

Ecological engineers' nests benefit plant recovery following fire in a semiarid grassland, New Mexico, USA

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Abstract

Questions: Ants and rodents are recognized as ecosystem engineers worldwide creating soil-modified nests and adjacent edges with superior resources. The influence of *Dipodomys spectabilis* (rat) and *Pogonomyrmex rugosus* (ant) on nests and edges would be similar in burned and unburned habitat on functional groups' cover, density, number of inflorescences and species number. We hypothesize that annual and perennial dicots would recover faster on rat patches than on burned grassland, dicots and grasses would recover faster on ant patches than on burned grassland, and annual dicots would recover faster on rat than on ant patches, whereas grasses would recover faster on ant than on rat patches.

Location: Semiarid grassland, Sevilleta National Wildlife Refuge, New Mexico, USA.

Methods: We analyzed annual and perennial dicots, grasses and subshrubs in burned and unburned plots at 80 nests during cool- and warm-seasons two years post-fire. Data were collected at nest top (mound), edge, and 20 m (control) from the edge.

Results: Cover, density and species richness of different functional groups were low on animal mounds in unburned and burned plots. Ant edges had greater perennial dicot cover, grass cover and richness while rat edges had lower grass density and richness than control sites at unburned and burned plots. Perennial dicot density and richness recovered faster at rat mounds and edges than control. Ant edges yielded faster recovery of grass inflorescences than control. Dicots recovered faster on rat than ant mounds whereas grasses grew faster on ant edges.

Conclusions: Rats create nests enhancing density of recovering dicots and ant edges facilitate reproduction of recovering grasses. Equal regeneration between animal nests and grassland occurred commonly when fire reduced grass competition. Dysochory, granivory and fire intensity may influence recovery. Nests may be sources of reestablishment and seed dispersal. Recovery of grassland may be amplified as plants infill from engineered nests.

KEYWORDS

ants, community ecology, dicots, grassland restoration, herbaceous community structure, nests, plant recovery facilitation, plant-animal interactions, rodent burrow, wildfire

1 | INTRODUCTION

Patches are an important element in community structure, fashioning an heterogeneous landscape and adding community diversity, differing plant species dynamics and population stability (Forman & Godron, 1986). Aridland ecosystems are undoubtedly driven by variable rainfall, yet they exhibit a mosaic of vegetation patches differing in their structure and dynamics. Fossorial animals contribute to this mosaic, creating nests that differ in soil nutrients, soil characteristics, water availability, seed banks and seed capture unique to the surrounding landscape. Thus, these patches can alter plant species composition (Alba-Lynn & Detling, 2008; Guo, 1996; Huntly & Inouye, 1988; MacMahon, Mull, & Crist, 2000) and increase richness and productivity (Nicolai, Smeins, & Cook, 2008; Whitford & DiMarco, 1995) including fecundity (Wagner & Jones, 2006; Nicolai et al., 2008). After a large-scale disturbance such as fire, plant colonization and regrowth may subsequently differ on nests. North American grasslands are dynamic ecosystems largely controlled by a disturbance regime consisting of large mammalian herbivory, variable precipitation, frequent fires and their interactions (Fuhlendorf & Smeins, 1997; Smeins & Merrill, 1988; Scasta et al., 2016). Directly after fire in semiarid grasslands, there is a decrease in woody taxa (Parmenter, 2008; Smeins & Merrill, 1988), grass biomass (Collins et al., 2017; Scheintaub, Derner, Kelly, & Knapp, 2009) and total above-ground plant biomass (Scheintaub et al., 2009). As a result, germination, establishment and survivorship of perennial grasses and dicot seedlings may increase (Snyman & Cowling, 2004; Zimmermann et al., 2008) along with perennial dicot productivity (Ladwig, Collins, Ford, & White, 2014; Parmenter, 2008; Scheintaub et al., 2009). With the reduction of vegetation biomass in these ecosystems, diversity may increase (Ladwig et al., 2014) or become more even (Drewa & Havstad, 2001).

Imbedded in semiarid grasslands are nest patches created by two ecosystem engineers (*sensu* Jones, Lawton, & Shachak, 1994), *Dipodomys spectabilis* (banner-tailed kangaroo rat; Edelman, 2012) and *Pogonomyrmex rugosus* (rough harvester ant; Farji-Brener & Werenkraut, 2017). Both species are long-lived; rarely moving their underground nests. Thus, their nests have time to develop soil resources and vegetation composition that often differs from areas adjacent to nests. Ant and rat nest patches share environmental conditions on their mounds; greater soil nutrients (Moorhead, Fisher, & Whitford, 1988; Platt, Kolb, Kunhardt, Milo, & New, 2016; Wagner & Jones, 2004), fungi (Hawkins, 1996), microbes and temperature (Lei, 2000). On ant mounds, water infiltration is higher than off mounds, whereas rat mounds have lower soil moisture. The rats' nest and mound are continually changed by construction and by throwing soil, excrement and plant debris outside the burrow (Guo, 1996). This results in a much greater amount of bare ground and soil disturbance than in surrounding uninhabited grassland (Koontz & Simpson, 2010). Similarly, ants in the genus *Pogonomyrmex* have a disturbed, bare soil disk on top of their nest by continually removing vegetation and by accumulating debris

