

Direct and indirect effects of a keystone engineer on a shrubland-prairie food web

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Abstract. Keystone engineers are critical drivers of biodiversity throughout ecosystems worldwide. Within the North American Great Plains, the black-tailed prairie dog is an imperiled ecosystem engineer and keystone species with well-documented impacts on the flora and fauna of rangeland systems. However, because this species affects ecosystem structure and function in myriad ways (i.e., as a consumer, a prey resource, and a disturbance vector), it is unclear which effects are most impactful for any given prairie dog associate. We applied structural equation models (SEM) to disentangle direct and indirect effects of prairie dogs on multiple trophic levels (vegetation, arthropods, and birds) in the Thunder Basin National Grassland. Arthropods did not show any direct response to prairie dog occupation, but multiple bird species and vegetation parameters were directly affected. Surprisingly, the direct impact of prairie dogs on colony-associated avifauna (Horned Lark [*Eremophila alpestris*] and Mountain Plover [*Charadrius montanus*]) had greater support than a mediated effect via vegetation structure, indicating that prairie dog disturbance may be greater than the sum of its parts in terms of impacts on localized vegetation structure. Overall, our models point to a combination of direct and indirect impacts of prairie dogs on associated vegetation, arthropods, and avifauna. The variation in these impacts highlights the importance of examining the various impacts of keystone engineers, as well as highlighting the diverse ways that black-tailed prairie dogs are critical for the conservation of associated species.

Key words: arthropod; black-tailed prairie dogs; Brewer's Sparrow; grassland; keystone species; Mountain Plover; structural equation modeling; trophic interaction; Western Meadowlark.

INTRODUCTION

Ecosystem engineers, or species that physically alter their environment (Jones et al. 1994), are also considered keystone species if the effects of these alterations on other species are “outsized” relative to the engineer’s abundance (Power et al. 1996, Prugh and Brashares, 2012). Keystone engineering by beavers (Rossel et al. 2005, Law et al. 2017), and burrowing rodents (Prugh and Brashares 2012) is linked with increased biodiversity. Thus, these species are of interest from a conservation standpoint (Mills et al. 1993) and in the study of community dynamics and trophic cascades (Lindeman 1942, Paine 1980, Pace et al. 1999).

The concepts of trophic interactions and trophic cascades have long guided our understanding of community and ecosystem dynamics (e.g., McCann et al. 1998, Kefi et al. 2012, Leroux and Loreau 2015). More recently,

greater attention has been given to more nuanced forms of species interactions among trophic levels, including behaviorally mediated (Winnie 2012) or structurally mediated (DeVore and Maerz 2014) interactions, as well as other non-trophic interactions (e.g., foundation species and some mutualisms; Borst et al. 2018). Integrating both trophic and non-trophic interactions into food web analysis is crucial to characterizing these systems. Because both types of interactions occur simultaneously and non-independently in the case of keystone engineers, we must incorporate both to truly understand their impacts (Sanders et al. 2014).

Social, herbivorous, burrowing mammals, such as black-tailed prairie dogs (*Cynomys ludovicianus*) are considered both keystone species (Paine 1966, Mills et al. 1993) and ecosystem engineers (Jones et al. 1994) because they drive diversity and species associations throughout the world’s arid and semiarid ecosystems (Kotliar et al. 1999, Davidson et al. 2012). However, the ways in which black-tailed prairie dogs specifically affect trophic vs. non-trophic interactions, and the relative importance of these interactions, remain unclear because of the complexity of these impacts. Black-tailed prairie

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dogs live at high densities, making them an ideal prey resource for predators. They continuously clip vegetation to maintain visibility of potential predators within social colonies (Hoogland 1995), creating clear “islands” of short structure habitat within a matrix of taller grasses or shrubs (Lomolino and Smith 2003). Black-tailed prairie dog disturbance is additive across years such that areas colonized for long periods show especially distinct habitat structure and vegetation composition (Garrett and Franklin 1988, Johnson-Nistler et al. 2004, Duchardt et al. 2019). By keeping vegetation in an earlier phenological state, prairie dogs can increase forage quality for herbivores (Connell et al. 2019). However, by reducing biomass, they reduce forage quantity, leading to competition with domestic livestock for forage (O’Meilia et al., Derner 2006). This conflict is especially salient on public lands in the western United States (Holecheck 1981), and finding the balance between the ecological services of prairie dogs and the needs of the ranching industry is an ongoing concern (Miller et al. 2007).

Prairie dogs influence the abundance of predators (Dobson and Lyles 2000, Lomolino and Smith 2004), arthropods (Davidson and Lightfoot 2007), small mammals (Shiple and Reading 2006), herptiles (Shiple and Reading 2006), and birds (Tipton et al. 2008, Augustine and Baker 2013, Duchardt et al. 2019), but the mechanisms driving these relationships are not always clear. Because of myriad ecosystem impacts of prairie dogs, their effects on other organisms can be both direct and indirect. For example, various bird species show strong associations with prairie dog colonies, and this association may be because prairie dogs alter vegetation structure to the shorter vegetation that these birds prefer (an indirect effect mediated by vegetation structure). Alternatively, prairie dogs may cause shifts in vegetation composition, leading to increased abundance of arthropods that are the main food source of these birds (an indirect effect mediated by vegetation composition and arthropod abundance). Another possibility is that prairie dog alarm calls provide birds with information about predator risk (a direct effect of social information), thus increasing habitat quality. Based on the discussion above, we suggest that the main mechanisms by which prairie dogs may directly or indirectly influence other taxa include altering (1) vegetation structure (via clipping vegetation around burrows), (2) vegetation biomass and quality, (3) plant species composition, (4) food resources for predators, (5) the scale and size of vegetation patches, and (6) social information (Kotliar et al. 1999, Bak et al. 2001, Connell et al. 2018). We built a conceptual model (Fig. 1) to summarize these potential mechanisms, as well as the potential for abiotic factors to mitigate these effects.

