

ECOLOGICAL INTERACTIONS BETWEEN TWO ECOSYSTEM ENGINEERS:  
GUNNISON'S PRAIRIE DOG AND BOTTA'S POCKET GOPHER

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ABSTRACT—We examined ecological interactions between two ecosystem engineers, Gunnison's prairie dogs (*Cynomys gunnisoni*) and Botta's pocket gophers (*Thomomys bottae*), across a 67,000-km<sup>2</sup> range of northern Arizona. We examined densities of burrows, composition of vegetation, and characteristics of soil associated with locations where each species occurred alone and compared them to where they were both present. Density of *T. bottae* was significantly lower in the presence of *C. gunnisoni* than where occurring alone, while density of *C. gunnisoni* more than doubled at locations where they occurred with *T. bottae* compared to where they were alone. Vegetational communities associated with locations where *C. gunnisoni* occurred alone were significantly different from locations where *T. bottae* occurred alone and where both species were present. We also detected that burrows of *T. bottae* and *C. gunnisoni* occurred in soils that did not differ significantly in depth, texture, or rock content, but characteristics of soil played an influential role in patterns observed in vegetational communities.

RESUMEN—Examinamos las interacciones ecológicas entre dos herbívoros clave: Los perros de la pradera de Gunnison (*Cynomys gunnisoni*) y los topos (*Thomomys bottae*) a través de 67,000 km<sup>2</sup> en la zona norte de Arizona. Examinamos las densidades de madrigueras, la composición de vegetación, y las características del suelo asociadas con las localidades donde cada especie ocurrió sola y se los comparó donde ambas estuvieron presentes. La densidad de *T. bottae* fue significativamente más baja en presencia de *C. gunnisoni* en comparación a donde existió sola, mientras que la densidad de *C. gunnisoni* fue más del doble en los lugares donde ocurrió con *T. bottae* en comparación a donde existió sola. Las comunidades de la vegetación asociadas con los lugares donde *C. gunnisoni* ocurrió sola fueron significativamente diferentes de los lugares donde *T. bottae* ocurrió sola, y donde ambas especies estuvieron presentes. También encontramos que las madrigueras de *T. bottae* y *C. gunnisoni* ocurrieron en suelos que no diferían significativamente en profundidad, textura, ni en contenido de rocas, pero las características del suelo pueden ser importantes en los patrones observados en las comunidades de vegetación.

Research involving keystone modifiers or ecosystem engineers, defined as a species that greatly affects habitat features and the survival of other species (Mills et al., 1993; Jones et al., 1994), has consistently focused on effects of single species and not the effects or interaction between two such species. Comparative and experimental evidence suggests that grassland and desert ecosystems harbor several ecosystem engineers, such as prairie dogs (*Cynomys*; Kotliar et al., 1999; Bangert and Slobodchikoff, 2000; Miller et al., 2000), pocket gophers (*Thomomys bottae* and *Geomys bursarius*; Huntly and Inouye, 1988; Cantor and Whitham, 1989), and kangaroo rats (*Dipodomys*; Brown and Heske, 1990). Be-

cause some of these species live sympatrically with one another, interactions must occur between them. The combination of effects by multiple ecosystem engineers could have properties different from those each species has individually.

The focus of our research was to explore possible interactions and ecological relationships between two demonstrated ecosystem engineers, Gunnison's prairie dog (*Cynomys gunnisoni*) and Botta's pocket gopher (*Thomomys bottae*). Both live sympatrically throughout much of northern Arizona (Hoffmeister, 1986), but it is common to find areas where each species occurs in absence of the other. This distributional pattern provides

a unique opportunity to observe densities of burrows and vegetational communities associated with Gunnison's prairie dogs and Botta's pocket gophers separately, and where both are present.

Prairie dogs (*Cynomys*) and pocket gophers (*Thomomys* and *Geomys*) both affect the environment directly, by foraging on vegetation, and indirectly, through burrowing activities. Foraging and burrowing activities by Gunnison's prairie dogs affect diversity of plants (Slobodchikoff et al., 1988), height and cover of vegetation (Davidson, 2005), and heterogeneity of landscape (Bangert and Slobodchikoff, 2000). Similarly, burrowing and foraging by pocket gophers increases diversity of plants (Martinsen et al., 1990), affects vegetational structure (Reichman and Smith, 1985) and heterogeneity of habitat (Huntly and Inouye, 1988), and prevents regeneration of forest (Cantor and Whitham, 1989). The large influence on ecosystems has led researchers to consider prairie dogs (Kotliar et al., 1999; Bangert and Slobodchikoff, 2000; Miller et al., 2000) and pocket gophers (Cantor and Whitham, 1989) as keystone species and ecosystem engineers (Jones et al., 1994).

Although prairie dogs and pocket gophers seem to have similar categorical effects on the environment through herbivory and burrowing, ecological differences between the two result in different disturbance regimes. Prairie dogs intensively graze on aboveground vegetation and live in colonies that support many individuals and can cover large areas (Whicker and Detling, 1988). Conversely, pocket gophers forage mostly below ground and around burrow openings (Hunter and Inouye, 1988). Pocket gophers are mostly solitary, and their burrow systems disturb less soil than those of social prairie dogs (Davidson and Lightfoot, 2006). The different disturbance regimes associated with prairie dog and pocket gopher activities could structure different vegetational communities.

Additionally, in areas where both species occur, the combination of disturbance by prairie dogs and pocket gophers could produce a distinctly different vegetational community. Davidson and Lightfoot (2006) reported that the combined effects of coexisting keystone species *Cynomys ludovicianus* and *Dipodomys spectabilis* did structure a unique biotic community compared to where each species occurred alone. Although many species benefit directly or indirectly from

actions of prairie dogs and pocket gophers, it is unknown if they positively or negatively influence each other. It is possible that they compete for food or subterranean space, or benefit from one another by creating vegetational communities that provide forage for each other. Davidson and Lightfoot (2006) reported abundances of *C. ludovicianus* and *D. spectabilis* were lower where they occurred together compared to where each occurred alone, likely the result of competition.