(MacMahon et al., 2000; Whitford & DiMarco, 1995). Encircling rat and ant mounds is an edge zone of lesser soil disturbance (Guo, 1996) but little is known about soils' resource levels. Vegetation structure and composition differ on rat mounds (Edelman, 2012; Fields, Coffin, & Gosz, 1999; Guo, 1996; Moorhead et al., 1988; Moroka, Beck, & Pieper, 1982) and mound edges (Edelman, 2012; Fields et al., 1999; Guo, 1996; Schooley, Bestelmeyer, & Kelly, 2000). Further, ant edge zones differ in composition, growth and seed production (Wagner & Jones, 2006; Whitford, Barnes, & Steinberger, 2008). Both species' nest taxa can dominate the nest patch's seed rain by locally depositing their seeds on nests (Koontz & Simpson, 2010; Nicolai & Boeken, 2012). Individuals from plant functional groups dominating rat and ant nest patches will colonize and regrow faster than individuals off nests after fire because they are already established on the nest, adapted to fire, or they are on a resource patch (mound and edge). By inhabiting a resource patch organisms can recover quicker after a large-scale disturbance. The aim of this study was to assess the influence of rat and ant nest patches on the structure, richness and dynamics of plant functional groups during the first two years following wildfire by comparing burned patches to unburned patches and their adjacent grasslands. Plant functional groups include annual and perennial dicots, grasses, shrubs and subshrubs during cool and warm seasons. Specifically, the null hypothesis is that influences of rat and ant nest patches would be similar in burned and unburned habitat on functional groups' cover, density, number of inflorescences and species number. We further hypothesize that after burning (a) annual and perennial dicots would recover faster on rat patches than in surrounding grassland, (b) annual and perennial dicots and grasses would recover faster on ant patches than in grassland, and (c) annual dicots would recover faster on rat patches than on ant patches, whereas grasses would recover faster on ant than on rat patches.

2 | METHODS

2.1 | Study site

The study was conducted as part of the Sevilleta Long Term Ecological Research Program, located on the Sevilleta National Wildlife Refuge (SNWR), New Mexico, US (1,600 m a.s.l.; 34°20'30" N, 106°43'30" W). Soils at the study site are Aridisols (Johnson, 1988). Vegetation is dominated by *Bouteloua eriopoda* (black grama) in a mixture of perennial grasses while shrubs and cacti dot 15% of the site and another 10% is subshrubs.

The climate is semiarid, mid-elevation continental with a cool season (December–March) and a warm season (July–September). Mean annual precipitation (1989–2009) is 237.8 mm/yr (Deep Well Station within 1 km of the study site; Moore, 2014). Mean temperatures are 25.3°C in July and 2.4°C in December (Station Records 1989–2009). Except for the first cool season after the fire, climate during the study was much dryer and warmer than average including 83% below it during the first warm season (Appendix S1: Figure 1).



This climate pattern results in two distinct plant growing seasons, and the amount of growth is due to total seasonal precipitation. Total cool season precipitation leads to most dicot and shrub seed production in April and May (Xia, Moore, Collins, & Muldavin, 2010). Total warm season precipitation leads to reproduction in a different suite of dicot species and most perennial grasses and subshrubs.

2.2 | Study animals

Banner-tailed kangaroo rat mounds are 3–5 m wide and about 1 m high (preliminary observations). The edge zone encircling the mound varies in width from 4 to 10 m. Density of active rat nests on burned and unburned study plots was 2.0 mounds/ha and did not vary during the two-year study.

A rough harvester ant colony has a disk on top of the nest approximately 1 m diameter (Rissing 1988; Whitford & DiMarco, 1995). Width of the edge zone is approximately 20 cm. Density of adult colonies on study plots was 3.0 and 4.8 colonies/ha and did not vary during the two-year study.

2.3 | Wildfire plots

The Black Butte Wildfire, 4 August 2009, resulted in nearly 100% of study plots' aboveground vegetation being consumed by fire, leaving scorched stubble. Post-fire observations indicated that vegetation and litter at rat and ant nest patches burned similarly to surrounding grassland, but no data were collected on fire intensity or spread at these patches.

A burn study plot was randomly selected in the continuous band of approximately 3300 ha of burned habitat. An unburned plot was placed 50 m from it to reduce heterogeneity of soils and vegetation community. Each plot measured 200 m × 500 m (10 ha). The following year, a second pair of 10 ha plots was randomly selected and added to the study area 0.5 km from the original plots. Plots were added to increase functional groups' sample sizes that were low during the drought. All plots consisted of the same vegetation composition, south-facing 5% slope and sandy loam soils. There were no significant differences between original and new plots.

2.4 | Animal nests and zones

To compare animal nest patch effects relative to grassland on unburned and recovering vegetation, three factors were tested: two wildfire (burned and unburned), two animal species, and three nest zones. Ten active rat nests and ten active ant colonies were randomly selected in each plot. Zones were established on top of the nest (mound), a ring (edge) immediately surrounding the mound, and 20 m (far) in random directions from the edge. Preliminary observations indicate that mounds and edge zones do not extend 20 m from the center of the mound, thus the far zone is considered the control. Mound and edge zones were clearly discernible for both species; rat mounds are taller and edges have greater bare ground than

surrounding habitat. Ant mounds were found by their bare 1 m disk and edge zones by less bare ground than surrounding habitat.

2.5 | Vegetation sampling

Plant data were collected during cool and warm seasons for two years. First samples were collected 22 and 23.05.2010 when peak biomass occurred, and 18 and 19.09.2010 when cover and reproduction peaked early. Two years after the wildfire, samples were collected 11 and 12.05.2011, and 22 and 23.10.2011.

Twenty nests were sampled for each species. One sample was collected randomly in each zone. One edge zone sample was selected randomly in the ring surrounding the mound starting from the mound's border and extending to 5 m for rats and 30 cm for ants. To reduce quadrat border inclusion errors, plant variables were sampled using a circular hoop measuring 0.86 m diameter (0.58 m² area). Due to the narrow width of ant edge zones relative to the hoop, the edge was divided into two, crescent-shaped subsamples that were summed. Plant variables collected for each species were percent cover (aerial for dicots, subshrubs and shrubs and basal for grasses) and number in the hoop (Bonham, 1989; Whittaker, 1965). Plants were counted if any rooted portion was in the sampling hoop. Individual perennial grasses were determined by counting the rooted plant if unattached to stolons or crown-producing adults. Counts were standardized to m⁻². Number of species was summed for each functional group. Beginning the first warm season, approximate numbers of inflorescences produced by an individual for each species were collected and placed into four broad categories; no inflorescences, few, moderate and abundant. Categories were tallied for each functional group.