When organisms can have complex effects on their environment via a combination of direct and indirect effects, Structural Equation Modeling (SEM) provides a framework to tease apart the ways in which one set of

organisms impacts other groups (Grace 2006). Specifically, SEM allows us to use prior knowledge about ecological systems to assess different hypothesized causal pathways within ecosystems (Grace 2006). As a result, SEM provides a way to describe the most important sets of interactions within an ecosystem and to test specific hypotheses about the direct and indirect effects that link organisms. We used an SEM approach to (1) describe the ways in which black-tailed prairie dogs (*Cynomys ludovicianus*) impact plant communities, vegetation structure, arthropod abundance, and bird species abundance in a grassland–shrubland landscape and (2) to test specific hypotheses about how the effects of prairie dogs on birds may be mediated by vegetation structure, plant community composition, or arthropod abundance. At each trophic level (plant communities, arthropods, and birds), we used SEM to compare the competing, but not mutually exclusive, hypotheses of direct and indirect influences of black-tailed prairie dogs. Based on the literature we anticipated that most effects on arthropods would be associated with burrowing and vegetation structure (Davidson and Lightfoot 2007) while birds (specifically non-raptors) would respond mainly to vegetation structure (Augustine and Baker 2013). Conversely, we expected direct effects of prairie dogs on both vegetation structure and community composition (Winter et al. 2002, Johnson-Nistler et al. 2004). In addition to elucidating these ecological mechanisms, this study was also intended to determine those aspects of prairie dog disturbance most critical for associated taxa, an important step in balancing ecological and economic services on public rangelands.

METHODS

Study area

Our study was conducted within the U.S. Forest Service (USFS) Thunder Basin National Grassland in Converse, Weston, and Campbell counties, Wyoming (Fig. 2). Mean annual precipitation ranged from 25 to 35 cm, and generally fell during spring and summer (Porensky et al. 2018). The study area included a mosaic of sagebrush (*Artemisia* spp.) grasslands and prairie dog colonies. In uncolonized areas, shrub species included Wyoming big sagebrush (*A. tridentata wyomingensis*), greasewood (*Sarcobatus vermiculatus*), broom snakeweed (*Gutierrezia sarothrae*), and other sagebrush species. Common graminoids included blue grama (*Bouteloua gracilis*), western wheatgrass (*Pascopyrum smithii*), Sandberg’s bluegrass (*Poa secunda*), needle-and-thread (*Heterostipa comata*), and threadleaf sedge (*Carex filifolia*). Prairie dog colonies were dominated by western wheatgrass, plains prickly pear (*Opuntia polyacantha*), and short-lived forb species.

In 2017, the total extent of prairie colonies on the public lands within our study area was >16,000 ha, which at the time represented the largest known colony

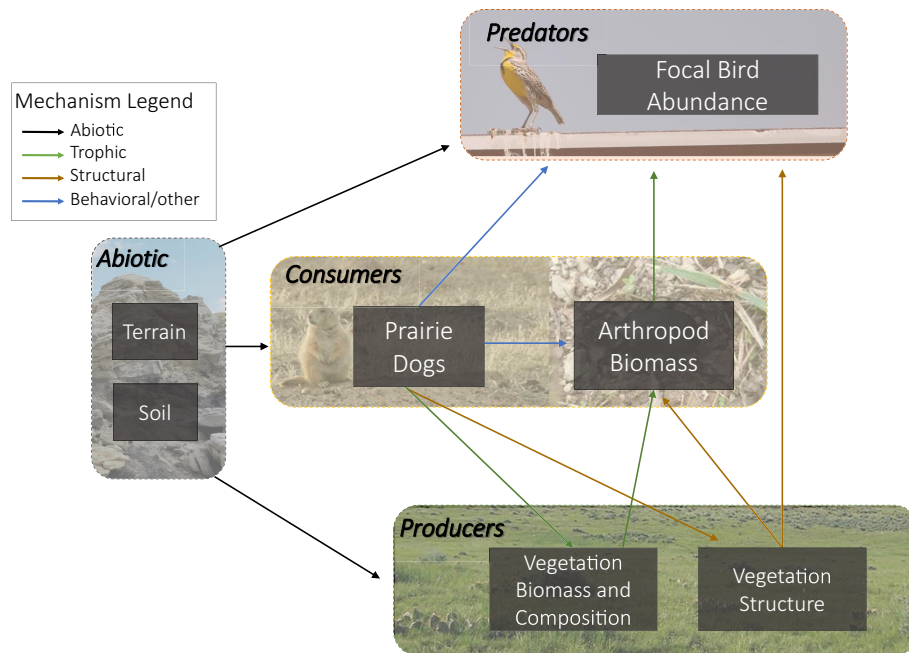


FIG. 1. Conceptual model of potential connections between multiple trophic levels and abiotic landscape features in the Thunder Basin National Grassland of northeastern Wyoming. Arrows indicate potential causal links. [Color figure can be viewed at wileyonlinelibrary.com]

complex in the world. Individual colonies ranged from 20 ha to 4,000 ha in size, the latter of which is an order of magnitude larger than prairie dog colonies typically found on National Grasslands in the western Great Plains over the past two decades (see Cully et al. 2010 and Johnson et al. 2011). This wide range in prairie dog colony size over space and time within our study area provided a unique opportunity to examine how colony distribution and size influences ecosystem dynamics.

Study design

To assess plant, insect, and bird responses to prairie dog disturbance, we used a point-transect-based sampling design (Fig. 2). We collected data at points along transects established for a multi-year study of songbird responses to prairie dogs (Duchardt et al. 2018, 2019). Transects were stratified into three groups: (1) “colony core” transects, which were randomly placed with the constraint that transects fell entirely within prairie dog colonies; (2) “sagebrush” transects, which were located non-randomly in 10 known areas of extensive sagebrush habitat; and (3) “colony edge” transects, which were randomly located with the requirement that transects crossed the edge of a prairie dog colony. For this project, we sampled at 35 transects, including 7 colony core transects, 21 edge transects, and 7 sagebrush transects. Along each transect, we sampled at one to three points selected from each transect to maximize variability in colony age and distance to colony edge. When selecting “edge”

points we ensured that at least one point was located outside the colony, while one or two were within the colony to ensure a fairly equal distribution of points inside and outside colonies. All points were separated by a minimum distance of 250 m.

