building (Moroka et al. 1982). The indirect effects of rodents on insect communities through the modification of the plant community are not well characterized. Our study was designed to increase the characterization of the indirect effects of rodents on insect communities

There have been many studies in the deserts of North America documenting plant-insect interactions (Ostoja et al. 2009) and rodent-insect interactions (Brown and Davidson 1977, Brown et al. 1979), but there are far fewer studies that compared these relationships across different desert ecosystems. The deserts of western North America vary in climate and have unique biotic communities. The Great Basin and the Mojave Desert share a border but are very different from one another, one is semi-arid while the other is hyper-arid. Despite these differences, both are facing a similar threat of changing fire regimes caused by invasive annual grasses. Because of their inherent differences, the biological communities in each desert may respond differently to these changes. The purpose of our study was to characterize the influence of fire and rodent exclusion on invertebrate community abundance and diversity in the Great Basin and Mojave Deserts and whether they were related to changes in the plant community.

METHODS

Study Site

Great Basin

Our Great Basin site is located in Rush Valley in southeast Toole Co., Utah (40°05’27”N 112°18’18”W). Elevation is 1650 m and mean annual temperature is 8.6° C, with an average mean January temperature of 3.2° C and an average mean July temperature of 22.3° C (Vernon GHCN:COOP, Utah Climate Center). The study site is dominated by Wyoming big sagebrush (*Artemesia tridentata wyomingensis*), and at the beginning of the experiment, only one other native plant was common, *Elymus elymoides*, a perennial bunch grass. There was little evidence of grazing and no evidence of fire in the last several decades prior to the start of the experiment in 2011.

Mojave Desert

Our Mojave Desert site is located at the Lytle Ranch Preserve, which is a 680-acre nature preserve owned and managed by Brigham Young University. Lytle Ranch is located in the Beaver Dam Wash in the northern Mojave Desert, in western Washington Co., Utah (37°08’54”N 114°00’50”W). Elevation is 915 m, mean annual temperature is 16.3° C, average mean January temperature is 6.2° C, and average mean July temperature is 28.1° C (Lytle Ranch GHCN, Utah Climate Center). Dominant plants in the study site are Joshua trees (*Yucca brevifolia*), Creosote bush (*Larrea tridentata*), and blackbrush (*Coleogyne ramosissima*). There has been no grazing in the last 30 years, and no evidence of fire in several decades.

Experimental Design

The experimental design at both sites is the same and consists of 60x60 m experimental blocks replicated 5 times. Each block is split into four equal (30x30 m) subplots. Each block was assigned 4 treatment combinations: burned or unburned, and rodent access or rodent exclusion, in a full factorial design (St. Clair et al. 2016). Each site is protected from cattle by a barb-wire fence, with enough room at the bottom to allow free movement of native wildlife. Rodent fences were established using 1 m tall welded-wire fencing which was buried 30 cm below the soil surface so that it extended 70 cm above the surface. The two plots in each block that were randomly assigned the rodent exclusion treatment had 20 cm of smooth metal flashing attached to the top of the fence to prevent rodents from climbing over the top. The two remaining plots had 12x10 cm openings cut in the bottom of the fence every 4 m to allow rodents freer movement in and out of the plots. For each of the five experimental blocks, one rodent exclusion and one rodent control plot were randomly selected and independently burned, completing the full factorial design. The burn treatments occurred in June, 2011 at the Mojave site and in September, 2011 at the Great Basin site. The fires were started with drip torches and resulted in high burn severity with a majority of the native plant cover removed (>90%) with the experimental burns. To facilitate the spread of fire between shrubs at the Great Basin site we placed 300 g m^{-2} of wheat straw in the shrub interspaces in our burn plots (St. Clair et al. 2016). Fire spread naturally without straw at the Mojave site.

Invertebrate Trapping

There were 4 pitfall traps placed in each experimental subplot (Andersen 1991), 10 m diagonally from each corner towards the center of the plot, each trap was 7.62 cm diameter. For each trapping session, traps were filled with approximately 90 ml of propylene glycol and left open for approximately 72 hrs. At the end of each trapping session, the contents of the traps were collected and placed in 70% isopropyl alcohol for later sorting and identification. Trapping sessions were performed at each location once a month from April through September 2016, five years after the treatments were imposed. Invertebrates were identified to family, where possible, and ants were identified to species. Once identified, the taxa were organized into four functional groups: ground-dwellers, flying-foragers, ground-foragers, and ants. We used the most abundant taxa from each group for our analysis. We excluded rare invertebrate families because it was impossible for us to determine whether they were simply rare in our system or rare because of our trapping method. The ground-dwelling group across both sites comprises data from the taxa Acari, Entomobryidae, Sminthuridae, and Meinertellidae. Our flying-forager group across both sites comprises data from the taxa Sarcophagidae, Sphecidae, Anthomyiidae, Geocoridae, Phoridae, Cicadellidae, Sciaridae, Bethylidae, micro-hymenoptera, and Cecidomyiidae. The ground-foraging group across both sites comprises data from the taxa Tenebrionidae, Carabidae, Histeridae, Acrididae, Araneae, Scarabaeidae, Solifugae, Elateridae, and Rhaphidophoridae (Tables 2.1 and 2.2).

Pitfall trapping does not efficiently capture all invertebrate species and can therefore skew indices of species diversity, it tends to favor non-flying invertebrates. Moreover, fluctuations in the abundances of dominant taxa have been shown to drive ecosystem services (Winfree et al. 2015). For this reason, we focused our analysis on the most abundant taxa that were represented at both sites. Because of the large spatial and temporal scale that we sampled and the specialized nature of identifying down to species, most invertebrates were identified to family and we only present abundance data. Ants all belong to the same family (Formicidae), and are established bioindicators of ecosystem function (Majer 1983). Pitfall trapping is a well-established method for capturing ants (Andersen 1991). Ants are also relatively easy to identify and are common in most ecosystems throughout the world. Therefore, we were able to identify ants to species and determine changes in richness and diversity of ant species in response to treatment conditions. Our results can also thus be readily compared to a wider range of studies.

Vegetation Surveys

Vegetation cover and density were measured at both sites. Cover was measured using the step point intercept method (Bonham 1989). Four 30 m transects were randomly placed parallel to each other in each plot. Starting at the two meter mark, a pin was dropped every 50 cm along each transect with a total of 46 points for each transect. Canopy, as well as first (next layer under canopy), second, and third foliar layers were recorded by species, and basal cover was also recorded. Cover measurements for each species for each plot were calculated by taking the total number of hits of each species across the four transects and dividing them by 184, and the resulting number was recorded as a percentage. In order to compare responses between sites, plant cover was separated into three groups for analysis: invasive herbaceous plants, native herbaceous plants, and shrubs.

