Burrowing rodents increase landscape heterogeneity in a desert grassland

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Abstract

Animals that modify their environment through engineering and herbivory have important impacts on ecosystems, yet the interactive roles of such species have rarely been studied. We studied the comparative and interactive effects of two burrowing herbivorous rodents, Gunnison's prairie dogs (*Cynomys gunnisoni*) and banner-tailed kangaroo rats (*Dipodomys spectabilis*), on vegetation where they co-occurred in a Chihuahuan Desert grassland. We found that their effects remained distinct and, thus, non-substitutable, where they co-occurred. The rodents differentially altered plant community structure relative to their different mound types, herbivory, and spatial scales of disturbance. Vegetation structure and plant species assemblages differed between mound and landscape patches occupied by prairie dogs and kangaroo rats. Where both species co-occurred, there was more soil disturbance, organic material from their fecal pellets, forb cover, and activity by other animals. The combined effect of these rodents increased the landscape heterogeneity and plant species richness by creating a mosaic of different habitat patches on the landscape. Our results demonstrate that these rodents had complementary, additive effects where they co-occurred, and suggest that multiple habitat-modifying species, especially those that play large ecological roles, can have important interactive effects on community structure and biodiversity.
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Keywords: Banner-tailed kangaroo rats; Biodiversity; Ecosystem engineers; Gunnison's prairie dogs; Keystone species

1. Introduction

Many animals modify their environments, generating habitats for other species, regulating community structure and dynamics, and altering ecosystem processes (Jones et al., 1994; Power et al., 1996). Animals modify their environments through a variety of mechanisms, but those that modify habitat structure through the physical process of ecosystem engineering and/or consumption of plant material have received increased attention over the last decade (Fuhlendorf and Engle, 2001; Joern, 2005; Knapp et al., 1999; Wright and Jones, 2006). Here referred to as habitat modifiers, these animals increase landscape heterogeneity and species diversity by creating unique patches of habitat that differ from the surrounding landscape (Fuhlendorf and

Engle, 2001; Wright et al., 2006). Well-known examples of such patches include beaver (*Castor canadensis*) dams, banner-tailed kangaroo rat (*Dipodomys spectabilis*) mounds, ant (Formicidae spp.) mounds, black-tailed prairie dog (*Cynomys ludovicianus*) colonies, and ungulate grazing lawns (McNaughton, 1984; Whicker and Detling, 1988; Wright et al., 2006). While all species interact with their environment to varying degrees, at one end of the spectrum, those habitat modifiers that have unique and disproportionately large impacts on other organisms and ecosystem processes are often termed keystone species (Kotliar, 2000; Power et al., 1996).

Most studies have focused on the effects of individual species on their environment. However, ecosystems are complex and species interactions can have non-intuitive outcomes on community organization and ecosystem processes (Brown et al., 2001), such that it is important to consider the combined effects of multiple species. Little is known about the interactive effects of co-existing habitat-modifying organisms, especially of those that are known to play keystone roles. Given that habitat-modifying species create unique patches of habitat, one would predict that if their effects are distinctive where they co-exist, then their combined impacts should be complementary and further increase heterogeneity and species diversity on the landscape. In this paper, we evaluate the comparative and interactive effects of two burrowing-herbivorous rodents, Gunnison's prairie dogs (*Cynomys gunnisoni*) and banner-tailed kangaroo rats, on desert grassland community structure.

Prairie dogs (*Cynomys* spp.) and banner-tailed kangaroo rats are often considered keystone species of grassland ecosystems of North America (Kotliar, 2000; Kotliar et al., 1999; Miller et al., 1994; Valone et al., 1995). Through their herbivory and ecosystem engineering these burrowing rodents dramatically modify grassland community structure and enhance heterogeneity on the landscape by creating unique patches of habitat for plants and animals (Ceballos et al., 1999; Hawkins and Nicoletto, 1992; Lomolino and Smith, 2003; Valone et al., 1995; Whicker and Detling, 1988). Prairie dogs transform grasslands by grazing grass and constructing numerous mounds with extensive burrow systems (Whicker and Detling, 1988, Fig. A1a). Within their colonies, they maintain a low, dense turf of rapidly growing plants dominated by forbs and grazing-tolerant grasses (Whicker and Detling, 1988), though most of what we know about the effects of prairie dogs on the vegetation is based on black-tailed prairie dog research. In contrast, banner-tailed kangaroo rats alter plant species composition and habitat structure by selectively harvesting seeds of large-seeded plants and constructing large, resource-rich mounds on the landscape (Brown and Heske, 1990; Mun and Whitford, 1990; Valone et al., 1995, Fig. A1b). Most research evaluating the roles of these rodents has been conducted in areas where each species occurs alone. Recently, however, we showed that black-tailed prairie dogs and banner-tailed kangaroo rats increased heterogeneity and diversity of vegetation in a desertified grassland system (Davidson and Lightfoot, 2006). In a subsequent study, we demonstrated a similar effect on arthropod communities (Davidson and Lightfoot, 2007).

Given that the roles of species are context dependent, our interest was to test the generality of the distinctive roles of these rodents and their interactive effects on grassland systems. To address this, we conducted similar research in an intact desert grassland system where Gunnison's prairie dogs and banner-tailed kangaroo rats co-occurred. Based on the findings of our previous research, we hypothesized that Gunnison's prairie dogs and banner-tailed kangaroo rats each would have large, unique effects on grassland community structure where they co-occur, and that as a result of their different foraging and mound-building behaviors, they also would have additive, complementary effects resulting in increased heterogeneity and diversity on the landscape. To test this hypothesis, we focused on the effects of their mounds on plant community structure in an area where the animals co-occurred, and conducted complementary research to understand how their mounds, soil disturbance, and herbivory affect the greater landscape.