In our study, we investigated ecological interactions between Gunnison's prairie dog and Botta's pocket gopher. Specifically, we addressed three hypotheses: 1) there will be a difference in density of prairie dog and pocket gopher burrows where each of these species occurs alone compared to where both are present, and 2) there will be different vegetational communities associated with locations that are inhabited by each species alone and where both are present. Because burrowing animals are dependent on characteristics of soil for placement of burrows (Bolen and Robinson, 1999), we investigated the role of soil in ecological interactions between Botta's pocket gopher and Gunnison's prairie dog, and hypothesized 3) that these species inhabit soils with similar characteristics.

**MATERIALS AND METHODS—Study Areas**—We collected data from three types of locations; locations where only Gunnison's prairie dog was present ( $n = 15$ ), locations where only Botta's pocket gopher was present ( $n = 15$ ), and locations where both species were present ( $n = 15$ ). By analyzing locations where Gunnison's prairie dogs (hereafter, *C. gunnisoni*) and Botta's pocket gophers (hereafter, *T. bottae*) each occur alone, we were able to establish patterns of density of burrows, associated vegetation, and characteristics of soils in which their burrows occurred, and then compare them to locations where both species were present.

We opportunistically chose study locations throughout northern Arizona (Fig. 1). We visited study locations 1 May–23 September 2000. Study locations spanned a substantial elevational gradient from 1,154 to 2,957 m and included several vegetation zones as described in Brown (1994). Vegetational communities at low elevation (<1,700 m) consisted of open semi-desert grasslands, whereas locations at high elevation (>2,000 m) consisted of subalpine meadows surrounded by montane conifer forests. Vegetational communities at intermediate elevation (1,700–2,000 m) consisted of a mixture of coniferous woodlands and grasslands. Sizes of colonies for both species ranged from 1 to 360 ha.

**Density of Burrows and Mounds**—We used density of active prairie dog burrows and mounds of pocket gopher burrows as a general indicator of use of space and abundance of animals. Although some authors have reported that number of active burrows provide a

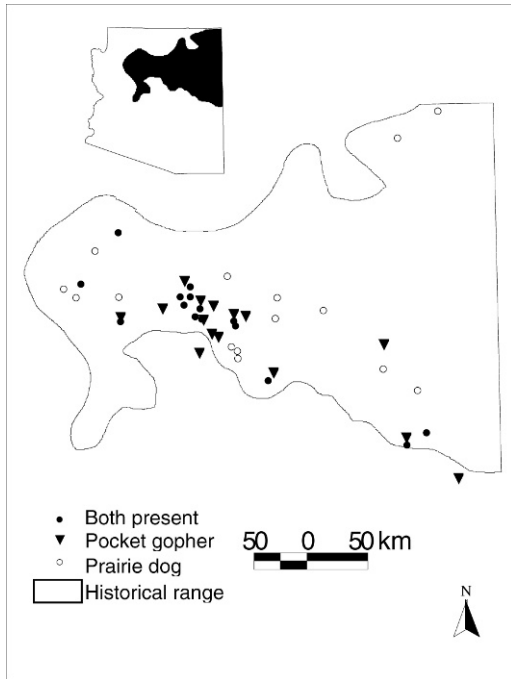


FIG. 1—Distribution of study locations in northern Arizona. The historical range of Gunnison's prairie dogs (*Cynomys gunnisoni*) in Arizona (Hoffmeister, 1986) is outlined. The range of Botta's pocket gophers (*Thomomys bottae*) completely encompasses Arizona.

weak index of actual populations of burrowing mammals (Powell et al., 1994), we did not use our data to generate specific population estimates. First, we reviewed literature for average size of territory of each species as the basis for selecting size of our density-sampling units. Rayor (1988) reported the median home range of individual *C. gunnisoni* to be 684 and 774 m<sup>2</sup> at two sites, whereas Hoogland (1999) reported mean size of territory of clans to be 6,700 m<sup>2</sup>. We selected a compromise between these two figures and used a 2,800-m<sup>2</sup> circular plot to sample density of prairie dog burrows. Reported mean size of home ranges for *T. bottae* vary considerably, ranging from 35 m<sup>2</sup> (Reichman et al., 1982) to 185 m<sup>2</sup> (Howard and Childs, 1959), and up to 474 m<sup>2</sup> (Bandoli, 1987). Due to the patchy distribution of activity of *T. bottae*, we opted for the higher value and selected 450-m<sup>2</sup> circular plots to sample density of pocket gopher mounds. Four density-sampling units were randomly placed within each study location. We then counted number of active burrows and mounds within the density-sampling units, designating a burrow of *C. gunnisoni* as active if there was fresh green scat around the burrow opening (Powell et al., 1994; Davidson et al., 1999) and a mound of *T. bottae* as active if it consisted of loose granular dirt and lacked vegetation (Smallwood and Erickson, 1995). Finally, we used a Mann-Whitney test to determine if densities of active burrows and mounds

were different between locations where each species occurred alone ( $n = 15$  for each species) and where both species occurred together ( $n = 15$ ).

**Vegetational Composition**—To determine if vegetation among the three treatments differed (*C. gunnisoni* alone, *T. bottae* alone, and both species present;  $n = 45$ ), we sampled vegetation characteristics in six randomly placed circular plots (diameter = 2 m) within each of the density-sampling units described above. We recorded percentage groundcover of grasses, forbs, shrubs, litter (dead plant and fecal material), and bare ground.