Statistical Analysis

We used repeated measures analysis of variance (ANOVA) models to test the main and interactive effects of fire and rodent exclusion across time (month) on the abundances of individuals for each of our three functional groups (Ground-dwellers, flying-foragers, and ground-foragers), as well as ant forager abundance, richness, and Shannon’s diversity index. We used Structural equation modeling (SEM) was used to estimate the indirect effects of fire and rodent exclusion, mediated through the plant community, on ant forager abundance, richness, and Shannon’s diversity index, as well as on the abundances of our three invertebrate functional groups (Lefcheck 2016). We ran Structural equation modeling (SEM) was run using the R package 'piecewiseSEM'(version 3.2.2 R Core Team, Vienna, Austria). We fit linear mixed effects models using the nlme package in R, and block was included as a random factor for each model (Pinheiro et al. 2016). We computed the conditional R^2 for each model was computed using the method of Nakagawa and Schielzeth (2013). We log transformed Ant forager abundance, ground-dweller abundance, and flying-forager abundance at both sites were log transformed to meet model assumptions of normality and homogeneity of variance. We used a square-root transformation of Ground-forager abundance at both sites were square-root transformed to meet model assumptions. Etc. Repeated measures ANOVA models were calculated using the program JMP (SAS Institute Inc., Cary, NC). In running the statistical analyses there weren't significant main effects of rodent exclusion or rodent exclusion by fire interactions. As a result, we present figures that show the main effects of fire and rodent exclusion over time.

RESULTS

We identified 101 families or orders identified on the Great Basin site. We also identified ten ant species representing nine genera in the Great Basin site. We identified 108 families or orders on the Mojave Desert site. We also identified twelve ant species representing nine genera in the Mojave Desert (Tables 2.3 and 2.4).

Fire Effects

Fire affected ant species richness and diversity at both sites (Tables 2.5 and 2.6), with higher species richness and diversity in unburned plots than in burned plots (Figure 2.1). In the Great Basin, the effect of fire on ant diversity was only significant in May and June (Table 2.6;

Figure 2.1). Fire did not significantly affect ant forager abundance at either site (Tables 2.5 and 2.6). Fire also had little effect on the abundances of ground-dwellers or ground-foragers at either site (Tables 2.5 and 2.6). Fire played a significant role in determining flying-forager abundance at the Great Basin site (Table 2.6), with higher flying-forager abundance in unburned areas than in burned areas (Figure 2.2), but fire had little effect on flying-forager abundance at the Mojave site (Table 2.5). Structural equation models suggest that the effects of fire on ant species richness and Shannon's diversity at both sites are mediated through changes in the plant communities (Tables 2.6 and 2.7; Figure 2.4). Specifically, fire had a positive influence on invasive plant cover, which then negatively influenced ant species richness and diversity (Tables 2.7 and 2.8; Figure 2.4).

Rodent Effects

Rodent treatments had little to no effect on ant forager abundance, richness, or diversity at either location when averaged across months (Table 2.5 and 2.4). At our Great Basin site, rodents had a significant effect on ant forager abundance depending on the month, with abundance being higher in rodent access plots than in rodent exclusion plots in May and June but being lower in rodent exclusion plots in August and September (Table 2.6; Figure 2.3). Rodent treatments had little to no effect on flying-forager abundance or ground-forager abundance at either site (Tables 2.5 and 2.6).

Fire and Rodent Interactions

Fire and rodent interaction terms in our models were generally not significant (Tables 2.5 and 2.6). The only exception to this was the abundance of ground-dweller invertebrates at our

Great Basin site (Table 2.6), in which abundance was higher in rodent exclusion plots, particularly in unburned conditions (Figure 2.3).

Time Effects

Ant forager abundance, species richness, and Shannon's diversity at both locations changed significantly across months (Tables 2.5 and 2.6), with abundance and species richness peaking in June at both locations (Figure 2.1). Ant diversity was highest in June in the Mojave, and highest in May in the Great Basin (Figure 2.1). At our Mojave site, ground-dweller abundance and flying-forager abundance were changed significantly across time (Table 2.5), with ground-dweller abundance peaking in June and flying-forager abundance being highest in April (Figure 2.2). At the Great Basin site, ground-dweller abundance, flying-forager abundance, and ground-forager abundance were all significantly affected by month (Table 2.6), with ground-dweller and flying-forager abundances peaking in June, and ground-forager abundance peaking in May (Figure 2.2).

DISCUSSION

This study documents that fire can significantly impact ant communities in both the Mojave and Great Basin deserts. The effects of fire on ant communities appears to be mediated by the loss of native shrubs and their replacement by invasive annuals. Most of our invertebrate groups at both sites were unaffected by both fire and rodent activity. Although rodents caused shifts in the types of invasive communities following fire this did not have strong effects on invertebrate communities. These patterns were fairly consistent between the Great Basin (semi-arid) and the Mojave (hyper-arid) desert sites despite their differences in climate, flora, and fauna.

Invertebrate Responses to Fire

Fire can have both positive and negative effects on invertebrate abundance and diversity (Swengel 2001), with the effects varying depending on the taxa measured and environmental conditions (Warren et al. 1987). In our study, fire had very little effect on ant forager abundance; however, fire reduced ant species diversity at both sites (Tables 2.5 and 2.6; Figures 2.1 and 2.2). Ostoja et al. (2009) reported lower ant diversity in cheatgrass dominated plots compared with sagebrush intact plots in the Great Basin which is a typical vegetation conversion after fire as seen in our plots. These results are consistent with our previous research at the Great Basin site, where ant species diversity was reduced in burned areas but ant forager abundance was unaffected (Day et al. 2018). In that study, the abundances of most species were reduced in burned plots, but the abundances of some dominant ant species increased, which kept overall ant forager abundance in burned areas similar to those in unburned areas. This same pattern occurred at our Mojave site, where reduction in abundance in some species of ants was balanced by the increase in abundance of others (Table 2.3). Among the dominant ant species that responded positively to fire were harvester ants in the genus *Pogonomyrmex* (Tables 2.3 and 2.4). Holbrook et al. (2016) reported increased *P. occidentalis* nest density in burned areas over unburned areas in the Great Basin. Our surveys show that *P. occidentalis* forager abundance increased in burned plots at our Great Basin site (Table 2.4) while P. rugosus forager abundance at our Mojave site nearly tripled in burned plots compared to unburned plots (Table 2.3). This increase in *Pogonomyrmex* abundance may be the result of shrub removal, allowing for increased colony densities (Sneva 1979, Day et al. 2018), or it may also be caused by increased seed resources from increases in annual plant cover.

The abundances of most of the invertebrate groups in our study were unaffected by fire (Tables 2.5 and 2.6; Figures 2.1 and 2.2). We did observe that the flying-forager group saw reductions in abundance in burned plots compared to unburned plots in the Great Basin (Table 2.6; Figure 2.2), which may be related to their avoidance of burned habitat. Gall midge (Diptera: Cecidomyiidae) larvae feed within plant tissues and some may have specific associations with native plants that are lost during fires. Welch (2005) reported 32 species of midges that induce galls on *A. tridentata*, so shrub removal of sagebrush may reduce host plant availability. Harper et al. (2000) observed reductions in some leafhoppers (Hemiptera: Cicadellidae) in burned areas.