2. Materials and methods

2.1. Study site

Research was conducted at the Sevilleta National Wildlife Refuge (SNWR) in central New Mexico, USA, 90 km south of Albuquerque, in Socorro County (NAD-27:34°24′N, 106°36′W, 1600 m elevation). Long-term mean annual precipitation was 243 mm, about 60% of which occurred during the summer. Long-term mean monthly temperatures for January and July were 1.5 and 25.1 °C, respectively. Gunnison's prairie dogs naturally colonized the study site in 1998, occurring within a 13 ha area during our study. The site has been

long inhabited by kangaroo rats, and represents typical northern Chihuahuan Desert grassland with deep clayey loam soils and burrograss (*Scleropogon brevifolius*), sand dropseed (*Sporobolus cryptandrus*), and black grama (*Bouteloua eriopoda*) as the dominant vegetation.

2.2. Mound-scale plots

To measure plant species composition and vegetation structure associated with mound disturbance patches we established replicate mound-scale plots, consisting of paired mound and non-mound control plots, a design similar to that used by Davidson and Lightfoot (2006), Guo (1996), Hawkins and Nicoletto (1992) and others (Fig. B1). Mound-scale plots were located in areas occupied by: (1) both species of rodents (Pdog + Krat plot) and (2) only kangaroo rats (Krat plot) (Fig. B1). Active mounds that were at least 10 m from other mounds of the same type were chosen in order to minimize impacts from adjacent mounds on the sampling points. Paired non-mound sampling points represented areas with minimal rodent disturbance (i.e., no rodent mound), systematically positioned 10 m from each study mound. Measurements were taken from 20 prairie dog mounds (fall 1999–spring 2002) and 20 kangaroo rat mounds (fall 2001 and spring 2002 only) on the Pdog + Krat plot, and around 20 kangaroo rat mounds on the Krat plot (fall 1999–spring 2002), as well as on paired non-mounds. Five-meter transects were located along the four compass directions centered on each mound. Plant canopy cover, maximum height of live foliage, feces, and animal soil surface disturbance were measured on 30 cm × 30 cm quadrats, located each meter along the transect lines. Sampling occurred during late spring and early fall.

2.3. Landscape-scale plots

While the focus of our study was on the mound-scale impacts of prairie dog and kangaroo rats, we also implemented complementary landscape-scale and exclosure plots to help us address their affects on the greater landscape. We compared vegetation on the Pdog + Krat plot, Krat plot, and also on a Transition plot, where both prairie dogs and kangaroo rats inhabited one-half of the plot and kangaroo rats inhabited the other half. For this paper, though, we focus our landscape comparisons primarily on the Pdog + Krat and Krat plots (Fig. B1). Historic extermination of prairie dogs at what is now the SNWR was extensive (John Ford, former officer for Animal Damage Control, personal communication 1999), leaving most of the grasslands inhabited only by kangaroo rats, and making it impossible to locate replicate sites (study plots) occupied by both species, exclusively by prairie dogs, or by neither species. Vegetation, fecal counts, and soil disturbance were sampled using a 180 m × 180 m (7 × 7) grid that extended across each plot (Fig. B1). Plant canopy cover, maximum height of live foliage, feces, and animal soil disturbance were measured at 30 m intervals on each grid using 1 m × 1 m quadrats. The method was similar to that developed by Huenneke et al. (2001), except that we measured total canopy cover per plant species within each quadrat. We counted fecal pellets of desert cottontail rabbits (*Sylvilagus auduboni*), black-tailed jackrabbits (*Lepus californicus*), kangaroo rats, and prairie dogs as a relative measure of their activity and nutrient input on the landscape. Soil surface disturbance by kangaroo rats, prairie dogs, and pronghorn antelope (*Antilocapra americana*) also was measured to evaluate the spatial distribution of their activity on the landscape. Soil disturbance was measured as the percentage of ground cover disturbed by animal tracks, digs, or mounds within each quadrat. Sampling occurred during late spring (April) and early fall (September), from fall 1999 to spring 2002. Prairie dog and kangaroo rat mounds within the 13 ha prairie dog colony area also were mapped using Global Positioning Systems from 1999 to 2002.

2.4. Experimental exclosure plots

To measure the response of vegetation to the exclusion of prairie dogs and kangaroo rats, 10 replicate split-plot exclosures were systematically installed on the Pdog + Krat plot (Fig. B1). We installed two types of exclosures, one that consisted of 5.08-cm-diameter mesh wire to exclude prairie dogs ($^{-}P^{+}K$ exclosure) and the other with 2.54-cm-diameter mesh wire to exclude both prairie dogs and kangaroo rats ($^{-}P^{-}K$ exclosure). The split-plot exclosures were each paired with an unfenced control plot ($^{+}P^{+}K$). A $^{-}K^{+}P$ exclosure plot was

not constructed, as it was impossible to exclude kangaroo rats while allowing larger prairie dogs through the fences. Nevertheless, as prairie dogs were excluded from both exclosure treatments, and kangaroo rats only from one, the difference between the two provided a measure of the effects of kangaroo rats alone. Each exclosure and control plot was $3.0 \, \text{m} \times 1.5 \, \text{m}$. The exclosures and controls contained two contiguous $0.5 \, \text{m} \times 1 \, \text{m}$ vegetation quadrats located in the center of each plot, $0.5 \, \text{m}$ from each fence-line to avoid potential fence effects and disturbance. Plant canopy cover and maximum height of live foliage were measured during spring and early fall. Exclosure plots were installed in January 2001. Pre-treatment data were collected in spring and fall 2000, and post-treatment data were collected from spring 2001 to fall 2002.

