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The Cascading Effects of Invasive Grasses in North American Deserts: The Interactions of Fire, Plants, and Small Mammals

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The Cascading Effects of Invasive Grasses in North American Deserts:

The Interactions of Fire, Plants, and Small Mammals

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A thesis submitted to the faculty of
Brigham Young University
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Master of Science

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ABSTRACT

The Cascading Effects of Invasive Grasses in North American Deserts: The Interactions of Fire, Plants, and Small Mammals

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The landscapes of the Great Basin and Mojave Deserts are changing due to plant invasion. Highly flammable invasive grasses increase the size and frequency of fire causing a cascade of effects through the plant and animal communities. One of the most influential animal groups in desert systems is small mammals. We sought to learn how small mammals are impacted by fire and how their influence on the plant community differs between burned and unburned habitat. Small mammals did not have higher rates of mortality as a direct result of a controlled burn. In the Great Basin, there were short-term reductions in abundance, richness, and diversity of the small mammal community in burned plots. In the Mojave, species richness and diversity increased in burned plots shortly after fire and no abundance differences were detected. These results correspond with our prediction based on the dominant small mammal species at each site.

Small mammals are primarily granivores; however, they also have strong impacts on the plant community via folivory. We tested for small mammal impacts on seedling survival in burned and unburned habitat. Small mammal access, burned vs. unburned habitat, and plant species were all important determinants of survival. Small mammals greatly reduced survival at both sites in burned and unburned habitat and often had a stronger impact in unburned than burned plots. Accounting for small mammal folivory may be a crucial step in successful post-fire rehabilitation.

Finally, we used seed trays to test how small mammals influence the persistence of seed on the landscape. Small mammals reduced persistence of an invasive and native plant species in the Great Basin in 2012, yet a year later when small mammal abundance was reduced, no small mammal effect was observed. In the Mojave, persistence was reduced for the majority of species both years of the study. Small mammals did not appear to avoid seed of invasive plant species as we had predicted and may be important consumers reducing the reproductive potential of these invaders. If small mammals do prefer non-native seedlings over natives and are also consuming non-native seed, they may be greatly reducing the presence of non-natives both on the unburned landscape as well as after fire. Non-native consumption by small mammals could aid in the biotic resistance of these desert ecosystems. This research further enforces the important role that small mammals play as consumers, dispersers, and regulators of the plant community.

Keywords: Great Basin Desert, Mojave Desert, folivory, granivory, seed, seedling, *Dipodomys merriami*, *Peromyscus maniculatus*, *Bromus* sp.

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Chapter 1: Direct and indirect effects of fire on small mammal abundance and diversity in the Great Basin and Mojave Deserts

Abstract

As invasive grasses and fire increase in frequency and extent in North American deserts, they have the potential to affect animal communities through bottom-up forces. We experimentally tested the direct and indirect effects of fire on small mammal communities of the Great Basin and Mojave Deserts. Apparent survival was unaffected by fire in both deserts, indicating that the direct effects of fire were minimal. However, fire indirectly decreased the abundance, richness, and diversity of small mammals in the Great Basin up to 11 months after fire. In the Mojave, abundance was unaffected and diversity and species richness were greater on burned than unburned plots 4 months after fire. The differences in effects between the deserts may be due to differences in the foraging preferences of the dominant species at each site. As these species are primarily herbivorous, short-term changes to the small mammal community could have long-term implications by affecting the recovery of the plant community after fire.

Introduction

The invasion of exotic grasses, particularly *Bromus* species, in North American deserts has dramatically increased the size and frequency of fire in this region (Brooks and Matchett 2006). These invasive plant species fill plant interspaces with fine fuels that allow wildfire to carry across large areas. This exotic vegetation recovers quickly after fire and matures and dies early in the season which can extend the fire season and has increased fire frequency from century to decadal time scales (Whisenant 1989, Kulpa et al. 2012, Bukowski and Baker 2013).

The altered fire regimes and subsequent changes to the plant community can impact small mammal communities.

The responses of different small mammal species to fire vary in desert ecosystems; some species commonly increase in abundance in response to fire, while others decrease. Typically, bipedal species (i.e. *Dipodomys* sp.) forage in open areas between shrubs in unburned habitat (Rosenzweig and Winakur 1969, Kotler 1984) and maintain or increase their abundance when shrub cover is reduced by fire (Simons 1991, Monroe et al. 2004, Monasmith et al. 2010, Horn et al. 2012). In contrast, quadrupedal species (e.g. *Perognathus* sp. and *Peromyscus* sp.) which often focus foraging efforts under and near shrubs in desert habitat (Rosenzweig and Winakur 1969, Kotler 1984, Falkenberg and Clarke 1998), decrease in abundance after fire (Groves and Steenhof 1988, Simons 1991, Monroe et al. 2004, Ostoja and Schupp 2009, Horn et al. 2012). These species-specific responses to altered fire regimes can shift the abundance, richness, and diversity of small mammal communities.

While direct mortality of adult small mammals due to fire is variable and often minimal (Howard et al. 1959, Simons 1989, Clark and Kaufman 1990, Esque et al. 2003); indirect impacts due to habitat changes can alter the richness, abundance, and diversity of small mammal communities. There is mixed evidence that species richness, diversity, or overall abundance of small mammal communities in deserts is sometimes greater on unburned than burned areas (Bock and Bock 1978, Groves and Steenhof 1988, Ostoja and Schupp 2009, Vamstad and Rotenberry 2010, Litt and Steidl 2011, Horn et al. 2012), although sometimes no difference is detected in one or more of these measures (Valone et al. 2002, Monroe et al. 2004, Ostoja and Schupp 2009, Monasmith et al. 2010, Vamstad and Rotenberry 2010). Despite the fact that small mammal responses to fire have been the focus of many studies, the overall results are inconclusive. In addition, the time frame of many previous studies has been at least a year after fire occurred (Groves and Steenhof 1988, Monroe et al. 2004, Ostoja and Schupp 2009, Horn et al. 2012). Little is known about immediate and short-term responses of small mammal communities to fire. Information collected before fire and soon after fire is vital to understanding how and when changes in richness, abundance, and diversity occur.

Small mammals are keystone species in western North American deserts (Brown and Heske 1990, Guo et al. 1995, Kerley and Whitford 2009), therefore changes to their richness, abundance, or diversity can have important biological feedbacks on plant community characteristics. Small mammals affect plant diversity and structure via folivory, granivory, and soil disturbance (Brown and Heske 1990, Kerley and Whitford 2009). Because small mammal responses to fire vary by species (Monasmith et al. 2010), fire can change the diversity and dynamics of the small mammal community thus impacting the plant community and possibly the way it recovers after fire. An improved understanding of the changes to the small mammal community soon after fire could inform our understanding of the regrowth of the plant community and ultimately the changes occurring after fire across desert ecosystems.

We designed an experiment utilizing mark-recapture methods to test the short-term effect of fire on small mammal communities in two North American deserts. We hypothesized that fire would indirectly impact the abundance, richness, and diversity of the small mammal community by limiting resource availability and altering habitat structure. Specifically, we predicted that: i) abundance of bipedal species (*Dipodomys* sp.) would be greater in burned than unburned plots or remain unchanged after fire; ii) abundances of quadrupedal species (e.g. *Peromyscus* sp., *Perognathus* sp.) would be greater in unburned than burned plots after fire; iii) small mammal species richness and diversity would decrease on burned plots; iv) fire would not decrease survival of small mammals; v) at a site dominated by a bipedal species (our Mojave site dominated by *Dipodomys merriami* (Merriam's kangaroo rat)), fewer changes to the small mammal community will be observed after fire than at a site dominated by a quadrupedal species (our Great Basin site dominated by *Peromyscus maniculatus* (deer mouse)).

Methods

Study Site

The study sites were located in the Great Basin and Mojave Deserts of Utah. The Great Basin site was located in a sage-steppe community on BLM land in Rush Valley (40°5'21.18"N, 112°18'26.88"W). Dominant vegetation was *Artemisia tridentata wyomingensis* (Wyoming sagebrus) and *Elymus elymoides* (bottlebrush squirreltail). The Mojave study area was located at Lytle Ranch Preserve in the Beaver Dam Wash region of southwestern Utah in mid elevation Mojave shrubland (37°8'53.46"N, 114°0'49.59"W). The dominant vegetation at this site was composed of *Yucca brevifolia* (Joshua tree), *Coleogyne ramosissima* (blackbrush), and *Larrea tridentata* (creosote bush). These study sites were established in 2011.

Plot Design

Each study site contained five replicates hereafter referred to as blocks. Each block was quartered into four adjacent square plots (30 m x 30 m) fenced with 1 cm welded wire fencing that extended 65 cm aboveground and 35 cm belowground. Plots were randomly assigned to the treatments: burned open (with small mammals), burned exclosure (without small mammals), unburned open, and unburned exclosure so that each treatment was represented once per block. Small mammal exclosure plots had 20 cm of metal flashing over the welded wire on the outward facing side to prevent entrance into these plots. To facilitate movement of small mammals into and out of open plots, a 15 cm x 15 cm hole was cut into the welded wire at ground level on both sides of the plot connected to the outside area. Burn treatments were applied to selected plots on June 18 (Mojave) and September 17 (Great Basin) of 2011.

Small mammal trapping

We sampled small mammals by live trapping within each plot and outside of each plot before and after controlled burns occurred. The Mojave site was sampled 3 weeks prior to the burn and 3 and 17 weeks after the burn. We attempted to sample the Great Basin site along the same timeline; however, due to burn restrictions the date of the fire was postponed. This site was therefore sampled 12 and 9 weeks prior to the burn and 3 weeks afterwards. Sampling continued at both sites three times annually (spring, summer, and fall) through April 2014. For each trapping session eight Sherman live traps were placed 1 m from the fencing inside each plot (two per side); four traps were placed 10 m from the fencing outside each plot (Figure 1.1). Each trap was baited with commercially available rodent seed mix. A total of 240 traps were set each night at each study area. Traps were set each evening and checked each morning for three consecutive nights. Polyester batting was added to traps if temperatures were predicted to drop below 4° C to reduce the likelihood of exposure. Small mammals received an individually numbered ear tag and the species, trap location, sex, age, reproductive condition, and mass were recorded for each animal. Because tags are occasionally lost from pocket mice with small ears (Parmenter et al. 2003), we also shaved a small patch of fur from these animals when captured to identify them as recaptures during subsequent nights within the capture session. All animals were released at the point of capture unless they were trapped inside an exclosure plot in which case they were released at the nearest point outside the exclosure.

To ensure that captures from traps near plot edges accurately represented the small mammal communities within plots, we used an additional trap layout in April 2014 at both sites (hereafter identified as the center layout). The original trap layout as specified above was first used for three nights according to the standard protocol; the following three nights the center layout was used. The center layout had six Sherman live traps placed in a circle centered in each plot; each trap was 3 m from the center of the plot, 3 m from neighboring traps within the same plot, and 12 m from the edge of the plot. All traps were baited, set, and checked with the same methods detailed for the original layout above; the only alteration was the location and number of traps used. 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).

Data Analysis

ANOVA tests were used to examine treatment effects. All analyses were performed with function lmer in package lme4 of program R (Bates et al. 2014, R Core Team 2014). Minimum number known alive (MNKA) was used as our measure of small mammal abundance and was calculated as the minimum number of individuals of each species recorded within burned and unburned plots with small mammal access for each time period. Species richness, overall abundance, reciprocal Simpson diversity index, and Shannon diversity index were calculated for each plot in each time period using function diversityresult in package BiodiversityR (Kindt and Coe 2005). These four values as well as the MNKA for each species were used as response variables for analyses. To determine if there were short-term effects of fire on small mammals, we tested for a treatment by time interaction with a separate model for response variables of each trapping period. An interaction model was chosen over an additive treatment and time model because we wanted to allow for differences between treatments to vary before and after the fire treatment was applied. When ANOVA tests were significant, Tukey adjusted pairwise comparisons of least squared means were conducted using function lsmeans in package lsmeans (Lenth 2014). These tests were used to determine if there were differences between unburned and burned plots in each time period as well as between the original and new trap layouts in April 2014.

To determine if there was a direct impact of fire on the survival of small mammals, apparent survival rates were calculated for animals in burned and unburned plots. Apparent survival was calculated as the number of individuals recaptured after the fire divided by the total number captured in the trapping period before the plots were burned. Apparent survival rates were calculated for each open plot separately. Two individuals in the Great Basin were captured before fire in the same burn treatment type in two different blocks (e.g. in the burned plot of block 1 and the burned plot of block 2); for this analysis, they were counted only for the first plot in which they were captured. There were two individuals in the Great Basin and three in the Mojave that were captured in both a burned and an unburned plot before fire; these were left out of the analysis. Comparisons were made using a t-test with function t.test in package stats in program R (R Core Team 2014).

Results

We had 1,018 captures of 487 individual small mammals in the Great Basin and 1,244 captures of 505 individuals in the Mojave over 12,960 total trap-nights. In decreasing order of abundance, species comprising the community in the Great Basin were *P. maniculatus*, *Dipodomys microps* (chisel-toothed kangaroo rat), *Perognathus parvus* (Great Basin pocket mouse), *Tamias minimus* (least chipmunk)*, Lemmiscus curtatus* (sagebrush vole), and *Onychomys leucogaster* (northern grasshopper mouse; Figure 1.2). In decreasing order of abundance, species comprising the community in the Mojave were *D. merriami*, *Chaetodipus formosus* (long-tailed pocket mouse), *Neotoma lepida* (desert woodrat), *Peromyscus crinitus* (canyon mouse), *O. leucogaster*, *Ammospermophilus leucurus* (white-tailed antelope squirrel), and *Sylvilagus audubonii* (desert cottontail).

In the Great Basin, we captured four species of small mammal in burned plots, five in unburned plots, and five outside of the plots. *D. microps*, *P. maniculatus*, *P. parvus*, and *T. minimus* were captured in burned plots. All of these species were captured in unburned plots and outside plots with the addition of *L. curtatus* in unburned plots and *O. leucogaster* outside the plots. We did not perform species specific abundance comparisons for *L. curtatus* or *O. leucogaster* due to the low number of captures for these species.

In the Mojave, we captured six species of small mammal in burned plots, seven in unburned plots, and seven outside of the plots. *D. merriami*, *C. formosus*, *N. lepida*, *P. crinitus*, *O. leucogaster*, and *A. leucurus* were captured in burned plots. All of these species and *S. audubonii* were captured within unburned plots and outside of the plots. We did not perform species specific abundance comparisons for *O. leucogaster*, *A. leucurus* or *S. audubonii* due to the low number of captures of these species.

Comparisons of the original and center trap layouts confirmed consistency in the results obtained by these two methods in both deserts. No differences were detected in richness, diversity, or abundance between burned and unburned plots at that time using either method (all $p>0.05$). Additionally, no differences were detected in richness, diversity, or abundance measures between the original and center layouts (all $p>0.05$).

Direct effects of fire on small mammals

We had no evidence of mortality of small mammals due to fire in either desert. In the Great Basin, apparent survival of animals captured in burned plots (0.18 ± 0.09) did not differ from unburned plots (0.43 ± 0.21; t=-1.08, p=0.34). The same was true in the Mojave where apparent survival in burned plots (0.40 ± 0.13) did not differ from unburned plots (0.39 ± 0.19; t=0.06, p=0.95).