Analysis of vegetational data consisted of using nonmetric multidimensional scaling (NMDS; DECODA software). NMDS is a measure of dissimilarities in vegetation composition (Faith et al., 1987; Minchin, 1987). This method plots each location from the three treatments in multidimensional space based on how similar they are to one another. Locations that are similar in vegetational composition will be closer together and locations that are dissimilar will be farther apart. We used an analysis of similarity (ANOSIM) to determine if the three treatments supported significantly different vegetational compositions (Faith et al., 1987; Minchin, 1987). A nonparametric multivariate method for comparing multiple samples, the ANOSIM test statistic  $R$ , is based on ranked dissimilarities between samples within and between treatments. If average rank-dissimilarity between treatments is greater than average rank within treatments, treatments will differ in composition. Finally, we used the vector-fitting procedure to determine which variables were most correlated with the ordination pattern (Wagner et al., 2000).

**Characteristics of Soil**—To determine if burrows of *C. gunnisoni* and *T. bottae* were located in different types of soil, we collected soil samples for texture analysis. Texture of soil often can determine where a burrowing animal will occur (Bolen and Robinson, 1999). We collected soil samples from the center of each density-sample unit. We used a soil auger 1.7-m long with a bucket 25-cm long and 8 cm in diameter to collect soil samples at a depth of 0.25 m and a standardized volume of a full bucket (about 700–900 g). Because both prairie dogs and pocket gophers affect texture of soil comprising mounds (Laycock and Richardson, 1975; Munn, 1993; Treveño-Villarreal et al., 1997), we collected soil samples away from mounds to avoid effects of burrowing activity. We determined soil texture by relative proportions of sand, silt, and clay particles (Tan, 1996; Brady and Weil, 1999). To determine soil texture, we followed the particle dispersion and sedimentation method outlined by Tan (1996).

In addition to sand, silt, and clay particles, rocks are a major component of soil. Presence of rocks can increase density of soil and make burrowing more energetically costly (Vleck, 1979). To determine if rock content of the soil differed among the three treatments ( $n = 45$ ), we removed all rocks >2 mm in diameter from soil samples and determined the percentage content of rock (by mass) of the soil. We used an analysis of variance (ANOVA) to determine if there were differences in amount of rock in the soil among the three treatments.

Depth of the soil also could influence location of burrows. To determine if depth of soil differed among the three treatments, we recorded depth of soil at the center of each density-sampling unit by using the soil auger to core into the soil to a maximum depth of 1.7 m (length of soil auger) or until it could not penetrate deeper. We used an ANOVA to determine if there were differences in depth of soil among the three treatments ( $n = 45$ ). Finally, we used NMDS, ANOSIM, and vector-fitting analyses to evaluate if there were differences in the characteristics of soil as a whole (percentage composition of sand, silt, and clay; rock content; and depth of soil) among the three treatments.

**RESULTS—Density—**Density of active *T. bottae* mounds was significantly lower at locations where *C. gunnisoni* ( $33.3 \pm 3.2$  SE mounds/plot) was present compared to locations where *T. bottae* occurred alone ( $73.8 \pm 12.5$  mounds/plot;  $U = 23.5$ ,  $201.5$ ,  $P < 0.001$ ). Despite density of active burrows of *C. gunnisoni* being 2.5 times greater at locations where *T. bottae* ( $18.6 \pm 4.8$  burrows/plot) was present compared to locations where *C. gunnisoni* occurred alone ( $7.3 \pm 0.65$  burrows/plot), the difference was not significant ( $U = 71$ ,  $154$ ,  $P = 0.089$ ).

**Vegetational Composition—**Vegetational composition was significantly different among the three treatments (Fig. 2; Table 1). Vegetation at locations where *C. gunnisoni* occurred alone was significantly different from vegetation at locations where *T. bottae* occurred alone and locations where both species were present. There was no difference in vegetational composition between locations where *T. bottae* occurred alone and locations where both species were present. Three of the five vegetational variables that were measured were significantly correlated with ordination pattern (Fig. 2) and consisted of two major gradients. A gradient of bare ground and grass (locations with high grass cover had low bare ground cover) was influential for separation of locations where *C. gunnisoni* occurred alone from locations where *T. bottae* occurred alone and where both species occurred together. The other gradient of litter and forb cover was not useful for separating treatments.

Analysis of variance quantified the significant difference in amount of bare ground cover among the three treatments ( $F_{2,42} = 8.98$ ,  $P = 0.001$ ; Fig. 3). Bare ground cover at locations where *C. gunnisoni* occurred alone ( $54.9 \pm 4.2\%$ ) was significantly greater than locations where *T. bottae* occurred alone ( $28.3 \pm 4.2\%$ ; Tukey's HSD used for all post hoc comparisons,  $P = 0.001$ )

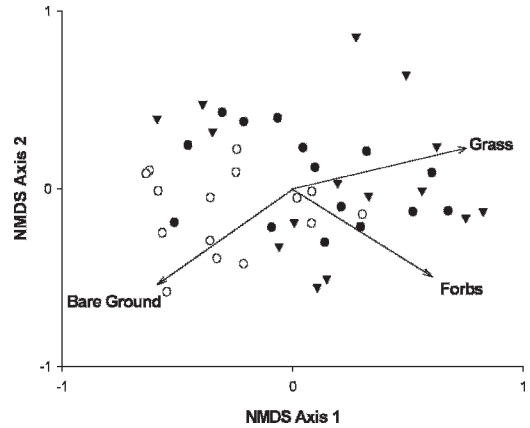


FIG. 2—Non-metric multidimensional scaling (NMDS) ordination of vegetational composition where *Cynomys gunnisoni* occurred alone ( $n = 15$ ; ○), where *Thomomys bottae* occurred alone ( $n = 15$ ; ▼), and where both species were present ( $n = 15$ ; ●) in northern Arizona, 2000. Vegetation was significantly different ( $\alpha = 0.05$ ) between *C. gunnisoni* and *T. bottae*, *C. gunnisoni* and both species present, but not between *T. bottae* and both species present. Vectors that were significantly correlated with the ordination pattern were bare ground cover (%;  $R_{max} = 0.967$ ,  $P < 0.001$ ), percentage cover of grass ( $R_{max} = 0.838$ ,  $P < 0.001$ ), and percentage cover of forbs ( $R_{max} = 0.798$ ,  $P < 0.001$ ).

and locations where both species were present ( $34.2 \pm 3.0\%$ ;  $P = 0.003$ ). Bare ground cover was not significantly different between locations where *T. bottae* occurred alone and where both species were present ( $P = 0.925$ ).