Indirect Effects of Fire Mediated Through Changes in Plant Communities

Vegetation structure and plant community composition are important determiners in invertebrate community composition (Bromham et al. 1999, Denno et al. 2002, Herrera and Dudley 2003, Pearson 2009). Lower ant diversity in burned plots may be a response to reduced resource availability or unfavorable abiotic conditions as a result of an altered plant community. Ant species richness and diversity were negatively influenced by invasive plant cover at both sites (Tables 2.7 and 2.8; Figures 2.4). This is consistent with findings of Ostoja et al. (2009) who found that ant diversity decreased in *B. tectorum* dominated sites compared to sagebrush intact sites in the Great Basin. Invasive plants were also reported to reduce ant species richness in a grassland (Lenda et al. 2013). Ants are generally thermophilic, but have varying levels of temperature tolerance (Hölldobler and Wilson 1990). In sagebrush systems, shrub removal increases soil surface temperature (Chambers and Linnerooth 2001), and reduces soil moisture in surface soils (Inouye 2006). This change in abiotic conditions may favor some ant species, such as *Pogonomyrmex* (Bucy and Breed 2006), but may restrict foraging time for other ant species. The abundances of arboreal ant species were reduced in burned plots at both sites; *Crematogaster depilis* in the Mojave was not found at all in burned areas during our study (Table 2.3), and *Camponotus vicinus* in the Great Basin was eight times more abundant in unburned plots than in burned plots during our study (Table 2.4). The life histories of more arboreal ants such as *C. depilis* and *C. vicinus* are closely tied to woody plants (Hölldobler and Wilson 1990), which are greatly reduced in burned plots. The carpenter ant, *C. vicinus*, was reported to stop foraging when temperatures reach 23° C (Bernstein 1979), so more shaded unburned areas may allow longer foraging times in summer. Nocturnal nectivorous ants, which may rely more on perennial plants for nectar resources, were also reduced in burned areas compared to unburned areas, *Myrmecocystus mexicanus* in the Mojave (Table 2.3) and *M. testaceus* in the Great Basin (Table 2.4).

Invertebrate Responses to Rodent Exclusion

Rodents can have strong top-down effects on Great Basin and Mojave plant communities (Sharp-Bowman et al. 2017a, Sharp-Bowman et al. 2017b). Previous research in our Great Basin plots show that rodent exclusion in burned areas dramatically increased the cover of *B. tectorum* leading to loss of plant biodiversity (St. Clair et al. 2016). We therefore expected to see top down effects of rodents on plant communities translate to shifts in invertebrate community composition and structure. However, we observed no significant main effects of rodent exclusion on ant community richness and diversity or invertebrate community abundance (Tables 2.5 and 2.6). Our results suggest that invasive plant cover strongly affects ant diversity (Tables 2.7 and 2.8; Figure 2.4), and while rodents may alter which types of invasive plants dominate in burned areas (St. Clair et al. 2016), they seem to have less effect on the percent cover of invasive plants in burned plots (Tables 2.7 and 2.8; Figure 2.4). For example, invasive plant cover in burned rodent-access (BA) and burned rodent-exclusion (BE) plots were nearly identical between sites (68% and 67% in BS plots in the Mojave and Great Basin respectively, and 72% in BE plots at both sites). This suggests that the loss of native shrubs and their replacement by invasive annuals following fire has a larger impact on invertebrate communities than differences in the composition of invasive annual communities (annual grasses vs. annual forbs) created by rodents (St. Clair et al. 2016). Abiotic changes associated with shifts from native perennial shrublands to invasive annual plant communities, to which invertebrates are sensitive, are likely much greater than differences between invasive annual grass and annual forb communities.

Invertebrate Responses Over Time

Seasonality played a significant role on invertebrate abundance and diversity in the Mojave (Table 2.5) and Great Basin (Table 2.6). In the Great Basin, the flying-forager functional group exhibited a more sustained abundance throughout the sampling season in unburned areas, as opposed to a late season decline in burned areas. We also see similar patterns in the abundances of ground-dwellers and ants over time at both sites. These effects are likely related to altered abiotic conditions favoring certain life history strategies. It is possible that altered vegetation dynamics could lead to different foraging patterns across seasons. For example, at the Great Basin site, leafhoppers exhibited a shift from more consistent abundance throughout the year in unburned areas, to a more concentrated abundance at the beginning of the year in burned areas. Insect abundance and presence has previously been linked with plant architecture (Stinson and Brown 1983). After a burn, annual grasses can quickly fill open space, and make the system more seasonal as they quickly dry out toward the end of spring (Billings et al. 1994, Knapp 1996). Changes in the seasonality of the vegetation likely alter the site selection of flying-foragers, such as leafhoppers, that utilize the area for forage or laying eggs (Stinson and Brown 1983).

Ant-plant interactions vary over seasons due to abiotic factors affecting both plants and ants (Rico-Gray et al 2012). Temperature and precipitation are known to drive seasonal changes in ant species richness and ant-plant interactions (Kaspari et al. 2000, Rico-Gray et al. 1998). Ant communities vary over the course of a year with changing plant phenology and may alternate food resources depending on the season (Rico-Gray 1993). The peak in ant forager abundance in early summer at both sites (Figure 2.1) is likely influenced by seed production, as most annual plants have gone to seed by June (Gordon et al. 2008). The peaks in ant species richness and Shannon's diversity in May and June in unburned plots in the Great Basin (Figure 2.1) may be related to flowering events, seed production (Pol et al. 2011), nectar production (Dattilo 2015), and increasing summer temperatures (Crist and MacMahon 1991). Because the burned plots have fewer perennial plants, especially shrubs, burned plots have increased seed production as a result of higher densities of annual plants, and less transpiration, resulting in higher soil surface temperatures. The Mojave site saw higher Shannon's diversity in unburned plots every month, but total abundance was significantly higher in burned plots in May, June and July (Figure 1). The Mojave site has much higher shrub diversity than the Great Basin site, so burned plots may be seeing more losses in ant-shrub mutualisms (like that of *C. depilis* and cacti (Chamberlain and Holland 2008)), lowering diversity throughout the study.

Desert Comparison

Ants in general responded similarly to treatments at both sites when averaged over the whole collecting season; however, the way those responses played out over time differed between sites. In the Mojave, ant richness and diversity were higher in unburned plots than in burned plots throughout the entire collecting season (Figure 2.1). In the Great Basin, however, the differences in ant richness and diversity between burn treatments were more variable (Figure 2.1). The Mojave site has higher mean temperatures than our Great Basin site through most of the year and plant diversity is much higher at our Mojave site than at our Great Basin site. Ant foraging rates are dependent on both temperature (Crist and MacMahon 1991, MacKay and MacKay 1989) and food availability (Gordon et al. 2008). The higher plant diversity and higher mean temperatures in the Mojave may allow for the sustained difference in ant richness and diversity through the season.