Indirect effects of fire on small mammals

In the Great Basin, small mammal abundance, richness, and diversity decreased in burned plots after fire. In October 2011, three weeks after fire, total abundance (burned: 1.0 ± 0.4; unburned: 4.2 ± 0.8; t=2.84, p=0.02), *P. maniculatus* abundance (burned: 0 ± 0; unburned: 2.6 ± 0.7; t=2.90, p=0.01), and species richness (burned: 0.8 ± 0.4; unburned: 2.0 ± 0.3; t=2.70, p=0.02) were greater in unburned than burned plots (Figure 1.3); these measures did not differ in any other time period (all p>0.05). In April 2012, seven months after the fire, *T. minimus* was more abundant in unburned (1.0 ± 0.3) than burned plots (0.2 ± 0.2; t=2.50, p=0.04); abundance of *T. minimus* did not differ in any other time period (all p>0.10). In August 2012, 11 months after fire, species diversity was greater in unburned than burned plots for both the inverse Simpson (burned: 1.34 ± 0.21; unburned: 2.14 ± 0.13; t=2.43, p=0.04) and Shannon (burned: 0.26 ± 0.16; unburned: 0.80 ± 0.07; t=2.90, p=0.01) indices; these measures did not differ in any other time period (p>0.05). Abundances of *D. microps* and *P. parvus* did not differ between burned and unburned plots in any time period (all p>0.10).

In the Mojave, small mammal diversity and species richness increased on burned plots after fire. In October 2011, four months after fire, species richness (burned: 2.2 ± 0.2; unburned: 0.8 ± 0.4; t=2.59, p=0.03) and Shannon's diversity index (burned: 0.66 ± 0.07;

unburned: 0.06 ± 0.06; t=2.90, p=0.01; Figure 1.4) were greater in burned than unburned plots; these measures did not differ in any other time period (all p>0.10). Simpson's diversity index, overall abundance, and all species specific abundances did not differ between burned and unburned plots in any time period (all p>0.10).

Comparison across deserts

We observed more differences in the small mammal community between burned and unburned plots in the Great Basin than the Mojave. Abundances of *P. maniculatus* and all species combined were greater in unburned than burned plots in the Great Basin three weeks after fire. Species richness was also greater in unburned than burned plots three weeks after fire. In addition, abundance of *T. minimus* (7 months after fire) and small mammal diversity (11 months after fire) were greater in unburned than burned plots within a year after the burn. However, no differences were detected in abundance between burned and unburned plots in any time period before fire or up to 34 months after fire in the Mojave. Species richness and Shannon's diversity index were greater in burned than unburned plots four months after fire, but no other differences were observed between treatments in the Mojave.

Discussion

Great Basin fire effects

In the Great Basin, we found no evidence that the small mammal community was directly affected by fire treatments. We did not detect any differences in apparent survival between animals in burned and unburned plots. This is consistent with other evidence that direct fire mortality tends to be low in forest (Lee and Tietje 2005, Tietje et al. 2008, Morris et al. 2011), prairie (Clark and Kaufman 1990), and arid ecosystems (Esque et al. 2003, Yarnell et al. 2008, D'Souza et al. 2013).

There were short term indirect effects of fire on the abundance of the small mammal community in the Great Basin. Abundances of *P. maniculatus* and all species combined were lower in burned plots than unburned plots three weeks after fire. The decline in overall abundance appears to be driven primarily by the change in *P. maniculatus* numbers as none were caught in burned plots at that time. As there is no evidence of higher mortality as a direct result of fire, the observed abundance difference is best explained as an avoidance of the recently burned plots by *P. maniculatus*. Lower abundance of *P. maniculatus* at burned than unburned sites has previously been demonstrated in desert habitat (Groves and Steenhof 1988); however, it is interesting to note that this species often exhibits a positive response to fire in forest and prairie habitats (Kaufman et al. 1988, Clark and Kaufman 1990, Zwolak and Foresman 2007, 2008, Zwolak et al. 2010). Differences in litter cover and interspecific competitors may be responsible for different fire responses in different habitats (Kaufman et al. 1988, Clark and Kaufman 1990, Zwolak and Foresman 2007).

In the Great Basin, the effects of fire on the small mammal community that we detected were all within one year of the burn; fire effects were not detected 1-2.5 years after fire. Likewise, previous research in the Great Basin found that diversity did not differ 6-17 years after fire (Ostoja and Schupp 2009). However, greater abundance and richness were found in unburned than burned habitat 1-17 years after fire (Groves and Steenhof 1988, Ostoja and Schupp 2009).

Mojave fire effects

In the Mojave, we found no evidence of direct effects of fire on small mammals. Animals captured in burned and unburned plots had equivalent apparent survival. Similarly, other studies have shown that mortality of small mammals during fire events is quite low in the desert (Esque et al. 2003, Yarnell et al. 2008, D'Souza et al. 2013).

In the Mojave, there were no indirect effects of fire on the abundance of the small mammal community and few effects on richness and diversity. Species richness and Shannon's diversity index were both greater in burned than unburned plots four months after fire; afterwards, no differences were detected in these measures. However, our results are inconsistent with those of a study performed on naturally occurring burned and unburned habitats near our Mojave study plots (Horn et al. 2012). At these nearby sites, the abundance of *D. merriami* increased, while the abundances of *C. formosus*, *P. crinitus*, and all species combined decreased on sites burned 4-5 years previously compared to unburned sites. That study also found reduced richness and diversity at burned sites. These changes in abundance, richness, and diversity may be the result of accumulated indirect effects of fire impacting the survival or reproductive rates of small mammals in burned areas over time. Similar changes to the small mammal community may be occurring on our site, yet they remain undetected at this relatively early time.

The fire effects that we detected on the small mammal community in the Mojave were all within four months of the burn; no differences were detected ten months to three years after fire. In contrast, previous studies have found that diversity has been greater in unburned than burned Mojave habitat two or more years after fire (Vamstad and Rotenberry 2010, Horn et al. 2012).

There is mixed evidence as to whether abundance and species richness are greater in unburned habitat (Horn et al. 2012) or do not differ (Vamstad and Rotenberry 2010) as in our study.

Desert comparisons

We hypothesized that the mode of locomotion of the most abundant species would influence how each community responded to fire. At our Great Basin site *P. maniculatus* is the most abundant species and is quadrupedal; quadrupedal species tend to prefer shrub cover (Rosenzweig and Winakur 1969, Kotler 1984, Falkenberg and Clarke 1998) which is decreased by fire. At our Mojave site, *D. merriami* is the most abundant and is bipedal; bipedal species tend to prefer open areas between shrubs which are increased by fire (Rosenzweig and Winakur 1969, Kotler 1984). We therefore expected more severe decreases in the abundance, richness, and diversity of small mammals in the Great Basin as their preferred habitat decreased after fire. Consistent with our prediction, we observed more indirect impacts of fire on the small mammal community in the Great Basin than in the Mojave (Figures 1.3-1.4). Similarly, other studies have found decreases in the abundance of quadrupedal species after fire (Groves and Steenhof 1988, Simons 1991, Monroe et al. 2004, Ostoja and Schupp 2009, Horn et al. 2012) and equal or increased abundances for bipedal species after fire (Simons 1991, Monroe et al. 2004, Monasmith et al. 2010, Horn et al. 2012).

As small mammals can play a keystone role in North American deserts (Brown and Heske 1990, Guo et al. 1995, Kerley and Whitford 2009), understanding their response to fire in this region is an important step to understand the regrowth of the plant community and to plan effective rehabilitation efforts for burned regions. Additionally understanding the longer term changes to the small mammal community through continued monitoring of burned regions will aid in the understanding of how these communities change over time. As these communities shift, the impact on the plant community will have an important influence on these desert landscapes and help to determine how they respond to fire and other disturbances.

Indirect impacts of fire were detected in both the Great Basin and Mojave Deserts. While there was no evidence of increased mortality in burned plots due to fire, indirect effects of fire were detected within a year after fire in both deserts. These indirect effects of fire were more numerous in the Great Basin than the Mojave and this difference may be due to the modes of locomotion of the dominant species at each site. These results add to our understanding of the changes occurring in the deserts of western North America as a result of alterations to the fire regime. This information can help us understand the post-fire dynamics of these ecosystems as a whole and inform management decisions regarding post-fire rehabilitation efforts.

The future of the Great Basin and Mojave Deserts is threatened by invasive grass and associated fire (Whisenant 1989, Brooks and Matchett 2006, Bukowski and Baker 2013). By improving our understanding of these systems we can implement effective management actions that will minimize the impacts of invasive species and preserve these unique ecosystems. Desert small mammals, as both plant consumers and dispersers, play an important role in determining the structure of the plant community (Brown and Heske 1990, Guo et al. 1995, Kerley and Whitford 2009). Understanding how small mammals are effected by fire, particularly in the short-term as plant communities are recovering, is pivotal to understanding how these systems respond to invasion and how the effects of invasion can be minimized.

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Chapter 1 Figures

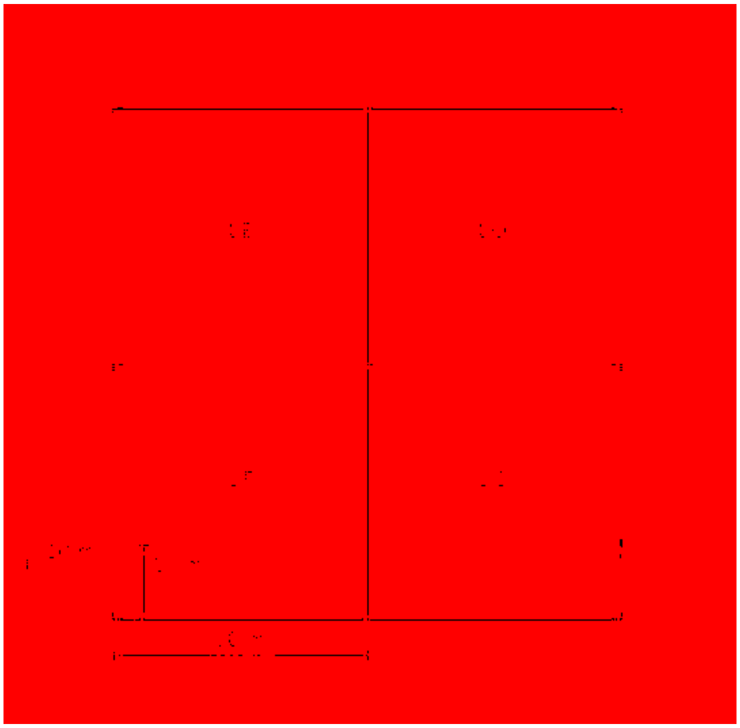

Figure 1.1. Trap layout for each block; each triangle represents a trap station with one Sherman live trap. Each block contains 4 adjacent plots (30 x 30 m each) with 8 traps inside each plot and 4 outside each plot. Plots are labeled BE for burned exclosure, BO for burned open, UE for unburned exclosure, and UO for unburned open.

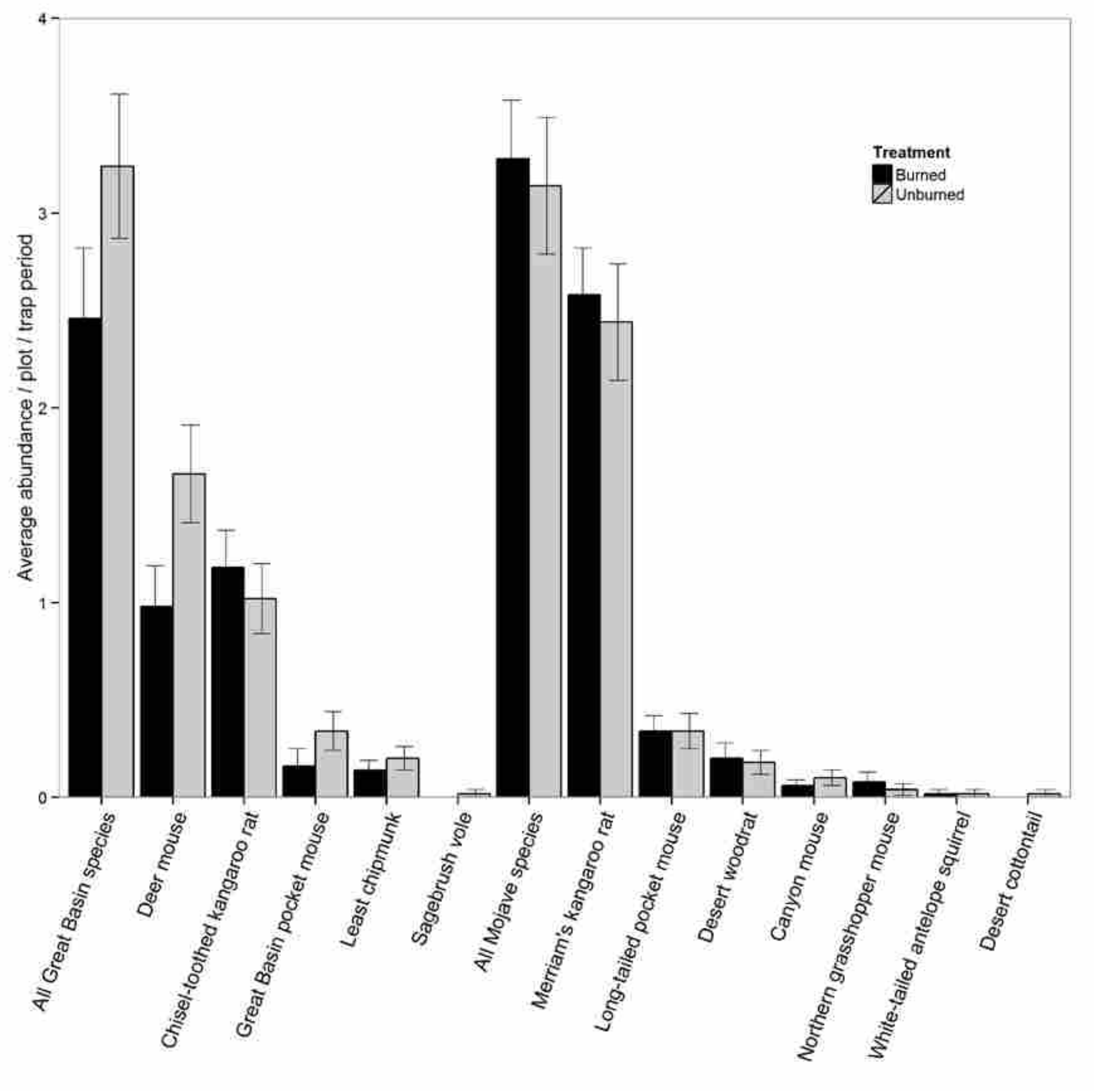

Figure 1.2. Relative abundance of small mammal species (+SE) captured in burned and unburned plots in the Great Basin and Mojave Deserts between May 2011 and April 2014.