Plants were identified to species and verified with specimens from the collection of the Plant Division, Museum of Southwestern Biology, University of New Mexico. Seed information and nomenclature were obtained from the USDA Plants Database (<http://plants.usda.gov>). Taxa sampled were grouped into five functional groups based on morphological characters and life span: annual dicot, perennial dicot, grass, shrub and subshrub. Moreover, in order to separate taxa into plants that were budding, flowering, and producing seeds in the cool or warm seasons, we used the Sevilleta Long Term Ecological Research records and observations during data collection.

2.6 | Soil properties

Soil texture, temperature and moisture were compared at fifteen ant nests and fifteen rat nests randomly chosen in burned and unburned habitat adjacent to the sample plots for a total of 30 animal nests. At every nest, three samples were collected, one from each zone from gaps in the vegetation and standing litter.

Soil samples were collected using a core of 4 cm diameter by 15 cm deep and then air-dried and passed through a 2 mm sieve. Soil texture was analyzed by the hydrometer method using an ASTM Hydrometer, 152H and 20°C (Day, 1965; Gee & Or, 2002). At the same nests, soil temperature and percent volume moisture were

collected with a probe at 10 cm depth on 25.01.2010. Weather conditions were cool and dry with minimal evaporation to obtain relatively similar data at species nests and their zones. Additional temperature and moisture samples were collected 8.05.2010 and 13.05.2011 to compare annual differences.

2.7 | Statistical analyses

Plant functional group variables were compared with regard to burn, animal species and zone using a three-way nested analysis of variance (ANOVA) design with species nested in burn. Animal species were nested because the wildfire scorched an almost continuous band; therefore, we were unable to randomize burn plots. Separate analyses were conducted each year for cool and warm season sampling periods to reduce the interacting variances caused by season and climate. Soil variables were compared using the same three-way nested ANOVA.

Shrubs were not analyzed because they were rarely counted during all sample periods. Grasses were pooled into the warm growing season because cool season species were rarely sampled. For each plant functional group, percent cover, density, number of species in a quadrat, and categories of number of inflorescences per individual were analyzed separately. Data were logarithm- or power-transformed for analyses when cover, density, number of species, or soil texture were non-normal

and variances unequal. Some distributions of data were highly skewed even after transformations; therefore, non-parametric ANOVA (Kruskal–Wallis) was used (Zar, 2014). Planned comparisons were conducted to determine differences among zones for each animal species.

A χ^2 test of association was used to compare the frequency of number of inflorescences per individual category with burn, animal species and zone. If expected counts for a category were below five, then two or more categories were pooled. Very few plants produced seed inflorescences during the second warm season following the burn, and thus, analyses were not conducted. Analyses were performed using SPSS (IBM SPSS Statistics for Windows, version 24; IBM Corp., Armonk, NY).

3 | RESULTS

Forty-three plant species were recorded with 77% of these taxa shared between burned or unburned habitat and 74% shared between animal species. Unburned banner-tailed kangaroo rat nest zones are co-dominated by annual and perennial dicots while the far zone, i.e. the control, is dominated by perennial grasses (Appendix S1). The few plants on unburned rough harvester ant mound zones are also dicots but edge zones are similar to far zones.