Data collection

Prairie dog occupancy data.—Prairie dog colony boundaries were partially or fully mapped in the Thunder Basin each fall by the USFS and partners since 2001. Disturbance by black-tailed prairie dogs differs from many other sources of biotic or abiotic disturbance in that it is continuous and additive, for example, areas that have been colonized for 10 yr generally differ in terms of vegetation structure and composition from those colonized for 2 yr (Garrett and Franklin 1988, Johnson-Nistler et al. 2004). As such, we generated a metric of colony age for each point based on the first year it was within the mapped prairie dog colony boundaries.

We calculated distance to colony edge and used it as a metric of spatial distribution of prairie dog disturbance. We used mapped colony layers from 2016 to represent colony habitat in 2017, because most colony growth occurs in summer and early fall (Garrett and Franklin 1988, Milne-Laux and Sweitzer 2006), and our data were collected in the spring. Concurrent with biomass data collection (see Plant biomass data), we counted all prairie dog burrows at least partially within 4 m of the biomass transect (8 m wide × 30 m long belt). We

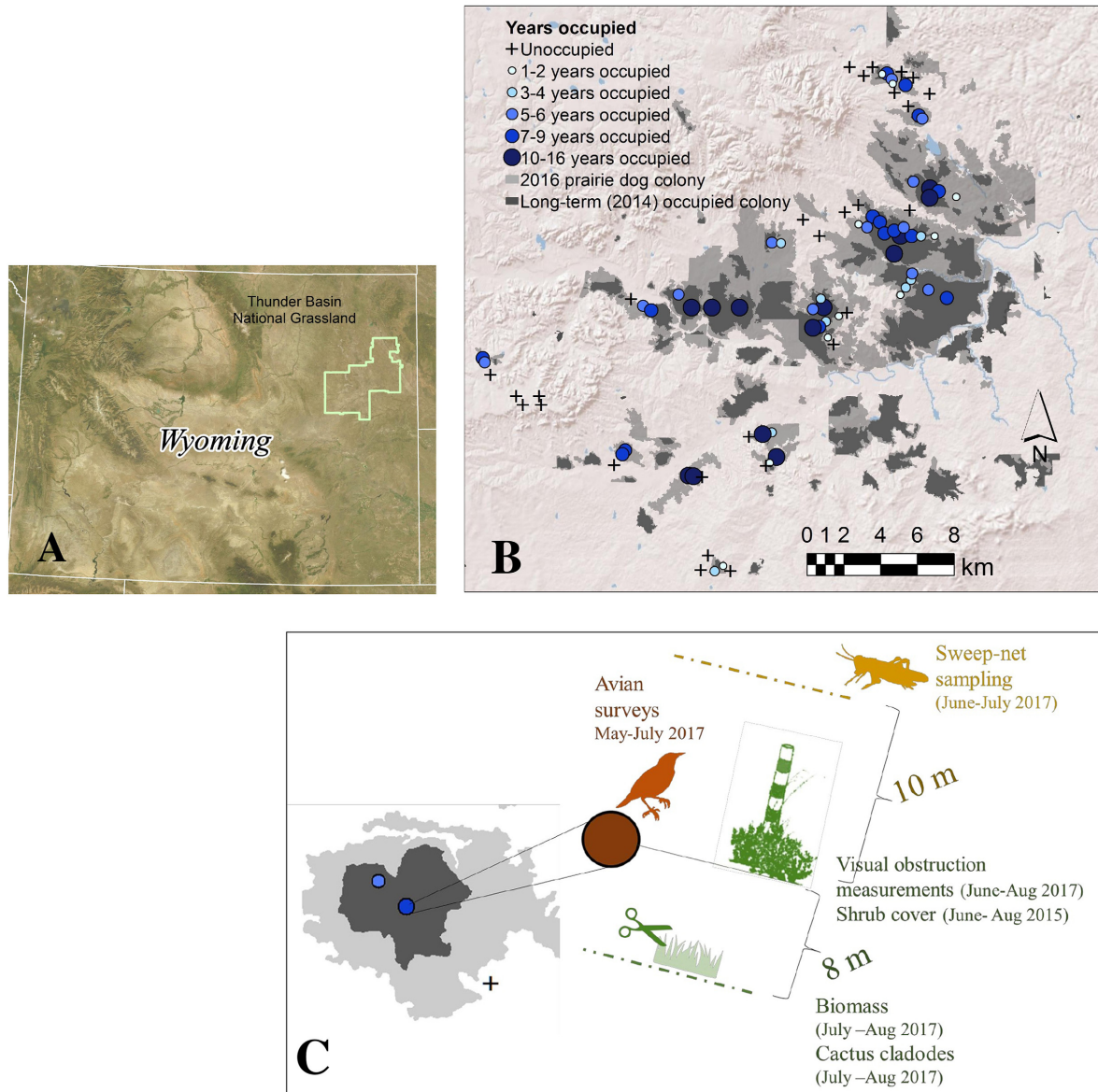


FIG. 2. Landscape-scale sampling design. (A) Location of Thunder Basin National Grassland within Wyoming, USA. (B) Sampled sites ($n = 88$) in the $\sim 400\text{-km}^2$ study area in Thunder Basin National Grassland. Shading of dots indicates the presence of prairie dog, and tan regions on the map are the outline of mapped prairie dog colonies. (C) Sampling design within each site, for estimating bird abundance, plant communities, plant structure, and arthropod biomass. [Color figure can be viewed at wileyonlinelibrary.com]

recorded burrows as either active or inactive based on presence of fresh scat, fresh diggings, or (for inactive burrows), the presence of spider webs and overgrown vegetation at the burrow entrance (Biggins and Miller 1993). We used these density data to calculate active and total burrows per hectare.

Because of moderate to high collinearity among four measures relating to prairie dogs (active prairie dog burrow density, total prairie dog burrow density, colony age, and distance to edge; Appendix S1: Table S1), we used detrended correspondence analysis (DCA) to identify two orthogonal axes of prairie dog impact. These two

axes (DCA1 and DCA2) accounted for 87% of variation in prairie dog measures, with DCA1 accounting for 71% and DCA2 accounting for 16%. DCA1 was related to active prairie dog burrows and, to a lesser extent, total prairie dog burrows (Appendix S1: Table S2). DCA2 was related to burrow densities as well as colony age (Appendix S1: Table S2). Thus, these two variables are hereafter referred to as prairie dog activity (DCA1) and prairie dog occupation intensity (DCA2).

