Keystone rodent interactions: prairie dogs and kangaroo rats structure the biotic composition of a desertified grassland

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Understanding the interactive effects of multiple keystone species where they co-occur may have important consequences for regional biodiversity. Additionally, understanding how the impacts of keystone species vary across different ecosystems is important for effectively guiding conservation and management. We conducted a large-scale field study in northern Mexico where the geographic distributions of black-tailed prairie dogs *Cynomys ludovicianus* and banner-tailed kangaroo rats *Dipodomys spectabilis* overlap. These species are considered both keystones and ecosystem engineers of grassland environments, but little is known about their separate and interacting roles in desertified systems where they co-occur. Our research evaluated 1) the independent impacts of black-tailed prairie dogs and banner-tailed kangaroo rats in a desertified annual grassland, and 2) their interactive effects on grassland community structure and biodiversity. Prairie dogs and kangaroo rats differentially affected vegetation structure, plant cover, species composition, and species richness across multiple spatial and temporal scales. The interactive effects of these keystone species resulted in enhanced landscape heterogeneity and biodiversity. Our results demonstrate the importance of prairie dogs and kangaroo rats in desertified grasslands, and have important implications for understanding the interactive effects and context-dependency of keystone species.

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Particular species play key regulatory roles in community structure and ecosystem processes, and can be of critical importance to maintaining biodiversity (Paine 1969, Jones et al. 1994, Power et al. 1996, Whitford and Kay 1999). Those species defined as keystones exhibit disproportionately large control over the structure and functioning of ecosystems relative to their abundance (Power et al. 1996). Some keystone species, such as starfish *Pisaster ochraceus*, sea otters *Enhydra lutris*, and wolves *Canis lupus*, have large influences on community structure through their predation, while other keystones, such as elephants *Loxodonta africana*,

gophers *Thomomys bottae* and *Geomys bursarius*, and beavers *Castor canadensis*, modify, create, and maintain habitats through their ecosystem engineering (hereafter, keystone engineer) (Jones et al. 1994, Lawton and Jones 1995, Power et al. 1996). The roles of keystone species are considered to be unique and not substitutable by functionally similar species (Power et al. 1996, Kotliar et al. 1999). Therefore, the loss of keystones can have dramatic consequences on the structure and function of ecosystems (Power et al. 1996, Kotliar 2000).

In this study, we evaluate the potential keystone roles of black-tailed prairie dogs *Cynomys ludovicianus* and

banner-tailed kangaroo rats *Dipodomys spectabilis* in a highly desertified grassland, and their potential double keystone effect in landscapes where they co-occur. Prairie dogs *Cynomys* spp. are considered to be keystone species of grassland ecosystems throughout central North America (Miller et al. 1994, Kotliar et al. 1999, Kotliar 2000). Along the southern edge of their range, the distribution of prairie dogs overlaps with banner-tailed kangaroo rats (hereafter, kangaroo rat) (Schmidly et al. 1993, Hoogland 1995), another species considered to be keystone in desert grassland systems (Valone et al. 1995). Many of the former grasslands throughout this region have become desertified, with the replacement of perennial grasses by annual species and the invasion of shrubs (Schlesinger et al. 1990, Whitford 2002, Ceballos et al. 2005). Due to the widespread loss of habitat and poisoning campaigns over the last century, areas where prairie dogs and banner-tailed kangaroo rats overlap are now rare (Findley et al. 1975, Whitford 1997, Waser and Ayers 2003, Johnson et al. 2003). The loss of arid grasslands to desertification and declines in similar keystone rodents is a world-wide phenomenon (Schlesinger et al. 1990, Whitford 1997, Branch et al. 1999, Whitford 2002, Lai and Smith 2003, Zhang et al. 2003). Therefore, determining the separate and interactive effects of these species is critical to understanding, preserving, and restoring grassland ecosystems.

Prairie dogs transform grassland landscapes through the construction of extensive burrow systems and intensive grazing. These activities create unique patches of habitat for plants and animals, and affect important ecosystem processes (Whicker and Detling 1988, Ceballos et al. 1999, Kotliar et al. 1999, Bangert and Slobodchikoff 2000, Lomolino and Smith 2003). Kangaroo rats also dramatically alter grassland plant and animal species composition and ecosystem processes by constructing large mounds and selectively harvesting seeds (Brown and Heske 1990, Valone and Brown 1995, Whitford and Kay 1999). However, the roles of keystone species are often context-dependent, and their ecological significance can vary across different environments and community assemblages (Menge et al. 1994, Power et al. 1996, Kotliar 2000). Most research evaluating the roles of prairie dogs and kangaroo rats has been conducted in relatively intact perennial grasslands or shrub-dominated communities where these rodents occur alone (Whicker and Detling 1988, Brown and Heske 1990, Kerley et al. 1997, Kotliar et al. 1999, Lomolino and Smith 2003). Little is known about the roles of prairie dogs in desert grasslands, and research on the engineering roles of both species is lacking in the highly disturbed grassland systems that characterize much of their geographic ranges. The impacts of prairie dogs and kangaroo rats may be considerably different in these desertified systems, which differ from the natural structure and function of intact grasslands. Additionally, little

is known about the interactive impacts of multiple keystone species where they co-exist. Given that keystone species dramatically alter community structure and increase biodiversity (Power et al. 1996), where they co-exist they may create unique communities and have important consequences for local and regional biodiversity.