CONCLUSION

Exotic invasive plants are changing desert fire regimes (D’Antonio and Vitousek 1992), and their downstream impacts on invertebrate communities can have important ecological consequences. Fire facilitates invasion (Brooks et al. 2004) and invasion in turn facilitates fire (Balch et al. 2013), creating a positive feedback loop and threshold resulting in potential state changes. Our data suggests that invertebrate community abundance is generally stable in response to desert fires but that species and taxonomic groups can vary dramatically. Invasive grass fire cycles pose a serious threat to arid systems where we may see significant modification to ecosystem function (Hooper et al. 2005), and perhaps local extinctions of some species. Biodiversity is already lower in arid systems than in more mesic systems because of abiotic limitations, and many of the species are operating near tolerance limits. This makes functional redundancy less likely in arid systems, which increases the importance of each invertebrate species in the system (Whitford 1996). Even within a genus, there are important physiological, behavioral, and life history differences between species that minimize competition and affect the role that the individual species play in the ecosystem (Whitford et al. 1976, Whitford 1978). The replacement of less common species with more common ones may not adequately replace the services provided by the less common species. Fires and exotic annual grass invasion are changing the world for invertebrates in desert ecosystems.

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FIGURES

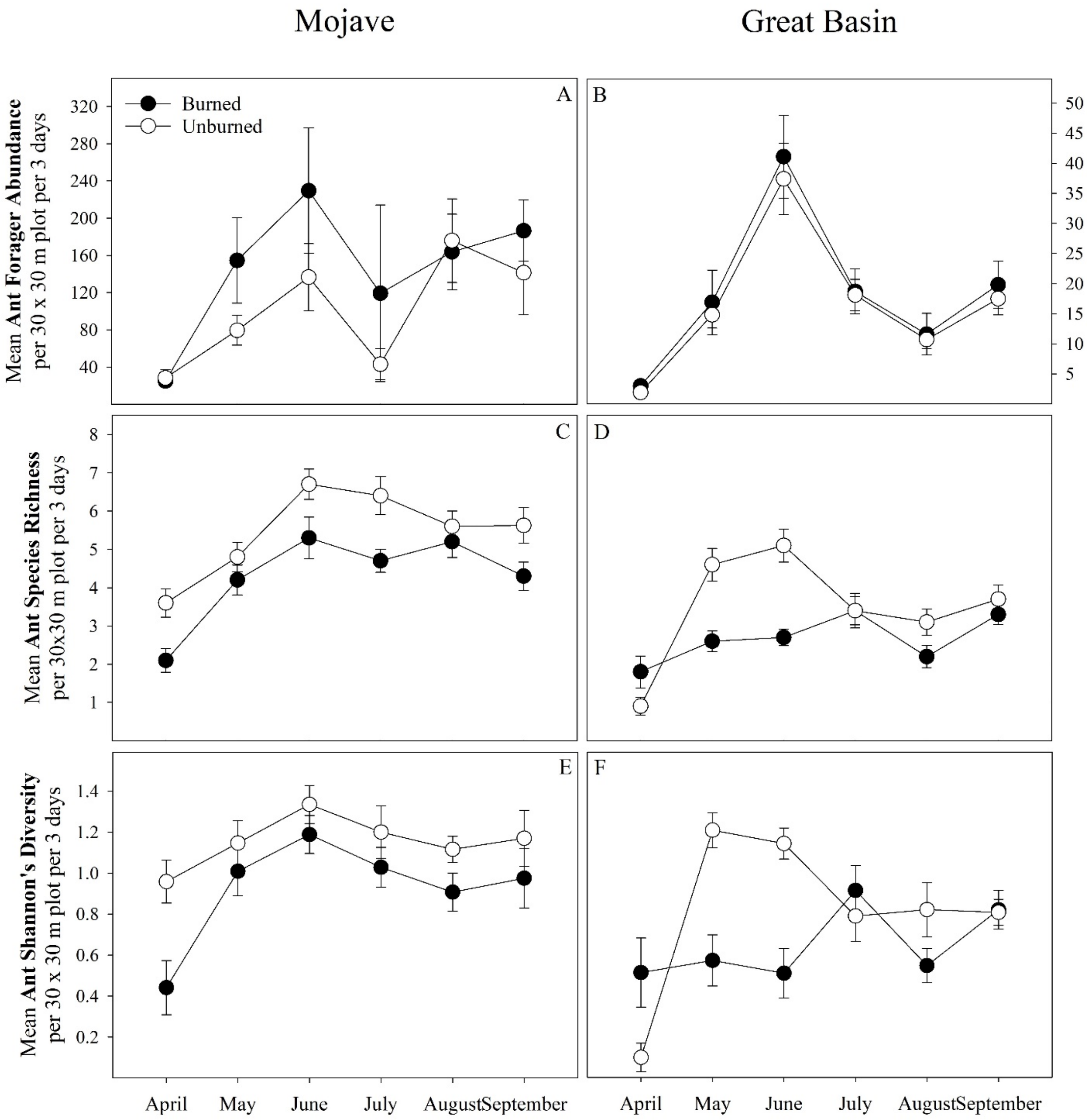

Figure 2.1. Ant forager abundance (A and B), species richness (C and D), and Shannon's diversity (E and F) responses to burn treatment separated by month and site. Error bars represent standard error.