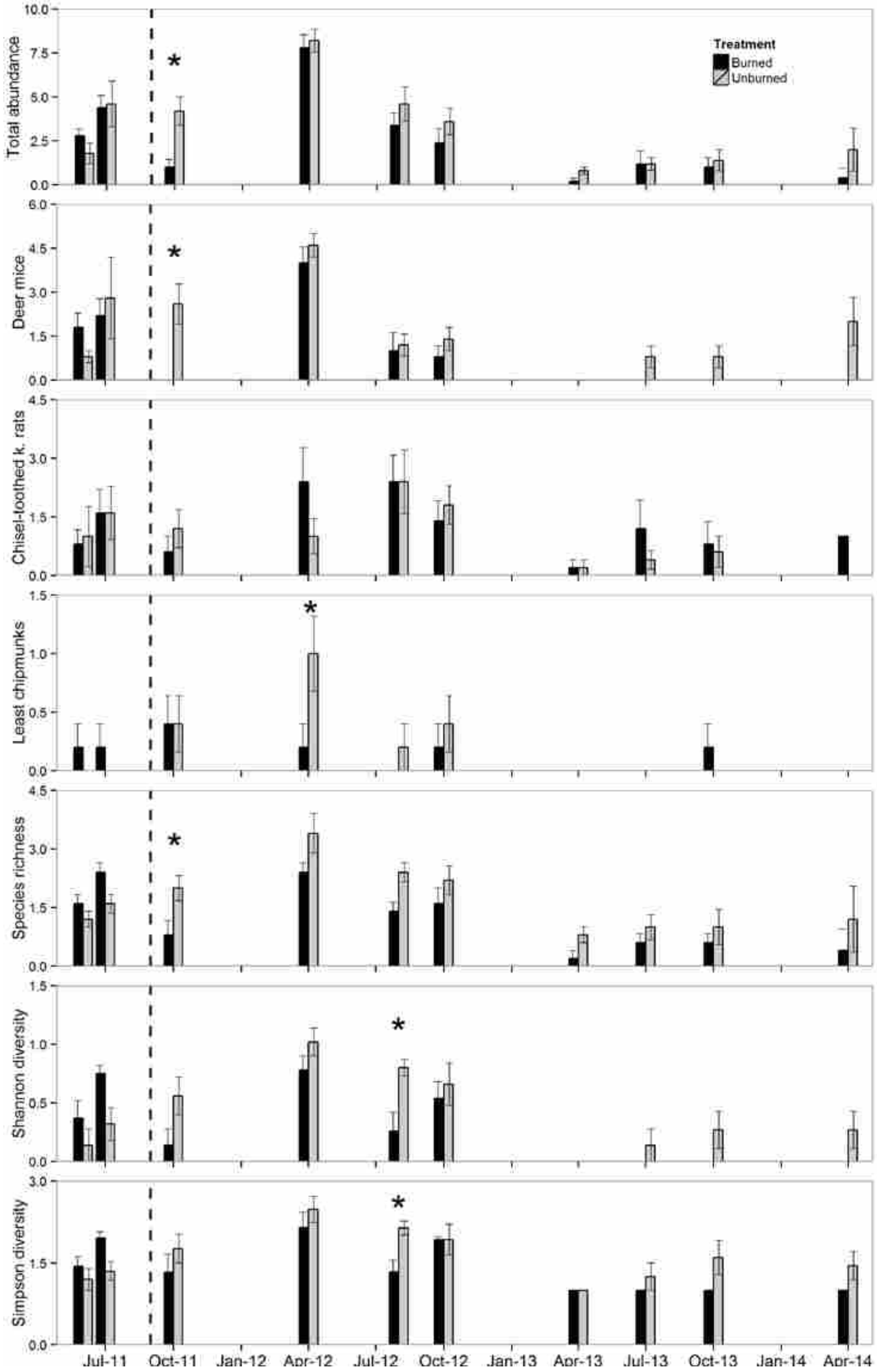

Figure 1.3. Abundance of all small mammal species, abundance of deer mice, abundance of chisel-toothed kangaroo rats, abundance of least chipmunks, species richness, Shannon and Simpson diversity indices in burned and unburned plots (+SE) in the Great Basin Desert between June 2011 and April 2014. The dashed line marks the time when plots were burned; * denotes significant difference ($p<0.05$) between burned and unburned plots for a given trapping occasion.

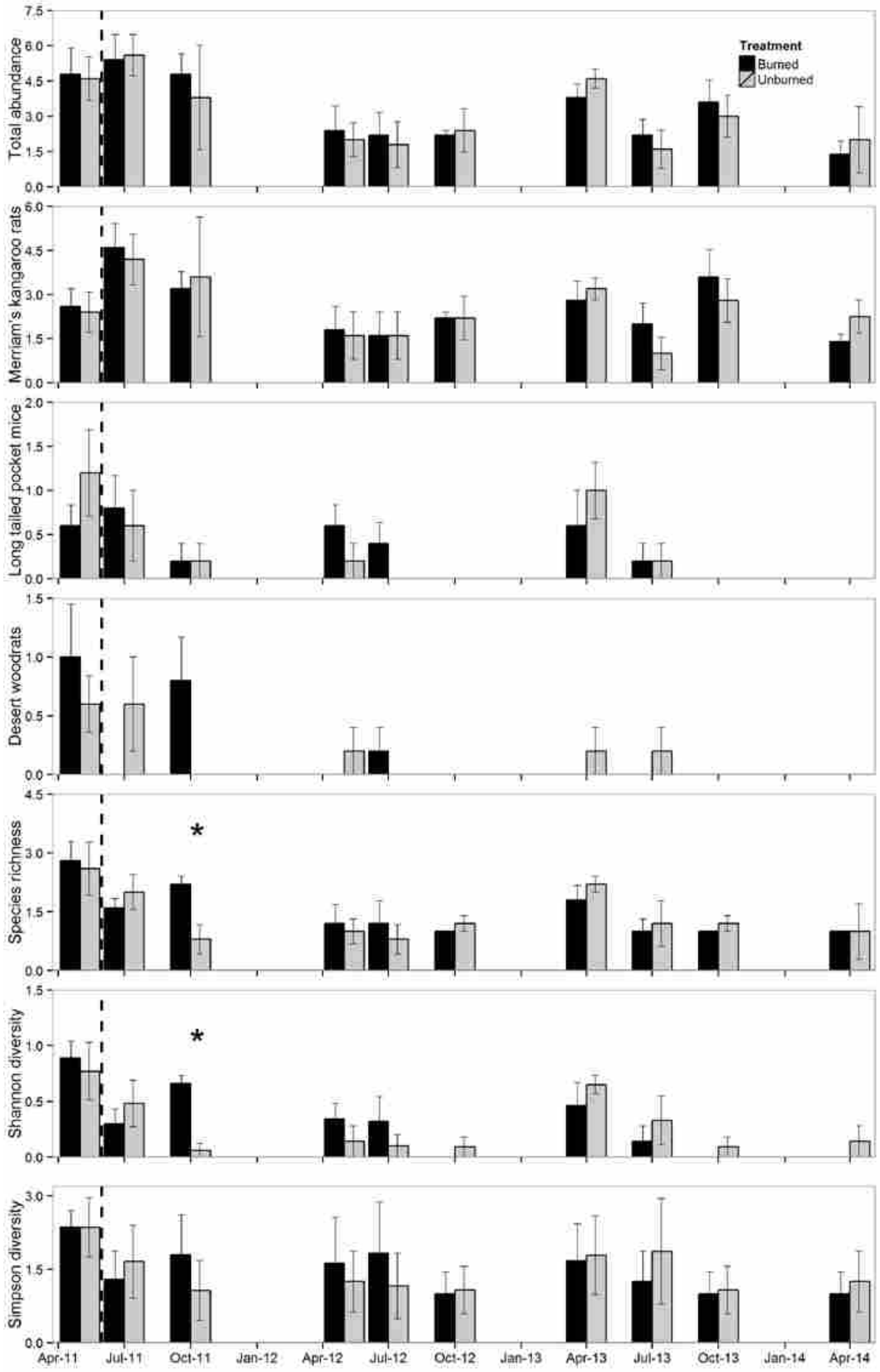

Figure 1.4. Overall abundance of small mammals (+SE), abundance of Merriam's kangaroo rats, abundance of long-tailed pocket mice, abundance of desert woodrats, species richness, Shannon's diversity index, and Simpson's diversity index in burned and unburned plots in the Mojave Desert 2011- 2014. The dashed line marks the time when plots were burned. Differences ($p<0.05$) between burned and unburned plots within a trapping occasion are marked with an asterisk (*).

Chapter 2: Drivers of desert plant communities: Interactions of small mammal folivory and fire in western North American deserts

Abstract

Invasive exotic grasses are increasing the frequency and size of wildfire in North American deserts resulting in alterations to the vegetation and wildlife communities in these regions. Desert small mammals impact the plant community via granivory, folivory, and seed dispersal. Small mammals may vary in their abundance and diversity between burned and unburned desert regions and thus their impact to the plant community could be altered by a changing fire regime. To better understand how desert wildfire may alter small mammal-plant interactions, we examined the influence of small mammal folivory on seedling survival in experimental plots in the Mojave and Great Basin Deserts. We used a randomized complete block experimental design to examine the interactive effects of small mammals (present vs. absent) and fire (burned vs. unburned). Seedlings of 14-15 common species were transplanted into experimental plots and survival was monitored daily. Small mammals had a negative effect on seedling survival in both years in both deserts. The impact of small mammals on seedling survival differed between burned and unburned regions. Desert seedling survival is heavily influenced by small mammals and this impact can differ between burned and unburned regions and vary across plant species. In regions impacted by exotic grass invasion and altered fire regimes, small mammal folivory may have a strong influence on the recovery of the plant community. After fire, the impact of small mammal folivory on the recovering plant community needs to be accounted for when planning rehabilitation efforts in ensure success.

Introduction

Small mammals play a keystone role in deserts via folivory and granivory (Brown and Heske 1990, Guo et al. 1995, Kerley et al. 1997, Kerley and Whitford 2009). Folivory by small mammals can have strong effects on the structure of plant communities (Guo et al. 1995, Kerley et al. 1997, Roth et al. 2009, Kerley and Whitford 2009); it can reduce the survival of seedlings, plant establishment, and seed production of various plant species (Pyke 1986, Valone and Thornhill 2001, Meyer and Pendleton 2005, Duval et al. 2005, Bestelmeyer et al. 2007, Suazo et al. 2013). Folivory by small mammals can also maintain disturbed sites in a degraded state (Roth et al. 2009) and may synergistically reduce survival of native plants in combination with competition with invasive grasses (Lei 2009). However, many aspects of small mammal folivory are still unclear including how folivory may be impacted by disturbance such as fire, how effects may vary between different small mammal communities, and the relative effect on different plant species,.

Increases in fire in North American deserts are occurring as invasive grasses increase the connectivity of fuels, altering the structure of the plant community (D’Antonio and Vitousek 1992, Brooks et al. 2004, Brooks and Matchett 2006). The rapid recovery of invasive grasses after fire provides abundant flammable biomass (Beatley 1969a, West and Hassan 1985). The positive feedback loop that results leads to shorter fire return intervals (Whisenant 1989, Bukowski and Baker 2013) and a loss of native shrub cover (Stewart and Hull 1949, Young and Evans 1978, Whisenant 1989). Reductions in shrub cover associated with disturbance such as fire can alter the abundance and diversity of small mammal communities (Beatley 1976, Simons 1991, Horn et al. 2012, Hall 2012, Freeman et al. 2014). These changes to the small mammal community likely affect the keystone role of small mammals in desert systems, yet what the specific impacts of disturbance may be and to what extent this may occur remain unknown.

The bottom-up effects of disturbance on the small mammal community may vary depending on the small mammal species present. Bipedal desert small mammals (i.e. *Dipodomys* sp.) prefer foraging in open areas between shrubs (Rosenzweig and Winakur 1969, Kotler 1984) and maintain or increase abundance in response to fire (Simons 1991, Monroe et al. 2004, Monasmith et al. 2010, Horn et al. 2012). At a site dominated by bipedal species, small mammals may forage equivalently in burned and unburned regions. In contrast, quadrupedal species (e.g. *Peromyscus* sp., *Perognathus* sp.) prefer foraging under and near shrub cover (Rosenzweig and Winakur 1969, Kotler 1984, Falkenberg and Clarke 1998) and their abundance is often reduced after fire (Groves and Steenhof 1988, Simons 1991, Monroe et al. 2004, Ostoja and Schupp 2009, Horn et al. 2012). At a site dominated by quadrupedal species, small mammals may avoid burned habitat and preferentially forage in unburned regions. Therefore, the relative abundance of bipedal and quadrupedal small mammals at a site may determine the intensity of top-down effects of small mammals after disturbance such as fire.

Our objective was to assess how folivory impacts plant survival and is altered by disturbance. Specifically, we evaluated the interactive effects of folivory by small mammals and fire on the survival of seedlings in two North American deserts. We addressed the following questions: 1) What is the impact of small mammals on the survival of seedlings of various plant species? 2) How will plant survival and small mammal effects differ between disturbed (burned) and undisturbed (unburned) habitat? 3) How will disturbance and small mammal effects differ between bipedal and quadrupedal communities?

Methods

Study Sites

The study sites were located in the Great Basin and Mojave Deserts of Utah. The Great Basin site was located in a sage-steppe community in Rush Valley on BLM land in west-central Utah (40°5'21.18"N, 112°18'26.88"W). Dominant vegetation was *Artemisia tridentata wyomingensis* (Wyoming sagebrush) and *Elymus elymoides* (bottlebrush squirreltail). Trapping at the Great Basin site revealed that the small mammal community is primarily comprised of (in order of descending abundance): *Peromyscus maniculatus* (deer mouse), *Dipodomys microps* (chisel-toothed kangaroo rat), and *Perognathus parvus* (Great Basin pocket mouse; Sharp Bowman 2015). The Mojave study area was located at Lytle Ranch Preserve in the Beaver Dam Wash region of southwestern Utah in mid elevation Mojave shrubland (37°8'53.46"N, 114°0'49.59"W). The dominant vegetation at this site was composed of *Yucca brevifolia* (Joshua tree), *Coleogyne ramosissima* (blackbrush), and *Larrea tridentata* (creosote bush). Trapping at the Mojave site revealed that the small mammal community is primarily comprised of (in order of descending abundance): *Dipodomys merriami* (Merriam's kangaroo rat), *Chaetodipus formosus* (long-tailed pocket mouse), and *Neotoma lepida* (desert woodrat; Horn et al. 2012, Sharp Bowman 2015). These sites were established in 2011.

Plot Design

We used a randomized complete block design to assess the effects of small mammals and fire on the survival of seedlings. Each of our study sites contained 5 replicates, hereafter referred to as blocks. Each 60 m x 60 m block was quartered into 4 adjacent square plots (30 m x 30 m). We installed 1 m tall welded wire fences that extended 65 cm aboveground and 35 cm belowground surrounding each plot. Each plot was randomly assigned to one of four treatments:

burned with small mammals (burned open), burned without small mammals (burned exclosure), unburned with small mammals (unburned open), and unburned without small mammals (unburned exclosure); each treatment was represented once per block. To facilitate movement of small mammals into and out of open plots, 10 x 12 cm holes were cut into the welded wire at ground level connecting plots to the outside area. To prevent access of small mammals into exclosure plots, 20 cm of metal flashing was installed over the welded wire on the outward facing side. However some larger species (e.g. *Tamias minimus* (least chipmunk) and *N. lepida)* were not completely excluded by the exclosure fencing.

Burn treatments were applied to selected plots on June 18 (Mojave) and September 17 (Great Basin) of 2011. Fires at both sites were ignited using drip torches. Due to low concentrations of fine fuels at the Great Basin site, 300 g/m^2 of wheat straw was added to plots using the methods of Esque et al. (2010) to allow fire to spread between shrubs. This concentration of straw is within concentrations of fine fuels found at Great Basin sites with *Bromus tectorum* (cheatgrass) invasion (Hulbert 1955). The burn severity was high; with greater than 95% plant mortality. At the Mojave site, straw additions were deemed unnecessary. In the Mojave, the burn severity was moderate; all herbaceous vegetation and the majority of shrubs were consumed by fire.

Seedling Experiment

To determine the effects of fire and small mammals on the survival of seedlings, we planted seedlings of 14 (Great Basin) or 15 (Mojave) species common to each desert in the plots and monitored their survival over the course of 1-2 weeks (Table 2.1). A preliminary trial in the greenhouse was conducted to determine the length of time each plant species needed to grow to a mean height of 2.5 cm. Each species of plant was grown from seed in a 4 inch square plastic pot in a mixture of 50% sand, 25% perlite, and 25% top soil watered daily. Results from this trial were used to determine planting times and germination rates to have 10-15 plants per pot timed to match the emergence of seedlings on the landscape at each site.