There also was a significant difference in amount of grass cover among the three treatments ( $F_{2,42} = 4.79$ ,  $P = 0.013$ ; Fig. 3). Grass cover at locations where *C. gunnisoni* occurred alone ( $22.3 \pm 4.4\%$ ) was significantly lower than locations where *T. bottae* occurred alone ( $38.2 \pm 4.4\%$ ; Tukey's HSD,  $P = 0.033$ ) and locations where both species were present ( $39.5 \pm 3.1\%$ ;  $P = 0.023$ ). There was no difference in grass cover between locations where *T. bottae* occurred alone and where both species were present ( $P = 0.988$ ).

Although it was not statistically significant, mean forb cover at locations where *T. bottae* occurred alone and where both species were present ( $11.2 \pm 1.9\%$  cover;  $9.1 \pm 1.3\%$ , respectively) was nearly double that of locations where *C. gunnisoni* occurred alone ( $4.8 \pm 1.9\%$ ;  $F_{2,42} = 3.17$ ,  $P = 0.052$ ; Fig. 3). There was no significant difference in litter cover ( $F_{2,42} = 0.23$ ,

TABLE 1—Results from analysis of similarity (ANOSIM) of vegetation composition and soil characteristics among locations occupied by *Cynomys gunnisoni* ( $n = 15$ ), *Thomomys bottae* ( $n = 15$ ), and both species ( $n = 15$ ) in northern Arizona, 2000.

Ordination	Treatment comparison	<i>R</i>	<i>P</i>
Vegetational composition	<i>C. gunnisoni</i> – <i>T. bottae</i>	0.224	0.002
	<i>C. gunnisoni</i> – both species	0.200	0.002
	<i>T. bottae</i> – both species	–0.020	0.603
Soil characteristics	<i>C. gunnisoni</i> – <i>T. bottae</i>	0.114	0.260
	<i>C. gunnisoni</i> – both species	0.369	<0.001
	<i>T. bottae</i> – both species	0.195	0.246

$P = 0.795$ ) or shrub cover ( $F_{2,42} = 0.44, P = 0.650$ ) among the three treatments.

**Characteristics of Soil**—There were few differences in characteristics of soil among the three treatments (Fig. 4, Table 1). This ordination pattern differed from the vegetation ordination in that points had less spacing between them, indicating that there was less variation in characteristics of soil than vegetation. Characteristics of soil where *C. gunnisoni* occurred alone were significantly different from those at locations where both species were present, but not different from those at locations where *T. bottae* occurred alone. Characteristics of soil where *T. bottae* occurred alone were not different from those at locations where both species were present. A gradient consisting of depth of soil and rock content of soil was influential in separation of locations where *C. gunnisoni* occurred alone from locations where both

species were present (Fig 4). Texture of soil (composition of silt, sand, and clay) was less influential in separation of treatments.

Silt was the only class of soil particles that differed among treatments ( $F_{2,40} = 6.61, P = 0.003$ ). The proportion of silt at locations where both species were present ( $42.7 \pm 2.9\%$ ) was significantly greater than locations where *C. gunnisoni* occurred alone ( $27.4 \pm 3.0\%$ ; Tukey’s HSD,  $P = 0.002$ ). The proportion of silt at locations where *T. bottae* occurred alone ( $35.3 \pm 3.0\%$ ) was not significantly different from locations where *C. gunnisoni* occurred alone ( $P = 0.172$ ) or where both species were present ( $P = 0.192$ ). There was no difference in proportion of sand ( $F_{2,40} = 0.942, P = 0.398$ ) or clay ( $F_{2,40} = 1.30, P = 0.283$ ) among treatments. Burrows of each species were located in a variety of soil textures. The most prevalent soil textures observed at locations where both species were present and locations where *T. bottae* occurred alone were medium and medium-fine soils (e.g., loam and silt loam), which consist of low amounts of clay, medium sand, and medium to high amounts of silt. Conversely, locations where *C. gunnisoni* occurred alone were often in medium-coarse (e.g., sandy loam; high in sand) and medium fine (e.g., clay loam; high in clay) textured soils.

There was a significant difference in depth of soil among treatments ( $F_{2,40} = 6.02, P = 0.005$ ). Depth of soil at locations where *C. gunnisoni* occurred alone ( $133.1 \pm 9.7$  cm) was significantly deeper than locations where both species were present ( $86.9 \pm 9.4$  cm; Tukey’s HSD,  $P = 0.004$ ). Depth of soil was not significantly different between locations where *T. bottae* occurred alone ( $101.9 \pm 9.7$  cm) and locations where *C. gunnisoni* occurred alone ( $P = 0.072$ ) or between locations where both species were present ( $P = 0.516$ ).