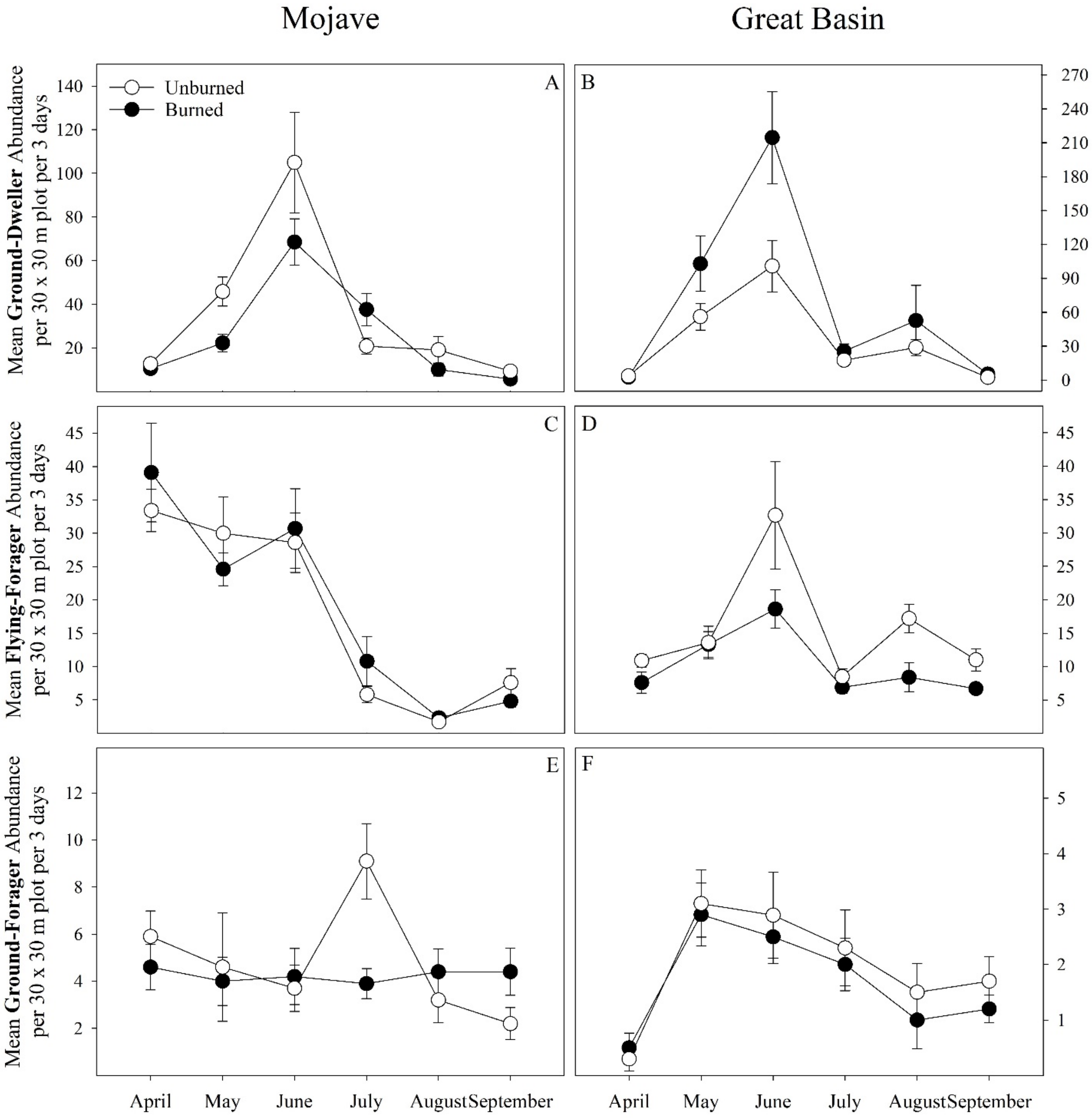

Figure 2.2. Ground-dweller abundance (A and B), flying-forager abundance (C and D), and ground-forager abundance (E and F) responses to burn treatments separated by month and site. Error bars represent standard error.

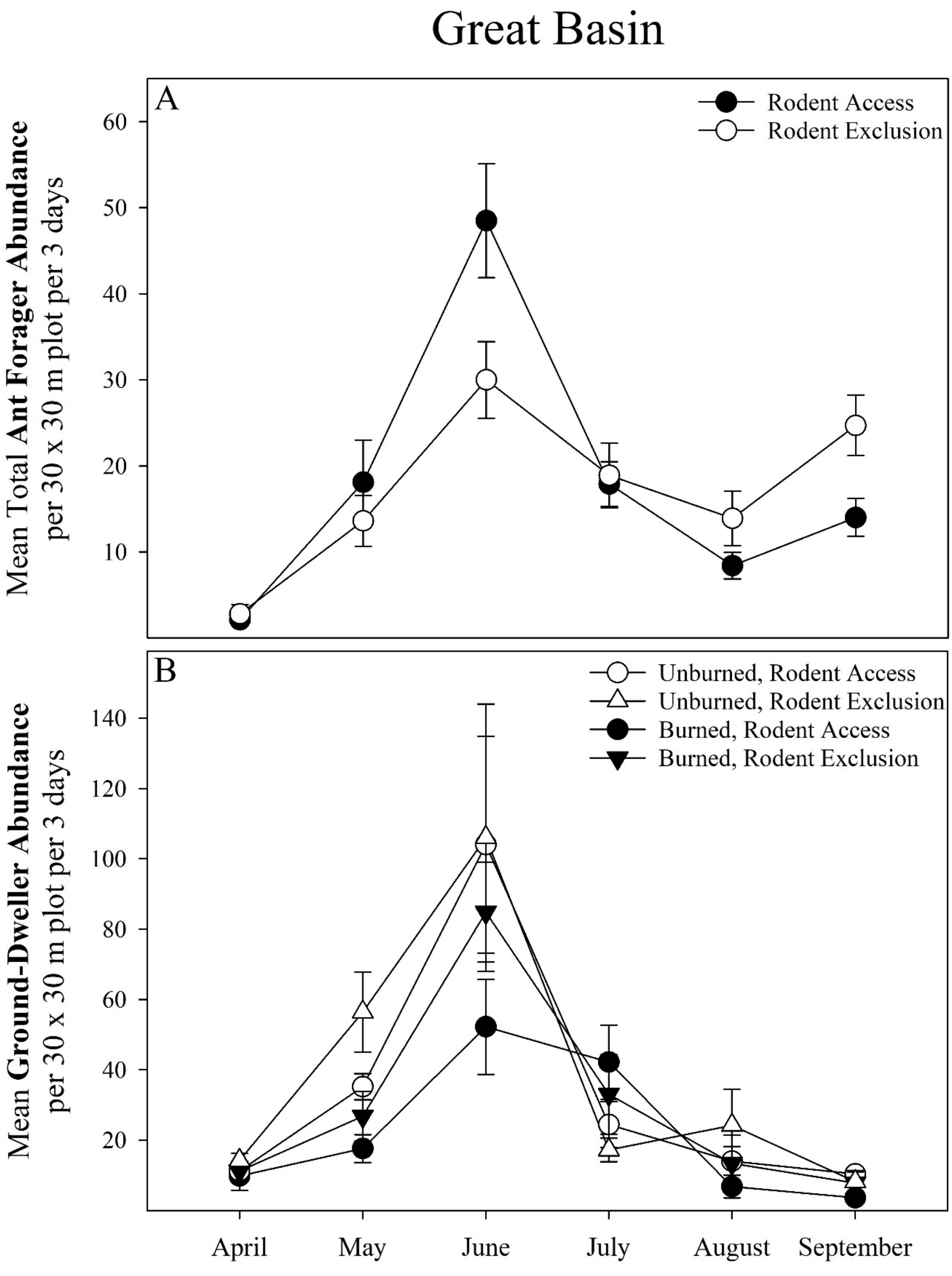

Figure 2.3. Responses of ant forager abundance to rodent treatment (A) and ground-dweller abundance to fire and rodent treatments (B) separated by month in the Great Basin. Error bars represent standard error.

