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Ecosystem engineering varies spatially: a test of the vegetation modification paradigm for prairie dogs

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Colonial, burrowing herbivores can be engineers of grassland and shrubland ecosystems worldwide. Spatial variation in landscapes suggests caution when extrapolating single-place studies of single species, but lack of data and the need to generalize often leads to 'model system' thinking and application of results beyond appropriate statistical inference. Generalizations about the engineering effects of prairie dogs (*Cynomys* sp.) developed largely from intensive study at a single complex of black-tailed prairie dogs *C. ludovicianus* in northern mixed prairie, but have been extrapolated to other ecoregions and prairie dog species in North America, and other colonial, burrowing herbivores. We tested the paradigm that prairie dogs decrease vegetation volume and the cover of grasses and tall shrubs, and increase bare ground and forb cover. We sampled vegetation on and off 279 colonies at 13 complexes of 3 prairie dog species widely distributed across 5 ecoregions in North America. The paradigm was generally supported at 7 black-tailed prairie dog complexes in northern mixed prairie, where vegetation volume, grass cover, and tall shrub cover were lower, and bare ground and forb cover were higher, on colonies than at paired off-colony sites. Outside the northern mixed prairie, all 3 prairie dog species consistently reduced vegetation volume, but their effects on cover of plant funcrional groups varied with prairie dog species and the grazing tolerance of dominant perennial grasses. White-tailed prairie dogs *C. leucurus* in sagebrush steppe did not reduce shrub cover, whereas black-tailed prairie dogs suppressed shrub cover at all complexes with tall shrubs in the surrounding habitat matrix. Black-tailed prairie dogs in shortgrass steppe and Gunnison's prairie dogs *C. gunnisoni* in Colorado Plateau grassland both had relatively minor effects on grass cover, which may reflect the dominance of grazing-tolerant shortgrasses at both complexes. Variation in modification of vegetation structure may be understood in terms of the responses of different dominant perennial grasses to intense defoliation and differences in foraging behavior among prairie dog species. Spatial variation in the engineering role of prairie dogs suggests spatial variation in their keystone role, and spatial variation in the roles of other ecosystem engineers. Thus, ecosystem engineering can have a spatial component not evident from single-place studies.

Ecosystem engineers affect physical and biological processes in grassland and shrubland habitats worldwide. Spatial variation in the inherent habitat matrix and functional variation among similar species of engineers may alter engineering processes, which can alter their keystone role. Colonial, burrowing herbivores can be both ecosystem engineers and keystone species that are widely distributed across diverse landscapes (Kotliar et al. 1999, Delibes-Mateos et al. 2011). Spatial variation in landscapes suggests caution before extrapolating single-place studies of single species, but lack of data and the need to generalize often leads to 'model system' thinking and application of results beyond appropriate statistical inference. Similarities in form and function of colonial, burrowing herbivores, and the ecosystems they engineer, suggest a model system approach is desirable, as it can generalize results from intensive studies of a single species at a single study site. Clearly, ecology benefits from this approach, but paradigms developed from intensive, single-place studies should be tested with extensive, multi-place studies.

Prairie dogs (*Cynomys* sp.) are colonial, burrowing, herbivorous rodents widely distributed in grasslands and shrublands of west-central North America. They have a complex social organization, with groups of families (coteries) comprising colonies, and groups of colonies comprising complexes (Hoogland 2006). Unsuitable or unoccupied land occurs within and among colonies; thus, complexes are a patchy aggregation of on- and off-colony sites. Prairie dogs are ecosystem engineers because they substantially modify the physical structure of vegetation and soils (Whicker and Detling 1988, Bangert and Slobodchikoff 2000, Davidson and Lightfoot 2008), and keystone species because they influence abundance, diversity, and population processes for many associated species (Kotliar et al. 1999,