The regions where prairie dogs and kangaroo rats overlap provide a unique opportunity to study this ecologically interesting and important question. The purpose of our study was two-fold. Our first objective was to evaluate the independent effects of prairie dogs and kangaroo rats on biotic communities in a highly desertified environment, focusing on the plant community. We tested the hypothesis that the effects of these rodents appear as statistical differences in plant species richness, composition, and cover between areas where they are present versus absent. Our second objective was to determine if prairie dogs and kangaroo rats have distinctive, interactive influences on the biotic communities in desertified grassland systems. We hypothesize that there is even greater habitat heterogeneity and plant species richness in areas where they co-occur compared to where they occur alone.

Methods

Study area

Our study was conducted in the Janos and Casas Grandes region of northwestern Mexico, located 75 km south of the United States-Mexico border. This region contains one of the largest remaining complexes of black-tailed prairie dogs. The area supports a high diversity of endangered animals, and co-existing populations of black-tailed prairie dogs and banner-tailed kangaroo rats (Marcé 2001, Ceballos et al. 2005). However, the prairie dog populations declined 36% between 1988 and 2001 due to habitat loss and poisoning, and extensive areas of perennial grassland in the region have become desertified to shrubland or annual grassland (Marcé 2001, Desmond 2004, Ceballos et al. 2005).

Our research was conducted at the El Cuervo prairie dog colony (NAD-27: 30°7′N, 108°3′W; 1500 m), the largest colony in the region (15 000 ha) (Marcé 2001). The site was located in a broad valley, characterized by an annual grassland that had been heavily grazed by cattle. Overgrazing has been largely responsible for the conversion of perennial grassland dominated by tabosa grass *Pleuraphis mutica*, burrograss *Scleropogon brevifolius*, and blue grama *Bouteloua gracilis* to ephemeral grassland dominated by annual grasses, needle grama *B. aristidoides*, sixweeks grama *B. barbata*, and sixweeks threeawn *Aristida adscensionis*, as well as numerous forbs (Desmond 2004, Ceballos et al. 2005).

Mean annual precipitation is 307 mm, with most occurring during the summer monsoon period. Cool winters and hot summers characterize the region, with temperatures ranging from $-15°C$ in winter to $50°C$ in summer, providing a mean annual temperature of $15.7°C$ (Ceballos et al. 1999).

Landscape-scale plots

Vegetation was sampled at the landscape-scale using four replicate 0.25 km^2 blocks. Each block consisted of three 100×100 m plots, for a total of 12 plots. We conducted a natural experiment (Diamond 1986), and established landscape-scale plots where the treatments were naturally intermixed within each block. The blocks were ca 0.5 km apart from each other. The 100 m plots on each block were located in areas occupied by prairie dogs only (Pdog plot), kangaroo rats only (Krat plot), and by both species (Pdog+Krat plot). We selected plots with similar numbers of active mounds within each treatment type in order to control for rodent activity (i.e. densities) across the plots. Kangaroo rats and/or prairie dogs occupied most of the grassland in the region, making it impossible to locate comparable habitats where neither species was present. Vegetation was sampled using 100×100 m (5×5) grid design that extended across each plot. Percent plant canopy cover and height of live foliage were measured at 25 m intervals on each grid using 1×1 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 rather than multiple volumetric measures needed to measure plant biomass.

To quantify the processes by which prairie dogs and kangaroo rats alter vegetation, their fecal counts and soil surface disturbance were measured in addition to vegetation. Soil disturbance was measured as the percentage of ground cover disturbed by rodent tracks, digs, or mounds within each quadrat. We also counted the number of fecal pellets from black-tailed jackrabbits *Lepus californicus* and the percent cover of soil disturbance by gophers *Thomomys bottae*, harvester ants *Pogonomyrmex barbatus* and *P. rugosus*, and cattle *Bos taurus*. The numbers of prairie dog, kangaroo rat, and harvester ant mounds on each 1 ha landscape-scale plot also were counted. Vegetation and animal soil impacts were measured at the end of the spring and summer growing seasons, in early autumn 2001 (September) and late spring 2002 (mid-April).

Mound-scale plots

To measure plant species composition and vegetation structure associated with mound disturbance patches, we established replicate mound-scale plots with paired "non-mound" control plots. Ten prairie dog and 10 kangaroo rat mounds were subjectively selected from each plot in such a way as to disperse the sample mounds to the greatest spatial extent across each plot. Mounds that were at least 15 m from other mounds were chosen in order to minimize impacts from adjacent mounds on the sampling points. Paired non-mound sampling points were systematically positioned 10 m to the north of each study mound. In order to represent areas with minimal rodent disturbance (i.e. no rodent mound), the non-mounds sometimes had to be moved clock-wise in one of the other cardinal directions from the paired mound. The paired mound and non-mound control plots were naturally intermixed within each landscape-scale plot as a result of the systematic placement of non-mound points among the existing mounds. Measurements were taken from 10 prairie dog mounds on each Pdog plot, 10 kangaroo rat mounds on each Krat plot, and 10 prairie dog and 10 kangaroo rat mounds on each Pdog+Krat plot, as well as on paired non-mounds. A 5 m transect extended from the centre of each mound toward the paired non-mound, and another 5 m transect extended from the centre of each non-mound toward the paired mound. Percent plant canopy cover, height of live foliage, fecal counts, and percentage of soil disturbance by prairie dogs and kangaroo rats were measured from 30×30 cm quadrats located at 1, 3, and 5 m along each transect line. Mound-scale measurements were collected in early autumn 2001 and late spring 2002.