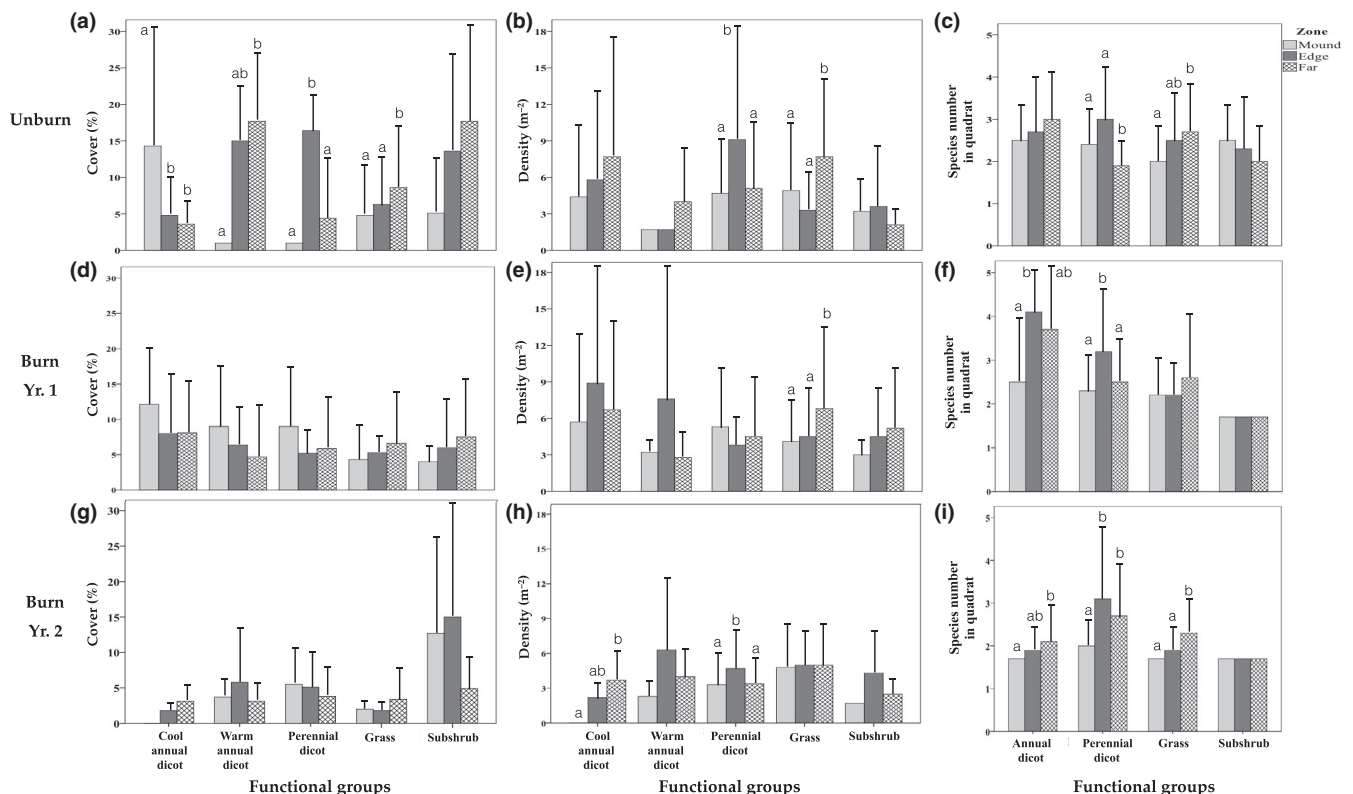


FIGURE 1 Mean (SD) functional group variables at rat mound, edge and far zones in Sevilleta National Wildlife Refuge, NM. Cover, density and number of species in the unburned plot the first year (a–c), burned plots the first year (d–f), and second year following fire (g–i). Means with different letters are significantly different Planned Comparisons at $p < 0.05$. Perennial dicots and subshrubs were pooled by season



3.1 | Modification of habitat by animals

Cover, density and species richness of all functional groups tended to be lower on rat mound zones compared to far the first year, except for significantly greater cover of cool season annual dicots (Figure 1a) and richness of perennial dicots (Figure 1c). Mounds had significantly less warm season annual dicot cover, grass basal cover (Appendix S2), species richness (Appendix S2) and density (Figure 1b; Appendix S2) than far zones. Moreover, there were less grass inflorescences produced on rat mounds compared to far plots (Table 1).

Edge zones had significantly greater perennial dicot cover and density than far zones. As a result, total plant cover was also greater (Table 2). However, grass species richness was lower by comparison.

The warmer and dryer second year lowered functional groups' responses so that most differences were not measurable. Nevertheless, significant differences unique to the second year were found; mounds matched edge results with significantly higher densities of cool season, perennial dicots compared to far zones (Figure 2b). In addition, edge zones had higher, nearly significant total plant density during the cool season (Table 2).

Mounds on ant nests had significantly lower total plant cover and density compared to edge and far zones, but edges had greater responses from grasses. Mounds had significantly less density of grasses (Figure 3b) and perennial dicots compared to edge and far zones. The first year, numbers of annual dicot and grass species were significantly lower on mound zones while subshrubs were less abundant on mounds compared to edges (Figure 3c).

Edge and far zones were generally similar, except that edges had significantly greater basal cover of grasses than far zones (Figure 3a). As a result, total warm season plant cover was greater on edge compared to far zones. Further, there were more grass inflorescences produced in edge zones.

Mound reductions in cover and density continued to be significant in the second year of the study. Nevertheless, significant

differences unique to the second year were found at edge zones; they had lower, nearly significant densities of cool season perennial dicots than far zones (Figure 2b). In contrast, edges had significantly greater cover of warm season perennial dicots (Figure 2a) and higher grass species richness compared to far zones (Figure 2c).

3.2 | Recovery of vegetation at animal nests

Density and number of species quickly recovered in rat zones after the fire. However, cover was lower than in unburned plots and was further reduced in the second dry year. Perennial dicot species richness recovered faster in edge than in far zones the first year (Figure 1f). Grass density in rat zones recovered to unburned levels (Figure 1e, Appendix S2) and by the second year grass richness had also recovered (Figure 1i, Appendix S2). Additionally, significantly less grass inflorescences were produced on rat mounds compared to far zones. However, basal cover of *B. eriopoda* was nearly double on burned mounds (mean 7.4%, *SD* 6.8%) compared to unburned mounds (mean 4.0%, *SD* 4.3%) due to seedling establishment (burned mean 5.8 m^{-2} , *SD* 4.3 m^{-2} , unburned mean 3.4 m^{-2} , *SD* 1.7 m^{-2}).

The results of grass cover, richness and abundance of inflorescences, and richness of perennial dicots found the first year in rat zones were similar the second year of the study, but were not statistically significant (Figure 1g–i). Nevertheless, differences unique to the second year were found in rat edge zones; perennial dicot density (Figure 2e) and warm season total plant density (Table 2) recovered faster than in far zones.

Ant mound reductions in cover (Figure 3d), density (Figure 3e) and species richness (Figure 3f) quickly recovered (Table 2; Appendix S2). Although generally not statistically significant, these reductions occurred in the dry year, too (Figure 3g–i).

Ant edge and far zones' densities (Figure 3e) and richness (Figure 3f) recovered toward unburned levels. Moreover, warm season perennial dicot cover (Figure 3d), grass basal cover (Figure 3d) and grass richness (Figure 3f), which showed greater edge responses compared to

TABLE 1 Frequency of the abundance of grass inflorescences per individual at rat mound and edge zones and ant edge zones during the first warm season following fire, Sevilleta National Wildlife Refuge, NM, USA

Location	Frequency of grass inflorescence categories		
	NoneCount/Expected Count	All other categories-Count/Expected Count	Row total
Burn Ant Edge	2/6.9	17/12.1	19
Unburn Ant Edge	3/6.2	14/10.8	17
Burn Rat Mound	5/2.2	1/3.8	6
Unburn Rat Mound	6/2.9	2/5.1	8
Burn Rat Edge	4/3.6	6/6.4	10
Unburn Rat Edge	3/3.3	6/5.7	9
Burn Far	12/10.1	16/17.9	28
Unburn Far	11/10.9	19/19.1	30
Column Total	46	81	127

Note: Abundances are categorized as none, few, moderate, and abundant and were pooled when 22% of the expected counts were <5. Ant mounds were eliminated because the expected count was always <5. Pearson's χ^2 : $\chi^2 = 19.6$, $p = 0.007$.