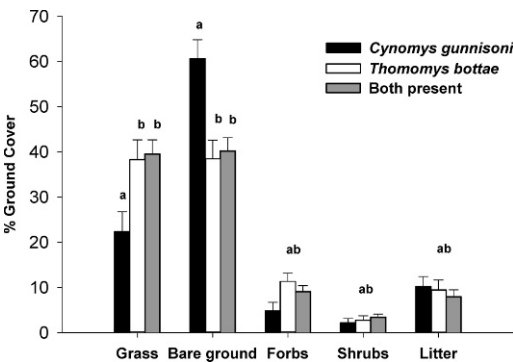


FIG. 3—Mean ( $\pm 1$  SE) percentage groundcover of grass, bare ground, and forbs at locations where *Cynomys gunnisoni* ( $n = 15$ ) and *Thomomys bottae* ( $n = 15$ ) each occurred alone and locations where both species were present ( $n = 15$ ) in northern Arizona, 2000. Groups a and b were significantly different ( $\alpha = 0.05$ ). Group ab was not significantly different.

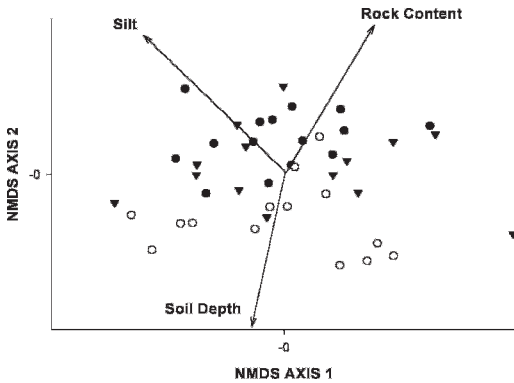


FIG. 4—Non-metric multidimensional scaling (NMDS) ordination of soil characteristics where *Cynomys gunnisoni* occurred alone ( $n = 15$ ; ○), where *Thomomys bottae* occurred alone ( $n = 15$ ; ▼), and where both species were present ( $n = 15$ ; ●) in northern Arizona, 2000. The only significant difference ( $\alpha = 0.05$ ) was between *C. gunnisoni* and both species present. Vectors that were significantly correlated with the ordination pattern were depth of soil (cm;  $R_{max} = 0.749$ ,  $P < 0.001$ ), rock content of soil (%;  $R_{max} = 0.760$ ,  $P < 0.001$ ), and silt composition of the soil (%;  $R_{max} = 0.640$ ,  $P < 0.001$ ).

Because depth of soil was negatively correlated with rock content of soil ( $r = -0.366$ ,  $P = 0.005$ ), locations that had shallow soil generally had high rock content. There was a significant difference in rock content of soil among treatments ( $F_{2,40} = 5.72$ ,  $P = 0.007$ ). The proportion of soil mass consisting of rock at locations where *C. gunnisoni* occurred alone ( $7.5 \pm 3.0\%$ ) was significantly lower than locations where both species were present ( $21.8 \pm 2.9\%$ ; Tukey's HSD,  $P = 0.005$ ). Similar to the pattern observed for depth of soil, rock content of soil at locations where *T. bottae* occurred alone ( $16.2 \pm 3.0\%$ ) was not significantly different from locations where *C. gunnisoni* occurred alone ( $P = 0.131$ ) or locations where both species were present ( $P = 0.373$ ).

DISCUSSION—*Effect of Ecosystem Engineers on Each Other*—We found the presence of one ecosystem engineer negatively associated with presence of the other. Vegetational cover and characteristics of soil were not significantly different between locations where *T. bottae* occurred alone and where both species were present, which suggests other, unmeasured effects of *C. gunnisoni* activity may limit density of *T. bottae*. Because both of these species are

burrowing herbivores, it is possible that direct competition exists for food or subterranean space. Food items of *T. bottae* could have been decreased by activity of *C. gunnisoni*. A comparison of diets for *C. gunnisoni* (Shalaway and Slobodchikoff, 1988) and *T. bottae* (Bandoli, 1981) near Flagstaff, Arizona, indicated that nearly 50% of food items overlapped between the two species. This suggests competition between *C. gunnisoni* and *T. bottae* is likely.

Densities of pocket gophers are limited by availability of food (Howard and Childs, 1959; Andersen and MacMahon, 1981; Rezsutek and Cameron, 1998), and they will selectively burrow in areas that have higher productivity of food (Reichman and Smith, 1985; Inouye et al., 1987; Benedix, 1993). Aboveground grazing by black-tailed prairie dogs (*C. ludovicianus*) decreases root biomass and annual net root production (Ingham and Detling, 1984). Roots and other belowground storage organs are crucial components of winter diet of pocket gophers (Vaughan, 1974; Andersen and MacMahon, 1981). Possible decreased root biomass from grazing by *C. gunnisoni* has the potential to limit availability of food and populations of *T. bottae*.

The fact that density of *T. bottae* mounds was negatively associated with presence of *C. gunnisoni* is interesting because the majority of research involving prairie dogs indicates their activities benefit other wildlife (Kotliar et al., 1999; Miller et al., 2000). Similarly, Davidson and Lightfoot (2006) reported abundances of prairie dogs (*C. ludovicianus*) and kangaroo rats (*D. spectabilis*) decreased where they coexisted compared to where they occurred alone. Keystone species have been associated with increasing habitat or species diversity (Paine, 1969), resulting in a higher number of individual species occupying a given area. More species in a given area increases the possibility of resource competition and the possibility that any one species is not able to dominate resources. Although habitat heterogeneity can alleviate competition through niche diversification, there is still undoubtedly overlap between resource needs of animals occupying colonies of prairie dogs (i.e., grass as a food source). As direct and indirect activities of *C. gunnisoni* increase landscape heterogeneity (Bangert and Slobodchikoff, 2000; Davidson, 2005), they potentially increase the number of niches within a landscape; however, these niches are now presumably

smaller than those of a less-diverse landscape. Thus, the niche of *T. bottae* may be reduced where it occurs with *C. gunnisoni* compared to where it occurs alone.