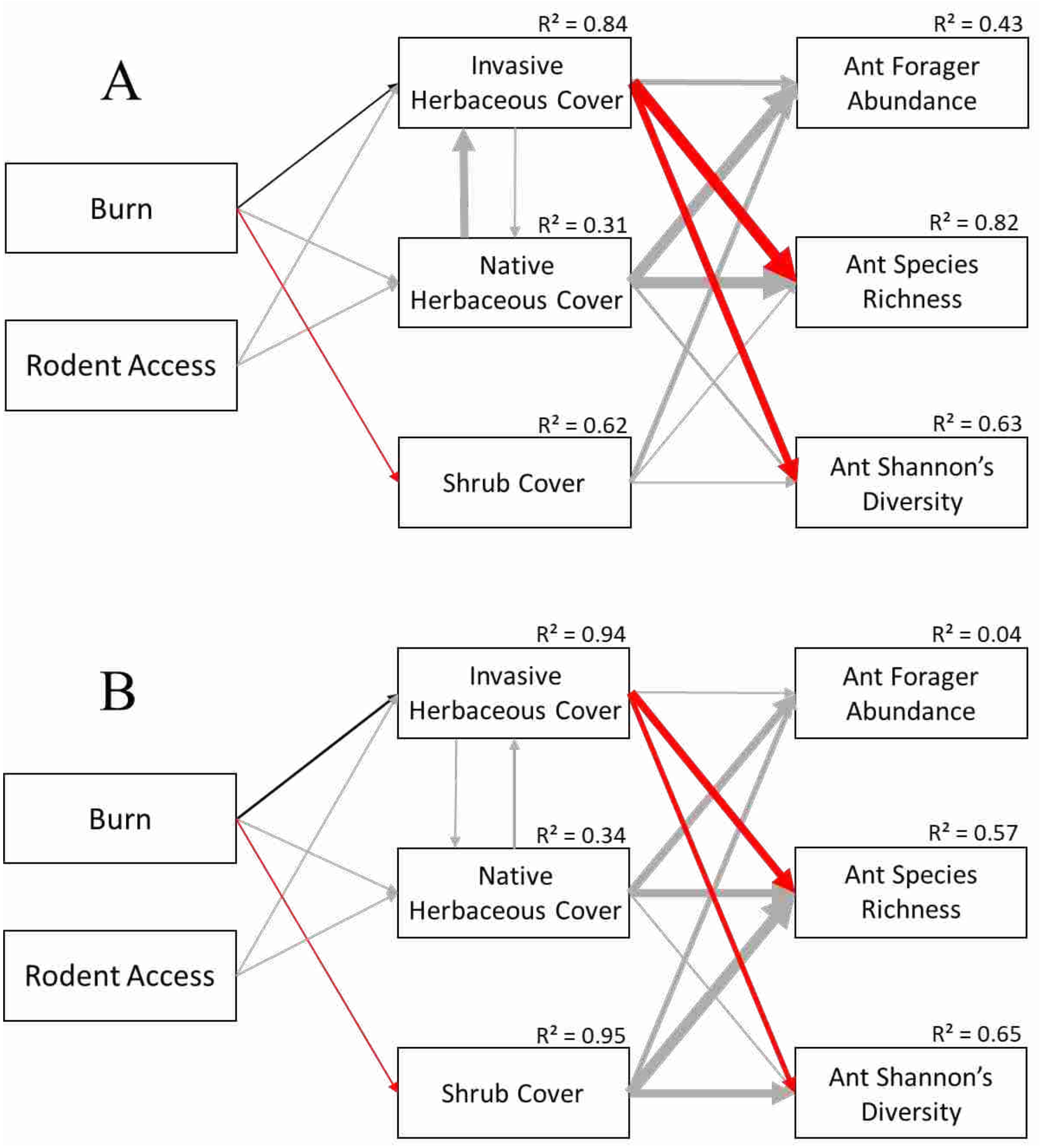

Figure 2.4. Structural equation models, showing relationships between burn treatments, rodent treatments, plant cover types and the forager abundance, species richness, and Shannon's diversity of the ant communities in the Mojave (A) and the Great Basin Deserts (B). R^2 values are shown for each model. Gray lines represent non-significant interactions ($p > 0.05$), black lines represent positive significant interactions ($p \leq 0.05$), red lines represent negative significant interactions ($p \leq 0.05$). Line width indicates strength of interaction, thicker lines mean stronger interaction.

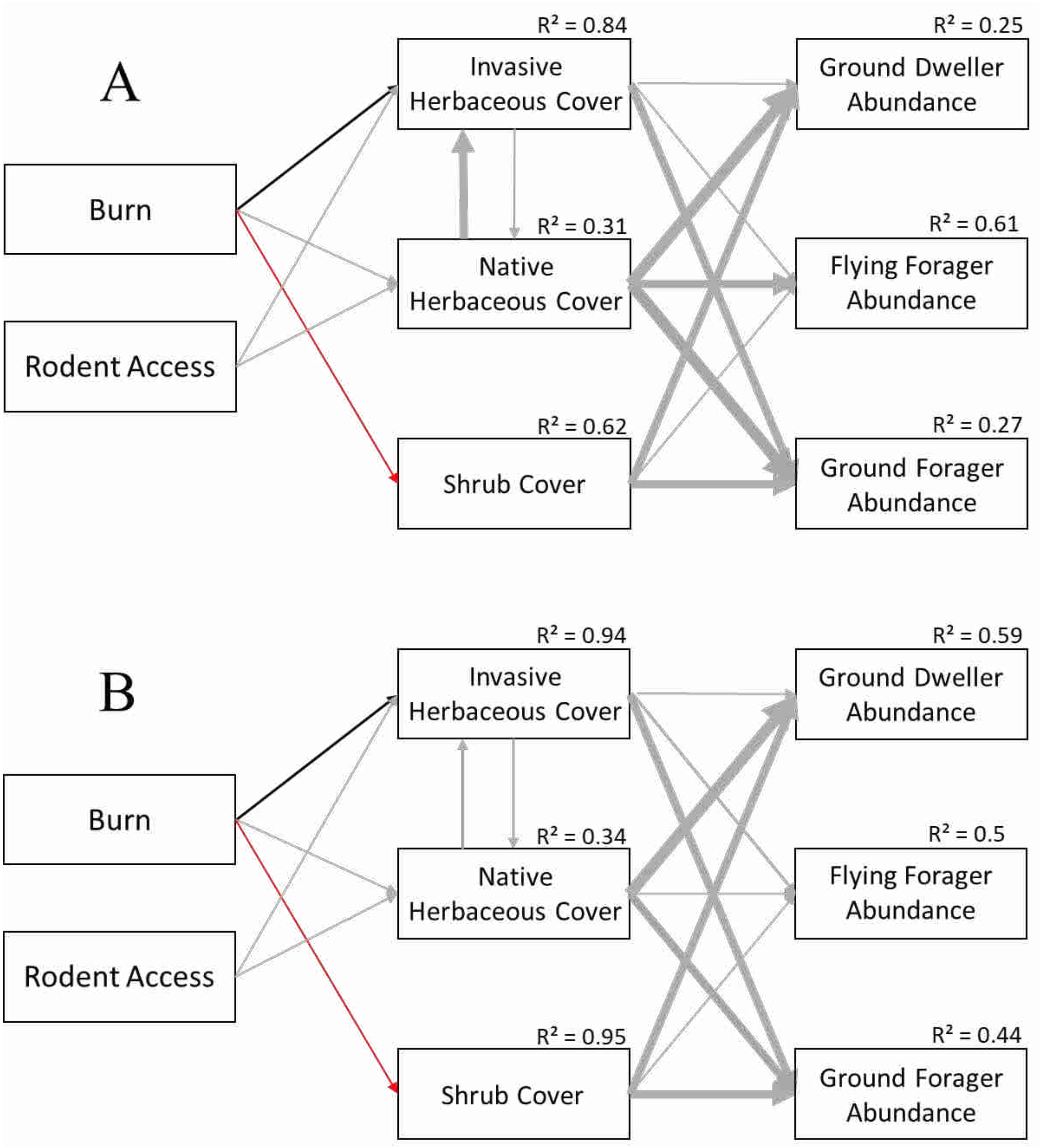

Figure 2.5. Structural equation models, showing relationships between burn treatments, rodent treatments, plant cover types and the ground-dweller abundance, flying-forager abundance, and ground-forager abundance in the Mojave (A) and the Great Basin Deserts (B). R^2 values are shown for each model. Grey lines represent non-significant interactions ($p > 0.05$), black lines represent positive significant interactions ($p \leq 0.05$), red lines represent negative significant interactions ($p \leq 0.05$). Line width indicates strength of interaction, thicker lines mean stronger interaction.