TABLE 2 Summary of nested ANOVA results for total plant cover (% basal for grasses, aerial for all others) and plant density (m^{-2}) effected by ant and rat mound, edge and far zones in burned and unburned grassland during the first two years following fire, Sevilleta National Wildlife Refuge, NM

Main effect	Cool season 2010 $n = 120$ zones				Cool season 2011 $n = 161$ zones		Warm season 2010 $n = 195$ zones				Warm season 2011 $n = 169$ zones			
	Cover ^b		Density ^b		Density ^f		Cover ^f		Density ^f		Cover ^f		Density ^b	
	F	p	F	p	H	p	F	p	H	p	F	p	F	p
Species	0.4	0.80	0.2	0.69 ^d	0.6	0.47	1.8	0.18 ^f	3.7	0.02	2.0	0.16	2.0	0.20
Zone	10.5	<0.001	30.3	<0.001	9.1	0.01 ^f	26.9	<0.001	23.3	<0.001	5.8	.004	24.8	<0.001
Species X Zone	5.6	0.005	0.9	0.40	N/A	N/A	13.3	<0.001	N/A	N/A	1.2	0.31	1.4	0.30
Burn	4.3	0.03	1.2	0.28	11.4	0.003	4.0	0.05	0.02	0.90	1.0	0.31	10.0	0.03

^aKruskal–Wallis Analysis.

^bLogarithm data transformation.

^c $\chi^{0.3}$ power data transformation.

^dMound Only Planned Comparisons $t = 2.7$, $p = 0.009$, Edges Only $t = 3.1$, $p = 0.002$.

^eMound Only Planned Comparisons $t = 3.1$, $p = 0.002$.

^fRat Only Planned Comparison $t = 1.9$, $p = 0.05$.

the unburned plots, recovered similarly. There were significantly more grass inflorescences and faster recovery in edge zones compared to far zones. All grass taxa on the edge produced at least one inflorescence per plant one year after the burn.

3.3 | Comparisons of animals in modifying habitat

Rat mounds had significantly higher densities of cool and warm season total plants than ant mounds (Table 2). Density of warm season perennial dicots (Appendix S1), warm season total cover (Table 2) and richness of perennial dicots (Appendix S1) was higher on rat mounds than on ant mounds. In addition, subshrub richness and cool season total plant density were higher on rat nests and edge zones, respectively. Pooled, warm season dicots had significantly more inflorescences in rat zones (74% of all zones) than ant zones (26% of all zones): Fisher's exact test $\chi^2(1, n = 62) = 7.6$, $p = 0.008$.

Grass cover, density and inflorescences were higher in ant compared to rat edge zones. Ant edges had greater cool season total cover than rat edges while it was higher on rat mounds than ant mounds (Table 2). Similar significant interactions were observed during the first warm season for grass density, perennial dicot cover (Appendix S1) and total cover.

Differences between species unique to the second year were found; rat mounds had significantly greater cover of warm season annual dicots compared to ant mounds (Figure 2d). Grass species richness was significantly higher in ant edges compared to rat edges (Figure 2h).

3.4 | Animal comparisons during recovery of vegetation

Vegetation in rat and ant zones quickly recovered from differences observed between them (Appendix S1). Rat mound zones had higher grass density and higher density and species richness of warm season

perennial dicots compared to ant mounds, demonstrating faster recovery on rat mounds. Although rat mounds quickly regained more total plant cover than ant mounds, ant edges were similar to rat edges. However, grass cover and grass density recovered faster in ant edges than in rat edges. Ant edge zones also had a greater number of grass inflorescences compared to rat zones.

In the second year, rat mounds continued to show faster recovery of perennial dicot richness compared to ant mounds. Additionally, they recovered differences observed the second year, including faster recovery of warm season annual dicot cover on rat than ant mounds (Figure 2e). In contrast, the number of grass species was higher and recovery was faster in ant edges compared to rat edges (Figure 2d).

3.5 | Soil properties

Soil texture in the upper 10–15 cm was sandy loam in both study plots; 77% sand, 17% clay, 7% silt and 0.4% pebble. Together, animal species edge zones had a significantly greater proportion of sand (83.7%, SD 4.5%) and pebble (3.6%, SD 5.5%) compared to far zones (sand 77.0%, SD 3.2%; pebble 0.4%, SD 0.7%). In addition, mound zones had a greater proportion of pebbles (2.5%, SD 2.8%) compared to far zones. Rat mounds had a significantly greater proportion of sand (77.6%, SD 6.8%) compared to ant mounds (74.8%, SD 4.2%).

Mean soil moisture was significantly higher the first year of the study (2.5% volume, SD 0.6%) compared to the second (1.3% volume, SD 0.3%; $F = 6.1$, $p < 0.001$). Soil moisture in January was significantly lower in mound zones (mean 8.8% volume, SD 1.8%) compared to far zones (mean 10.3% volume, SD 2.2%; $F = 6.62$, $p < 0.001$). In addition, moisture was significantly lower in rat mound zones (1.7% volume, SD 0.5%) compared to far zones (2.6% volume, SD 0.7%) during the first cool season ($F = 3.0$, $p < 0.05$). Mean soil temperature was 29.8°C (SD 1.2°C) and was similar between species and their zones.