Opposite of what we observed with *T. bottae*, density of active *C. gunnisoni* burrows was >2 times as high where they co-occurred with *T. bottae* compared to locations where *C. gunnisoni* occurred alone. One explanation for this pattern may be related to dominant vegetation associated with different elevations. Locations at high elevation (majority of locations where both were present) consisted of subalpine meadows surrounded by forests, which limit expansion of colonies and dispersal of individuals to other colonies (Travis et al., 1997), thereby increasing density. Locations at low elevation (majority of locations for *C. gunnisoni*) consisted of open grasslands that do not seem to pose major limitations to expansion of colonies or dispersal.

An alternative hypothesis is that the presence of *T. bottae* benefited *C. gunnisoni*. Mounds of excavated soil created by *T. bottae* serve as areas of high seed catchment (McDonough, 1974) and forb growth (Martinsen et al., 1990). Seeds are an important component of the diet of *C. gunnisoni* in early spring (Shalaway and Slobodchikoff, 1988). Excavated mounds become dominated by annuals and eventually perennials, which may provide areas for *C. gunnisoni* to graze. Investigations into effects of habitat quality on *C. gunnisoni* revealed that more productive habitats yield an increase in growth rates, sexual maturation, and ultimately productivity (Rayor, 1988). If activity of *T. bottae* increases food resources of *C. gunnisoni*, then the presence of *T. bottae* may benefit *C. gunnisoni*. This potential relationship represents a poorly studied aspect of the ecology of prairie dogs. Most research involving prairie dogs examines their effects on vegetation, other wildlife, or ecosystem processes. Yet, we know little about how other rodents, grazing ungulates, or predators affect prairie dogs. Grazing by bison (*Bison bison*) was reported to benefit *C. ludovicianus* by improving foraging conditions (Krueger, 1986), whereas simulated livestock grazing negatively affected the Utah prairie dog (*C. parvidens*; Cheng and Ritchie, 2006). Although ecosystem engineers are known to affect many aspects of their biotic community, they also are affected by other species.

*Ecosystem Engineers Associated with Different Vegetational Communities*—We detected different vegetational communities associated with locations where *T. bottae* and *C. gunnisoni* each occurred alone, which was likely due to differences in disturbance regime. The fact that soil characteristics and elevation were not different between these two treatments supported our hypothesis that different ecosystem engineers and disturbance regimes are associated with different vegetational communities. Locations with *T. bottae* were associated with significantly more cover of grass and forbs and significantly less bare ground than locations with *C. gunnisoni*. The nature of disturbance by pocket gophers involves continuous excavation of soil onto the surface. Freshly excavated soil provides a colonization opportunity for disturbance-dependent plants (McDonough, 1974; Martinsen et al., 1990) and facilitates regeneration of vegetational cover that was lost to herbivory or production of soil mounds. Burrowing by prairie dogs provides fewer colonization opportunities for plants because construction or maintenance of burrows does not occur frequently (Fitzgerald and Lechleinter, 1974), whereas mounds from pocket gophers are created throughout the year (Bandoli, 1981). The larger amount of bare ground at *C. gunnisoni* locations also could be attributed to the fact that prairie dogs exhibit more intensive grazing than pocket gophers. Pocket gophers are limited to feeding on roots within their tunnel systems and vegetation in the immediate vicinity of their burrow openings, whereas prairie dogs graze over much larger areas (Hoffmeister, 1986). Because prairie dogs live in territorial clans (Rayor, 1988; Hoogland, 1999), their grazing is likely more intense than the herbivory of solitary pocket gophers.

We partially supported our hypothesis that the combination of two disturbance regimes would produce a unique vegetational community, because locations where both species were present were different from those of *C. gunnisoni* alone, but not from *T. bottae* alone. Presence of *C. gunnisoni* should have increased the amount of bare ground and fewer *T. bottae* would turn over less soil, creating less opportunity for growth of forbs and grasses. The conflicting results from different disturbance regimes warrant consideration of other factors that influence vegetational communities.

To reconcile vegetation-community patterns, we compared differences in soil characteristics and elevation between treatment locations. Vegetational communities that were not significantly different (both species present and *T. bottae* alone) were located at sites that did not differ in elevation or soil characteristics. Conversely, vegetational communities that were significantly different (both species present and *C. gunnisoni* alone) also differed in elevation, although not significantly, and soil characteristics. Higher elevations (majority of sites with both species present and *T. bottae* alone) receive more precipitation, which could be responsible for the increase in vegetational cover, despite the increase in disturbance and herbivory. Higher-elevation locations often were located in loamy soils with high proportions of silt. These types of soil have physical and chemical properties that are ideal for growth of plants (Raven et al., 1981). Fertile soils and high precipitation may explain why an increased herbivory and disturbance did not reduce plant cover at locations where both species were present compared to where *T. bottae* occurred alone. Although ecosystem engineers and keystone species have profound effects on biotic communities, these effects can be overshadowed by the influence of soil conditions or climate. This was the case when Grant-Hoffman and Detling (2006) detected no difference in vegetation between sites on and off colonies of *C. gunnisoni*, but conceded that a persistent drought in that area likely masked potential differences. Experiments involving addition of species (e.g., Davidson et al., 1999) into separate areas of similar vegetation, soil composition, and elevation would be an excellent way to observe how a vegetational community is changed in response to different disturbance regimes.