In 2012, due to time constraints the seedlings were put out into plots over 2 days: May 1 (3 blocks) and May 2 (2 blocks) in the Mojave and May 29 (3 blocks) and May 30 (2 blocks) in the Great Basin. The entire pot was planted so that the soil level in the pot (approximately 1 cm below the lip) was even with ground level. Pots were planted 0.3 meters apart along a randomly placed transect line within each plot. The number of plants alive per pot was recorded every day or every other day for 8 days from the beginning of the experiment. Plants were counted as dead if no whole leaves remained or if they were too dry to stand upright. After counting each pot received approximately 20 ml of water.

In 2013, all blocks at a given site were planted on a single day and timed to match the experiments performed the previous year (May 2 in the Mojave and May 30 in the Great Basin). To ensure independence among species, pots were planted 3 meters apart and 3 meters from the edge of the plot in a regular linear pattern. Number of seedlings alive in each pot were counted at the time of planting and then subsequently daily or every other day over the course of 8 days. Plants were counted as dead if no whole leaves remained or if they were too dry to stand upright. After counting each pot received approximately 20 ml of water.

Data analysis

We used mixed effects Cox proportional hazards analysis to investigate how small mammal treatment, burned or unburned treatment, and plant species influenced the survival of seedlings. Survival data was divided into four datasets based on site and timing: Mojave 2012, Great Basin 2012, Mojave 2013, and Great Basin 2013. For each dataset, we fit models using all combinations of the three fixed factors (small mammal treatment, burn treatment, and plant species) and their interactions as well as a random term for block and then selected the best model using AIC_c. Analyses were performed using package coxme in program R (Therneau 2012a, R Core Team 2014). Pairwise comparisons were made using package lsmeans on fixed effect Cox proportional hazards models from package survival in program R (Therneau 2012b, Lenth 2014). The top model from the mixed effect analysis for each dataset was created using the survival package with block included as an additive fixed effect. Pairwise comparisons were made for each species and treatment combination within each dataset.

Results

We monitored the fates of 3925 seedlings in the Great Basin in 2012, 3888 in the Great Basin in 2013, 3022 in the Mojave in 2012, and 3028 in the Mojave in 2013. At both sites and during both years, the survival of seedlings was affected by small mammal and burn treatments (Figure 2.1, Table 2.2). Plant species was also an important factor determining survival for all datasets. The top model for each dataset was the three-way interaction (Mammals*Burned*Species; for all w_i=1.00).

Small mammals reduced seedling survival and this impact differed between burned and unburned plots (Figure 2.1, Tables 2.3-2.4). Small mammals reduced survival for fewer plant species in burned than unburned Great Basin plots in both years (Figures 2.1-2.3, Table 2.3). In the Mojave, small mammals reduced survival for all 15 plant species, except for *Krascheninnikovia lanata* (winterfat) in both burned and unburned plots in 2012 (Figures 2.4-

2.5, Table 2.4). However in 2013, small mammals in the Mojave reduced survival for more species in unburned plots than burned plots.

Small mammal access to plots often shifted patterns of seedling survival between burned and unburned habitat (Figure 2.1, Tables 2.3-2.4). In the Great Basin in 2012, survival was higher in burned than unburned plots both with and without small mammal access (Table 2.3). However, in 2013 at this site survival was greater in burned plots only with small mammal access; no other factors altered survival rates between burned and unburned exclosures (Table 2.3). The small mammal effect in the Great Basin appears to be similar in unburned and burned plots in 2012, yet stronger in unburned than burned plots in 2013. In small mammal exclosures, survival was higher in burned than unburned Mojave plots in 2012 (Table 2.4); however, when small mammals had access to plots this trend shifted to higher survival in unburned plots. In 2013, a different pattern in survival was observed: survival was greater in unburned than burned exclosures, yet in plots open to small mammals no difference in survival between burn treatments was detected (Table 2.4). The small mammal effect in the Mojave appears to be greater in burned plots in 2012 and in unburned plots in 2013.

While generally small mammals decreased the survival of seedlings, there were some species with the opposite pattern (Figures 2.1-2.3, Table 2.3). In 2013, the following four Great Basin species had higher survival with small mammals than without them in burned plots: *L. lewisii* , *P. juncea* , and *E. wawawaiensis* (Table 2.3); in unburned plots *P. secunda* had higher survival with small mammals (Table 2.3). However, the survival of these four species was reduced by small mammals in their respective burn treatments in 2012 (Table 2.3).

The survival of seedlings differed between 2012 and 2013 at both sites (Figure 2.1, Tables 2.3-2.4) and these differences were correlated with distinct changes to the population levels of herbivores at each site. In the Mojave, 2013 was a year of high grasshopper abundance, while 2012 had lesser abundance; the increase in grasshoppers is associated with low survival of seedlings in all plots in 2013. In the spring of 2012 in the Great Basin small mammal abundance in the plots was 16 times greater (average minimum number known alive per open plot was 8.0 in April 2012 and 0.5 in April 2013) than in the spring of 2013 ($t=13.33$, $df=9$, $p<0.01$); lesser small mammal abundance in 2013 was correlated with much higher survival of seedlings in all plots. Nevertheless, even in 2013 with lesser small mammal abundance in the Great Basin and high folivory by grasshoppers in the Mojave, small mammal folivory effects remained distinguishable.

Discussion

This study is the first to compare small mammal folivory in burned and unburned habitat across a wide suite of plant species. We found that folivory was an important driver of seedling survival, as has previously been shown on a smaller scale (Meyer and Pendleton 2005). This may be an additional way that small mammals act as keystone species regulating the plant community in deserts (Brown and Heske 1990b, Guo et al. 1995, Kerley et al. 1997, Kerley and Whitford 2009). Small mammal folivory differed between burned and unburned habitat and the relative abundance of bipedal and quadrupedal small mammals may drive patterns of folivory in burned landscapes, influencing post-fire recovery and revegetation efforts.

Small mammal folivory

Small mammals in North American deserts, even those considered granivores, consume vegetative plant matter. Vegetation is a source of moisture in dry environments (Nagy and Gruchacz 1994, Sipos et al. 2002) as well as a possible trigger for reproduction (Beatley 1969b, Reichman and van de Graaff 1975). Although green plant matter is a small portion of their diet (Reichman 1975), folivory by small mammals can alter the structure of desert plant communities (Kerley et al. 1997, Kerley and Whitford 2009). We found that small mammal folivory was highly influential on the survival of seedlings at both our Great Basin and Mojave sites (Figure 2.1, Tables 2.3-2.4), even with large changes to the abundance of herbivores.

Temporal fluctuations in herbivore population size influenced the shape of survival curves, but did not obscure small mammal effects. Grasshopper abundance is variable, can be impacted by fire (Bock and Bock 1991, Joern 2004), and can greatly influence the plant community (Burleson and Hewitt 1982). In the Mojave, extensive invertebrate folivory in year 2 of our study diminished the survival of seedlings (Figure 2.1). Yet small mammal effects were still evident, indicating the stability of small mammal folivory in this system even in the presence of other strong herbivory effects (Table 2.4). In the Great Basin, when small mammal abundance decreased by nearly 94% in year 2, the effect of small mammal folivory was still an important determinant of survival (Figure 2.1, Table 2.3). As small mammal abundance can fluctuate over time (Brown and Heske 1990a) and be altered by disturbances such as fire (Bock and Bock 1978, Groves and Steenhof 1988, Simons 1991, Monroe et al. 2004, Ostoja and Schupp 2009, Monasmith et al. 2010, Bock et al. 2011, Horn et al. 2012), it's important to note that even at very low abundances small mammals have strong effects on the plant community.

Small mammals and fire

We had evidence that small mammal foraging differed between burned and unburned habitat. In the Great Basin, small mammals had a stronger impact on seedling survival in unburned than burned plots both years of our study (Figures 2.1-2.3, Table 2.3). In the Mojave, the small mammal effect differed between the two years of the study. In year 1, although small mammals reduced survival for the same plant species in both fire treatments, average survival was reduced more by small mammals in burned than unburned plots (Figures 2.1 and 2.5, Table 2.4). This is consistent with another study that found that small mammals forage equally or more intensively in burned than unburned habitat (Duval et al. 2005). However, in year 2 of our study in the Mojave, the small mammal effect was greater in unburned than burned plots (Figures 2.1 and 2.5, Table 2.4). In agreement with our Great Basin and second year's Mojave data, another study found that small mammal folivory reduced survival more in unburned than burned habitat (Suazo et al. 2013).

Bipedal vs. quadrupedal small mammal communities

In the Great Basin, the largely quadrupedal small mammal community had a stronger impact on the survival of seedlings in unburned than burned plots (Figure 2.1, Table 2.3). This is probably due to quadrupedal small mammals focusing foraging efforts under and near shrub cover (i.e. in unburned habitat) (Rosenzweig and Winakur 1969, Kotler 1984, Falkenberg and Clarke 1998). Quadrupedal small mammal communities may have a lessor impact on the survival of seedlings and establishment of plants in burned than in nearby unburned desert regions and this foraging behavior may promote recovery of vegetation following fire. However, bipedal species that are present in lower numbers before fire may become more prevalent in burned regions over time (Clements and Young 1996) and eventually exert the same top-down effect on plants that quadrupedal species do in unburned areas.

In the Mojave, small mammals impacted the survival of seedlings differently in the two years of our study. Bipedal small mammals prefer foraging in more open (e.g. burned) habitat (Rosenzweig and Winakur 1969, Kotler 1984) and we expected that the small mammal effect on seedling survival at this site would be equivalent or greater in burned than unburned plots. Results from year 1 of our study confirmed this idea; however, in year 2 small mammal foraging was stronger in unburned than burned habitat indicating that small mammals may have been avoiding burned plots (Figure 2.1, Table 2.4). If the effects of folivory are the same or increased in burned regions, then small mammal folivory could delay recovery of vegetation and hinder revegetation efforts. Further study is necessary to fully understand the relative impact of folivory by bipedal small mammals in burned and unburned habitat.

Management Implications

Federal spending on wildfire suppression often exceeds a billion dollars annually in the United States (U.S. Department of Agriculture 2006, National Interagency Coordination Center 2014); the significant costs of rehabilitation drive these costs even higher. Integrating our knowledge of the ecology of these systems into management actions can help to ensure the efficient and effective use of these resources. It can aid in the conservation of desert landscapes and continue to make them functional areas both for the conservation of ecosystems and species as well as for human-oriented activities including grazing. The efficient use of management resources is particularly important as invasive grasses continue to drive fire in North American desert landscapes.

Just as addition of diversionary seed may shift small mammal granivory pressure and increase the germination success of desirable plant species (Longland and Ostoja 2013), accounting for small mammal impacts beyond the seed stage may aid restoration efforts. Small mammal folivory can be highly influential on plant survival after germination. Successful rehabilitation methods should consider seedling predation and take actions to protect plants from folivory to increase seedling survival (Meyer and Pendleton 2005, Orrock et al. 2009). Even if implemented on a relatively small spatial scale across the landscape, this may aid in the successful reestablishment of native and desirable plant species. As the production of secondary metabolites by plants increases, consumption by small mammals should decrease (Sorensen et al. 2005). However, further research is necessary to understand which plant species and life stages may be vulnerable to and need protection from small mammal folivory.

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Chapter 2 Tables

Table 2.1. Plant species used in survival experiments in the Great Basin and Mojave Deserts with their origin and abbreviation.

Plant species	Origin*	Abbreviation
Great Basin		
Achillea millefolium (yarrow)	Native	ACMI
Agropyron cristatum (crested wheatgrass)	Introduced	AGCR
Agropyron fragile (Siberian wheatgrass)	Introduced	AGFR
Artemisia tridentata (sagebrush)	Native	ARTR
Atriplex canescens (fourwing saltbush)	Native	ATCA
Elymus wawawaiensis (Snake River wheatgrass)	Native	ELWA
Linum lewisii (Lewis flax)	Native	LILE
Medicago sativa (alfalfa)	Introduced	MESA
Pascopyrum smithii (western wheatgrass)	Native	PASM
Poa secunda spp. canbyi (Canby bluegrass)	Native	POCA
Poa secunda (Sandberg bluegrass)	Native	POSE
Psathyrostachys juncea (Russian wildrye)	Introduced	PSJU
Pseudoroegneria spicata (bluebunch wheatgrass)	Native	PSSP
Purshia glandulosa (desert bitterbrush)	Native	PUGL
Mojave		
Ambrosia dumosa (white bursage)	Native	AMDU
Atriplex canescens (fourwing saltbush)	Native	ATCA
Baileya multiradiata (desert marigold)	Native	BAMU
Coleogyne ramosissima (blackbrush)	Native	CORA
Encelia farinosa (brittlebrush)	Native	ENFA
Ephedra nevadensis (Nevada ephedra)	Native	EPNE
Ephedra viridis (green ephedra)	Native	EPVI
Eriogonum fasciculatum (Mojave buckwheat)	Native	ERFA
Erodium cicutarium (redstem stork's bill)	Introduced	ERCI
Krascheninnikovia lanata (winterfat)	Native	EULA
Larrea tridentata (creosote bush)	Native	LATR
Lupinus sparsiflorus (desert lupine)	Native	LUSP
Phacelia campanularia (desert bluebell)	Native	PHCA
Purshia glandulosa (desert bitterbrush)	Native	PUGL
Sphaeralcea ambigua (desert globemallow)	Native	SPAM

*according to USDA PLANTS Database (USDA, NRCS 2014)

Table 2.2. Results of model selection of Cox proportional hazards models. Models were compared within each dataset (site and year combination). All combinations of the three fixed factors (B=burned or unburned treatments; M=small mammals present or absent; and S=plant species) with a random block factor were modeled; only the top two models for each dataset are shown. Akaike weights (w_i) give the probability that a given model is the best of those tested to explain patterns in each dataset.

Model	Number of Parameters	ΔAIC_c	w_i
Great Basin 2012			
M*B*S	56	0	1.00
M*S+B	29	50.28	0.00
Great Basin 2013			
M*B*S	56	0	1.00
M*S+B	29	220.55	0.00
Mojave 2012			
M*B*S	60	0	1.00
M*S+B	31	155.61	0.00
Mojave 2013			
M*B*S	60	0	1.00
M*S+B	31	129.64	0.00

Table 2.3. Results of pairwise comparisons from fixed effects Cox proportional hazards analysis testing combinations of the effects of small mammal access, and burned vs. unburned habitat on seedling survival for various plant species and averaged across all fourteen plant species in the Great Basin Desert in 2012 and 2013. Reported values are z-statistics for each comparison. Significance is indicated by asterisks: *p<0.05; **p<0.01; ***p<0.001.

	Burned vs. unburned[1]				Small mammals[2]			
	2012		2013		2012		2013	
Plant Species	Open	Exclosure	Open	Exclosure	Burned	Unburned	Burned	Unburned
MESA	10.13***	4.52***	5.87***	0.53	**4.64*****	**10.00*****	**2.41**	**5.51*****
PUGL	4.67***	4.70***	*1.67*	*0.19*	**5.90*****	**7.13*****	**4.20*****	**3.52****
LILE	9.65***	9.41***	3.93***	*1.65*	**5.36*****	**5.15*****	3.29**	**2.37**
PSSP	5.71***	5.69***	2.41	*2.51*	**6.83*****	**6.93*****	1.48	**3.33****
POCA	8.27***	5.41***	3.47**	3.87***	**2.52**	**5.46*****	0.18	0.56
AGCR	10.44***	7.60***	7.37***	2.61*	**7.12*****	**9.33*****	**2.04**	**7.00*****
ATCA	11.07***	7.86***	2.07	*0.82*	**6.62*****	**8.92*****	1.19	**1.68**
PSJU	9.80***	5.35***	3.16**	*4.55****	**4.72*****	**8.76*****	2.82*	**4.84*****
ARTR	8.55***	4.92***	3.65**	0.62	**2.41**	**6.00*****	**0.24**	**3.30****
POSE	5.24***	5.87***	2.76*	4.02***	**3.69****	**2.79***	1.36	2.84*
AGFR	7.47***	7.22***	6.10***	*3.06**	**7.54*****	**7.35*****	0.32	**6.56*****
ELWA	9.15***	4.25***	4.06***	*2.94**	**4.63*****	**9.40*****	3.63**	**3.39****
PASM	11.05***	5.62***	1.42	1.99	**6.45*****	**11.94*****	0.76	1.31
ACMI	8.28***	6.73***	1.65	1.34	**4.70*****	**5.82*****	**3.29****	**4.19*****
All Sp.	29.40***	21.73***	12.44***	0.42	**19.61*****	**26.21*****	**1.45**	**12.18*****

[1] Italicized values indicate greater survival in unburned than burned plot; otherwise survival was greater in burned plot

[2] Bolded values indicate greater survival in exclosure plots (without small mammal access) than open plots (with small mammals); otherwise survival was greater in open plots.