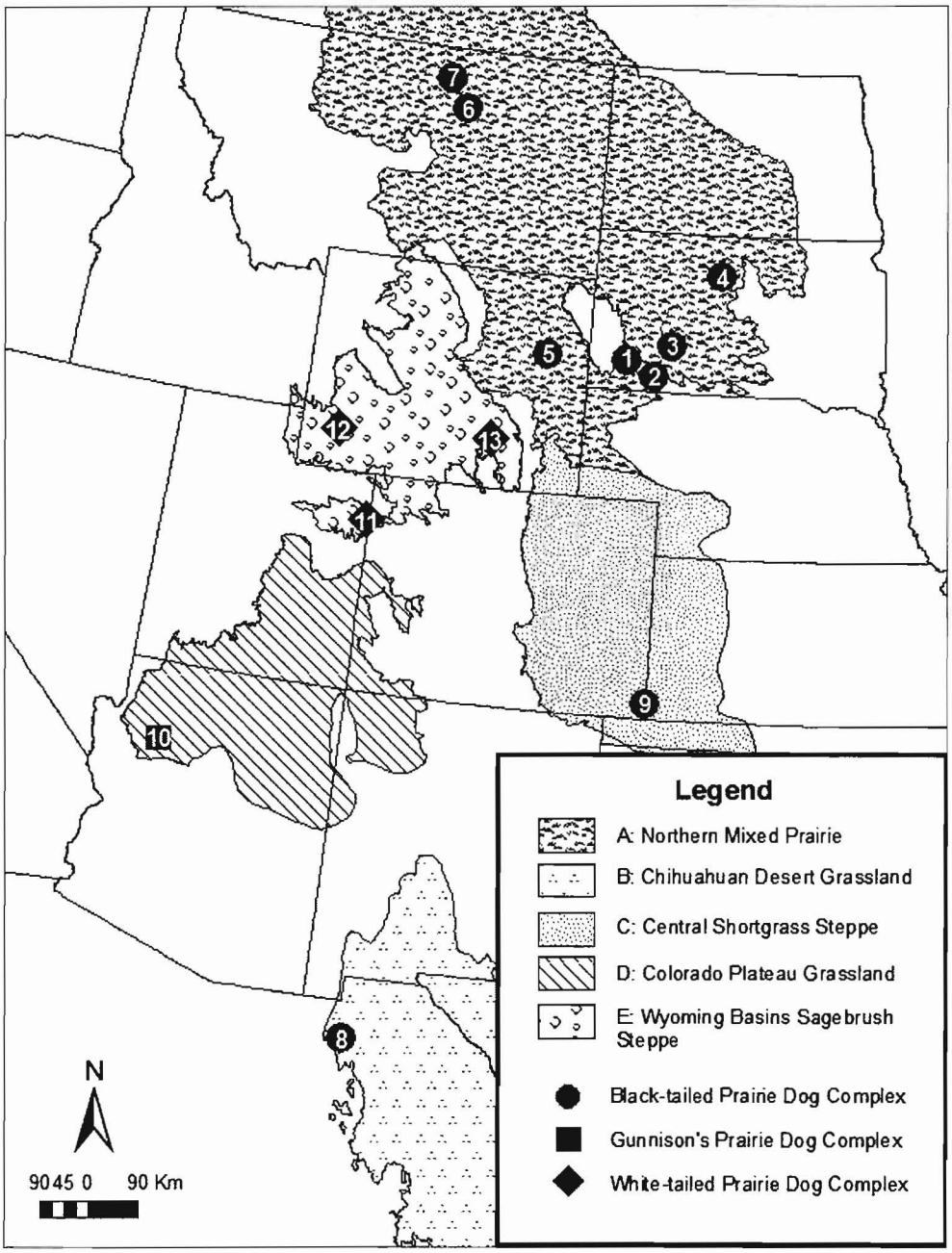

Figure 1. Locations of 13 complexes of 3 prairie dog species where vegetation attributes were measured in western North America. Complexes are shown relative to 5 ecoregions (A–E) whose boundaries were delineated through The Nature Conservancy's ecoregional planning process (TNC 1999). 1 = Wind Cave National Park; 2 = Pine Ridge Indian Reservation; 3 = Badlands National Park and Buffalo Gap National Grassland; 4 = Cheyenne River Indian Reservation; 5 = Thunder Basin National Grassland; 6 = Phillips County Public Lands (Bureau of Land Management [BLM] and C. M. Russell National Wildlife Refuge); 7 = Fort Belknap Indian Reservation; 8 = Janos – Casas Grandes region of Chihuahua, Mexico; 9 = Comanche and Cimarron National Grasslands; 10 = Aubrey Valley, Big Boquillas Ranch; 11 = Coyote Basin Public Lands (BLM and Dinosaur National Monument); 12 = Moxa Arch Public Lands (BLM); 13 = Shirley Basin Public Lands (BLM).

shrub component, primarily *Artemisia tridentata* and *A. cana*. All complexes were grazed by domestic cattle except Wind Cave and the Badlands portion of Badlands–Buffalo Gap, which were national parks grazed by bison *Bison bison*.

At each complex, colonies were selected using agency maps and were > 20 ha in size and active at the time of sampling (prairie dogs or fresh scat present at burrows). Paired off-colony sites were located by observing colony boundaries, and identifying nearby (~0.5–2.0 km) sites with similar topography, soils, and current grazing management, but lacking prairie dogs. We sampled all colonies within a complex that met these criteria, with the exception that we sampled about half of the colonies at the 2 largest complexes due to time constraints (Badlands–Buffalo Gap and Thunder Basin). We assumed that on- and off-colony sites