Avian data.—We surveyed the avian community at each point twice between late May and late June 2017. During

each 6-minute count, we recorded all species detected from the survey point. We recorded the distance and direction of each detection to facilitate distance sampling. Surveys occurred between 30 minutes before sunrise and 10:00 on days without high wind or rain (Pavlacky et al. 2017). By traveling to a subset of points via off-road vehicle, we ensured more effective detection of Mountain Plovers (*Charadrius montanus*), which display cryptic behavior in response to observers on foot (Dinsmore 2003). To adjust for detectability, we modeled avian abundance using Program DISTANCE (version 6.0) for five focal species: Mountain Plover, Horned Lark (*Eremophila alpestris*), Western Meadowlark (*Sturnella neglecta*), Lark Bunting (*Calamospiza melanocorys*), and Brewer's Sparrow (*Spizella breweri*). These species represent a range of preferred habitat types (shortgrass, midgrass, sagebrush) and conservation priority. For more detailed survey and adjustment methods, see Duchardt et al. (2019).

Vegetation structure data.—We measured vegetation structure at each survey point in June–July 2017, following bird point counts. Line-point intercept data were collected every 1 m along 30-m transects radiating from each point, perpendicular to the axis of the point count transect (Fig. 2; Herrick et al. 2009). These data consisted of basal hits for vegetation, bare ground, and litter. We measured visual obstruction, a metric incorporating both vegetation height and density, using a Robel pole (Robel et al. 1970) at 5-m increments along transects. In 2015, we collected shrub cover data along these transects using the line-intercept method (Herrick et al. 2009). Because shrub canopy cover likely varies minimally over 2 yr, we used these data to calculate percent cover of shrubs at each point in 2017.

Plant biomass data.—From July to August 2017, we established an additional 30-m transect parallel to and 8 m away from the vegetation structure transect (Fig. 2). At 10 and 20 m along this new transect, we placed a 0.5 × 1 m quadrat on the side of the tape facing away from the established vegetation structure transect. We recorded all species rooted inside each 0.5 × 1 m quadrat, then clipped all herbaceous biomass rooted inside the quadrat by functional group. Functional group assignments were based on the USDA plants database (USDA 2019) and included C₃ perennial graminoids, C₄ perennial grasses, native annual grasses, annual *Bromus* spp. (Japanese brome, *B. arvensis* and cheatgrass, *B. tectorum*), short-lived (annual or biennial) forbs, perennial forbs, and subshrubs. For cacti (mostly *Opuntia polyacantha*), we did not clip, but we recorded the number of cactus cladodes rooted within each quadrat.

Arthropod data.—We sampled arthropods along a 30-m transect that was located parallel to and 10 m away from the vegetation structure transects at each point (Fig 2). Arthropod collection occurred between 20 June and 5

July 2017, and samples were collected between 11:00 and 16:00 during periods of fair weather with low (<20 km/h) wind speeds. Arthropods along each transect were collected using sweep samples, completing 60 sweeps per 30-m transect resulting in a sampling of roughly 60 m² of vegetation. Arthropods were killed, and total dry biomass was weighed separately for grasshoppers and other arthropods. Because wind speed may affect detectability or capture rate of arthropods, we recorded wind speed (using a handheld anemometer) at each point and found it to be unrelated to arthropod biomass sample (Pearson's correlation, $r = -0.02$, $n = 84$, $P = 0.84$).

Topography and soils data.—We quantified topography within 100 m of each point. We chose this 100-m scale as it was large enough to capture variation in these variables within a “territory scale” for most focal bird species, but also small enough to minimize overlap between adjacent point-count locations. We used a digital elevation model to generate a topographic roughness index (roughness) and topographic wetness index (TWI; Gesch 2007, Porensky et al. 2018).

We collected soil cores at 10 and 20 m along each biomass transect. We used a standard soil auger (7 cm diameter) and took a composite sample of soil from 0 to 10 cm depth. Samples from the two cores per transect were pooled and a subsample of the homogenized material was extracted for texture analysis. Subsamples were air dried and passed through a 2-mm sieve. Soil particle size was determined using the hydrometer method (Bouyoucos 1962).

Data analysis

We used structural equation modeling (SEM) analysis to consider the effects of prairie dogs on three trophic levels: plants, arthropods, and birds. We used this model to parse out indirect and direct effects of prairie dogs, as well as trophic (consumptive) vs. structural or behavioral (non-consumptive) effects of prairie dogs. To begin the process of SEM, we created an SEM meta-model (Grace et al. 2010), which represents our hypothesized causal links relating prairie dog impact to aspects of vegetation, arthropods, and birds (Fig. 1, Appendix S1: Table S3). Our meta-model made the following assertions to limit the possible hypotheses linking impacts of prairie dogs to other organisms: (1) prairie dogs may have direct impacts on any trophic level via trophic interactions with plants, and behavioral interactions with arthropods and birds; (2) with the exception of prairie dog impacts on vegetation, top-down control of energy flow in this system is minimal, such that, in the time frame of this study, arthropod abundance does not affect vegetation abundance, nor does bird abundance affect arthropod abundance; (3) prairie dogs may impact total vegetation biomass, composition (biomass of particular plant groups), and vegetation structure; vegetation biomass and composition in turn affect arthropods as a food

resource, while vegetation structure affects arthropods and birds as habitat structure; (4) to account for collinearity with abiotic environment, aspects of abiotic environment (terrain ruggedness, TWI, and soils) can affect prairie dog impact as well as each of the other trophic levels; and (5) we concentrated on understanding links between trophic levels, and allowed for unexplained covariation between variables within trophic levels (plants, arthropod, and birds).

Using this approach, we constructed a full model that contained all causal links described above (Appendix S1: Table S4). We used the R package *lavaan* (Rosseel 2012) to fit and assess structural equation models using maximum likelihood estimation. The full model poorly fit the data (Appendix S1: Table S4). We reduced the full model using an iterative process of removing links that lacked statistical support ($P > 0.1$). During this process, we observed that grasshopper biomass and cactus cladode density were uncorrelated with any other variable in the model, so these variables were removed. We then calculated modification indices of links that were not in the reduced model, which may suggest missing causal links that are important to explaining the data. The modification index for an effect of invasive bromes (BROME) on the abundance of Western Meadowlarks (WEME) was 6.02, suggesting that this link might improve the fit of the model to the data (Grace 2006). Retention of this link improved fit to the data above a reduced model that lacked this link (reduction of model χ^2 of 7.2), so, despite its absence from our initial meta-model (Fig. 1), we added an effect of invasive bromes on Western Meadowlarks as a novel hypothesis about the habitat for this generalist grassland bird species. In order to assess the effects of small sample size to model estimates, we compared the reduced model parameters estimated by maximum likelihood in *lavaan*, to those of the same model estimated with Bayesian techniques that are more robust to small sample sizes using the R package *blaavan*. Estimates using *blaavan* did not differ substantially (on average <1%) from those obtained using maximum likelihood estimation, so we report maximum likelihood results from *lavaan*.