TABLES

Table 2.1. Total numbers of individuals of each taxa for the Mojave site, with the taxa separated by functional group. Numbers are separated by treatment combination: Unburned-Rodent Access (US), Unburned-Rodent Exclusion (UN), Burned-Rodent Access (BS), Burned-Rodent Exclusion (BN). Numbers represent total amounts collected for 2016 season.

Functional group/Taxon	**BS**	**BN**	**Total Burned**	**US**	**UN**	**Total Unburned**
Ground-dwellers						
Acari	482	586	**1068**	703	870	**1573**
Sminthuridae	22	13	**35**	9	62	**71**
Entomobryidae	146	281	**427**	269	180	**449**
Meinertellidae	11	5	**16**	15	19	**34**
Flying-foragers						
Cicadellidae	227	325	**552**	189	192	**381**
Anthomyiidae	17	8	**25**	7	18	**25**
Hymenoptera	15	31	**46**	29	31	**60**
Sciaridae	36	63	**99**	39	33	**72**
Bethylidae	30	25	**55**	26	12	**38**
Cecidomyiidae	41	43	**84**	78	134	**212**
Phoridae	53	62	**115**	79	59	**138**
Sphecidae	13	14	**27**	19	14	**33**
Sarcophagidae	10	4	**14**	12	23	**35**
Geocoridae	56	50	**106**	30	47	**77**
Ground-foragers						
Carabidae	9	22	**31**	17	7	**24**
Tenebrionidae	29	12	**41**	23	39	**62**
Acrididae	8	4	**12**	2	2	**4**
Rhaphidophoridae	13	19	**32**	31	16	**47**
Histeridae	23	18	**41**	42	9	**51**
Scarabaeidae	28	24	**52**	9	18	**27**
Solifugae	9	3	**12**	5	10	**15**
Elateridae	9	15	**24**	25	32	**57**

Table 2.2. Total numbers of individuals of each taxa for the Great Basin site, with the taxa separated by functional group. Numbers are separated by treatment combination: Unburned-Rodent Access (US), Unburned-Rodent Exclusion (UN), Burned-Rodent Access (BS), Burned-Rodent Exclusion (BN). Numbers represent total amounts collected for 2016 season.

Functional group/Taxon	**BS**	**BN**	**Total Burned**	**US**	**UN**	**Total Unburned**
Ground-dwellers						
Acari	714	484	**1198**	892	485	**1377**
Sminthuridae	168	71	**239**	65	81	**146**
Entomobryidae	555	2045	**2600**	277	191	**468**
Meinertellidae	1	0	**1**	1	2	**3**
Flying-foragers						
Cicadellidae	75	84	**159**	109	127	**236**
Anthomyiidae	57	62	**119**	81	65	**146**
Hymenoptera	33	11	**44**	20	20	**40**
Sciaridae	18	14	**32**	9	81	**90**
Bethylidae	15	10	**25**	14	10	**24**
Cecidomyiidae	14	29	**43**	88	103	**191**
Phoridae	32	26	**58**	60	42	**102**
Sphecidae	25	26	**51**	12	13	**25**
Sarcophagidae	18	6	**24**	30	15	**45**
Geocoridae	42	18	**60**	5	2	**7**
Ground-foragers						
Carabidae	13	4	**17**	8	3	**11**
Tenebrionidae	13	7	**20**	13	2	**15**
Acrididae	11	24	**35**	23	32	**55**
Rhaphidophoridae	7	3	**10**	10	5	**15**
Histeridae	3	1	**4**	1	1	**2**
Scarabaeidae	2	1	**3**	1	1	**2**
Solifugae	4	8	**12**	4	8	**12**
Elateridae	0	0	**0**	3	0	**3**

Table 2.3. Total numbers of individual ants of each species for the Mojave site, with the species separated by subfamily. Numbers are separated by treatment combination: Unburned-Rodent Access (US), Unburned-Rodent Exclusion (UN), Burned-Rodent Access (BS), Burned-Rodent Exclusion (BN). Numbers represent total amounts collected for 2016 season.

Subfamily/*Species*	**BS**	**BN**	**Total Burned**	**US**	**UN**	**Total Unburned**
Dolichoderinae						
Forelius pruinosus	463	395	**858**	692	320	**1012**
Dorymyrmex pyramicus	30	5	**35**	47	41	**88**
Formicinae						
Myrmecocystus mexicanus	80	25	**105**	205	306	**511**
Myrmecocystus semirufus	4	2	**6**	2	0	**2**
Myrmicinae						
Monomorium ergatogyna	18	0	**18**	1	1	**2**
Tetramorium hispidum	1	4	**5**	14	33	**47**
Pheidole desertorum	32	14	**46**	611	246	**857**
Pheidole gilvescens	209	280	**489**	286	187	**473**
Pogonomyrmex rugosus	1787	2414	**4201**	795	681	**1476**
Solenopsis molesta	0	3	**3**	0	0	**0**
Solenopsis xyloni	2063	938	**3001**	649	582	**1231**
Crematogaster depilis	0	0	**0**	18	30	**48**

Table 2.4. Total numbers of individual ants of each species for the Great Basin site, with the species separated by subfamily. Numbers are separated by treatment combination: Unburned-Rodent Access (US), Unburned-Rodent Exclusion (UN), Burned-Rodent Access (BS), Burned-Rodent Exclusion (BN). Numbers represent total amounts collected for 2016 season.

Subfamily/*species*	**BS**	**BN**	**Total Burned**	**US**	**UN**	**Total Unburned**
Dolichoderinae						
Forelius pruinosus	81	73	**154**	200	125	**325**
Formicinae						
Camponotus vicinus	7	3	**10**	41	39	**80**
Myrmecocystus hammettensis	13	2	**15**	8	4	**12**
Myrmecocystus testaceus	2	2	**4**	4	57	**61**
Myrmicinae						
Monomorium ergatogyna	25	207	**232**	15	16	**31**
Myrmica lobifrons	0	10	**10**	7	6	**13**
Pheidole jtl-222	4	19	**23**	4	7	**11**
Pogonomyrmex occidentalis	389	229	**618**	239	191	**430**
Solenopsis molesta	11	17	**28**	4	4	**8**
Temnothorax nevadensis	6	9	**15**	13	16	**29**

Table 2.5. F values from repeated measures ANOVA models for Mojave Desert invertebrate functional group and ant community responses to treatments. Bold = P < 0.1, * = P < 0.05, ** = P <0.01, *** = P <0.001.