*Characteristics of Soil*—Our comparison of characteristics of soil between locations where *C. gunnisoni* and *T. bottae* each occurred alone revealed few differences. Both species seemed to be soil generalists because they inhabited all types of soil textures, but were more prevalent in medium-textured soils (e.g., loam, silt loam), which have a balance between being loose enough for burrowing, but compact enough to maintain burrow infrastructure. The high variability in soil texture supports previous research that suggests prairie dogs and pocket gophers are more limited by the depth of soil and rock content of the soil than by texture of soil (Collier

and Spillett, 1975; Wagner and Drickamer, 2004). Different characteristics of soils where *C. gunnisoni* occurred alone and where both species were present does not reflect a niche shift or competitive exclusion. Rather, the confines of the natural distribution of our treatment sites influenced these results. Locations where we found *C. gunnisoni* alone were most common at low elevation, which consisted of desert grasslands with deep (>1.0 m), sandy soil and low amounts of rock, whereas the majority of locations where both species were present were located at high and intermediate elevations and consisted of shallower, silty soils with higher rock content. Although these species have slightly different burrowing needs and behaviors, these differences did not result in requiring different subterranean habitats.

Although communities that harbor two ecosystem engineers might not be common, each community could have multiple species that play crucial roles in maintaining diversity and stability in that system. Each ecosystem engineer has a unique disturbance regime that shapes communities differently, and the interaction of multiple disturbance regimes could have properties that are unique relative to the effects of each species alone. Most ecosystems probably are not maintained by a single ecosystem engineer or keystone species, but rather by the activities and interactions of several influential species, in addition to the important influences of soils and elevation that ultimately dictate presence of certain species of plants and wildlife. The grasslands of northern Arizona occur on a patchwork of different soil types, with each focal ecosystem engineer occurring alone and co-occurring with each other. The patchwork of soils and three disturbance regimes likely play an important role in the habitat and landscape diversity that is present.

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## LITERATURE CITED

- ANDERSEN, D. C., AND J. A. MACMAHON. 1981. Population dynamics and bioenergetics of a fossorial herbivore, *Thomomys talpoides* (Rodentia: Geomyidae), in a spruce-fir sere. *Ecological Monographs* 51:179–182.
- BANDOLI, J. H. 1981. Factors influencing seasonal burrowing activity in the pocket gopher, *Thomomys bottae*. *Journal of Mammalogy* 62:293–303.
- BANDOLI, J. H. 1987. Activity and plural occupancy of burrows in Botta's pocket gopher *Thomomys bottae*. *American Midland Naturalist* 118:10–14.
- BANGERT, R. K., AND C. N. SLOBODCHIKOFF. 2000. The Gunnison's prairie dog structures in a high desert grassland as a keystone engineer. *Journal of Arid Environments* 46:357–369.
- BENEDIX, J. H. JR. 1993. Area-restricted search by the plains pocket gopher (*Geomys bursarius*) in tallgrass prairie habitat. *Behavioral Ecology* 4:318–324.
- BOLEN, E. G., AND W. L. ROBINSON. 1999. *Wildlife ecology and management*. Fourth edition. Prentice Hall, Inc., Upper Saddle River, New Jersey.
- BRADY, N. C., AND R. R. WEIL. 1999. *The nature and properties of soils*. Twelfth edition. Prentice Hall, Inc., Upper Saddle River, New Jersey.
- BROWN, D. E. 1994. *Biotic communities: southwestern United States and northwestern Mexico*. University of Utah Press, Salt Lake City.
- BROWN, J. H., AND E. J. HESKE. 1990. Control of a desert-grassland transition by a keystone rodent guild. *Science* 250:1705–1707.
- CANTOR, L. F., AND T. G. WHITHAM. 1989. Importance of belowground herbivory: pocket gophers may limit aspen to rock outcrop refugia. *Ecology* 70:962–970.
- CHENG, E., AND M. E. RITCHIE. 2006. Impacts of simulated grazing on Utah prairie dogs (*Cynomys parvidens*) in a low productivity ecosystem. *Oecologia* 147:546–555.
- COLLIER, G. D., AND J. J. SPILLETT. 1975. Factors influencing the distribution of the Utah prairie dog, *Cynomys parvidens* (Sciuridae). *Southwestern Naturalist* 20:151–158.
- DAVIDSON, A. D. 2005. The comparative and interactive effects of prairie dogs and banner-tailed kangaroo rats on plants and animals in the northern Chihuahuan Desert. Ph.D. dissertation, University of New Mexico, Albuquerque.
- DAVIDSON, A. D., AND D. C. LIGHTFOOT. 2006. Keystone rodent interactions: prairie dogs and kangaroo rats structure the biotic composition of a desertified grassland. *Ecography* 29:755–765.
- DAVIDSON, A. D., R. R. PARMENTER, AND J. R. GOSZ. 1999. Response of small mammals and vegetation to a reintroduction of Gunnison's prairie dogs. *Journal of Mammalogy* 80:1311–1324.
- FAITH, D. P., P. R. MINCHIN, AND L. BELBIN. 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* 69:57–68.
- GRANT-HOFFMAN, M. N., AND J. K. DETLING. 2006. Vegetation on Gunnison's prairie dog colonies in southwestern Colorado. *Rangeland Ecology and Management* 59:73–79.
- HOFFMEISTER, D. F. 1986. *Mammals of Arizona*. University of Arizona Press and Arizona Game and Fish Department, Tucson.
- HOOGLAND, J. L. 1999. Philopatry, dispersal, and social organization of Gunnison's prairie dogs. *Journal of Mammalogy* 80:243–251.
- HOWARD, W. E., AND H. E. CHILDS, JR. 1959. Ecology of pocket gophers with emphasis on *Thomomys bottae meva*. *Hilgardia* 29:277–355.
- HUNTLY, N., AND R. S. INOUE. 1988. Pocket gophers in ecosystems: patterns and mechanisms. *BioScience* 38:786–792.
- INGHAM, R. E., AND J. K. DETLING. 1984. Plant-herbivore interactions in a North American mixedgrass prairie III. Soil nematode populations and root biomass on *Cynomys ludovicianus* colonies and adjacent uncolonized areas. *Oecologia* 63:307–313.
- INOUE, R. S., N. J. HUNTLY, D. TILMAN, AND J. R. TESTER. 1987. Pocket gopher (*Geomys bursarius*), vegetation, and soil nitrogen along a successional sere in east central Minnesota. *Oecologia* 72:178–184.
- JONES, C. G., J. H. LAWTON, AND M. SHACHAK. 1994. Organisms as ecosystem engineers. *Oikos* 69:373–386.
- KOTLIAR, N. B., B. W. BAKER, A. D. WHICKER, AND G. PLUMB. 1999. A critical review of assumptions about the prairie dog as a keystone species. *Environmental Management* 24:177–192.
- KRUEGER, K. 1986. Feeding relationships among bison, pronghorn, and prairie dogs: an experimental analysis. *Ecology* 67:760–770.
- LAYCOCK, W. A., AND B. Z. RICHARDSON. 1975. Long-term effects of pocket gopher control on vegetation and soils of a subalpine grassland. *Journal of Range Management* 28:458–462.
- MARTINSEN, G. D., J. H. CUSHMAN, AND T. G. WHITHAM. 1990. Impact of pocket gopher disturbance of plant species diversity in a shortgrass prairie community. *Oecologia* 83:132–138.
- MCDONOUGH, W. T. 1974. Revegetation of gopher mounds on aspen range in Utah. *Great Basin Naturalist* 34:267–275.
- MILLER, B., R. READING, J. HOOGLAND, T. CLARK, G. CEBALLOS, R. LIST, S. FORREST, L. HANEBURY, P. MANZANO, J. PACHECO, AND D. URESK. 2000. The role of prairie dogs as a keystone species: response to Stapp. *Conservation Biology* 14:318–321.
- MILLS, L. S., M. E. SOULÉ, AND D. F. DOAK. 1993. The keystone-species concept in ecology and conservation. *BioScience* 43:219–224.
- MINCHIN, P. R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* 69:89–107.
- MUNN, L. C. 1993. Effects of prairie dogs on physical and chemical properties of soils. Pages 11–17 in