We then tested three hypotheses about mediation in this system: (1) that the effect of prairie dogs (DCA1) on each of the five bird species was mediated by prairie dog impacts on vegetation structure (ROBEL, SHRUB COVER, BARE GROUND); (2) that the emergent effect of invasive brome grasses on Western Meadowlark was mediated by the impacts of brome grasses on arthropod biomass; and (3) that the effect of prairie dogs on arthropod biomass was mediated by prairie dog impacts on visual obstruction and brome grasses. To do this, we constructed a model that included all links needed to test whether a causal link was fully mediated, partially mediated, or not mediated by a third factor (Grace 2006). Because many links that are implicit in our hypotheses of mediation were removed in the model reduction process, this involved adding those links back

to the model to test explicitly for mediation. We assessed the evidence for hypotheses of full mediation ($A \rightarrow B \rightarrow C$), partial mediation ($A \rightarrow B \rightarrow C$; $A \rightarrow C$), and no mediation ($A \rightarrow C$) in two ways: (1) by comparing path coefficients of $A \rightarrow B \rightarrow C$ vs. $A \rightarrow C$ in a model that allowed for partial mediation and (2) assessing the difference in Akaike Information Criterion corrected for sample size (ΔAIC_c ; Burnham and Anderson 2002) between global SEMs that included full mediation, partial mediation, or no mediation of a given hypothesis.

RESULTS

Measures of prairie dog abundance were not strongly correlated with total plant biomass (Figs. 3a, 4); however, we observed a trade-off where burrow density was positively correlated with forb biomass and negatively correlated with grass biomass (Fig. 3a), reflecting a dramatic shift in biomass composition with increasing prairie dog disturbance. Common graminoid species included the perennials *P. smithii*, *B. gracilis*, and *P. secunda* and the annual *Vulpia octoflora*. Other common species included the perennial forbs *Sphaeralcea coccinea* and *Phlox hoodii*, the annual forbs *Plantago patagonica*, *Chamaesyce glyptosperma*, and *Salsola tragus*, and the cactus *O. polyacantha*. Like other graminoid species, biomass of nonnative annual brome species was lower on prairie dog colonies (Fig. 4).

The most common non-grasshopper arthropods collected were leafhoppers and plant hoppers (Cicadellidae and Fulgoridae; 31%), wasps/bees/ants (23%), plant bugs (Miridae; 10%), flies (8%), and spiders (2%). Non-grasshopper arthropods were correlated with multiple variables including visual obstruction (Fig. 3f). Although grasshopper biomass was not correlated with other variables and thus were not used in analyses, the most common species were *Trachyrhachys kiowa* (26%), *Melanoplus sanguinipes* (15%), *Cordillacris occipitalis* (14%), and *Psoloessa delicatula* (13%; (I. S. Pearce et al., unpublished manuscript). Western Meadowlarks were the most abundant bird species in our study, with 335 observations off-colony and 213 observations on prairie dog colonies. Brewer's Sparrows and Lark Buntings were also more abundant off prairie dog colonies (80% and 77% of observations, respectively). Conversely, Mountain Plovers and Horned Larks were more abundant on prairie dog colonies (96% and 84% of observations, respectively); both species were especially correlated with one component of DCA1, prairie dog burrow density (Fig. 3e).

Structural equation model

We created a structural equation model to explore the important causal links among prairie dogs, vegetation structure, vegetation composition, arthropods, and birds (Fig. 4). The reduced structural equation model of the prairie dog ecosystem, estimated as described above, had 83 degrees of freedom (Fig. 4). The reduced model had