2.5. Statistical analyses

Data were normalized by log transforms and all analyses were performed using SAS version 8.2 (SAS Institute, 2001). *t*-tests were used to test for differences in plant species cover, height, and richness, and percentage of soil disturbance and number of fecal pellets between the Pdog + Krat and Krat plots, and to test for differences between mound types within the Pdog + Krat plot. The landscape plots were not replicated, so the interpretation of all results from these plots are limited to the differences between the two plots. Paired *t*-tests were used to compare vegetation, soil disturbance, and fecal pellet variables between paired mound and non-mound plots. Repeated measures analysis of variance (RMANOVA) was used to evaluate the effects of rodent removal on vegetation over time. Mixed-linear models (MLM) with Bonferroni adjustments also were used to analyze differences in vegetation cover and height among the exclosure plots. Each model included exclosure treatment types as fixed effects, and a random exclosure effect that allowed for correlated responses among the paired exclosure treatments. Data were pooled when analyzing across sample periods, and for each mound-scale plot ($n = 20$) and exclosure plot ($n = 10$).

Canonical discriminant function analysis (CDFA) provided a multivariate analysis of variance (MANOVA) test for potential differences among mound and landscape-scale treatment plots based on simultaneous analysis of all plant species. Very rare species were removed from the analyses (McCune and Grace, 2002). The Proc CANDISC procedure calculated the Mahalanobis distance measures (D^2) to provide a measure of difference in plant species composition between the treatment types, and provided *F*-tests and *P*-values of equal mean vectors, based on the D^2 (SAS Institute, 2004).

3. Results

3.1. Precipitation patterns

Precipitation was highly variable during our study, but was typical for the SNWR. Winter and spring rains were below average in 2000, high in 2001, and very scant in spring through late summer 2002, while summer rains were approximately average in 1999, very wet in 2000, and below normal in 2001. Precipitation had a large influence on the temporal vegetation patterns at our site, most notably during the spring, but the overall treatment effects were consistent across years.

3.2. Vegetation cover and structure

Cover of forbs was up to two-times greater on the Pdog + Krat plot than on the Krat plot (*t*-test: $t_{38} = -4.56$, $P < 0.0001$; Fig. 1), and was greater on kangaroo rat mounds (on the Krat plot) and prairie dog mounds than on non-mounds over all years (paired *t*-test: $t_{19} = 4.60$, $P = 0.0002$; $t_{19} = 2.42$, $P = 0.025$, respectively). Heights of forbs were greater on kangaroo rat mounds than paired non-mounds over all years on the Krat plot (paired *t*-test: $t_{19} = 2.31$, $P = 0.03$), but height of summer forbs was lower on kangaroo rat mounds than non-mounds on the Pdog + Krat plot (paired *t*-test: $t_{19} = -2.74$, $P = 0.01$). No differences were present between forb height on prairie dog mounds and paired non-mounds. Cover of summer forbs was significantly greater on kangaroo rat mounds than on prairie dog mounds on the Pdog + Krat plot (*t*-test: $t_{38} = 2.88$, $P = 0.006$; Fig. 1), but height did not differ. Although kangaroo rat mounds on the Pdog + Krat plot were sampled for two seasons (fall 2001 and spring 2002), spring forbs were
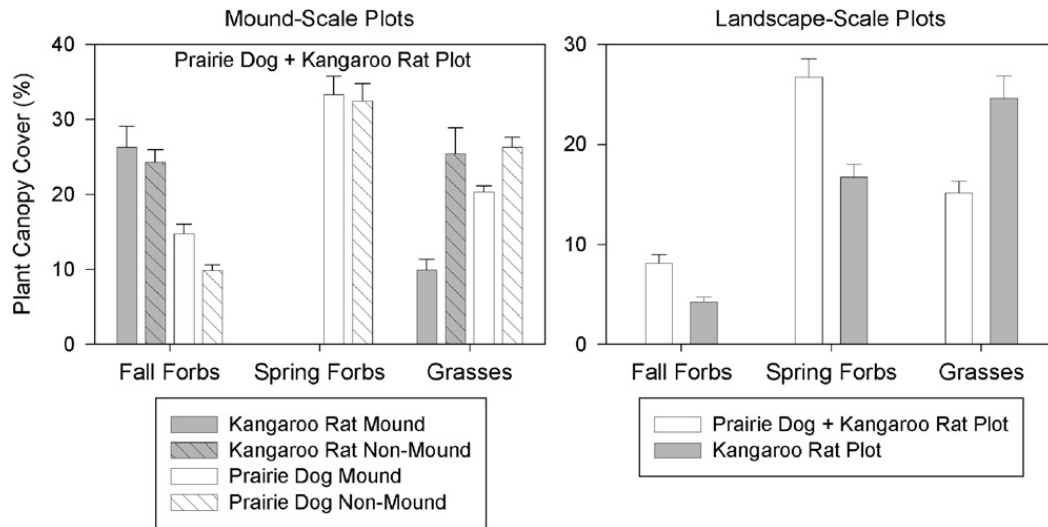
Fig. 1. Mean percentage plant canopy cover (+SE) on mound and landscape-scale plots over all years sampled (fall 1999–spring 2002), but kangaroo rat mounds were sampled in fall 2001 and spring 2002 only.
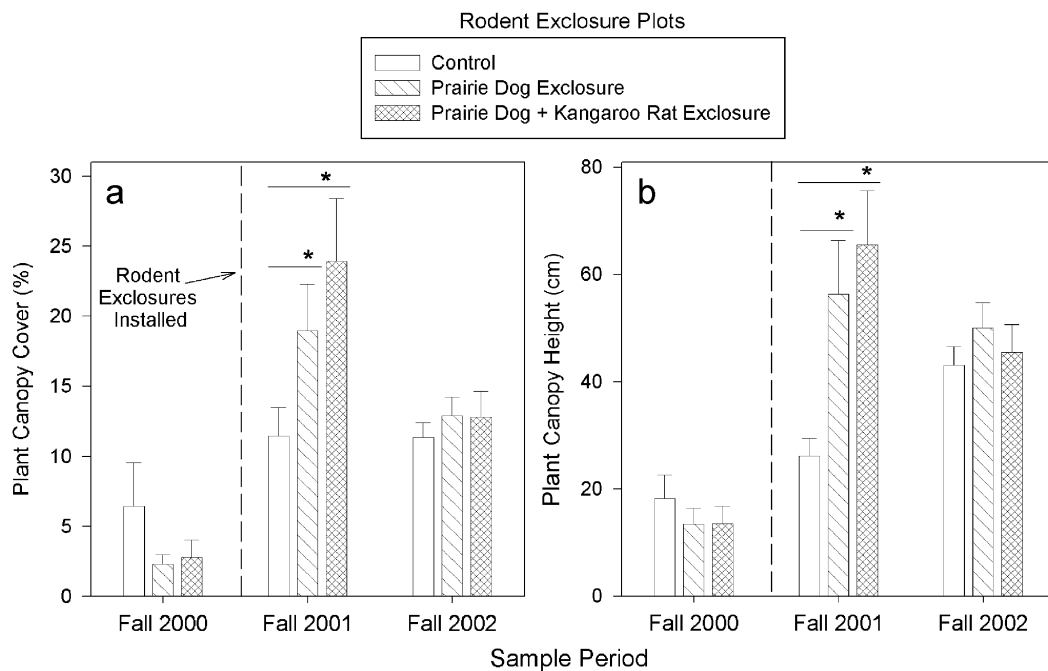