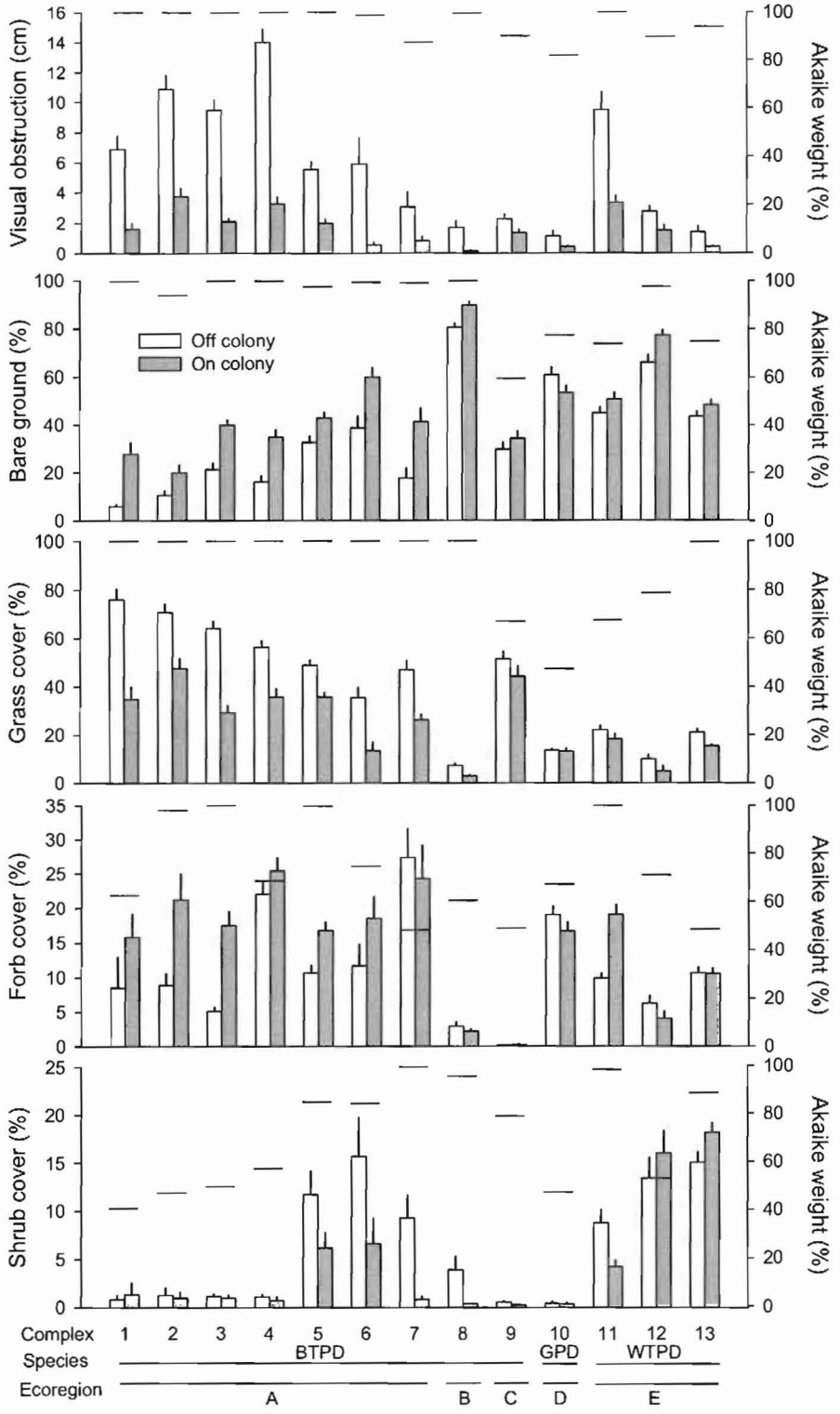

Figure 2. Comparison of 5 vegetation attributes measured off (open bars) and on (shaded bars) 279 prairie dog colonies at 13 complexes of 3 prairie dog species located in 5 ecoregions (Fig. 1). Akaike weight (0–100%) in support of a difference shown with horizontal bars; ± 1 standard error shown with vertical bars.

For WTPDs in the sagebrush steppe (complex no. 11–13), VO was lower on than off colonies at all 3 complexes. However, effects on bare ground, grass cover, and forb cover were weak and inconsistent. Shrub cover was lower on than off colonies at complex no. 11, but was slightly higher on colonies at complex no. 12 and 13. Shrubs at all 3 complexes were dominated by tall species, such as *A. tridentata*. Weak effects of WTPDs on tall shrubs in sagebrush steppe

Finally, factors beyond the scope of this investigation likely mitigate prairie dog effects on vegetation. For example, plague can reduce the size and persistence of prairie dog colonies, which can reduce the magnitude of vegetation effects (Augustine et al. 2008, Hartley et al. 2009). At the time of our study, plague effects varied from recent (complex no. 9) to unaffected (South Dakota complexes) to unknown. In general, colonies can remain in the same location following recovery from plague (Wyoming and Montana) or move location (shortgrass steppe; Augustine et al. 2008). In shortgrass steppe, less vegetation in the habitat matrix, greater grazing resistance of dominant shortgrasses, and less frequent occupancy of prairie dogs in a given location due to plague epizootics may all contribute to reduced prairie dog effects on vegetation structure. In this study, we focused on spatial variation but ignored temporal variation. Interannual variation in precipitation influences vegetation structure in the habitat matrix, which likely influences prairie dog effects. Thus, plague, temporal variation, and other factors likely influenced prairie dog effects observed in this study of spatial variation.

Spatial variation in the keystone role of prairie dogs

How does spatial variation in the engineering role of prairie dogs apply to their keystone role? Vegetation volume was lower on than off colonies at all 13 complexes despite spatial variation in the habitat matrix. Colonies occurred as relatively homogenous patches of short, sparse vegetation within a more heterogeneous matrix; thus, prairie dogs increased heterogeneity at the landscape scale. Spatial heterogeneity in vegetation structure is a key factor contributing to diverse faunal communities, and has been closely linked to habitat for grassland and shrubland birds (Fuhlendorf et al. 2006, Derner et al. 2009).