Table 2.4. Results of pairwise comparisons from fixed effects Cox proportional hazards analysis testing combinations of the effects of small mammal access, and burned vs. unburned habitat on seedling survival for various plant species and averaged across all fifteen plant species in the Mojave Desert in 2012 and 2013. Reported values are z-statistics for each comparison. Significance is indicated by asterisks: *p<0.05; **p<0.01; ***p<0.001.

	Burned vs. unburned[1]				Small mammals[2]			
	2012		2013		2012		2013	
Plant Species	Open	Exclosure	Open	Exclosure	Burned	Unburned	Burned	Unburned
BAMU	4.58***	3.30**	0.22	_3.87***_	__5.94***__	__7.89***__	0.85	__3.05*__
CORA	_1.91_	1.71	0.97	_0.92_	__7.98***__	__7.01***__	__1.60__	__2.56__
LATR	_3.38**_	_0.61_	_1.04_	_3.44**_	__6.87***__	__4.97***__	__3.14**__	__6.59***__
PUGL	4.01***	2.07	_0.40_	_2.90*_	__2.99*__	__4.95***__	__2.66*__	__4.70***__
PHCA	_4.36***_	_1.40_	1.24	_5.56***_	__11.08***__	__7.99***__	__4.40***__	__10.18***__
SPAM	1.04	1.02	0.42	_4.11***_	__5.45***__	__5.59***__	1.38	__2.83*__
LUSP	_0.16_	2.62*	_1.95_	_1.11_	__4.88***__	__3.71**__	__3.01*__	__2.18__
ENFA	_2.83*_	_0.84_	_4.32***_	_3.25**_	__6.97***__	__5.13***__	__3.82***__	__2.73*__
ERCI	_5.12***_	1.15	_0.97_	_7.75***_	__9.61***__	__3.68**__	__2.04__	__8.68***__
EPNE	_3.65**_	_0.12_	_1.23_	1.57	__8.52***__	__7.16***__	__10.60***__	__9.58***__
ATCA	_0.85_	0.59	0.60	_2.00_	__8.10***__	__6.74***__	__1.28__	__3.97***__
EPVI	_3.42**_	2.29	3.89***	0.31	__9.12***__	__7.35***__	__8.39***__	__11.80***__
ERFA	_1.70_	3.18**	_0.07_	_7.80***_	__8.89***__	__5.21***__	__0.55__	__8.26***__
AMDU	_4.30***_	4.34***	2.79*	_3.06*_	__11.40***__	__4.62***__	__6.65***__	__12.32***__
EULA	_2.50_	0.16	_0.12_	_2.19_	__2.06__	0.41	1.44	__0.75__
All Sp.	_4.81***_	4.61***	_0.10_	_9.65***_	__23.08***__	__18.20***__	__9.47***__	__18.62***__

[1] Italicized values indicate greater survival in unburned than burned plot; otherwise survival was greater in burned plot

[2] Bolded values indicate greater survival in exclosure plots (without small mammal access) than open plots (with small mammals); otherwise survival was greater in open plots.

Chapter 2 Figures

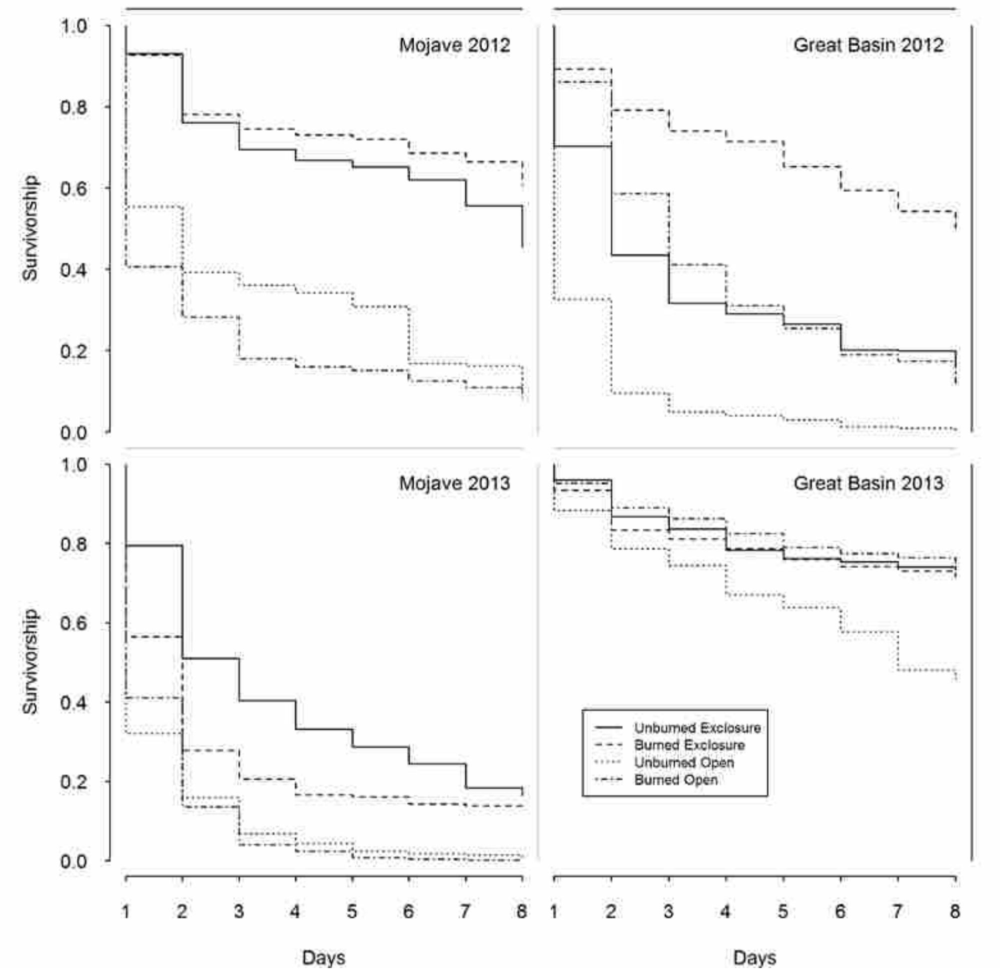

Figure 2.1. Survival curves demonstrating the effects of small mammals and fire on the survival of seedlings in the Great Basin and Mojave Deserts during May and June of 2012 and 2013. Exclosure plots were fenced to keep out small mammals while open plots allowed them access. A controlled burn treatment was applied to burned plots in 2011.

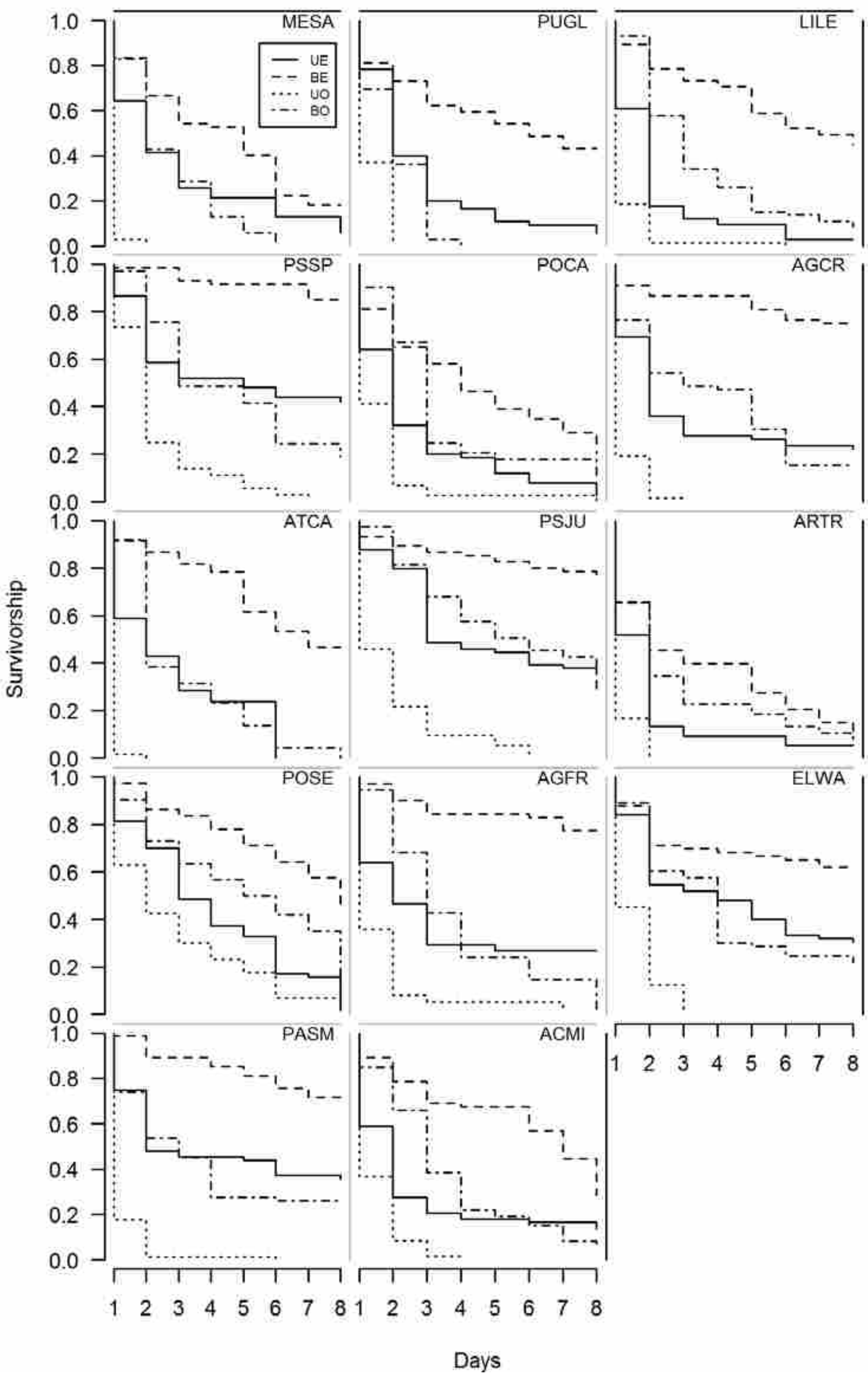

Figure 2.2. Survival curves demonstrating the effects of small mammal and fire treatments on the survival of seedlings of 14 species in the Great Basin Desert during May-June 2012. Four treatments were applied: unburned plots with small mammal exclosure (UE, solid line), burned plots with small mammal exclosure (BE, dashed line), unburned plots open to small mammals (UO, dotted line), and burned plots open to small mammals (BO, dot-dashed line).

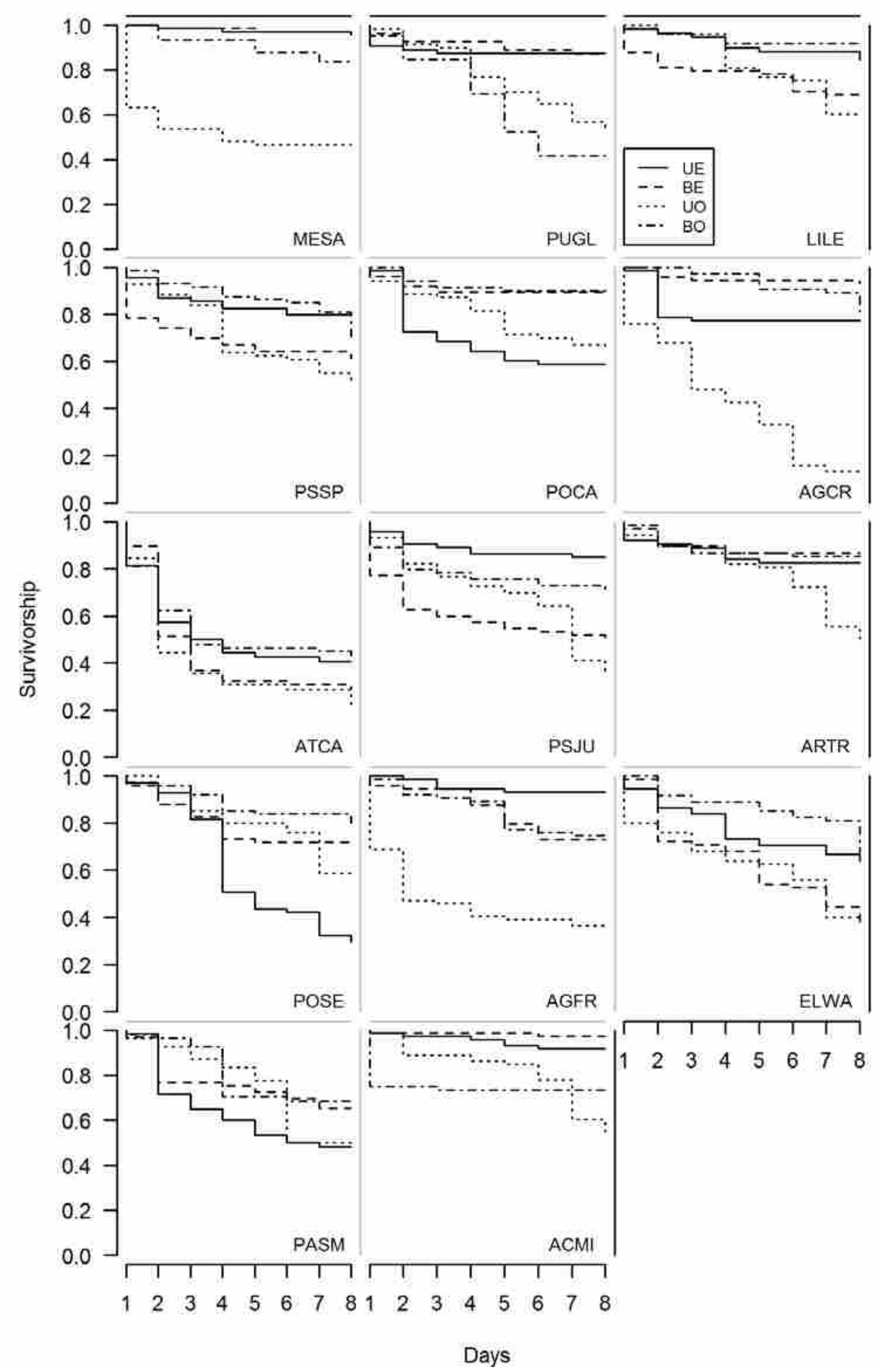

Figure 2.3. Survival curves demonstrating the effects of small mammal and fire treatments on the survival of seedlings of 14 species in the Great Basin Desert during May-June 2013. Four treatments were applied: unburned plots with small mammal exclosure (UE, solid line), burned plots with small mammal exclosure (BE, dashed line), unburned plots open to small mammals (UO, dotted line), and burned plots open to small mammals (BO, dot-dashed line).