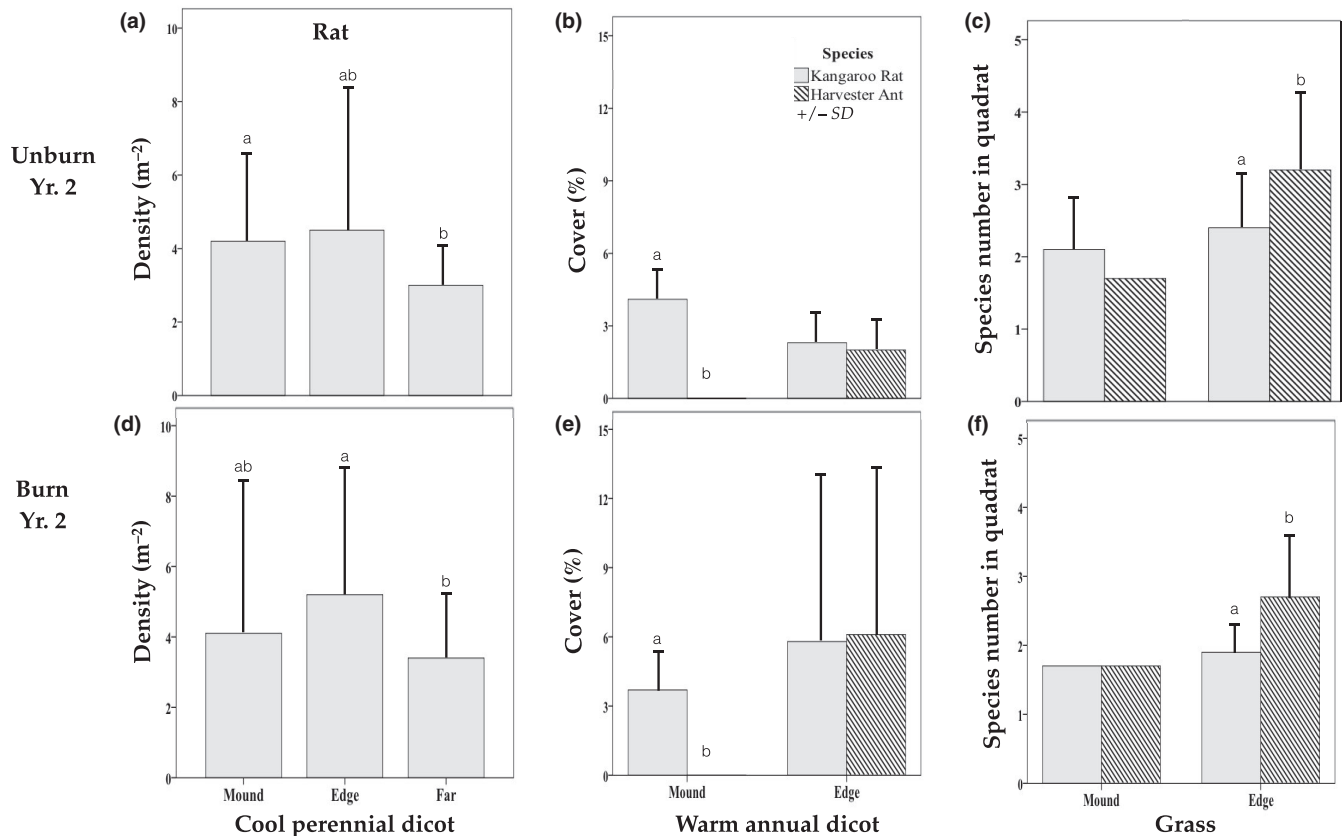


FIGURE 2 Mean (SD) annual and perennial dicot and grass variables following fire with unique second year responses at rat and ant mound, edge and far zones in Sevilleta National Wildlife Refuge, NM. Cover, density and number of species in unburned (a–c) and burned plots (d–f). Means with different letters are significantly different Planned Comparisons at $p < 0.05$

4 | DISCUSSION

In semiarid grasslands of the Sevilleta National Wildlife Refuge, *D. spectabilis* and *P. rugosus* nest patches differentially modified herbaceous functional groups, corresponding to prior studies. Nearly 60% of their modifications to vegetation recovered by the end of the second year following wildfire, thus partially supporting the null hypothesis. These results were due to species' resumption of activities shortly after the wildfire. As predicted, faster recovery of perennial dicots occurred in kangaroo rat edge zones and of grasses in harvester ant edges. Further, the results supported the third hypothesis that grasses would recover faster in ant edges compared to rat patches. Edges could provide improved resources for faster recovery than surrounding grasslands.

Recovery of controls was slow during the second dry year when density was lower than the first year whereas density at edges was higher, suggesting edges have resources that contribute to greater seedling establishment and faster recovery. Rat and ant edge zones were found to have greater proportions of sand and pebble compared to controls, perhaps resulting in higher water infiltration rates. Ant edges rapidly recovered grass reproductive allocation and these plants recovered faster there compared to surrounding habitat during both post-fire years, supporting the second hypothesis. This result is also reported for another species of harvester ant following a severe drought (Nicolai et al., 2008).

Guo (1996) found that rat mounds had greater biomass of small-seeded, annual dicot species compared to surrounding desert. Gutierrez and Whitford (1987) showed such species responded to additional nitrogen found in rat mounds. We also found fugitive taxa dominating cool season species composition and cover on mounds. In fact, when these taxa were encountered in unburned controls, individuals were diminutive. After the burn, annual cover was evenly distributed among zones and was no longer restricted to mounds. Fire perhaps increased levels of soil nitrogen, leaving uniform levels of it among zones and resulting in the even cover distribution of these taxa.