Statistical analyses

Data were normalized by square root transforms and all analyses were performed using SAS ver. 8.2 (Anon. 2001). Separate analyses of variance (ANOVA) tests with Bonferroni adjustments were used to analyse differences in total plant species, summer annual grasses and forbs, spring forbs, and each plant species among the landscape-scale plots factored by plant canopy cover, height, and species richness. Similar ANOVAs also were used to compare percentage of soil disturbance by prairie dogs, kangaroo rats, gophers, harvester ants, and cattle, the number of prairie dog, kangaroo rat, gopher, and ant mounds, and the number of fecal pellets from prairie dogs, kangaroo rats, and rabbits among the landscape-scale plots. Data were pooled when analysing across both sample periods, and were pooled for each landscape-scale plot (n =12). A block effect was included in the ANOVA models. Least-squares regression analyses were conducted to evaluate the potential covariance of ant, gopher, rabbit, and cattle activity with response variables.

ANOVAs were used to analyse the same vegetation, soil, and fecal variables between prairie dog and

kangaroo rat mounds on the Pdog+Krat plots. Each model included a block effect and a block by mound interaction term. Mixed-linear models (MLM) were used to analyse the same vegetation, soil, and fecal variables between paired mounds and non-mounds. The fixed effects for each model were the mound treatment types, blocks, and the interaction between the mound treatments and blocks. Each model included a random mound effect, which allowed for correlated responses on the paired mound and non-mound plots. Unless distance from mound was of interest, data were pooled across quads for each mound-scale plot, providing each mound treatment with 40 replicate samples. Mixed-linear models with Bonferroni adjustments were used to analyse the same variables at 1, 3, and 5 m distances away from mound and non-mound centres. The fixed effects for each model were the quadrat distances, blocks, and the interaction between the quadrat distances and blocks. Each model included a random quadrat effect, which allowed for correlated responses among the quadrats within the mound-scale plots.

Canonical discriminant function analysis (CDFA) was used to evaluate differences among the mound and landscape treatment plots based on plant species canopy cover. This procedure provided a multivariate analysis of variance (MANOVA) test for potential differences based on simultaneous analysis of all plant species. We conducted separate CDFAs to compare the species composition of all plants, spring forbs, and summer forbs and grasses among the mound-scale plots. The mound-scale data also was used to conduct similar CDFAs to compare species composition among the landscape-scale plots. Very rare species ($<2\%$ cover) 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 (Anon. 2004).

Results

Plant cover and structure

The cover and structure of vegetation differed between the mound-scale plots, and along a gradient extending away from prairie dog and kangaroo rat mound centres. Percent cover and height of all plants, summer forbs and grasses, and spring forbs was significantly lower ($p < 0.05$, in all cases but one) on both prairie dog and kangaroo rat mounds compared to their paired non-mounds on all landscape-scale plots (Fig. 1, Appendix A and B). Total plant cover and height decreased up to 5 m away from kangaroo rat mound centres on the Krat plot (MLM: cover $F_{2,72} = 47.10$, $p < 0.0001$; height $F_{2,72} = 40.05$, $p < 0.0001$) and Pdog+Krat plot (MLM: cover
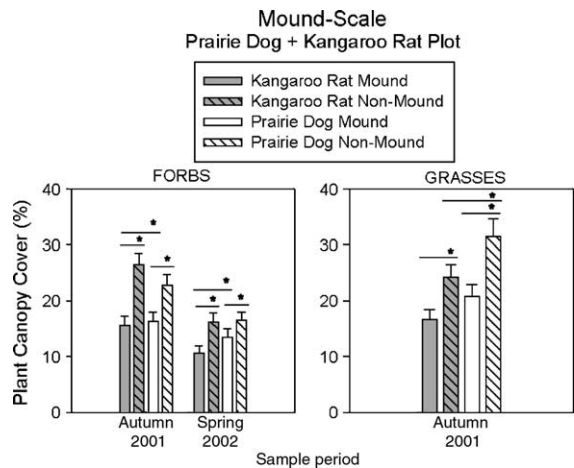

Fig. 1. Mean percentage plant canopy cover ($+SE$) of spring and summer forbs and summer grasses among mound-scale plots. $*p < 0.05$.

$F_{2,72} = 81.16$, $p < 0.0001$; height $F_{2,72} = 47.10$, $p < 0.0001$). In contrast, total plant cover and height decreased only up to 3 m away from prairie dog mounds on the Pdog plot (MLM: cover $F_{2,72} = 57.57$, $p < 0.0001$; height $F_{2,72} = 36.83$, $p < 0.0001$) and Pdog+Krat plot (MLM: cover $F_{2,72} = 37.38$, $p < 0.0001$; height $F_{2,72} = 31.69$, $p < 0.0001$). On the Pdog+Krat plots, prairie dog mounds had significantly greater cover of summer forbs and potentially also greater cover of spring forbs than kangaroo rat mounds (ANOVA: summer forbs $F_{1,72} = 3.38$, $p = 0.02$; spring forbs $B \times M$ $F_{3,72} = 5.05$, $p = 0.03$). Plant cover and structure did not show strong differences among the landscape-scale plots. However, summer annual grasses were almost two times taller on the Pdog+Krat and Krat plots than on the Pdog plots (ANOVA: $F_{2,6} = 11.02$, $p = 0.009$).