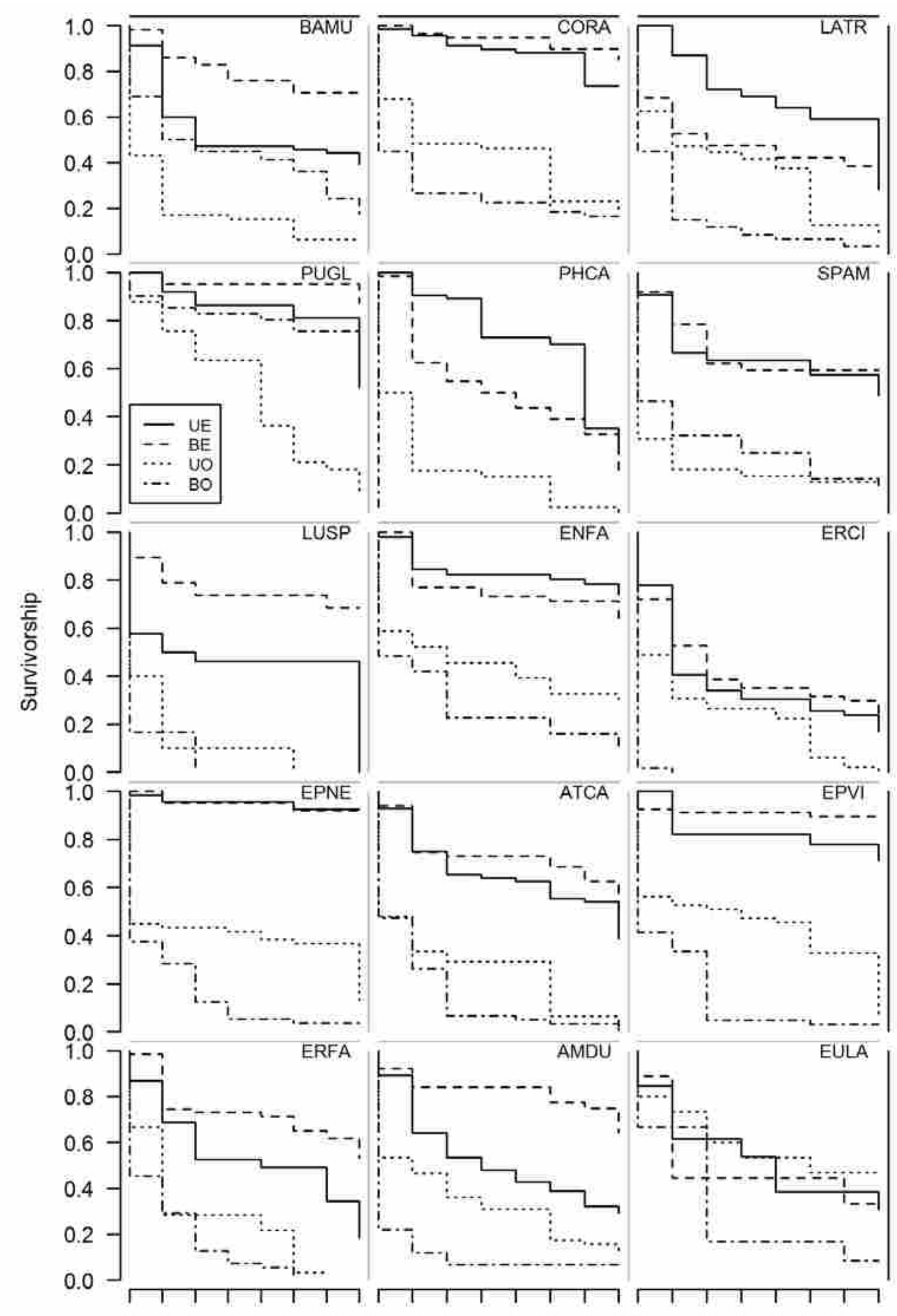

Figure 2.4. Survival curves demonstrating the effects of small mammal and fire treatments on the survival of seedlings of 15 species in the Mojave Desert during May 2012. Four treatments were applied: unburned plots with small mammal exclosure (UE, solid line), burned plots with small mammal exclosure (BE, dashed line), unburned plots open to small mammals (UO, dotted line), and burned plots open to small mammals (BO, dot-dashed line).

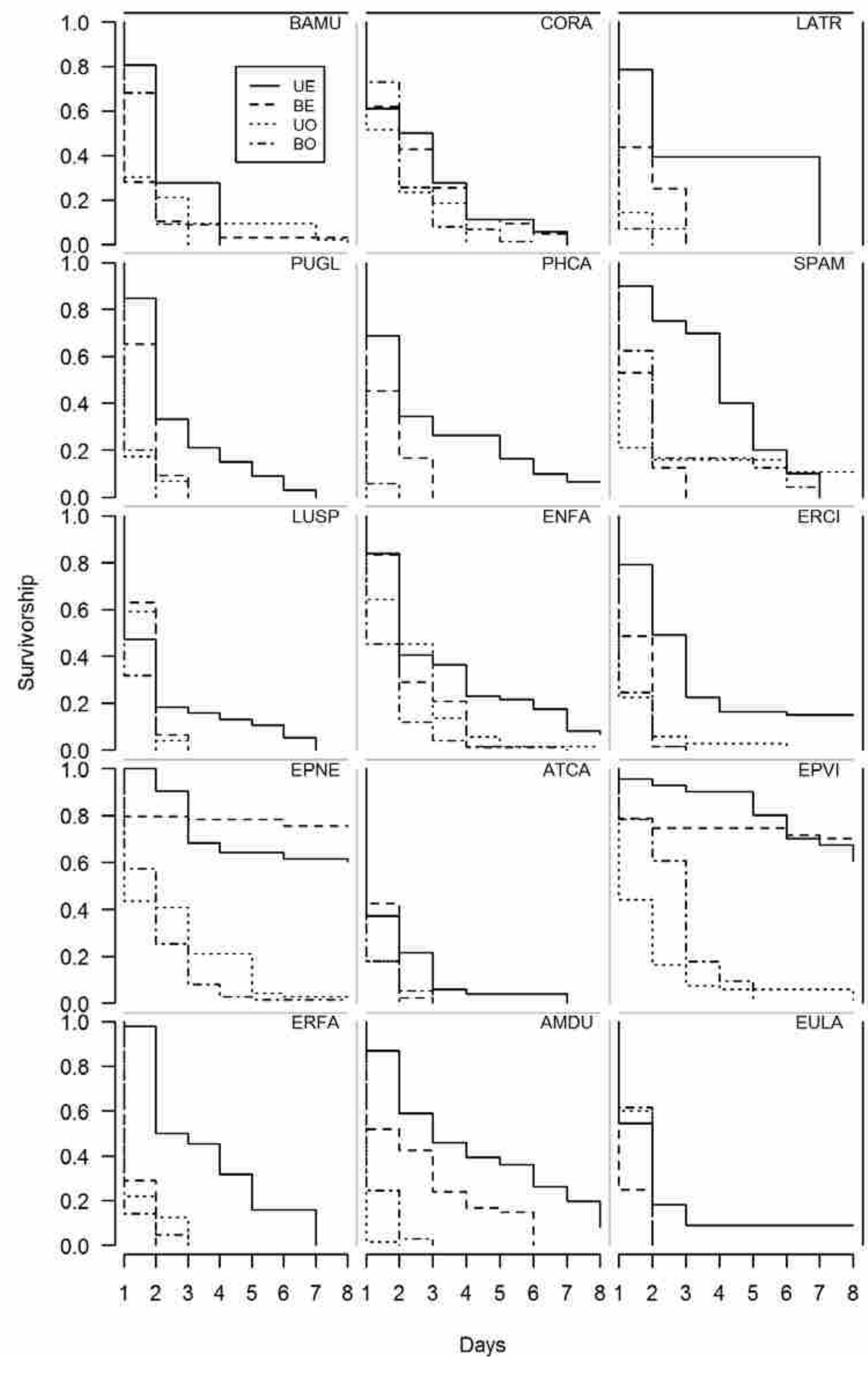

Figure 2.5. Survival curves demonstrating the effects of small mammal and fire treatments on the survival of seedlings of 15 species in the Mojave Desert during May 2013. Four treatments were applied: unburned plots with small mammal exclosure (UE, solid line), burned plots with small mammal exclosure (BE, dashed line), unburned plots open to small mammals (UO, dotted line), and burned plots open to small mammals (BO, dot-dashed line).

Chapter 3: How small mammal granivory and fire affect invasive and native desert plant communities

Abstract

Invasive grasses are increasing the size and frequency of fire in the Great Basin and Mojave Deserts, altering the plant community as well as higher trophic levels. Among those impacted are small mammals; as keystone species in North American desert systems these animals impact vegetation via granivory, herbivory, and seed dispersal. Using seed trays, we tested how small mammal granivory differs between burned and unburned habitat and how it varies between native and nonnative plant species in the Great Basin and Mojave Deserts. In three of our datasets there was no difference in persistence of seed between burned and unburned habitat; however, in 2013 at our Mojave site persistence was greater in burned than unburned plots. In the Great Basin, small mammals reduced persistence of seed of *Bromus tectorum* and *Linum lewisii* in 2012 when the abundance of small mammals was high. No small mammal effect was observed in 2013 in the Great Basin when small mammal abundance had decreased to nearly a third of its value the previous year. In the Mojave, small mammals reduced the persistence of seed for four out of five plant species both years of the study. Contrary to our prediction, small mammals did not demonstrate a preference for native species of seed over those of non-natives at either site. Seed collection and caching by small mammals is likely influential on the composition of plant communities post-fire. The lack of avoidance of non-native species indicates that small mammals are important collectors and possibly predators of these less desirable species.

Introduction

The structure of some deserts of North America is shifting as invasive grasses increase the size and frequency of wildfire (Whisenant 1989, Brooks and Matchett 2006), altering both plant and animal communities. The sagebrush steppe of the Great Basin traditionally burned on the scale of centuries, but is increasingly burning on the scale of decades (Whisenant 1989, Bukowski and Baker 2013). Native plants, adapted to a longer interval between fires, become less prevalent (Stewart and Hull 1949, Young and Evans 1978); meanwhile invasive grasses that are adapted to fire increase in density and abundance (Stewart and Hull 1949, Young and Evans 1978). Similar shifts occur in the Mojave Desert (Brooks and Matchett 2003). These changes to the vegetation affect higher trophic levels including the small mammal community. Changes to the vegetation upon which these herbivorous species depend can lead to reductions in abundance, species richness, and diversity in burned regions (Bock and Bock 1978, Groves and Steenhof 1988, Ostoja and Schupp 2009, Vamstad and Rotenberry 2010, Litt and Steidl 2011, Horn et al. 2012). Alterations to the small mammal community can then have a dramatic influence on the structure of vegetation (Brown and Heske 1990, Guo et al. 1995, Kerley et al. 1997, Kerley and Whitford 2009).

Granivory by small mammals has the potential to either inhibit or aid the proliferation of invasive grasses after fire. Small mammals typically do not prefer seed of invasive *Bromus tectorum* (cheatgrass) (Everett et al. 1978, Kelrick et al. 1986, Ostoja et al. 2013, Beard et al. 2013). Therefore preferential consumption of seed from native species after fire could reduce the native seed bank and promote the dominance of invasive grasses. However, small mammals have been known to harvest unexpectedly high quantities of both *B. tectorum* (Richardson et al. 2013) and *B. rubens* (red brome) (Hardy 1945, Rowland and Turner 1964). If small mammals preferentially harvest or consume seed of invasive grasses after fire, they could give native species an advantage in post-fire recovery. Whether granivory promotes the recovery of native or invasive species after fire is unclear; yet foraging by small mammals is likely a strong force determining the fate of these deserts.

The bottom-up impacts of fire on small mammals may be determined by their habitat preferences. Bipedal species (*Dipodomys* sp.) focus foraging efforts in open habitat between shrubs (Rosenzweig and Winakur 1969, Kotler 1984). They can increase or maintain abundance levels when habitat is opened up by fire (Simons 1991, Monroe et al. 2004, Monasmith et al. 2010, Horn et al. 2012). Therefore, sites numerically dominated by bipedal species may have equivalent foraging in burned and unburned regions or even increases in foraging in burned regions (Duval et al. 2005, Suazo et al. 2013). Conversely, quadrupedal species (pocket mice, and *Peromyscus* sp.) typically focus foraging efforts under and near shrub cover (Rosenzweig and Winakur 1969, Kotler 1984, Falkenberg and Clarke 1998); these species often decrease in abundance after fire in the desert (Groves and Steenhof 1988, Simons 1991, Monroe et al. 2004, Horn et al. 2012). Sites dominated by quadrupedal species may expect to see reductions in foraging in burned regions. The composition of a small mammal community likely determines its response to fire and consequently the top-down influence on the plant community post-fire.

Our objective was to determine the interactive effects of small mammals and fire on rates of removal of native and invasive seeds. We hypothesized that as the small mammal community is affected by fire, persistence of seeds would be influenced by an interaction between small mammals and fire. Further, this interaction would vary between the Great Basin and Mojave Deserts according to the relative abundance of bipedal and quadrupedal small mammals. Specifically, we predicted that: (i) at our site in the Great Basin where the small mammal community is dominated by *P. maniculatus* (deer mouse), a quadrupedal species, seed removal by small mammals would be greater in unburned than burned habitat; (ii) at our site in the Mojave where the small mammal community is dominated by *D. merriami* (Merriam's kangaroo rat), a bipedal species, seed removal by small mammals would be equivalent or slightly greater in burned than unburned habitat; (iii) small mammals would prefer native seed species to invasive seed; and (iv) removal rates would vary proportionally with changes in small mammal abundance over time.

Methods

Study Sites

The study sites were located in the Mojave and Great Basin Deserts in Utah. The Mojave study area was located at Lytle Ranch Preserve in the Beaver Dam Wash region of southwestern Utah in mid-elevation Mojave shrubland (37°8'53.46"N, 114°0'49.59"W). The dominant vegetation at this site was primarily comprised of *Yucca brevifolia* (Joshua tree), *Coleogyne ramosissima* (blackbrush), and *Larrea tridentata* (creosote bush). Trapping at the Mojave site revealed that the small mammal community is primarily comprised of (in order of descending abundance): *D. merriami* (Merriam's kangaroo rat), *Chaetodipus formosus* (long-tailed pocket mouse), and *Neotoma lepida* (desert woodrat) (Sharp Bowman 2015). The Great Basin site was located in a sage-steppe community in Rush Valley in the west central Great Basin Desert of Utah (40°5'21.18"N, 112°18'26.88"W). The vegetation was primarily comprised of *Artemisia tridentata wyomingensis* (Wyoming sagebrush) and *Elymus elymoides* (bottlebrush squirreltail). Trapping at the Great Basin site revealed that the small mammal community is primarily comprised of (in order of descending abundance): *Peromyscus maniculatus* (deer mouse), *Dipodomys microps* (chisel-toothed kangaroo rat), and *Perognathus parvus* (Great Basin pocket mouse) (Sharp Bowman 2015). Plots were established in 2011.