Fig. 2. (a) Mean percentage plant canopy cover and (b) height of live foliage (+SE) of summer forbs on the $^-P^+K$ and $^-P^-K$ exclosures and the $^+P^+K$ control plots. *$P < 0.05$.

absent during the drought of 2002. Grass cover and height were significantly greater on the Krat plot than on the Pdog + Krat plot and on non-mounds than on mounds over all years ($P < 0.0004$, for all tests; see Fig. 1). The effects of kangaroo rat mound disturbance on the vegetation also were greater where they co-occurred with prairie dogs. For example, summer forb cover around kangaroo rat mounds on the Pdog + Krat plot was up to threefold greater than around those on the Krat plot (t-test: $t_{38} = -4.92$, $P < 0.0001$), even at 5 m from the mound centers.

Cover and height of vegetation was greater inside the rodent exclosures. The largest differences between the exclosure and the control plots occurred during the first year, and summer forbs showed the greatest response to rodent exclusion (Fig. 2, C1, Table A1). Differences were less pronounced during the second year, when the prairie dog population had declined following the 2002 spring drought. Summer forb cover was significantly

greater in both the $^-P^+K$ and $^-P^-K$ exclosure plots than in the $^+P^+K$ control plots during fall 2001 (MLM: $F_{2,18} = 10.95$, $P = 0.001$), but no differences were present during fall 2002. Summer forb height showed a similar pattern (MLM: $F_{2,18} = 15.10$, $P = 0.0002$). Repeated measures ANOVA revealed a significant time effect for responses of summer forbs to the treatments ($P < 0.001$, for each). There also was a significant time by treatment interaction of summer forbs between both the $^-P^+K$ and $^-P^-K$ exclosures and the $^+P^+K$ control plots (RMANOVA: cover $F_{2,36} = 3.64$, $P = 0.037$; $F_{2,36} = 3.45$, $P = 0.04$, respectively; height $F_{2,36} = 6.93$, $P = 0.001$; $F_{2,36} = 8.20$, $P = 0.003$, respectively). However, there was no significant time by treatment interaction between the $^-P^+K$ and $^-P^-K$ exclosures. For grasses and spring forbs a significant time effect was present ($P < 0.001$, for each analysis), but no time by treatment interaction was detected.

Several plant species had greater height and cover in the rodent exclosures than in the control plots (Table A1). *Salsola kali*, was four to five times taller and about two times greater in cover in the exclosures plots than in the control plots during fall 2001, and in spring 2001 this species was present only in the $^-P^-K$ exclosures. Similar patterns were found for the spring forb, *Malacothrix fendleri*, and summer forb, *Aphanostephus ramosissimus*. The only perennial grass species that showed significant differences between the exclosure and control plots was the dominant tall grass at the site, *S. cryptandrus*, which was about twice as tall within the exclosure plots compared with the control plots during fall 2001. We frequently observed rodent herbivory (browse damage) on *S. kali*, *A. ramosissimus*, and *S. cryptandrus* outside of the exclosures, to a lesser degree within the $^-P^+K$ exclosure, but not in the $^-P^-K$ exclosure.

3.3. Plant species composition

The mound and landscape-scale plots supported unique combinations of plant species (Table 1, Fig. 3). CDFA indicated that plant species composition differed significantly between mounds and non-mounds, prairie dog mounds and kangaroo rat mounds, and the Pdog+Krat plot and Krat plot (MANOVA, all P-values < 0.05). However, we found no overall difference in species composition between exclosure treatments following rodent exclusion (MANOVA, $P > 0.05$). Mahalanobis distance measures further demonstrated that the distances based on the plant species composition were significantly different between the mound and landscape-scale plots (Table 1). However, plant species assemblages on kangaroo rat mounds were more distinct from paired non-mounds than prairie dog mounds were to paired non-mounds.