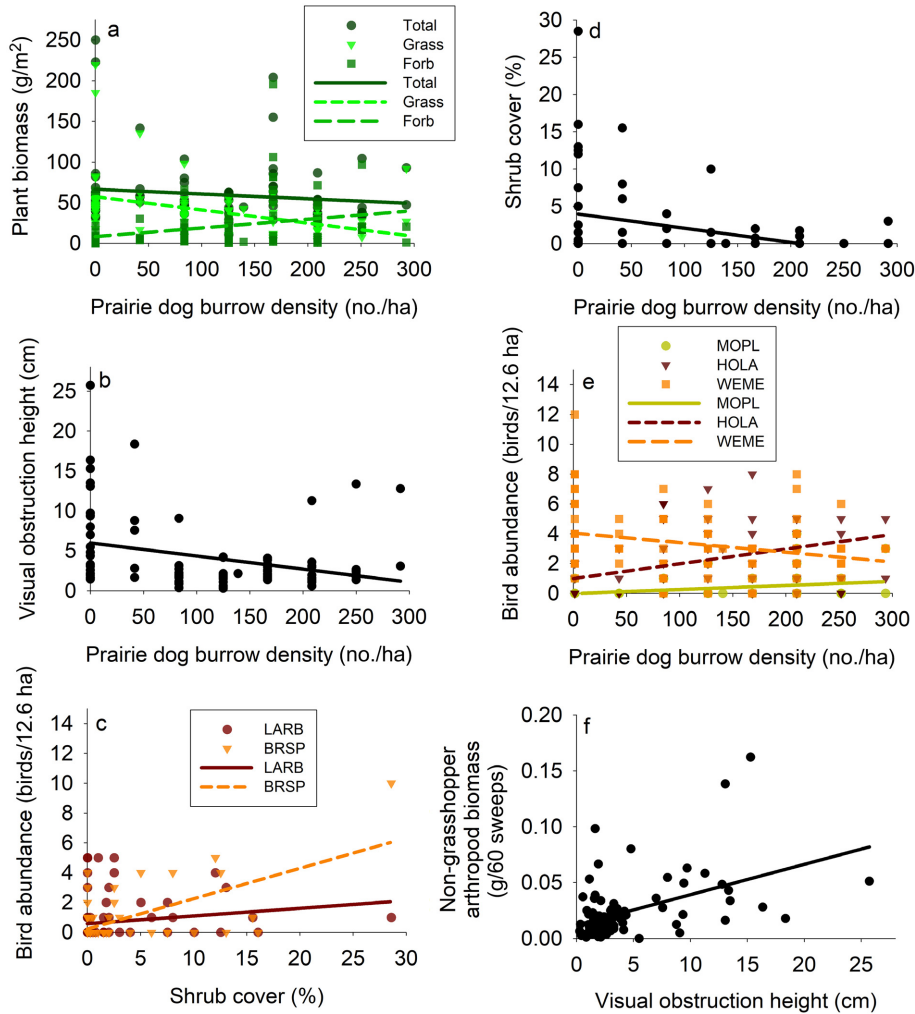


Fig. 3. Correlation structures between covariates in the Thunder Basin National Grassland in 2017. Panels A, B, D, and E represent correlation between total (active and inactive) prairie dog burrow density and plant biomass, visual obstruction, shrub cover, and three bird species, respectively. Panel C shows the correlation between shrub cover and density of two bird species, while panel F depicts the correlation between non-grasshopper arthropod biomass and visual obstruction. Lines represent simple bivariate relationships, though the structural equation modeling (SEM) analysis incorporates more complex correlation structures. [Color figure can be viewed at wileyonlinelibrary.com]

a good fit to the data, where χ^2 estimates indicated goodness of fit ($\chi^2 = 73.1, P = 0.77$) as did all alternative goodness of fit measures reported in lavaan. The model accounted for a high proportion of variation in some aspects of the prairie dog ecosystem (e.g., Horned Lark abundance, $R^2 = 0.53$), but only a small amount of variation in other aspects (e.g., bare ground $R^2 = 0.04$). We also note that while abiotic effects were incorporated in the model because they are known to impact relationships at multiple trophic levels, we do not discuss abiotic effects at length here. However, soil and topography had moderate to strong effects on prairie dog colonies as well as vegetation structure and community composition (Appendix S1: Table S5). Although our main focus was not on elucidating abiotic relationships, we note that

prairie dog burrows were more abundant at sites with smoother terrain (Appendix S1: Table S5).

Prairie dogs affected aspects of vegetation structure, vegetation community, and bird abundance (Figs. 3, 4). Effects of prairie dog activity (DCA1) were consistently greater than those of prairie dog occupation intensity (DCA2), and the effects of these two components of prairie dog footprint on the ecosystem were always in the same direction (Fig. 4). Prairie dog occupancy was related to reduced vegetation structure (shrub cover and Robel measurements; Fig. 3b and d, Fig. 4) and a shift in biomass composition from grasses to forbs, while having no impact on total plant biomass (Fig. 3a). Prairie dog disturbance was linked with increased abundance of Horned Larks (HOLA) and Mountain Plovers (MOPL),

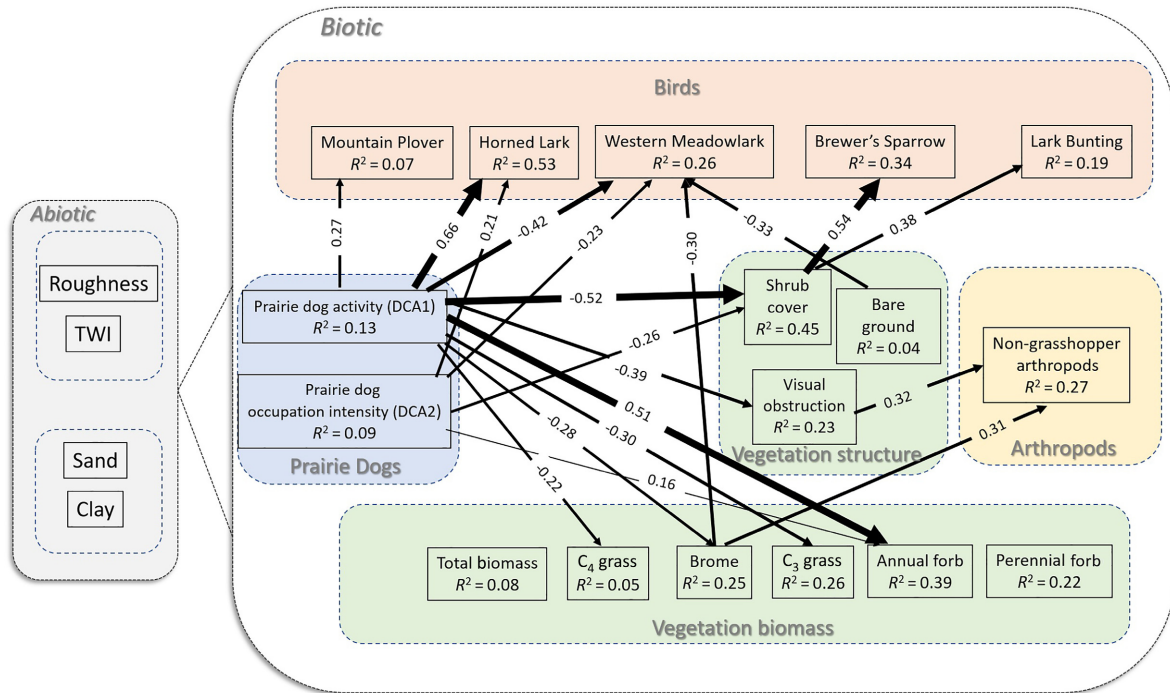


FIG. 4. Path diagram for the best structural equation model explaining biotic interactions. Connections between abiotic effects, shown in gray, and other model components are detailed in Table S4. Two parameters, grasshopper abundance and cactus cladode density, were removed during the model selection process. [Color figure can be viewed at wileyonlinelibrary.com]

and decreased abundance of Western Meadowlarks (WEME; Figs. 3e, 4).