Plot Design

We used a randomized complete block design to test for the effects of fire and small mammals on the plant community. Each of our study sites contained 5 replicates, hereafter referred to as blocks. Each 60 m x 60 m block was quartered into 4 adjacent plots (30 m x 30 m). We installed 1 cm welded wire fencing that extended 65 cm aboveground and 35 cm belowground surrounding each plot. Each plot was randomly assigned to one of four treatments: burned with small mammals (burned open), burned without small mammals (burned exclosure), unburned with small mammals (unburned open), and unburned without small mammals (unburned exclosure); each treatment was represented once per block. To facilitate movement of small mammals into and out of open plots, a 15 cm x 15 cm hole was cut into the welded wire on each outward facing side of the plot at ground level. To prevent entrance of small mammals into exclosure plots, 20 cm of metal flashing was installed over the welded wire on the outward facing side. However, some larger species (e.g., least chipmunks, white-tailed antelope squirrels, and desert woodrats) were not completely excluded by the exclosure fencing. Burn treatments were applied to selected plots on June 18 (Mojave) and September 17 (Great Basin) of 2011.

Seed Persistence

To determine the interactive effects of small mammals and fire on the persistence of seeds, we estimated the rate of seed removal in each plot. We performed four experiments: two in the Great Basin (one in 2012 and one in 2013) and two in the Mojave (one in 2012 and one in 2013). These experiments occurred in June and were initiated at the Mojave site 5 days before the Great Basin site. We used four to five plant species simultaneously for each experiment

(Table 3.1). We selected species that are commonly found in each desert region; we included common invasive species at each site when seed was available.

The same experimental protocol was used at both the Great Basin and Mojave sites. Each species was placed in a separate plastic 15 cm petri dish filled with approximately 125 mL of soil and 100 seeds (as determined by weight with the exception of *Halogeton glomeratus* (halogeton), which was counted). Sets of dishes, containing one dish of each species, were placed in a line with 30 cm between each dish within a set. Each plot received four sets that were parallel to and spaced 5 m away from one another. All sets were placed 1 m away from and perpendicular to an edge of the plot. All dishes were set out on the same day and one set was collected from each plot after each time period had elapsed (1, 3, 7, and 14 days). At the time of collection, the contents of each dish were sealed in a zip-top plastic bag and its contents were later sorted in the lab. For large-seeded species, samples were passed through a sieve and seed was collected and weighed. For small-seeded species, samples were more efficiently processed using the Valve Method (Lucero et al. 2012). All seed was oven dried at 60° C for 48 hours before being weighed after the use of both methods.

Two changes occurred to the above methods in 2013 for the second year of the study. The first change was implemented to ensure consistent weighing methods of seeds. In 2013, all seeds were dried for 48 hours at 60° C before being weighed both before going out into the field and after samples were collected and processed by either method. The second change was implemented to increase the independence of samples. In 2013, seed dishes were placed in a regular linear pattern; each dish was spaced 3 m from its nearest neighbor and 1 m from the edge of the plots. Besides these two changes methods were identical between the two years.

Data analysis

Data were divided into four datasets, each comprising the samples from a given desert and year of the study: Great Basin 2012, Great Basin 2013, Mojave 2012, and Mojave 2013. Although the data would ideally have been analyzed with binomial models, these models did not converge. As a result, linear mixed effects models were utilized (Suazo et al. 2013, Mattos et al. 2013). We used an arcsine square root transformation on the proportion of seeds persisting in dishes at the time of collection as the response (Suazo et al. 2013, Mattos et al. 2013). Random effects in the models included block and number of days the seeds were in the field; both random effects were included in all models. Fixed effects included presence vs. absence of small mammals, burned vs. unburned habitat, and seed species. Models including all three fixed effects with all combinations of both additive and interactive terms were run and the best model for each dataset was selected using AIC_c. Models were run using package lme4 and subsequent pairwise comparisons were made using package multcomp in program R (Hothorn et al. 2008, Bates et al. 2014, R Core Team 2014).

To determine if small mammals exhibited a preference for native seed and whether preferences differed between burned and unburned plots, we compared persistence of each plant species. The most preferred species would be consumed first and thus have the smallest area under their persistence curve in open plots. However, it was necessary to account for other seed predators (i.e. ants and birds) which had access to both open and exclosure plots to avoid confounding preferences of small mammals with those of other species. We assumed that differences in seed removal between the burned open and the burned exclosure plots from the same block were due to small mammals. Likewise, unburned open plots were compared with unburned exclosure plots from the same block. Differences in removal were measured over the course of the two week experiment and a value was obtained for the cumulative difference for each species in both burned and unburned habitat for each block. These values were scaled between species for each block to produce a preference index for each species ranging from 0 to 1; a species with a value of 1 was the most preferred. A Friedman test was used to test for differences in preference among species in program R (R Core Team 2014); differences in preference were tested for in burned and unburned plots separately. When significant results were obtained from the Friedman test, subsequent pairwise comparisons were made between species using package nparcomp in program R (Konietschke 2012, R Core Team 2014).

Results

The model that best described persistence of seed varied among datasets. The top model included a plant species by small mammal interaction and an additive burn effect for the Great Basin in 2012 and for the Mojave in 2012 and 2013 (M*S+B; Table 3.2; Figures 3.1-3.3). In the Great Basin in 2013 the best model was the additive model (M+S+B; Table 3.2; Figure 3.4).

The effects of fire and small mammals

Fire treatments often had no impact on persistence of seed and there was not strong evidence of an interaction between fire and small mammal effects in any dataset (Table 3.2). There was no difference between persistence of seed in burned and unburned plots in the Great Basin either year (2012: $z=1.06$, $p=0.29$; 2013: $z=1.17$, $p=0.24$) or in the Mojave in 2012 ($z=0.39$, $p=0.69$). In the Mojave in 2013 the proportion of seed persisting was greater in burned than unburned plots ($z=2.96$, $p<0.01$; Figure 3.2).

In the Great Basin, small mammals reduced seed persistence for some species in one year, but for no species the other year. In 2012, small mammals reduced the persistence of *B.*

tectorum (z=6.83, p<0.01) and *Linum lewisii* (Lewis flax; z= 4.01, p<0.01; Figure 3.3). Small mammals had no effect on persistence of *Achillea millefolium* (yarrow; z=0.02, p=1.00) or *Poa secunda* (Sandberg bluegrass; z=2.01, p=0.47). However, in 2013 small mammals had no effect on persistence of seed for any species (z=0.20, p=0.84; Figure 3.4).

In the Mojave, small mammals reduced seed persistence for most species in both years of the study. In 2012, small mammals reduced persistence for *C. ramosissima* (z=13.11, p<0.01), *L. tridentata* (z=10.85, p<0.01), *Ambrosia dumosa* (white bursage; z=4.98, p<0.01), and *Encelia farinosa* (brittlebrush; z=4.06 , p<0.01; Figure 3.1). Small mammals had no effect on persistence of *Eriogonum fasciculatum* (Mojave buckwheat; z=0.08, p=1.00). In 2013, small mammals reduced persistence for *C. ramosissima* (z=10.94; p<0.01), *L. tridentata* (z=5.80; p<0.01), *Bromus rubens* (red brome; z=5.06; p<0.01), and *A. dumosa* (z=3.25; p=0.04; Figure 3.2). Small mammals had no effect on persistence of *E. farinosa* in 2013 (z=2.23; p=0.44).

The effect of plant species on preference

There were no differences in preference among the seed species used in the Great Basin in either burned (2012: Friedman χ^2=4.50, df=2, p=0.11; 2013: Friedman χ^2=7.40, df=4, p=0.12) or unburned plots (2012: Friedman χ^2=1.50, df=3, p=0.68; 2013: Friedman χ^2=9.40, df=4, p=0.05; Table 3.1). There were also no preference differences in the Mojave in unburned plots (2012: Friedman χ^2=6.88, df=4, p=0.14; 2013: Friedman χ^2=9.12, df=4, p=0.06). However, in burned Mojave plots small mammals did have preferences (2012: Friedman χ^2=15.68, df=4, p<0.01; 2013: Friedman χ^2=13.92, df=4, p<0.01). Preferences for *C. ramosissima* (2012: 0.95 ± 0.05, 2013: 0.87 ± 0.13) and *L. tridentata* (2012: 0.92 ± 0.05, 2013: 0.62 ±0.12) were greater than those for *E. farinosa* (2012: 0.36 ± 0.03, 2013: 0.22 ± 0.05), *A. dumosa* (2012: 0.36 ± 0.17, 2013: 0.16 ± 0.04), and *E. fasciculatum* (2012: 0.21 ± 0.15; all

$p<0.03$). *B. rubens* had a mid-level of preference (0.44 ± 0.15) which did not differ from the preferences for any other species (all $p>0.33$).

The effect of small mammal abundance

The effect of small mammals on persistence of seed was positively correlated with small mammal abundance. The average abundance of small mammals within the open Great Basin plots was greater in 2012 (4.0 ± 0.6) than 2013 (1.2 ± 0.4; $p<0.01$; Sharp Bowman 2015). When abundance was low in 2013, no small mammal effect was detected; when abundance was more than 3 times higher in 2012, small mammals reduced persistence for half of the seed species. The average abundance of small mammals within the open Mojave plots did not differ between 2012 (2.0 ± 0.65) and 2013 (1.9 ± 0.50; $p=0.89$). Likewise, the effect of small mammals on persistence of seed is more consistent across years in the Mojave.

Discussion

Persistence of seed was influenced by all three manipulated factors in our experiments: small mammals, seed species, and burned vs. unburned habitat. Of the three, burned vs. unburned habitat had the smallest effect while small mammals and seed species often interacted to strongly influence persistence. Small mammals are known to be important consumers of seed in North American deserts and to have preferences for certain species (Everett et al. 1978, Kelrick et al. 1986, Sivy et al. 2011, Beard et al. 2013). However, little is known regarding how consumption of seeds may vary across burned and unburned habitat or how granivory may influence the plant community post-fire.

In the Great Basin, there was not strong evidence of an interaction between the fire and small mammal effects. We predicted that removal of seed by small mammals at this quadruped dominated site would be reduced in burned habitat. However, small mammal foraging was equivalent between the two burn treatments. We are unaware of other studies that have tested for differences in granivory between burned and unburned habitat by quadrupedal small mammals in a North American desert. While more studies are needed to corroborate our findings, it appears that the foraging behavior of quadrupedal small mammals is similar in burned and unburned habitat.

In the Mojave, there was no evidence of an interaction between the fire and small mammal effects. We predicted that removal of seed by small mammals at this biped dominated site would be equivalent in burned and unburned plots or reduced in unburned habitat. As there was no evidence of differences in the small mammal effect between burned and unburned plots, our prediction was upheld; small mammal granivory effects were equivalent among burn treatments. There was evidence of differences in persistence between burned and unburned habitats in the Mojave in 2013, but this difference was independent of small mammal presence. This burn effect may be the result of decreased granivory by ants in burned habitat (Suazo et al. 2013), though why this difference was detected in only one year of the study remains unknown. Previous studies of granivory by small mammal communities dominated by bipedal species have had mixed results. There is evidence that these small mammals exert an equivalent or greater granivory pressure in burned than unburned habitat (Duval et al. 2005). However, another study suggests that the relative granivory effect in burned and unburned habitat may differ depending on seed species (Suazo et al. 2013).

Small mammals did not demonstrate a preference for or against invasive species (*B. tectorum*, *H. glomeratus*, and *B. rubens*) in burned or unburned plots. Intermediate preference for *B. tectorum* has been previously demonstrated (Veech 2001). However, the majority of research indicates that *Bromus* seed is a less preferred food (Everett et al. 1978, Kelrick et al. 1986, Beard et al. 2013), although it can also be collected and cached in abundance (Hardy 1945, Rowland and Turner 1964, Richardson et al. 2013). Our data suggest that small mammals have no preference for or aversion to seed of *Bromus* sp. or *H. glomeratus*.

The impact that small mammals have on persistence of seed is demonstrated twice in this study. First, it has been tested for by comparisons between plots with and without small mammals. Second, it is revealed by the comparison between extremes in the abundance of small mammals in the Great Basin. When abundance was high in 2012 there was a reduction in seed persistence due to small mammals. Yet a year later on the same plots, when abundance had declined severely (a 70% decrease), the small mammal effect was undetectable. Meanwhile, on the Mojave plots abundance remained consistent over time and the effect of small mammals was detectable in both years. The abundance of small mammals is an important determinant of the impact of these animals on the persistence of seed; locations with few small mammals may not be strongly impacted.

Selection by small mammals for or against seed of invasive plants could strongly influence the future of North American deserts. Granivory by small mammals could determine the ability of plants to invade a site, dominate the plant community post-fire, and ultimately impact the fire regime. Small mammals may be important predators of invasive seed (Hardy 1945, Rowland and Turner 1964, Richardson et al. 2013), reducing successful reproductive efforts of these invaders. However, removal of seed is not necessarily equivalent to predation of seed (Vander Wall et al. 2005). If small mammals collect and cache invasive seed, yet fail to harvest these caches, they may act as dispersers rather than consumers of invasive species.

Further study on predation of seed is necessary to understand the net effect that small mammals have on *Bromus, Halogeton,* and other invasive species in North American deserts.

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Chapter 3 Tables

Table 3.1. Seed species used, their abbreviation, status, and preference of small mammals (± SE) in burned and unburned plots in 2012 and 2013 in the Great Basin and Mojave Deserts. Higher preference values correspond to more preferred species.

		2012		2013	
Species	Status [a]	Burned	Unburned	Burned	Unburned
Great Basin					
Achillea millefolium [b]	Native	0.18 ± 0.08	0.33 ± 0.17	0.21 ± 0.10	0.19 ± 0.16
Bromus tectorum	Introduced	0.88 ± 0.12	0.75 ± 0.15	0.86 ± 0.14	0.94 ± 0.06
Halogeton glomeratus	Introduced			0.23 ± 0.13	0.26 ± 0.11
Linum lewisii [b]	Native	0.65 ± 0.22	0.50 ± 0.21	0.33 ± 0.15	0.58 ± 0.20
Poa secunda [b]	Native	0.59 [c]	0.34 ± 0.14	0.53 ± 0.20	0.32 ± 0.15
Mojave					
Ambrosia dumosa	Native	0.36 ± 0.17*	0.53 ± 0.16	0.16 ± 0.04*	0.42 ± 0.13
Bromus rubens	Introduced			0.44 ± 0.15	0.56 ± 0.15
Coleogyne ramosissima	Native	0.95 ± 0.05*	0.61 ± 0.17	0.87 ± 0.13*	0.99 ± 0.01
Encelia farinosa	Native	0.36 ± 0.03*	0.47 ± 0.13	0.22 ± 0.05*	0.39 ± 0.08
Eriogonum fasciculatum	Native	0.21 ± 0.15*	0.24 ± 0.11		
Larrea tridentata	Native	0.92 ± 0.05*	0.85 ± 0.06	0.62 ± 0.12*	0.63 ± 0.14

[a] According to USDA PLANTS Database (USDA, NRCS 2014)

[b] Denotes species whose seeds were removed from samples via flotation

c Miscounting of samples for *Poa secunda* in burned 2012 plots left 1 block in which a preference index could be calculated ; this data point was omitted from the preference analysis.