That dicots increase after fire is commonly observed in semiarid grasslands (Collins et al., 2017; Ladwig et al., 2014; Scheintaub et al., 2009; Snyman & Cowling, 2004) and is usually attributed to reduced interspecific competition with dominant grasses (Smeins & Merrill, 1988; Sasaki & Lauenroth, 2011). In this study, the higher abundance of perennial and cool season annual dicots in the control zone compared to unburned grassland could be caused by a considerable cover loss of dominant perennial grasses and a reduced number of grass species (personal observation; Mulhouse, Hallett, & Collins, 2017).

On rat mounds, the constant disturbance of plants kills perennial grasses, potential competitors of dicots, which reduces competition between functional groups (Suding & Goldberg, 2001). If

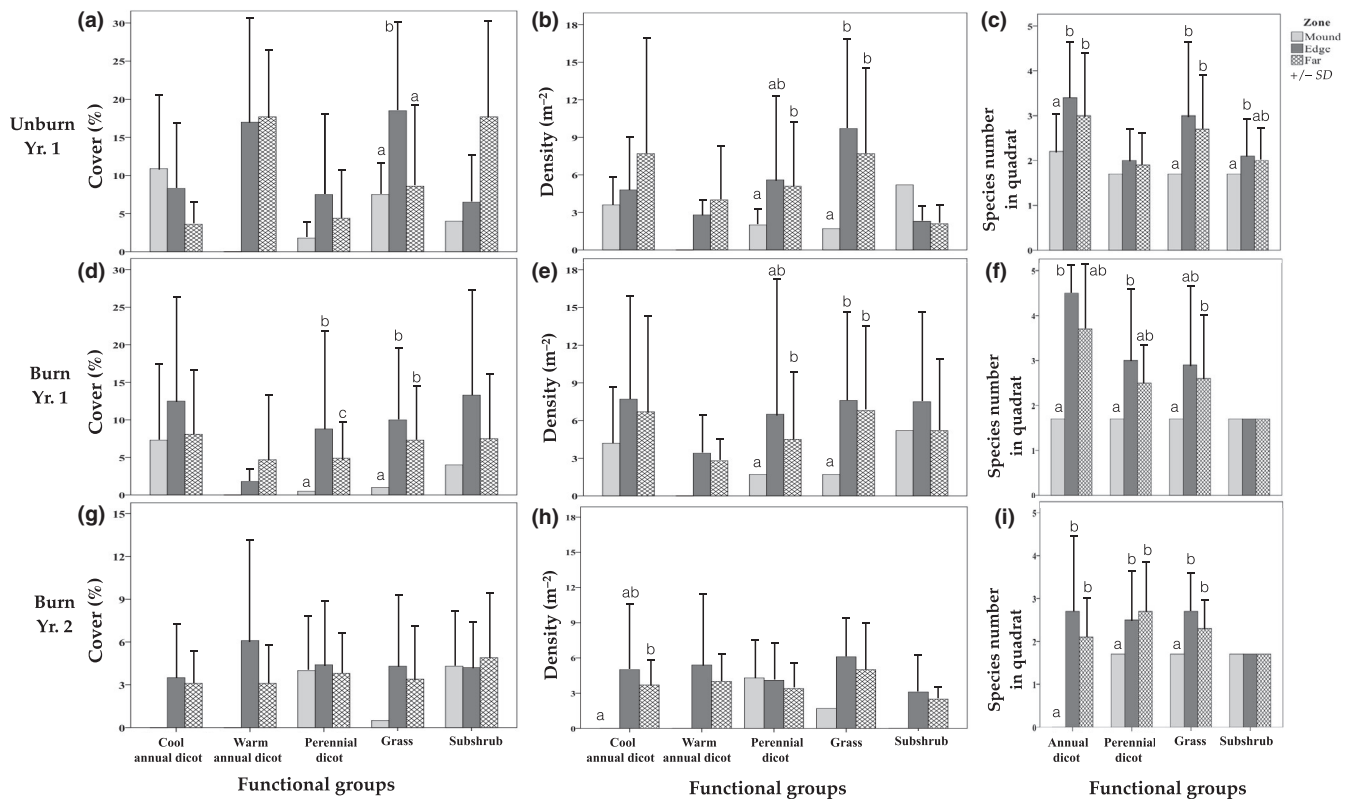


FIGURE 3 Mean (SD) functional group variables at ant mound, edge and far zones in Sevilleta National Wildlife Refuge, NM. Cover, density and number of species in the unburned plot the first year (a–c), burned plots the first year (d–f), and second year following fire (g–i). Means with different letters are significantly different Planned Comparisons at $p < 0.05$. Perennial dicots and subshrubs were pooled by season. Cover scales vary

rats remove potential competitors in unburned habitat, then the density, cover and richness of dicots in nest zones should be significantly greater compared to those in control sites. However, the wildfire also removed competitors, especially dominant perennial grasses. Thus, dicots would not necessarily be restricted to nest zones in burned plots and the even distribution of variables among zones is expected. Cover of perennial and cool season annual dicots, perennial richness and in the second year, perennial cool season density are consistent with these predictions. Differences were not caused by altered species composition. These results do not support the null hypothesis, instead rat disturbance creates a gap in grasses, reducing competitive intensity and allowing some dicots to flourish (Suding & Goldberg, 2001).

Another mechanism whereby rats could directly influence dicots could be due to rat seed caching. Banner-tailed kangaroo rats disperse herbaceous seeds by dyschory; storing them in multiple seed caches buried shallowly and scattered throughout the edge zone (Best, 1988). Seeds in caches can have higher rates of seedling establishment than in non-cache soil (Longland, Jenkins, Vander Wall, Veech, & Pyare, 2001). Specifically, we found *Sphaeralcea* (globemallow) species had double the abundance in edge zones compared to controls; these species are known to be highly collected by rats (Best, 1988; Hope & Parmenter, 2007). Thus, increased edge richness and density could be partially explained by

establishment from caches. Surprisingly, inflorescence production was uniform regardless of patch resources or competition with grasses.