Vegetation structure and community had variable direct effects on arthropod biomass and bird species. Higher Robel readings (indicating taller and denser vegetation) were correlated with increased non-grasshopper arthropod abundance (Fig. 3f), and higher shrub cover increased the abundance of the two sage-steppe associated bird species (Figs. 3c, 4). Western Meadowlarks were less abundant at sites with high bare ground cover (Fig. 4). We found two unexpected direct effects of invasive annual brome grasses (Fig. 4). Bromes increased the presence of non-grasshopper arthropods (Fig. 4), and no other aspect of vegetation community or biomass affected arthropod biomass. Bromes had a negative effect on the abundance of Western Meadowlark, a generalist grassland bird (Fig. 4). Arthropod abundance did not affect the abundance of any bird species.

Tests of mediation

The SEM suggested several important indirect interactions within the prairie dog ecosystem, and it also suggested several unexpected direct effects. Therefore, we conducted explicit tests of mediation to address three questions:

1. Are the effects of prairie dogs on each of the five bird species mediated by their reduction of vegetation

structure (as measured by sage cover, Robel index of visual obstruction, and low cover of bare ground)? We found strong evidence that the negative effects of prairie dogs on the abundance of sage-steppe-associated bird species (Brewer's Sparrow and Lark Bunting) were mediated by decreased shrub cover (Table 1). However, the model retained only direct effects of prairie dogs on grassland-associated bird species (positive effect on Mountain Plover and Horned Lark, and negative effect on Western Meadowlark; Table 1).

2. Is the emergent negative impact of invasive brome grasses on Western Meadowlarks mediated by arthropods? In our initial meta-model (Fig. 1), we did not anticipate direct effects of plant composition on bird species abundance. However, in the modeling process, it was apparent that the sites with abundant invasive brome grasses tended to have fewer Western Meadowlarks, so this link was added to the final model. A test of mediation suggested that this effect was not mediated by changes in arthropod abundance with increasing brome grasses (Table 1).
3. Are the effects of prairie dogs on arthropod biomass mediated by their impacts on vegetation structure and plant communities? The negative effects of prairie dogs on arthropods were fully mediated by prairie dog effects on visual obstruction and invasive brome grasses (Table 1).

TABLE 1. Tests of mediation to support direct and indirect effects in the prairie dog food web.

Question	Path coefficients					ΔAIC _c			Conclusion		
	Mediating variable (A→B→C)					Not mediated (A→C)	Fully mediated	Partially mediated		Not mediated	
1. Mediation of prairie dog effects on birds	Bare ground	Robel	Shrub cover	Arthropods	Brome						
Is the effect of prairie dogs on Lark Bunting mediated by vegetation structure (bare ground, Robel, and shrub cover)?	-0.01	0.08	-0.19**			-0.09	0	4.8	6.7	fully mediated by shrub cover	
Is the effect of prairie dogs on Brewer's Sparrow mediated by vegetation structure (bare ground, Robel, and shrub cover)?	0.06	-0.03	-0.23**			-0.04	0	4.8	44.7	fully mediated by shrub cover	
Is the effect of prairie dogs on Western Meadowlark mediated by vegetation structure (bare ground, Robel, and shrub cover)?	-0.05	-0.02	-0.04			-0.38**	18.7	17.7	0	not mediated	
Is the effect of prairie dogs on Horned Lark mediated by vegetation structure (bare ground, Robel, and shrub cover)?	0.01	0.03	0.03			0.60**	51.7	13	0	not mediated	
Is the effect of prairie dogs on Mountain Plover mediated by vegetation structure (bare ground, Robel, and shrub cover)?	0.01	-0.03	0.01			0.26**	14.4	14.8	0	not mediated	
2. Mediation of vegetation effects on birds											
Is the effect of invasive brome grasses on Western Meadowlark mediated by arthropods?				0.04		-0.36	7.1	6	0	not mediated	
3. Mediation of prairie dog effects on arthropods											
Is the effect of prairie dogs on arthropods mediated by vegetation height (Robel) and invasive brome grass?		-0.12**				-0.09**	-0.02	0	7.9	13.1	fully mediated by vegetation height and brome

Note: ΔAIC_c, change in the Akaike information criterion corrected for sample size.
 ** $P < 0.001$, * $P < 0.05$.

DISCUSSION

Our structural equation model representing interactions within a prairie dog ecosystem confirmed several long-held expectations about this system and suggested some novel hypotheses about how prairie dogs interact with plants, arthropods, and birds. Broadly, prairie dogs influenced all trophic levels either directly (shortgrass bird species as well as vegetation composition and structure) or indirectly via effects on vegetation (sagebrush bird species and arthropod abundance). The strong

relationships between prairie dogs and multiple trophic levels reinforces the importance of this species as a keystone engineer in rangeland ecosystems.

Direct effects of prairie dogs on vegetation supported previous findings in the literature. Prairie dog disturbance was associated with a shift from C₃ and C₄ perennial graminoids to annual forbs (Fig. 3A; Coppock et al. 1983, Johnson-Nistler et al. 2004) as well as decreased shrub cover (Johnson-Nistler et al. 2004) and visual obstruction (Winter et al. 2002). Because annual forbs provide lower quality livestock forage than perennial

grasses, our findings help explain how prairie dogs can reduce available forage for livestock while also having minimal effects on total herbaceous biomass (Derner et al. 2006, Augustine and Springer 2013, Connell et al. 2018).

These effects of prairie dogs on vegetation in turn influenced both arthropods and sagebrush birds (Fig. 4, Table 1). Non-grasshopper arthropods were more abundant with areas with greater visual obstruction, likely as a function of greater niche space associated with greater vertical structure (MacArthur and MacArthur 1961). Brewer's Sparrows and Lark Buntings, respectively obligate and facultative sagebrush species in this system (Duchardt et al. 2018), decreased in areas with lower sagebrush cover, and thus responded indirectly to prairie dogs.

Other relationships identified in our analyses were more novel. Given the ubiquity in the literature of the importance of bare ground for Mountain Plovers (Knopf and Miller 1994, Goguen 2012, Duchardt et al. 2020), and the evidence that prairie dogs often generate high proportions of bare ground (Johnson-Nistler et al. 2004, Goguen 2012), it may seem extremely surprising that neither of these relationships were included in our final model. Overall, bare ground was poorly characterized in the model ($R^2 = 0.04$), potentially because of extreme heterogeneity across the landscape: for example, bare ground was negatively correlated with topographic wetness index, which varied widely both in colonized and uncolonized areas. Although bare ground has been previously linked to prairie dog disturbance in this system (Duchardt et al. 2019), our analysis was more spatially and temporally restricted and our sample size may not have been adequate to overcome the heterogeneity in this system.