In this study, most of the statistical tests that indicated a significant treatment effect had a non-significant block by mound (or block by quad) interaction. Where interactions were significant, those effects were less ($p > 0.01$) than the treatment effects ($p < 0.0002$), indicating that the treatment effects were minimally influenced by the blocks (Gotelli and Ellison 2004). Here, we only report significant ($p < 0.05$) mound by block interactions ($M \times B$) (or quadrat by block interactions) when the treatment effects were not significant ($p > 0.05$). In those cases, a significant interaction term indicates a potential treatment effect, but that those effects were not consistent among all blocks.

Plant species composition

Plant species composition differed with the presence or absence of the rodents at both the mound and landscape-scales (Fig. 2, Table 1). Based on univariate analyses, 21 of 110 species differed significantly among the
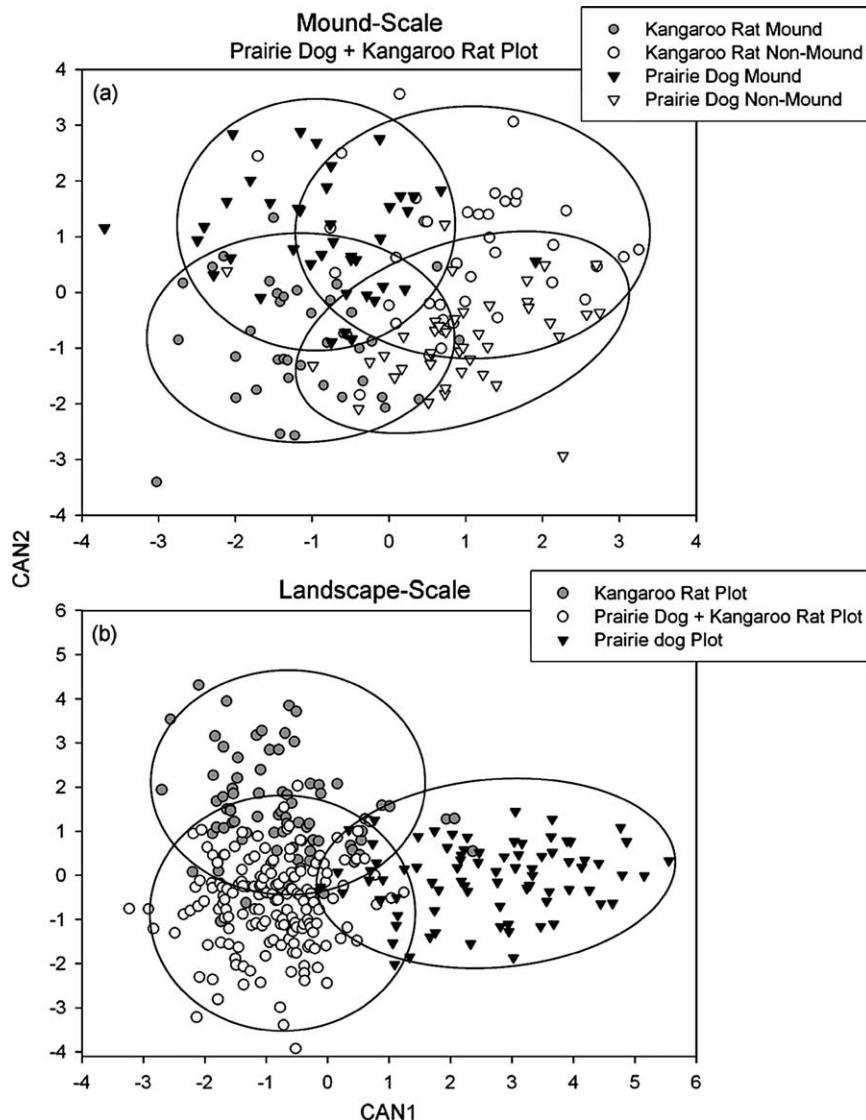
Fig. 2. Ordination of canonical variates for (a) mound-scale plots (MANOVA: $F_{123,348.5} = 1.8$, $p < 0.0001$) and (b) landscape-scale plots (MANOVA: $F_{98,544} = 7.47$, $p < 0.0001$). Ordinations represent differences in total plant species composition among plots based on mound-scale data. Ellipses represent 95% confidence intervals for each group. Similar patterns were seen for spring forbs and summer forbs and grasses among plots. Note that (a) shows groupings of mound-scale plots within the Pdog+Krat plot, which is plotted in (b).

mound-scale plots, and 9 of 104 species differed significantly among the landscape-scale plots ($p < 0.05$, for all tests). Many species were too rare to detect significant differences among the mound and landscape-scale plots (e.g. 47 and 29 species, respectively, occurred at $< 2\%$ cover). A number of species occurred exclusively on one treatment type. However, most of the differences in species composition among the treatment plots were due to differences in relative abundances of species, which likely explains the overlap among groups in the CDFA ordinations (Fig. 2). Despite overlap, each treatment type supported distinctive combinations of plant species. The CDFA indicated that the composition of spring

forbs, summer forbs and grasses, as well as of all plant species differed significantly between the mounds and non-mounds, prairie dog mounds and kangaroo rat mounds, and also among the Pdog+Krat, Krat, and Pdog plots (MANOVA: $p < 0.001$, for all tests). The Mahalanobis distance measures also demonstrated significant differences between the treatment plots, based on spring forbs, summer forbs and grasses, and total plant species composition (Table 1).