Spatial variation in prairie dog effects likely affects associated fauna. For example, the mountain plover *Charadrius montanus* is a grassland bird species that breeds in areas with short, sparse vegetation. In sagebrush steppe, where bare ground cover already is high in the vegetation matrix, mountain plovers can be found in areas both with and without prairie dog disturbance (Plumb et al. 2005). In contrast, where the vegetation matrix is more dense, mountain plovers occur at higher densities (shortgrass steppe, Augustine 2011) or almost exclusively (northern mixed prairie; Dinsmore et al. 2005) on prairie dog colonies.

Shifts in vegetation structure induced by prairie dogs may also influence small mammal (Stapp 2007, Cully et al. 2010), large mammal (Krueger 1986), arthropod (Davidson and Lightfoot 2007), and herpetofaunal communities (Kretzer and Cully 2001). Specifically, Cully et al. (2010) found BTPDs consistently altered rodent species composition at many of the same complexes as in our study, with effects that varied along latitudinal and longitudinal gradients. In addition to effects on vegetation structure, prairie dogs affect associated species via development of burrow systems and serving as prey for a variety of species. Placed in context with previous prairie dog research, our large-scale study shows that spatial variation in how prairie dogs modify vegetation structure should be considered as one of several interacting effects that underlie spatial variation in the keystone role of prairie dogs.

Spatial variation in other ecosystem engineers

Given observed spatial variation in vegetation modification by prairie dogs, what patterns can be predicted for other ecosystem engineers? Colonial, burrowing herbivores occur on most continents, and like prairie dogs, are often considered ecosystem engineers. In Argentina, the plains vizcacha *Lagostomus maximus* is a colonial, burrowing rodent of semiarid scrub and grassland that decreases height and cover of grasses and shrubs, increases forb cover, and provides habitat for associated species (Branch et al. 1996). In Mongolian steppe, the colonial, burrowing Siberian marmot *Marmota sibirica* creates distinct patches within the grassland matrix, increasing complexity at the landscape scale (Van Staalduinen and Werger 2007). In Europe, the warrens and grazing activities of European rabbits *Oryctolagus cuniculus* increase plant heterogeneity and species richness (Gálvez-Bravo et al. 2011). In Australia, the burrowing bettong *Bettongia lesueur* is a colonial, burrowing marsupial that formerly was widespread and abundant in semi-arid and arid mainland. Before declining in abundance, they reduced shrub encroachment and likely altered vegetation structure in ways similar to prairie dogs (Baker and Noble 1999).

As with prairie dogs, we may expect to find spatial variation in vegetation modification by these species, which in turn is linked to their keystone effect on associated taxa. Our findings provide a baseline to evaluate variation among and within species relative to effects on vegetation structure in different ecosystems. Given similarities in engineering and keystone roles among colonial, burrowing herbivores across continents, and spatial variation in how prairie dogs modify vegetation structure, we suggest understanding spatial variation is critical to fully understanding the engineering and keystone effects of many other species.

Conclusions

We found that BTPD effects on vegetation structure in northern mixed prairie cannot be consistently extrapolated to other ecoregions or prairie dog species. Black-tailed prairie dog effects on grass cover and bare ground were less in shortgrass steppe and Colorado Plateau grassland than in northern mixed prairie. This may be explained by the dominance of grazing-tolerant shortgrasses in the matrix vegetation of shortgrass steppe and Colorado Plateau versus the dominance of taller-structured perennial grasses in northern mixed prairie. With respect to variation among prairie dog species, where shrubs occur in the matrix vegetation, shrub cover was consistently lower on BTPD colonies but not WTPD colonies. Differences may be due to greater burrow densities of BTPDs and their behavior of cutting shrubs to enhance visibility. In spite of spatial variation in their effects, all 3 species of prairie dog significantly reduced vegetation volume in all 5 ecoregions. We suggest that future efforts to understand prairie dog effects focus on sagebrush

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