Mojave Desert

Treatments	Ant Forager Abundance	Ant Species Richness	Ant Shannon's Diversity	Ground-Dwellers Abundance	Flying-Foragers Abundance	Ground-Foragers Abundance
Fire	0.6	**11****	**7.1***	3.1	0.1	0.3
Rodents	0.1	1.0	0.1	0.1	0.1	0.4
Month	**19*****	**24*****	**6.5****	**49*****	**63*****	3.2
FirexRodents	0.0	0.2	0.4	0.6	0.6	0.1
FirexMonth	1.7	1.8	0.5	2.7	0.2	1.2
RodentsxMonth	0.6	1.1	0.8	3.1	0.4	0.3
FirexRodentsxMonth	0.4	0.2	0.2	1.6	0.5	1.3

Table 2.6. F values from repeated measures ANOVA models for Great Basin invertebrate and ant community responses to treatments averaged for the whole year. Bold = P < 0.1, * = P < 0.05, ** = P <0.01, *** = P <0.001.

Great Basin Desert

Treatments	Ant Foraging Abundance	Ant Species Richness	Ant Shannon's Diversity	Ground-Dwellers Abundance	Flying-Foragers Abundance	Ground-Foragers Abundance
Fire	0.1	**7.7***	3.9	1.3	**15****	0.4
Rodents	0.3	0.1	0.0	0.6	0.0	0.2
Month	**41*****	**12****	**7.5***	**34*****	**9.5****	**24*****
FirexRodents	0.7	0.0	0.1	**4.9***	0.8	0.0
FirexMonth	1.0	**7.5***	**8.8***	1.4	1.4	0.6
RodentsxMonth	**4.1***	1.9	1.1	0.2	0.2	2.1
FirexRodentsxMonth	2.4	1.6	1.2	1.5	0.6	0.6

Table 2.7. Path estimates, standard error, and p-value for Mojave Desert structural equation models. P values <0.05 were bolded for emphasis.

Response	Predictor	Estimate	Std. Error	P value
Invasive Herbaceous Cover	Burn	0.188	0.031	**0.000**
Invasive Herbaceous Cover	Rodent Access	0.019	0.031	0.554
Invasive Herbaceous Cover	Native Herbaceous Cover	3.470	2.332	0.163
Native Herbaceous Cover	Burn	0.003	0.005	0.567
Native Herbaceous Cover	Rodent Access	-0.006	0.003	0.082
Native Herbaceous Cover	Invasive Herbaceous Cover	0.016	0.016	0.361
Shrub Cover	Burn	-0.159	0.031	**0.000**
Ant Shannon's Diversity	Invasive Herbaceous Cover	-1.090	0.304	**0.004**
Ant Shannon's Diversity	Native Herbaceous Cover	-0.516	4.583	0.912
Ant Shannon's Diversity	Shrub Cover	0.257	0.407	0.539
Ant Species Richness	Invasive Herbaceous Cover	-5.098	1.309	**0.002**
Ant Species Richness	Native Herbaceous Cover	-19.261	16.142	0.256
Ant Species Richness	Shrub Cover	-0.296	1.519	0.849
Ant Forager Abundance	Invasive Herbaceous Cover	0.881	1.248	0.494
Ant Forager Abundance	Native Herbaceous Cover	-10.372	16.103	0.532
Ant Forager Abundance	Shrub Cover	-0.958	1.495	0.534
Ground-Dweller Abundance	Invasive Herbaceous Cover	-0.066	1.095	0.953
Ground-Dweller Abundance	Native Herbaceous Cover	13.395	14.903	0.386
Ground-Dweller Abundance	Shrub Cover	1.257	1.363	0.375
Flying-Forager Abundance	Invasive Herbaceous Cover	0.040	0.586	0.946
Flying-Forager Abundance	Native Herbaceous Cover	1.131	6.975	0.874
Flying-Forager Abundance	Shrub Cover	0.006	0.663	0.994
Ground-Forager Abundance	Invasive Herbaceous Cover	1.050	0.916	0.274
Ground-Forager Abundance	Native Herbaceous Cover	-14.541	11.697	0.238
Ground-Forager Abundance	Shrub Cover	1.088	1.089	0.338

Table 2.8. Path estimates, standard error, and p-value for Great Basin Desert structural equation models. P values <0.05 were bolded for emphasis.

Response	Predictor	Estimate	Std. Error	P value
Invasive Herbaceous Cover	Burn	0.568	0.038	**0.000**
Invasive Herbaceous Cover	Rodent Access	-0.052	0.037	0.190
Invasive Herbaceous Cover	Native Herbaceous Cover	-0.548	0.638	0.407
Native Herbaceous Cover	Burn	-0.009	0.052	0.864
Native Herbaceous Cover	Rodent Access	-0.027	0.014	0.085
Native Herbaceous Cover	Invasive Herbaceous Cover	-0.034	0.086	0.703
Shrub Cover	Burn	-0.196	0.010	**0.000**
Ant Shannon's Diversity	Invasive Herbaceous Cover	-0.818	0.324	**0.026**
Ant Shannon's Diversity	Native Herbaceous Cover	0.147	0.946	0.879
Ant Shannon's Diversity	Shrub Cover	-1.620	0.939	0.110
Ant Species Richness	Invasive Herbaceous Cover	-2.879	1.267	**0.042**
Ant Species Richness	Native Herbaceous Cover	4.320	3.699	0.266
Ant Species Richness	Shrub Cover	-5.331	3.693	0.175
Ant Forager Abundance	Invasive Herbaceous Cover	0.437	0.874	0.626
Ant Forager Abundance	Native Herbaceous Cover	1.465	2.548	0.576
Ant Forager Abundance	Shrub Cover	0.917	2.566	0.727
Ground-Dweller Abundance	Invasive Herbaceous Cover	-0.349	1.118	0.760
Ground-Dweller Abundance	Native Herbaceous Cover	-6.380	3.269	0.075
Ground-Dweller Abundance	Shrub Cover	-3.712	3.252	0.276
Flying-Forager Abundance	Invasive Herbaceous Cover	-0.571	0.653	0.399
Flying-Forager Abundance	Native Herbaceous Cover	0.462	1.908	0.813
Flying-Forager Abundance	Shrub Cover	0.405	1.907	0.835
Ground-Forager Abundance	Invasive Herbaceous Cover	-1.396	0.761	0.091
Ground-Forager Abundance	Native Herbaceous Cover	1.152	2.222	0.614
Ground-Forager Abundance	Shrub Cover	-3.250	2.215	0.168