In general, at the mound-scale, most species had significantly greater cover on non-mound plots than on prairie dog or kangaroo rat mounds, especially the perennial forb, *Sida abutifolia*, and the dominant annual

Table 1. Pairwise Mahalanobis distances (D^2 showing differences in total plant species composition between the mound-scale plots and between the landscape-scale plots during autumn 2001 and spring 2002. (a) Above the diagonal are the distance values between the paired kangaroo rat mounds (KM) and kangaroo rat non-mounds (KN) on the kangaroo rat (K) plot (n =80, DF =33, 49) as well as the distance values between the paired prairie dog mounds (PM) and prairie dog non-mounds (PN) on the prairie dog (P) plot (n =80, DF =32, 47). Below the diagonal are distance values for comparisons between KM, KN, PM, and PN on the prairie dog+kangaroo rat (PK) plot (n =160, DF =123, 348.5). (b) Distance values between the PK, K, and P landscape-scale plots (n =160, DF =49, 272). * p <0.05, ** p <0.01, *** p <0.001.

Pairwise Mahalanobis distances (D^2)

(a) Mound-scale plots

	KM	KN	PM	PN
KM	0	8.58***		
KN	6.75***	0		
PM	5.01**	3.56	0	6.74**
PN	4.50*	4.48*	6.61***	0

(b) Landscape-scale plots

	K	P	PK
K	0	12.94***	4.31***
P	12.94***	0	12.33***
PK	4.31***	12.33***	0

grasses, *B. barbata* and *B. aristidoides*. The most prominent species on mounds was the summer annual, *Tidestromia lanuginosa*. The annual forbs, *Chenopodium* species 1 and *Solanum heterodoxum*, also showed particularly strong associations with kangaroo rat mounds. Other species such as the perennial forb, *Hoffmanseggia glauca*, and the annual grass, *A. adscensionis*, were strongly associated with prairie dog mounds. Overall, the cover of perennial forbs and annual grasses was significantly greater on non-mounds than on mounds (p <0.02, for all tests; Appendix B), but perennial forb cover was significantly greater on prairie dog mounds than kangaroo rat mounds (ANOVA: $F_{1,72} = 18.84$, p <0.0001). The primary pattern among the landscape-scale plots was the greater dissimilarity in species composition between the Krat plots and Pdog plots relative to the Pdog+Krat plots (Fig. 2, Table 1).

Plant species richness

Prairie dogs and kangaroo rats also influenced plant species diversity patterns at the mound and landscape-scales (Fig. 3). Species richness was consistently greater on the non-mounds than on the prairie dog or kangaroo rat mounds (Fig. 3). Mean species richness around kangaroo rat mounds (KM) and prairie dog mounds (PM) was >2 times greater at 3 m (5.35–6.10) and 5 m (6.35–6.64) than at 1 m (1.92–3.15) away from the mound centres (MLM: KM-Krat Plot $F_{2,72} = 79.19$, p < 0.0001; KM-Pdog+Krat plot $F_{2,72} = 106.86$, p <0.0001; PM-Pdog plot $F_{2,72} = 38.28$, p <0.0001; PM-Pdog+Krat plot $F_{2,72} = 40.90$, p <0.0001). Prairie dog mounds had greater plant species richness at both 1 and 3 m from their mounds compared to 1 and 3 m from kangaroo rat mounds (ANOVA: 1 m $F_{1,72} = 5.94$, p =0.02; 3 m $F_{1,72} = 4.61$, p =0.04). At the landscape-scale, plant species richness was consistently greater on the Pdog+Krat plots than on either the Krat plots or the Pdog plots during both spring and autumn seasons, but the difference was only significant during the spring (ANOVA: $F_{2,6} = 6.27$, p =0.02) (Fig. 3).

Animal soil disturbance and nutrient input

Prairie dog and kangaroo rat mounds represented highly disturbed patches of soil and concentrated areas of nutrient input via their fecal pellets. Prairie dog and kangaroo rat mounds had 4–6 times greater soil disturbance and 4–175 times the number of fecal pellets compared to paired non-mound areas. Similar to their effects on plant cover and height, soil disturbance decreased up to 5 m away from kangaroo rat mound centres on the Krat plot (ANOVA: $F_{2,72} = 487.36$, p < 0.0001) and Pdog+Krat plot (MLM: $F_{2,72} = 223.08$, p <0.0001). In contrast, soil disturbance decreased only up to 3 m away from prairie dog mounds on the Pdog plot (MLM: $F_{2,72} = 324.71$, p <0.0001) and Pdog+Krat plot (MLM: $F_{2,72} = 177.42$, p <0.0001). Kangaroo rat mounds also had significantly greater percentage of disturbed soil at 1 m from their mounds compared to 1 m from prairie dog mounds (MLM: $F_{1,72} = 7.6$, p = 0.007).