On the other hand, the seeming lack of relationship between vegetation structure and shortgrass birds including Mountain Plover and Horned Lark may also highlight the complex role of prairie dogs in this ecosystem. Although there were weak to moderate correlations between shortgrass bird species and vegetation structure variables (Appendix S1: Table S1), direct correlations between each species and prairie dog activity were much greater (0.66 between horned larks and DCA1, and 0.27 between Mountain Plovers and DCA1). Because the modeling process balances parsimony with characterizing the system, the best model contained only these direct effects. We therefore highlight that these results should not be interpreted to mean that structural variables are unimportant, but rather that prairie dog disturbance encompasses these variables as well as other aspects of habitat quality. In other words, prairie dog disturbance is more than the sum of its observed (or at least typically measured) parts when it comes to shortgrass bird habitat.

Size was another trait of prairie dog colonies that may be important for some associated species (Duchardt et al. 2019); although size was a component of our

measured variable of distance to colony edge, it was not assessed directly here. Another component of prairie dog disturbance that may affect habitat quality for birds is social information provided by prairie dogs (Danchin et al. 2004). For example, social alarm calls that provide information about imminent threats to other prairie dogs may inadvertently benefit other species (Bryan and Wunder 2014). As such, prairie dog colonies may represent safer environments because birds have more information about predator presence and behavior. Other potential mechanisms by which prairie dogs may influence habitat quality warrant further exploration; this includes the role of prairie dog burrow density, which was positively related to the abundance of shortgrass bird species in our study.

Another novel observation in this study was the negative effect of annual brome biomass on Western Meadowlarks. While negative impacts of bare ground on Meadowlarks was expected given their reliance on litter cover for nesting (Davis and Lanyon 2008), the strong negative effect of nonnative bromes was not. Nonnative bromes in this system consist mainly of cheatgrass and field brome. The former is synonymous with poor rangeland quality and linked with altered fire regimes that reduce sagebrush cover in much of the western United States (D'Antonio and Vitousek 1992, Balch et al. 2013, Bradley et al. 2018). While some studies have examined the indirect effects of cheatgrass on sagebrush birds via fire (Knick et al. 2005), studies examining the effects of annual bromes on grassland obligate birds are few. Early research showed little direct response of mid-grass species like Grasshopper Sparrows (*Ammodramus saviarum*) or Western Meadowlarks to cheatgrass (Wiens and Rotenberry 1985) and a similar number of studies indicate avoidance (e.g., Earnst and Holmes 2012) or affinity (e.g., Schuler et al. 1993). Where other relatively thick grasses are available, cheatgrass is likely underutilized because it provides poor material for building large dome nests (Davis and Lanyon 2008), and rapid senescence may make nests more visible to predators.

Finally, we found no relationship between grasshopper biomass and any other variable within the model. The absence of a direct link between birds and grasshopper or other arthropod biomass was in keeping with the literature (Wiens 1974). Although adults of the focal bird species rely on arthropods for 25–100% of their diet in the breeding season and young are provisioned almost entirely with arthropods (Beason 1995, Knopf and Wunder 2020), other studies have also shown a lack of resource limitation in these species during the breeding season and a stronger response to vegetation structure (Wiens 1974, Fisher and Davis 2010). The absence of bottom-up control of grasshoppers was more surprising. We offer two non-mutually exclusive hypotheses to address this lack of relationship. First, this result may be a function of the diversity of grasshoppers in this system: at least 18 species of grasshopper are found in the Thunder Basin, and these species show highly diverse and

often opposing habitat preferences (Pearse et al., *unpublished manuscript*). If different grasshopper species respond inversely to certain habitat traits, this may not have been captured by our guild-level analysis. Second, grasshoppers are notorious for experiencing extreme fluctuations in abundance between years (Gage and Mukerji 1977), and this variability may overwhelm other relationships in the system.

Broader impacts

Across a wide variety of food webs and types of species interactions, there is debate about the relative importance of consumptive and non-consumptive effects of species interactions in food webs (Preisser et al. 2007). In aquatic food webs, the presence of caged predators that cannot attack prey still cause high mortality of prey that exhibit avoidance behaviors (McCauley et al. 2011). In forest ecosystems, deer can reduce the abundance of nonpalatable plants to nearly the same degree as palatable plants due to soil compaction (Heckel et al. 2010). Prairie dogs alter the surrounding vegetation both because they consume plants, and also because they trim vegetation as a defense against predators, the latter of which is a non-consumptive effect (Hoogland 1995). In our study, the resulting lowered vegetation structure and reduction of shrub density reduced nesting habitat for shrub-nesting birds (Brewer's Sparrow) and birds that build dome nests in thicker grasses and litter (Western Meadowlark), while increasing habitat for shortgrass ground-nesters (Mountain Plover and Horned Lark). Some species responded directly to prairie dog disturbance, which we speculate may be an effect linked to colony size or heterospecific social information, the latter of which mitigates the impact of predators. In summary, prairie dogs have profound impacts on shrubland-prairie food webs. Most of these impacts are non-consumptive and involve anti-predator behaviors and habitat preferences.

Understanding how prairie dogs impact other organisms is important because prairie dog colonies are extremely dynamic and landscapes with large proportions of prairie dogs are home to several species of conservation concern, including Mountain Plovers. Our model suggests that some of our intuition about interactions within this system (Fig. 1) was accurate to the degree that it explained variation of species at a landscape scale. In other cases, we show that the effects of prairie dogs on other organisms may be due to mechanisms other than those typically considered and deserve further exploration. Exploring these effects will be especially critical in systems where prairie dogs are controlled either partially or entirely for the purpose of livestock grazing. To examine these possibilities in the future, it will be informative to monitor the prairie dog ecosystem over the boom and bust cycles of prairie dog abundance, incorporating controlled field experiments to identify specific mechanisms of prairie dog disturbance and characterize their impacts on associated species.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.3195/supinfo>

DATA AVAILABILITY

Data are available from the USGS Science Base repository at <https://doi.org/10.5066/P9GI27PX>.