Rat seed consumption or removal to the nest, rather than caching, may lower grasses density and richness in nest patches within at least 6 m of the mound (Schroder, 1979). For example, the co-dominant grass *Bouteloua gracilis* was not counted on mounds and edge zones in either burn level and grass richness was significantly lower. Disturbances and seed collection may inhibit grass recovery. However, establishment of *Bouteloua eriopoda* seedlings on mounds helped to equalize grass basal cover among zones.

Ant edges had lower cover and density of warm season, perennial dicots compared to control zones due to competition with grasses or granivory. When wildfire removed competitors, they became evenly distributed between edges and control sites. However, harvester ant colonies are known to switch seed preferences, alter numbers collected and discard uneaten stored seeds in the edge zones when habitat conditions change (Whitford, 1978; Wagner & Jones, 2004; Nicolai, Cook, & Smeins, 2007). However, Zimmer and Parmenter (1998) noted that rates of specific food items returned to the nest were equivalent in Sevilleta National Wildlife Refuge burned and unburned grassland. More study is needed to determine the role granivory plays in perennial dicot recovery compared to competitive release from grasses.



With their large size, greater bare ground and less litter for fuel (Edelman, 2012; personal observations), rat edge zones may be less flammable, leaving more individuals, regenerative organs and seeds available for recovery than in the control zones (Joseph, Seymour, Cumming, Mahlangu, & Cumming, 2013; Simkin, Michener, & Wyatt, 2004). Nevertheless, the wildfire's intensity appeared homogeneous across rat zones but it was not measured.

In contrast, higher litter on rat mounds (Koontz & Simpson, 2010) and in ant edge zones (personal observations) may intensify fire, overheating nest soils and damaging regenerative organs and seeds (Deák et al., 2014; Eriksson, 1989). Over half of rat mounds lost their subshrubs compared to increased density in controls, thus fire damage may have affected subshrub recovery. Most taxa recorded in the animals' zones display high mortality when exposed to fire (Parmenter, 2008), and in this study, they did not recover. Grasses in ant edges did not regain their greater cover or species richness possibly due to greater fire damage to tiller buds (Deák et al., 2014; Eriksson, 1989) because some fire-adapted species such as *B. gracilis* (Parmenter, 2008) recovered slower in edge than control zones.

During the second dry year, number of grass species was higher in unburned ant edges than in any combination of animal species, burn and zone. It did not recover faster in burned edge zones as predicted, though. Subordinate grass taxa survived or reestablished from seeds and tiller buds on the burned nests. However, *B. eriopoda*, and to a lesser extent *Sporobolus cryptandrus* (sand dropseed) were missing from half the nests. High fire mortality and slow recovery are documented for these two species (Gosz & Gosz, 1996; Humphrey & Schupp, 1999; Stinson & Wright, 1969). As a result, the distribution of grass richness became more even between edge and far zones.

Slower recovery of grass cover in ant edges may be partly caused by plants allocating nest resources for reproduction instead of above-ground growth. When nitrogen was added to a tall-grass prairie, C_4 grasses produced more seed inflorescences than leaf biomass compared to plants in untreated areas (HilleRisLambers, Harpole, Schnitzer, Tilman, & Reich, 2009).

As predicted, the grass functional group recovered faster in ant edge compared to rat edge zones. To our knowledge, studies have not compared available resources in the two species' patches. Soil temperature and proportions of sand and pebble were comparable between species. Still, grasses in ant edges may have an advantage over grasses in rat edges because they grow adjacent to the nest with its better soils conditions. Roots may be able to grow into the nest for resources in addition to using them at the edge. Wagner and Jones (2006) demonstrated that an annual grass growing in rough harvester ant edge zones was capable of using nitrogen from the nest.

Differing granivory rates and seed selections occur between harvester ants and kangaroo rats (Samson, Philippi, & Davidson, 1992). Specifically, no *B. gracilis* was found in rat edge zones whereas ant edges resembled the surrounding habitat. Due to the higher establishment and survival of grasses in ant edge zones, basal cover was also higher than on rat nests. By calculating grass density to cover

ratios of rat (1:1.1) and ant (1:1.3) zones, we determined that ants confer greater growth to a slight degree.

Dicot functional groups recovered faster on rat than ant patches, supporting the third hypothesis. Two mechanisms may contribute to these results; first, not all dicots in ant edge zones grow roots into nests to obtain resources (Wagner & Jones, 2006). Second, rat edges may facilitate establishment and survivorship, especially during dry conditions.

Our results in this semiarid ecosystem have ramifications for research in disturbance ecology and ecosystem engineering. Although the results are broadly consistent with the competitive reduction hypothesis, they also suggest that these ecosystem engineers create patches with superior soil conditions, enhancing the establishment and survivorship of recovering dicots and reproduction of recovering grasses. Dysochory and granivory could also influence recovery. It is unknown how fire intensity may add to nest patch recovery. As areas of high grass reproduction during recovery, ant patches may act as foci for seed dispersal into surrounding habitat. With greater dicot establishment, richness and, crucially, survivorship during dry periods, rat mounds and edges may be sources for reestablishment. Recovery of a grassland may be amplified as plants infill from these patches. Recovery of the ecosystem after large-scale disturbances may be facilitated by numerous small-scale modifications by these little engineers.

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DATA ACCESSIBILITY

The research data supporting this publication are available upon request to the author.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Figures of climate, relative frequency, and comparisons of animals

Appendix S2. ANOVA tables of cover, richness and density

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