Our data demonstrated that the activity and likely the densities of both prairie dogs and kangaroo rats were lower where they co-occurred than where either species occurred alone. The mean number of kangaroo rat mounds per ha was two-times lower on the Pdog+Krat plots (4.75) than on the Krat plots (11). The mean number of prairie dog mounds also was relatively lower on the Pdog+Krat plots (41) than on the Pdog plots (60.75). Our soil disturbance and fecal count data support these results (Fig. 4). Mean percentage soil

Fig. 3. Plant species richness (+SE) on the mound and landscape-scale plots during autumn 2001 and spring 2002. *p <0.05 between mound-scale plots and between the prairie dog+ kangaroo rat (PK) plot and the kangaroo rat plot. •p <0.05 between the PK plot and the prairie dog plot.
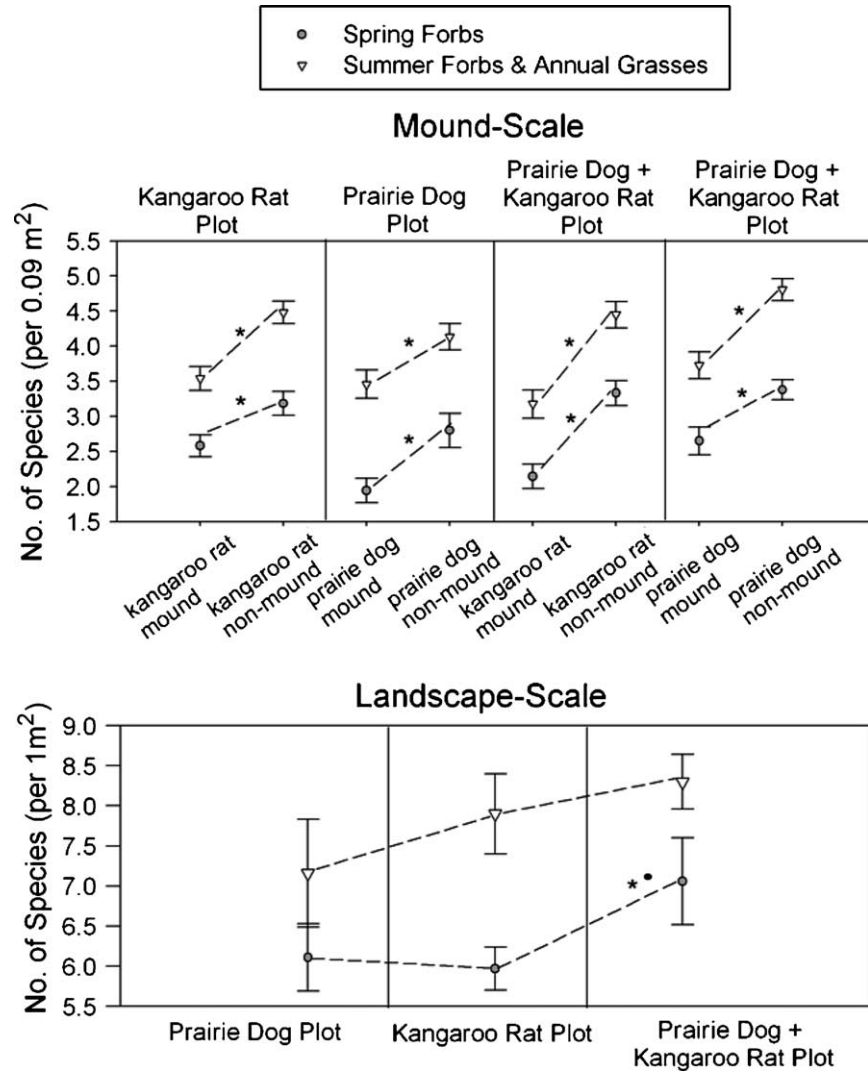
disturbance by prairie dogs (sdp) and kangaroo rats (sdk) and prairie dog fecal pellet counts (pf) were significantly greater on the plots where the rodents occurred alone than where they co-occurred (ANOVA: sdp $F_{2,6} = 10.99$, p =0.01; sdk $F_{2,6} = 8.19$, p =0.02; pf $F_{2,6} = 12.50$, p =0.007).

This grassland received significant soil disturbance by prairie dogs, kangaroo rats, harvester ants, cattle, and gophers (Fig. 4). The average number of active prairie dog, kangaroo rat, harvester ant, and gopher mounds per hectare were 50.9, 7.87, 19.58, and 12.4, respectively. Note that a gopher mound was comprised of a cluster of individual mounds <0.5 m apart. The relative activities of gophers, ants, rabbits, and cattle differed among the landscape-scale plots (Fig. 4), yet their activities did not covary with the vegetation variables evaluated in this study. Gophers had the highest percentage of soil disturbance on the Pdog+Krat plots compared to the

Pdog and Krat plots (ANOVA: $F_{2,6} = 5.86$, p =0.04). The number of harvester ant mounds was significantly greater on the Krat plots than the Pdog and Pdog+Krat plots (ANOVA: $F_{2,6} = 7.28$, p =0.02). Cattle soil disturbance (i.e. tracks) was about two-times higher on plots where only prairie dogs occurred, but differences among plots were not significant (p >0.05). The magnitude of soil disturbance and fecal material from prairie dogs was from 2 to 20 times greater than that from kangaroo rats, ants, gophers, and cattle (Fig. 4).