Table 1
Pairwise Mahalanobis distances (D^2) showing differences in plant species composition between mound-scale plots and between landscape-scale plots

	KM	KN	PM	PN
(a) *Mound-scale plots*				
KM	0	10.46*	11.07*	12.29*
KN	7.0*	0	9.29*	7.61
PM	–	–	0	3.75
PN	–	–	5.70*	0

	K	PK	T
(b) *Landscape-scale plots*			
K	0	–	–
PK	26.24*	0	–
T	14.58*	24.33*	0

(a) Below diagonal are distance values between paired kangaroo rat mounds (KM) and non-mounds (KN) on the kangaroo rat plot (K), and distance values between paired prairie dog mounds (PM) and non-mounds (PN) on the prairie dog + Kangaroo rat plot (PK) from fall 1999 to fall 2002. Above diagonal are distance values for comparisons between KM, KN, PM, and PN on the PK plot during fall 2001. (b) Distance values between the PK, K, and transition (T) plots from fall 1999 to fall 2002.
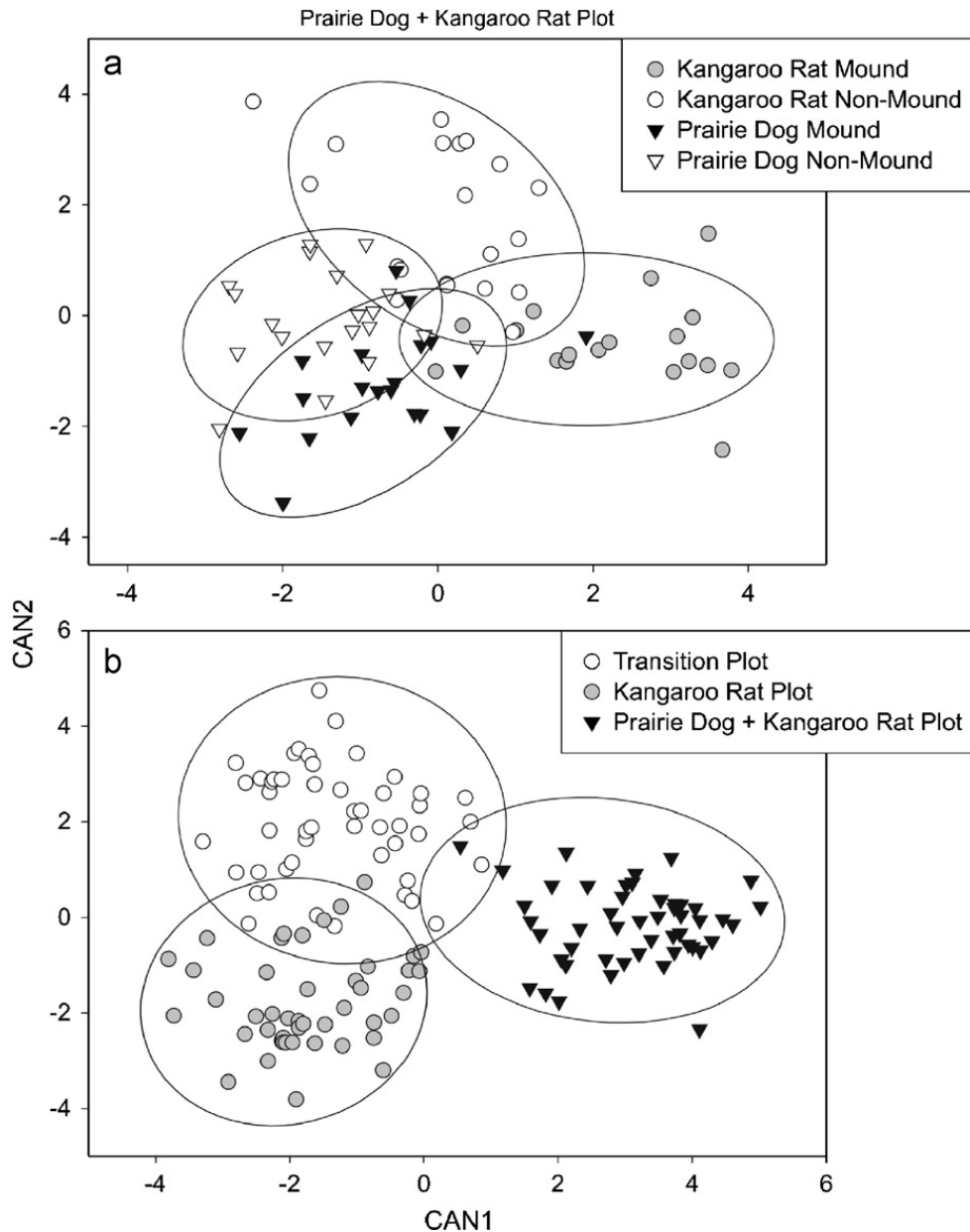   *$P < 0.05$.

Fig. 3. Ordination of canonical variates for (a) mound-scale plots during fall 2001 (MANOVA: $F_{93,133} = 1.58$, $P = 0.008$) and (b) landscape-scale plots over all years sampled, fall 1999–2001 (MANOVA: $F_{114, 176} = 5.45$, $P < 0.0001$) based on differences in plant species composition among plots. Ellipses represent 95% confidence intervals for each group. Note that (a) shows groupings of mound-scale plots within the Pdog + Krat plot, which is plotted in (b).