- Proceedings of the symposium on the management of prairie dog complexes for the reintroduction of the black-footed ferret (J. L. Oldemeyer, D. E. Biggens, B. J. Miller, and R. Crete, editors). United States Fish and Wildlife Service, Department of the Interior, Biological Report 13, Washington, D.C.
- PAINE, R. T. 1969. A note on trophic complexity and community complexity. *American Naturalist* 103:91–93.
- POWELL, K. L., R. J. ROBEL, K. E. KEMP, AND M. D. NELLIS. 1994. Aboveground counts of black tailed prairie dogs: temporal nature and relationship to burrow entrance density. *Journal of Wildlife Management* 58:361–366.
- RAVEN, P. H., R. F. EVERT, AND H. CURTIS. 1981. *Biology of plants*. Third edition. Worth Publishers, Inc., New York.
- RAYOR, L. S. 1988. Social organization and space-use in Gunnison's prairie dog. *Behavioral Ecology and Sociobiology* 22:69–78.
- REICHMAN, O. J., AND S. C. SMITH. 1985. Impact of pocket gopher burrows on overlying vegetation. *Journal of Mammalogy* 66:720–725.
- REICHMAN, O. J., T. G. WHITHAM, AND G. A. RUFFNER. 1982. Adaptive geometry of burrow spacing in two pocket gopher populations. *Ecology* 63:687–695.
- REZSUTEK, M., AND G. N. CAMERON. 1998. Influence of resource removal on demography of Attwater's pocket gopher. *Journal of Mammalogy* 79:538–550.
- SHALAWAY, S., AND C. N. SLOBODCHIKOFF. 1988. Seasonal changes in the diet of Gunnison's prairie dog. *Journal of Mammalogy* 69:835–841.
- SLOBODCHIKOFF, C. N., A. ROBINSON, AND C. SCHAACK. 1988. Habitat use by Gunnison's prairie dogs. Pages 403–408 in *Management of amphibians, reptiles, and small mammals in North America* (R. C. Szaro, K. E. Severson, and D. R. Patton, editors). United States Forest Service General Technical Report RM-166, Washington, D.C.
- SMALLWOOD, K. S., AND W. A. ERICKSON. 1995. Estimating gopher populations and their abatement in forest plantations. *Forest Science* 41:284–296.
- TAN, K. H. 1996. *Soil sampling, preparation, and analysis*. Marcel Dekker, Inc., New York.
- TRAVIS, S. E., C. N. SLOBODCHIKOFF, AND P. KEIM. 1997. DNA fingerprinting reveals low genetic diversity in Gunnison's prairie dogs (*Cynomys gunnisoni*). *Journal of Mammalogy* 78:725–732.
- TREVEIÑO-VILLARREAL, J., W. E. GRANT, AND A. CARDONA-ESTRADA. 1997. Characterization of soil texture in Mexican prairie dog (*Cynomys mexicanus*) colonies. *Texas Journal of Science* 49:207–214.
- VAUGHAN, T. A. 1974. Resource allocation in some sympatric, subalpine rodents. *Journal of Mammalogy* 55:764–795.
- VLECK, D. 1979. The energy cost of burrowing by the pocket gopher *Thomomys bottae*. *Physiological Zoology* 52:122–135.
- WAGNER, D. M., AND L. C. DRICKAMER. 2004. Abiotic habitat correlates of Gunnison's prairie dog in Arizona. *Journal of Wildlife Management* 68:188–197.
- WAGNER, D. M., G. A. FELDHAMER, AND J. A. NEWMAN. 2000. Microhabitat selection by golden mice (*Ochrotomys nuttalli*) at arboreal nest sites. *American Midland Naturalist* 144:220–225.
- WHICKER, A. D., AND J. K. DETLING. 1988. Ecological consequences of prairie dog disturbances. *BioScience* 38:778–785.

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