* Denotes a species whose preference differed from at least one other species in that burn treatment

Table 3.2. Model selection table with the top two models for each dataset and their respective model weights for data collected in the Great Basin and Mojave Deserts in 2012 and 2013. M=small mammal presence/exclosure; B=burned/unburned habitat type; S=plant species

Model	Number of Parameters	ΔAIC_c	w_i
Great Basin 2012			
M*S+B	9	0	0.985
M+S+B	6	8.666	0.013
Mojave 2012			
M*S+B	11	0	1.000
M*S*B	20	32.436	0.000
Great Basin 2013			
M+B+S	7	0	0.849
M*B+S	8	3.456	0.151
Mojave 2013			
M*S+B	11	0	1.000
M+S+B	7	21.605	0.000

Chapter 3 Figures

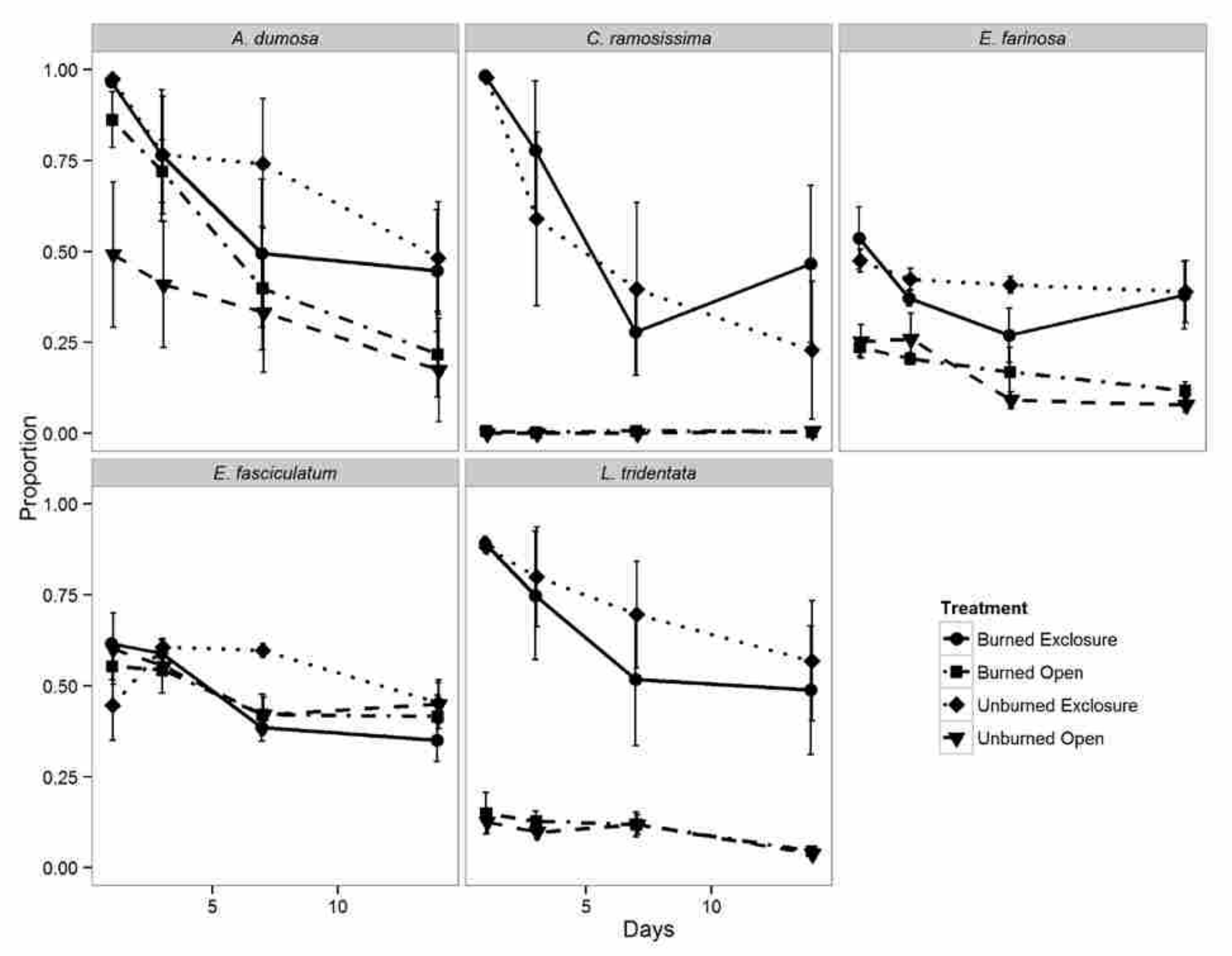

Figure 3.1. Proportion of seed persisting in seed dishes left in plots for 1, 3, 7, or 14 days in burned and unburned Mojave plots in 2012 by species. Exclosures are plots without small mammals; open plots have small mammal access.

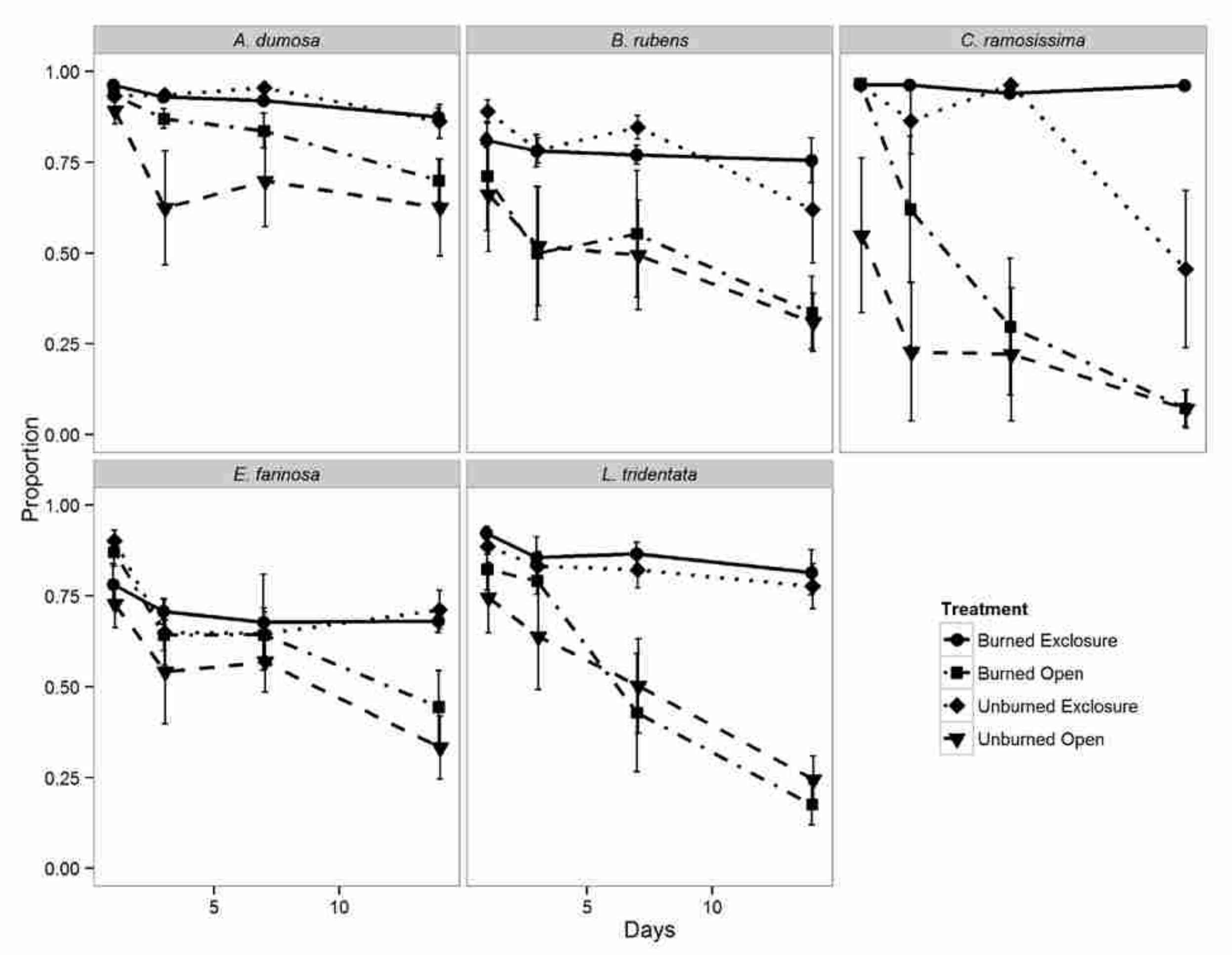

Figure 3.2. Proportion of seed persisting in seed dishes left in plots for 1, 3, 7, or 14 days in burned and unburned Mojave plots in 2013 by species. Exclosures are plots without small mammals; open plots have small mammal access.

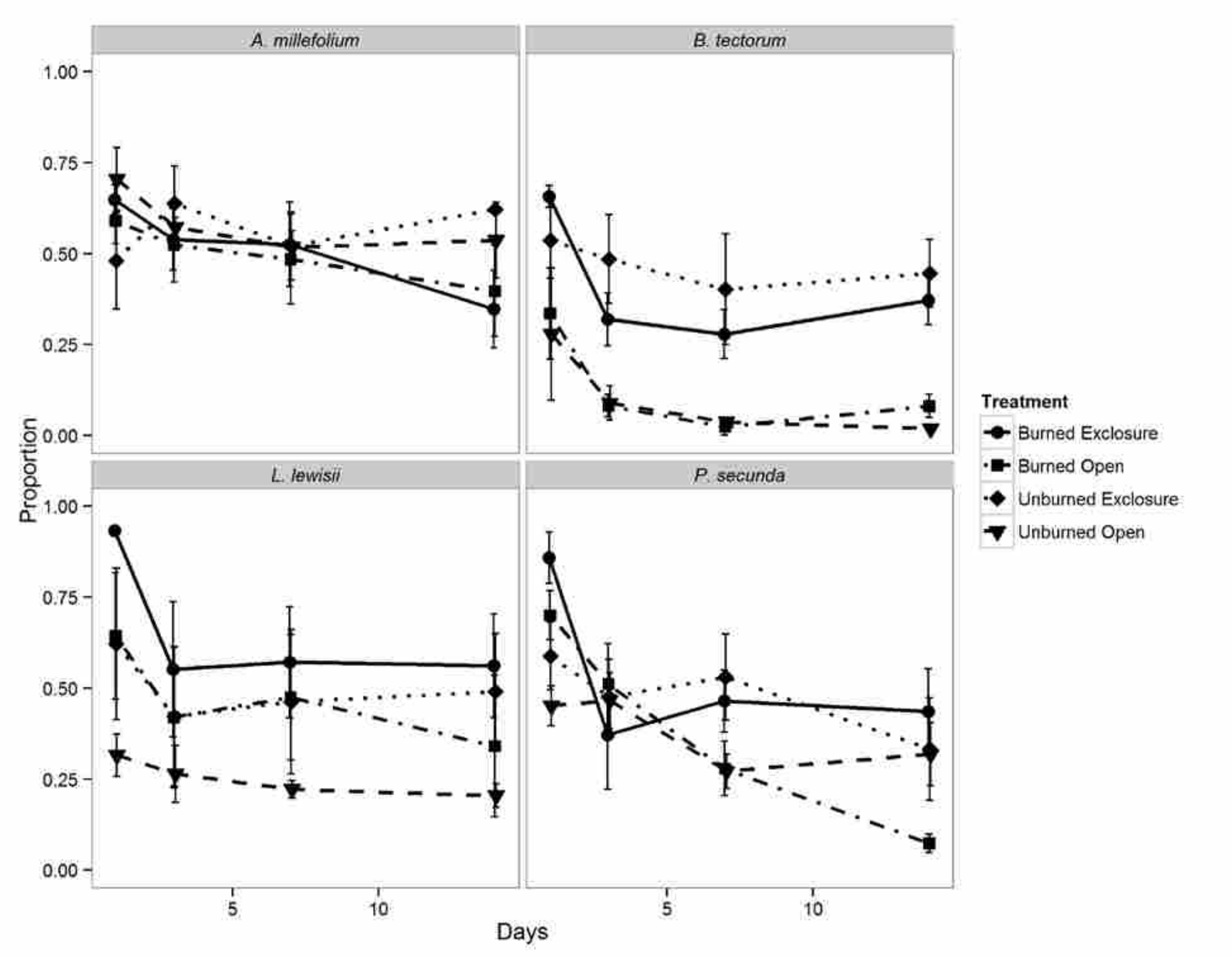

Figure 3.3. Proportion of seed persisting in seed dishes left in plots for 1, 3, 7, or 14 days in burned and unburned Great Basin plots in 2012 by species. Exclosures are plots without small mammals; open plots have small mammal access.

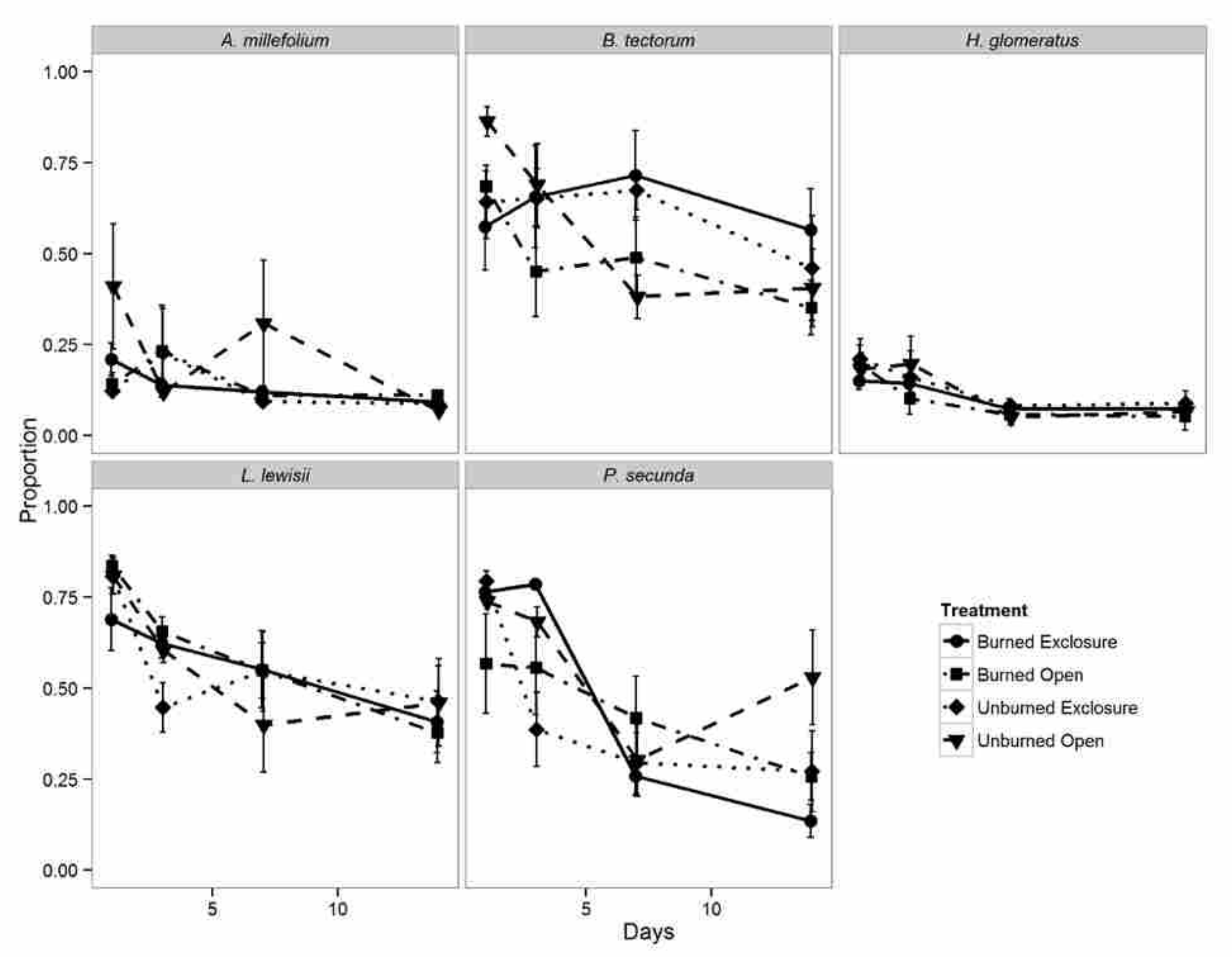

Figure 3.4. Proportion of seed persisting in seed dishes left in plots for 1, 3, 7, or 14 days in burned and unburned Great Basin plots in 2013 by species. Exclosures are plots without small mammals; open plots have small mammal access.