Of the 111 plant species, we found significant differences in 21 species at the landscape-scale and 19 species at the mound-scale, based on univariate analyses (Table A2). These species accounted for most of the variation in species composition between plots as indicated by the CDFA loadings. Many species were found exclusively on one treatment type, but were too rare for differences to be detected statistically. In general, summer annual forbs, annual grasses, and the spring forb, *Descurainia pinnata*, were most strongly associated with prairie dog and kangaroo rat mounds and also were most abundant on the Pdog + Krat plot. Other spring forbs, perennial forbs, and perennial grasses were most common on non-mounds. The perennial grass, *S. contractus*, and the summer annual forb, *Eriogonum rotundifolium*, were highly associated with kangaroo rat mounds, whereas, the annual grass, *B. barbata*, and perennial grasses associated more strongly with prairie dog mounds.
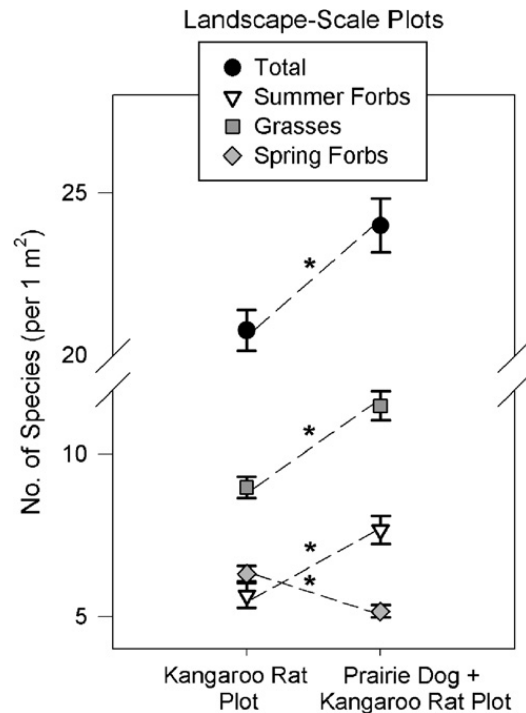
Fig. 4. Plant species richness patterns (+SE) on the landscape-scale plots over all years. *$P < 0.05$.

3.4. Plant species richness

The activities of prairie dogs and kangaroo rats also affected plant species richness. Although species richness did not differ between the rodent mounds and non-mounds, richness was greater on prairie dog mounds than on kangaroo rat mounds on the Pdog+Krat plot (t-test: $t_{38} = -4.58$, $P < 0.0001$). At the landscape-scale, the Pdog+Krat plot had greater species richness than the Krat plot over all years (t-test: $t_{96} = -3.32$, $P = 0.001$; Fig. 4). This difference reflected the greater species richness of summer forbs and grasses, which comprised about 85% of the total species pool. Spring forbs showed an opposite pattern, being more species rich on the Krat plot than the Pdog+Krat plot (t-test: $t_{96} = 3.71$, $P = 0.0003$).

3.5. Animal soil disturbance and nutrient input

The spatial area and percentage of disturbed soil around kangaroo rat mounds was two times greater than around prairie dog mounds. The mean percentage of disturbance around kangaroo rat mounds (56%) compared to the non-mounds (11%) also was greater than around prairie dog mounds (21%) compared to paired non-mounds (5%). In addition, the extent of the disturbed patches around kangaroo rat mounds was greater on the Pdog+Krat plot compared to the Krat plot. On the Krat plot, at 5 m from the mound center, soil disturbance became similar to non-mounds, but on the Pdog+Krat plot at the same distance (5 m) from the mound center, soil disturbance was still significantly greater than on the non-mounds (paired t-test: $t_{19} = 2.81$, $P = 0.01$).