Discussion

Our research demonstrates that in this desertified grassland ecosystem prairie dogs and kangaroo rats played keystone roles both where they co-occurred and where they occurred alone. Through a combination of mound
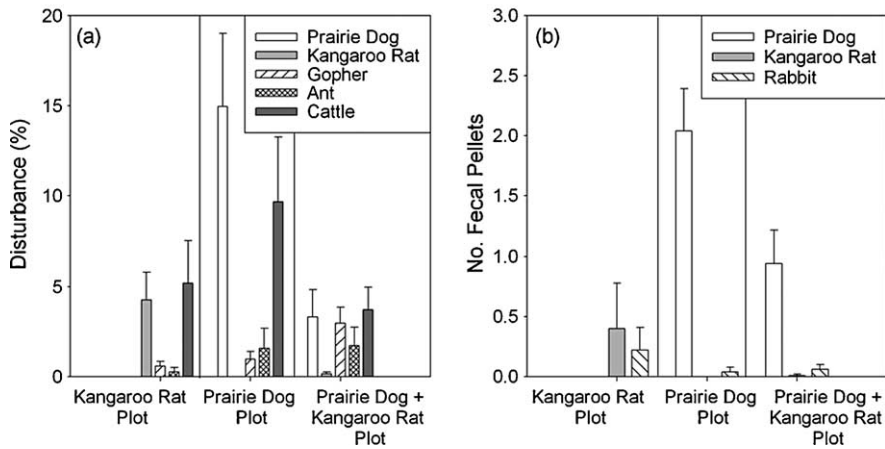
Fig. 4. (a) Mean percentage of soil disturbance (+SE) by prairie dogs, kangaroo rats, gophers, harvester ants, and cattle on the landscape-scale plots during autumn 2001 and spring 2002. (b) Mean number of fecal pellets 1 m^{-2} (+SE) from prairie dogs, kangaroo rats, and rabbits on the landscape-scale plots during autumn 2001 and spring 2002.

building, soil disturbance, nutrient input, and foraging, these rodents created a mosaic of habitat patches on the landscape across multiple scales. Their mounds provided unique habitat structure and supported distinctive combinations of plant species relative to surrounding areas, and areas where these rodents co-occurred had greater landscape heterogeneity and species richness compared to where they occurred alone. While many studies have demonstrated that these animals play keystone roles in grasslands (Whicker and Detling 1988, Brown and Heske 1990, Kerley et al. 1997, Kotliar et al. 1999, Lomolino and Smith 2003), few studies have evaluated their effects in desertified annual grasslands (Desmond 2004). Even rarer are studies evaluating the interactive effects of multiple keystone species in the same system (Fahnestock and Detling 2002). Our results are particularly interesting because these rodents played keystone roles even in this highly desertified system, and when these keystone species co-occurred they created unique communities and enhanced biodiversity.

Prairie dogs and kangaroo rats had similar effects in this desertified desert grassland as compared to relatively intact perennial grassland systems by having important regulatory roles on plant community structure. In perennial grasslands, these rodents create mound disturbance patches that suppress perennial grasses and reduce plant competition (Pickett and White 1985). These mound patches provide microsites where early successional forbs become established (Pickett and White 1985, Guo 1996, Farrar 2002). Yet, desertified annual grasslands lack these typical successional relationships because the entire area is disturbed and dominated by annual grasses and forbs (Heady 1977, Denslow 1985). Nevertheless, prairie dog and kangaroo rat mounds in the desertified grassland still acted as unique patches of habitat that differed in plant species composition, structure, and diversity from surrounding areas, as seen in other grassland systems (Mun and Whitford 1990, Guo 1996, Farrar 2002, Davidson 2005).

The differences we observed in the plant community were likely driven by differences in soil texture and nutrients around the mounds (Whitford and Kay 1999). Additionally, within early successional plant communities some species prefer more disturbed patches than others (Pickett and White 1985), which likely contributed to the differences in the plant communities on and off mounds.

The finding that prairie dogs and kangaroo rats had additive effects on plant community structure and biodiversity is consistent with the keystone species definition that keystones are not only those species that have disproportionately large impacts on community structure, but also, their roles are functionally unique (Power et al. 1996, Kotliar 2000). The different engineering and foraging roles of these rodents likely explain why they had unique impacts on the plant community. First, kangaroo rat mounds are much larger areas of disturbance and are shallower than prairie dog mounds; the mounds extend 3–6 m in diameter and consist of shallow networks of tunnels that extend ca 1 m deep (Best 1988). In contrast, prairie dog mounds are hard-packed, conical or turret-shaped and average about 1–2 m in diameter with a single tunnel that extends several meters below the ground surface (Hoogland 1995). Given the different burrow depth and size and structure of the mounds, the mounds undoubtedly differ in soil nutrients, texture, and water infiltration rates. In our system, species such as *S. heterodoxum* were clearly associated with the highly disturbed soils on the tops of kangaroo rat mounds, whereas, perennial forbs like *H. glauca* and the annual grass *A. adscensionis* were abundant on the relatively less disturbed soils around prairie dog mounds. These findings also are consistent with kangaroo rat removal experiments in the Chihuahuan Desert, which have demonstrated that kangaroo rat granivory and soil disturbance greatly reduces the cover of *A. adscensionis* (Brown and Heske 1990).

Second, prairie dogs disturb greater amounts of soil on the landscape than kangaroo rats. The impacts of prairie dogs through soil disturbance and fecal pellets (i.e. nutrient input) exceeded that of all other species known to have large influences in the Janos-Casas Grandes landscape, including kangaroo rats, gophers, harvester ants, and cattle (see Fig. 4). Prairie dogs have been shown to move as much as 4759–9731 kg of soil per hectare through the construction of their mounds in the Janos-Casas Grandes grassland (Ceballos et al. 1999), and our study demonstrates that they created 2 to 7 times more mounds per hectare than any other mound-building animals in this system. The greater impact of prairie dogs on soils was probably due to their naturally higher population densities compared to kangaroo rats, and because they are colonial animals that construct more mounds on the landscape compared to solitary kangaroo rats (Best 1988, Hoogland 1995).