At the landscape-scale, the Pdog+Krat plot received more soil disturbance and fecal matter than the Krat plot, most of which was due to prairie dogs (Fig. 5). Although the presence of pronghorn antelope and rabbits at the site was generally low, pronghorn disturbance, rabbit feces, and kangaroo rat feces were significantly greater on the Pdog+Krat plot than on the Krat plot over all years (t-test: Pronghorn $t_{96} = -2.43$, $P = 0.017$; Rabbit $t_{96} = -2.41$, $P = 0.018$; Kangaroo Rat $t_{96} = -2.22$, $P = 0.028$, respectively; Fig. 5). On the Pdog+Krat plot, prairie dogs created 30 mounds per ha, while kangaroo rats created 5 mounds per ha. The disturbance and feces from pronghorn antelope, kangaroo rats, rabbits, as well as prairie dogs resulted in significantly greater total soil disturbance (t-test: $t_{96} = -2.74$, $P = 0.007$) and fecal counts (t-test: $t_{96} = -7.18$, $P < 0.0001$) on the Pdog+Krat plot than the Krat plot. Disturbance by prairie dogs and kangaroo rats
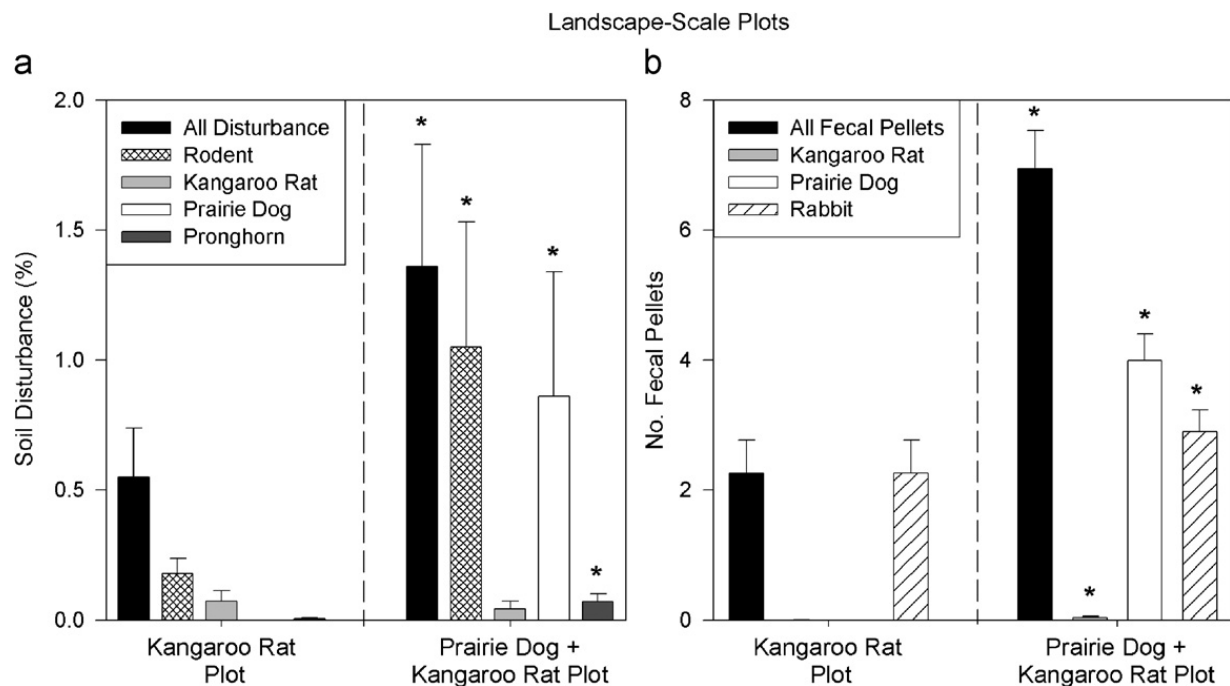
Fig. 5. (a) Mean percentage of soil disturbance (+SE) by all animals, rodents (prairie dogs, kangaroo rats, and other rodents), prairie dogs, kangaroo rats, and pronghorn antelope between the landscape-scale plots (fall 1999–2001). (b) Mean number of fecal pellets per $1 \, m^2$ (+SE) from kangaroo rats, prairie dogs, rabbits, and from all these animals between the landscape-scale plots over all years. *$P < 0.05$.

significantly impacted soils on the landscape-scale plots, but the observed differences in vegetation between the landscape-scale plots may not be entirely due to the activities of prairie dogs and kangaroo rats.

4. Discussion

Our results demonstrate that Gunnison's prairie dogs and banner-tailed kangaroo rats each had large, unique effects on plant community composition and structure through their mound building, soil disturbance, nutrient input, and foraging. The combination of their different activities resulted in a mosaic of distinct habitat patches on the landscape, increasing habitat heterogeneity and biodiversity where they co-occurred. While prairie dogs and kangaroo rats are known to play large ecological roles in areas where they occur alone (e.g., Bangert and Slobodchikoff, 2000; Brown and Heske, 1990; Kerley et al., 1997; Kotliar et al., 1999; Valone et al., 1995; Whicker and Detling, 1988), our results show that similar roles are exhibited and remain unique even where they co-occur.

Especially interesting was our finding that these rodents had complementary effects on plant community structure where they co-occurred. Mounds of burrowing mammals are known to provide important small-scale patches of disturbed soil, creating microsites for distinct assemblages of forbs (Farrar, 2002; Guo, 1996; Mun and Whitford, 1990; Whitford and Kay, 1999). Our results are consistent with these findings, but interestingly, prairie dog and kangaroo rat mounds provided different habitats with distinct patterns in vegetation structure and unique combinations of species. These differences likely resulted from the different structural and functional properties of their mounds (Fig. A1). Prairie dogs generally clip vegetation around their mounds and burrow deeply into the soil with a single tunnel, creating small (1–2 m), compact mounds that are usually devoid of vegetation (Hoogland, 1995; Whicker and Detling, 1988). In contrast, kangaroo rat mounds are larger (3–5 m), with networks of shallow tunnels that extend ca. 1 m deep (Valone et al., 1995), and unlike prairie dogs, kangaroo rats do not intensively clip vegetation around their mounds. Differences in mound architecture and maintenance behavior likely resulted in different soil properties, water infiltration rates, and disturbance intensity that, in turn, influenced the plant communities. Age differences between kangaroo rat and prairie dog mounds at the study site also could have played a role, but such differences are

common, as prairie dog mounds are highly dynamic and with the introduction of sylvatic plague so are colonies.

Prairie dogs and kangaroo rats also seem to modify each other's effects, as evidenced by the much larger, more disturbed kangaroo rat mound patches found on the prairie dog colony. Prairie dog mounds were common immediately around kangaroo rat mounds, and the extent of disturbance around the kangaroo rat mounds was probably further enhanced by the presence of both prairie dogs and their mounds. The combined activity of prairie dogs and kangaroo rats also created a landscape with greater soil disturbance, which enhanced forbs and caused apparent increases in those animals that preferentially forage on forbs (Fig. 5). Yet, the impact of these rodents on the landscape was constrained by seasonal precipitation. For example, during years with far below-average precipitation, such as spring 2000 and especially 2002, there was little germination of ephemeral plants in areas disturbed by the rodents, resulting in large areas of bare soil, a marked contrast from wet years.

Our exclosure experiment revealed that prairie dog removal had a greater impact on the vegetation than kangaroo rat removal. We detected a significant vegetation response to the release from prairie dog activity, but no measurable effect of kangaroo rat activity. However, vegetation responses were consistently greater in the exclosure where both animals were excluded compared to where only prairie dogs were excluded, which may reflect an additive impact of herbivory by the two species that was not strong enough to be detected statistically. This result likely reflects key differences in the foraging behavior of these two rodents. Gunnison's prairie dogs are primarily folivorous, consuming both grasses and forbs, though also feeding on seeds to some extent (Shalaway and Slobodchikoff, 1988). In contrast, kangaroo rats are primarily granivorous, and influence grassland vegetation predominantly through the effects of seed harvesting and caching that can take years to take effect (Brown and Heske, 1990), but they also feed on grasses to some extent (Kerley et al., 1997; Sipos et al., 2002). Both rodent species are known to forage on the plant species that increased most within our exclosures (Bonham and Lerwick, 1976; Holdenried, 1957; Kerley et al., 1997; Koford, 1958), and the dominant grass, *S. cryptandrus*, was likely subjected to greater herbivory relative to the other grasses because of its tall stature and high palatability (Allred, 1993). Although the exotic species, *S. kali*, showed a particularly strong increase in response to experimental rodent exclusion, it occurs primarily on disturbed soil (Farrar, 2002; Koford, 1958; Winter et al., 2002), so its increase may be a temporary phenomenon, dependent on the lingering effects of the disturbed soil associated with abandoned mounds. In general, the removal of folivorous prairie dogs appears to have elicited a greater and likely more rapid response by vegetation than the response to removal of granivorous kangaroo rats. Sampling over longer periods may further elucidate the distinctive impacts of prairie dog and kangaroo rat herbivory in areas where they co-occur. Additionally, it may take substantial time for their removal to affect plant community composition as a result of differential reproduction and survival of plant species.

The effects of prairie dogs and kangaroo rats also differed spatially across the landscape. Prairie dogs provided spatially extensive patches of small-scale disturbance because their effects extended well beyond their mounds. Prairie dogs created almost six times the number of mounds and twenty-times more soil disturbance on the landscape than kangaroo rats (Fig. 5), and their removal elicited the only significant response by vegetation within the exclosures. Additionally, the landscape where Gunnison's prairie dogs occurred had significantly greater forb cover, lower perennial grass cover, and lower vegetation height than where only kangaroo rats occurred, which typifies vegetation characteristics found on black-tailed prairie dog colonies (e.g., Whicker and Detling, 1988; Winter et al., 2002). The more widespread impacts of prairie dogs on vegetation occurred probably because they created numerous smaller mounds, live in dense colonies, and graze widely across the landscape (Fitzgerald and Lechleitner, 1973; Hoogland, 1995). In contrast, kangaroo rats had more intensive, localized impacts on vegetation, probably because behaviorally they confine their activities to their mounds and local foraging trails, and they create much larger mound disturbance patches that are more widely dispersed on the landscape (Valone et al., 1995). Kangaroo rats clearly play large, important roles in shaping plant community structure (Brown and Heske, 1990; Guo, 1996; Mun and Whitford, 1990), but their landscape effects may not be as dramatic (see Baez et al., 2006), at least in the short-term (Brown and Heske, 1990), as those exhibited by prairie dogs.

The independent effects of prairie dogs and kangaroo rats on plant community organization are consistent with recent insights from research on other habitat-modifying organisms in a wide range of ecosystems

(Badano et al., 2006; Moore et al., 2004; Wright et al., 2006), as well as with the common effects of burrowing-herbivorous rodents in other grassland systems (Whitford and Kay, 1999). The disturbed patches created by habitat modifiers such as beaver dams, bison (*Bison bison*) wallows, the mounds of gophers (*Geomys* and *Thomomys* spp.), plains vizcachas (*Lagostomus maximus*), zokors (*Myospalax fontanierii*), and badgers (*Taxidea taxis*), and the digs of Indian crested porcupines (*Hystrix indica*), provide novel habitats that favor distinct assemblages of species relative to the surrounding unmodified landscapes (Branch et al., 1999; Wright et al., 2006; Zhang et al., 2003). Our findings support the work of others, showing that while these modified habitat patches may vary in being more or less species rich, when both modified and unmodified patches are combined on the greater landscape, heterogeneity and species diversity are increased (Fuhlendorf and Engle, 2001; Joern, 2005; Wright et al., 2002, 2006).

Our study also demonstrates that when two ecologically important habitat modifiers co-exist their combined effects increase landscape heterogeneity to an even greater extent. Even though prairie dogs and kangaroo rats are both burrowing-herbivorous rodents, having somewhat similar ecological roles, their effects remained distinct and, thus, non-substitutable, where they co-occurred. Therefore, as predicted, the combination of both rodents had a complementary, additive effect, increasing heterogeneity and biodiversity as a result of different mound types, foraging behaviors, and spatial scales of impact on the landscape. These results are consistent with the interactive effects of black-tailed prairie dogs and banner-tailed kangaroo rats on heterogeneity and biodiversity in an entirely different grassland system (Davidson and Lightfoot, 2006) and with their effects on arthropod communities (Davidson and Lightfoot, 2007). This consistency across the different grassland systems, taxonomic groups, prairie dog colony ages, and species of prairie dogs demonstrates the generality of the interactive effects of these rodents on the landscape. The combined effects of multiple disturbance types such as fire and bison in the tallgrass prairie show similar effects on heterogeneity and species diversity (Joern, 2005), and research evaluating different types of interactions, such as the effect of salmon and bears on nitrogen budgets in the riparian forests of Alaska demonstrates that the combined effect of multiple keystone species can be greater than that by either species individually (Helfield and Naiman, 2006). We suggest that when managing for biodiversity it is important to consider habitat-modifying species, especially those that play large ecological roles. When these species are lost from ecosystems their functional roles may not be replaceable, affecting entire suites of species that associate with the habitats they create.

Acknowledgments

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jaridenv.2007.12.015.

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