Third, prairie dogs and kangaroo rats differ in their foraging behaviour. Kangaroo rats feed primarily on seeds, and selectively deplete soil seed reserves of large seeded annual plants and grasses (Brown and Heske 1990). In contrast, prairie dogs feed predominantly on grass foliage, and maintain a low, dense turf of rapidly growing plants dominated by forbs and grazing-tolerant grasses (Whicker and Detling 1988, Detling 1998). Indeed, consistent with the known effects of prairie dog herbivory, the prairie dog colony exhibited significantly lower grass height compared to areas occupied by kangaroo rats (Whicker and Detling 1988). However, there is probably some overlap in foraging niches since kangaroo rats are known to eat grass and prairie dogs also forage on large seeds (Fagerstone et al. 1981, Kerley et al. 1997, Sipos et al. 2002), which may explain why the activities (i.e. abundances) of prairie dogs and kangaroo rats were lower where they co-occurred than where they occurred alone in this resource-limited system.

The influences of prairie dogs and kangaroo rats on soils and the plant community have been shown to cascade throughout the ecosystem and affect other animal species (Whicker and Detling 1988, Brown and Heske 1990, Hawkins and Nicoletto 1992, Detling 1998, Kotliar et al. 1999). Our research supports these findings, but also indicates that the effects of prairie dogs and kangaroo rats on soils and vegetation were sufficiently unique in order to elicit different influences on the activities of other important animals in this system: gophers and ants (Fig. 4). Gophers were most abundant on the Pdog+Krat plots where forbs and plants with large root tubers were especially common, which reflects the belowground foraging behaviour of these fossorial rodents (Huntly and Inouye 1988). Additionally, harvester ant mounds were most numerous on plots where only kangaroo rats occurred, and were often observed near kangaroo rat mounds. The ants may have benefited from altered soil texture and seed composition and reduced plant cover near the kangaroo rat mounds (Schooley et al. 2000). The interactions of prairie dogs and kangaroo rats with gophers and ants are not well understood, and inherent differences in soil, vegetation, and other factors among the landscape plots also may have influenced their distribution.

Our study highlights several important points regarding prairie dogs, kangaroo rats, and other burrowing mammals in similar grassland systems. Small to medium sized burrowing, herbivorous mammals are native to grasslands throughout the world, including mole rats (Bathyergidae spp.) of South Africa, southern hairy-nosed wombats *Lasiorhinus latifrons* of Australia, gophers *Geomys* and *Thomomys* spp. of North America, zokors *Myospalax fontanierii* of the Tibetan Plateau, and plains vizcachas *Lagostomus maximus* of Argentina. Interestingly, the impacts of these other burrowing mammals are remarkably similar to those demonstrated by prairie dogs and kangaroo rats. Like prairie dogs and kangaroo rats, they transform grasslands through burrowing and herbivory, and many are considered to have keystone-level effects because they exert strong controls on the structure of grassland communities and ecosystem processes (Huntly and Inouye 1988, Jones et al. 1994, Power et al. 1996, Whitford 1997, Branch et al. 1999, Cameron 2000, Reichman and Seabloom 2002, Zhang et al. 2003, Machicote et al. 2004).

Keystone species that are defined largely by their engineering role may have more consistent effects on ecosystem processes than species that are defined primarily by their trophic role (Power et al. 1996, Table 2). For example, well-known keystone predators, such as sea otters and starfish have been shown to exhibit system-altering impacts in some environments but not in others (Paine 1969, Menge et al. 1994, Power et al. 1996). Yet, our research demonstrates that prairie dogs and kangaroo rats play similar roles in both highly degraded environments and relatively intact grasslands, primarily due to their engineering roles. These rodents appear to act as keystones across a wide-range of geographic space, environmental conditions, and habitat types (Whicker and Detling 1988, Brown and Heske 1990, Valone et al. 1995, Kerley et al. 1997, Ceballos et al. 1999, Kotliar et al. 1999, Kotliar 2000, Lomolino and Smith 2003), suggesting that their roles are less context-dependent than trophically defined keystones. The roles of keystone engineers may be similar across habitat types due to the consistent effects of large architectural features, such as rodent mounds, termitairia, or ungulate wallows on soil and vegetation dynamics.

Although different kinds of burrowing mammals have somewhat similar impacts in grassland systems, our research demonstrates that the ecological roles of prairie dogs and kangaroo rats are not functionally substitutable. These animals created different patch types across

multiple temporal and spatial scales. Their combined effects resulted in a mosaic of unique habitats, enhancing species diversity and the structural complexity of the landscape. These results are consistent with the emerging paradigm that the interplay of multiple disturbance types increases heterogeneity, an important mechanism for increasing biodiversity (Huston 1994, Fuhlendorf and Engle 2001, Joern 2005). Similar patterns are caused by different disturbance mechanisms in other systems, such as the interaction of bison grazing and fire in tallgrass prairie (Collins et al. 1998, Joern 2005). There also is growing evidence from research in other systems that the interactive effects of multiple species elicit unique consequences on the structure and function of ecosystems (Pringle et al. 1999, Duffy et al. 2003, Bakker et al. 2004, Boyer and Fong 2005, but see Fahnestock and Detling 2002). Therefore, although the loss of some species may result in compensatory responses from functionally similar species (Brown et al. 2001, Tilman et al. 2001), our research suggests that the roles of some keystones, especially those defined in part by their engineering roles, are not only unique but interact to create unique communities in time and space.

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