Testing for Thresholds in a Semiarid Grassland: The Influence of Prairie Dogs and Plague

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David J. Augustine,[1] Justin D. Derner,[2] and James K. Detling[3]

Authors are [1]Research Ecologist and [2]Research Leader and Rangeland Scientist, US Department of Agriculture–Agricultural Research Service, Rangeland Resources Research Unit, Cheyenne, WY 82009, and Fort Collins, CO 80526, USA; and [3]Professor Emeritus, Department of Biology and Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523, USA.

Abstract

State-and-transition models for semiarid grasslands in the North American Great Plains suggest that the presence of herbivorous black-tailed prairie dogs (*Cynomys ludovicianus*) on a site 1) creates a vegetation state characterized by increased dominance of annual forbs and unpalatable bunchgrasses and increased bare soil exposure and 2) requires long-term (> 40 yr) prairie dog removal to transition back to a vegetation state dominated by palatable perennial grasses. Here, we examine 1) how the recent history of prairie dog occupancy on a site (1–10 yr) influences the magnitude of prairie dog effects on vegetation composition and 2) how occupancy history affects vegetation dynamics following extirpation of prairie dogs. We used a natural experiment in the shortgrass steppe of northeastern Colorado, USA, where prairie dogs were extirpated from multiple sites during an outbreak of epizootic plague. On sites occupied by prairie dogs for 1–4 yr prior to extirpation, plant cover and composition recovered to conditions similar to unoccupied sites within a single growing season. Larger reductions in perennial C_4 grasses occurred on sites occupied for the prior 7–10 yr compared to sites with shorter occupancy histories (< 6 yr). On sites occupied for the prior 7–10 yr, C_4 perennial grasses recovered after 5 yr following prairie dog extirpation; in addition, C_3 perennial graminoids and forbs remained more abundant (compared to sites with no history of prairie dogs) throughout the 5-yr period. Our findings showcase that prior site occupancy (up to 10 yr) by prairie dogs did not induce irreversible shifts in vegetation state in this semiarid grassland. Rather, vegetation changes induced by prairie dogs represent primarily a phase shift in landscapes where prairie dog populations are regulated by epizootic plague.

Key Words: ecological sites, grazing intensity, resilience, shortgrass steppe, state-and-transition models, western Great Plains

INTRODUCTION

State-and-transition models (STMs) provide a conceptual framework for understanding spatial variation and temporal changes in grassland vegetation as well as implications of management practices and strategies (Westoby et al. 1989; Stringham et al. 2003; Briske et al. 2005, 2008; Bestelmeyer et al. 2009). STMs are founded on the idea that plant communities can undergo transitions that are either readily reversible (referred to as phase shifts) or not readily reversible (referred to as transitions among alternate stable states; Briske et al. 2005). A key challenge in developing STMs is identifying those conditions, processes, and ecological interactions that can result in phase shifts vs. state transitions. The latter are generally linked to an ecological threshold whereby a change in ecosystem conditions past the threshold alters ecological processes that previously would have been capable of reversing the shift (Briske et al. 2008). Examples of such thresholds include changes in fire behavior (e.g., due to shifts in woody vs.

herbaceous vegetation abundance; Van Langevelde et al. 2003; Ansley and Castellano 2006) and loss of surface soil fertility or water-holding capacity (e.g., due to loss of vegetation cover; Suding et al. 2004; van de Koppel and Rietkerk 2004; Chartier and Rotagno 2006; Bestelmeyer et al. 2013). Phase shifts within a vegetation state can occur in response to natural events or management and represent changes that can be readily reversed if the driver causing the phase shift is removed (Briske et al. 2008).

One of the most frequently cited factors inducing transitions among ecological states in grasslands of North America is grazing management (Twidwell et al. 2013). In western North America, existing STMs typically focus on the effects of livestock grazing, particularly with regard to the timing, intensity, and duration of grazing. In some rangelands, the effects of grazing by native herbivores, including colonial, burrowing mammals, can also have dramatic effects on vegetation structure and composition and can additionally have important effects on biodiversity of native plants and vertebrates (Kotliar et al. 1999; Davidson et al. 2012; Augustine and Baker 2013). In the western Great Plains of North America, black-tailed prairie dogs (*Cynomys ludovicianus*) are colonial, burrowing rodents that historically were widespread throughout the region and were ecologically important components of the disturbance regime (Knowles et al. 2002). Although their distribution and abundance have been substantially reduced over the past two centuries, black-tailed prairie dogs have significant effects on vegetation composition and structure where they remain locally abundant (Coppock et al. 1983; Whicker and Detling 1988; Cid et al. 1991; Hartley et

al. 2009; Baker et al. 2013). These effects include decreases in height, cover, and biomass of palatable graminoids together with increases in cover and biomass of forbs, and the magnitude of these changes in vegetation typically increases with the time an area has been occupied by prairie dogs (Coppock et al. 1983; Archer et al. 1987). Because of the importance of these grasslands for livestock grazing, a key issue is the degree and time period over which such effects are reversible following prairie dog removal. Within the range of the black-tailed prairie dog, currently published STMs often include an alternative state characterized by increased bare ground exposure and increased dominance of an unpalatable bunchgrass (red threeawn, *Aristida purpurea* Nutt.) and annual forbs (US Department of Agriculture–Natural Resources Conservation Service [USDA-NRCS] 2007). These STMs suggest the *Aristida*–bare ground state may transition back to rangeland dominated by palatable perennial grasses only through long-term (> 40 yr) prairie dog removal (USDA-NRCS 2007). However, few empirical data are available to support these predictions.

Given the importance of such models for informing rangeland management and policy, empirical studies that assess temporal and spatial variation in plant communities in order to test the assumptions of STMs are clearly needed (e.g., Bagchi et al. 2012; Bestelmeyer et al. 2013). Here, we examine 1) how the recent history (previous 10 yr) of prairie dog occupancy influences the magnitude of prairie dog effects on vegetation composition in the shortgrass steppe of Colorado, USA, and 2) how occupancy history affects vegetation dynamics over a 5-yr period following the local extirpation of prairie dogs by an epizootic plague event. To address the first objective, we examined how variation in plant community composition was related to variation in the number of years that prairie dogs had occupied a site. To address the second objective, we quantified temporal dynamics in the abundance of four plant functional groups (C4 perennial grasses, C3 perennial graminoids, annual forbs, and perennial forbs) and changes in the spatial pattern of plant cover over time following prairie dog extirpation.

METHODS

Study Area
We conducted this study in native shortgrass steppe at the Central Plains Experimental Range approximately 12 km northeast of Nunn, Colorado, USA (lat 40°50′N, long 104°43′W). Long-term mean annual precipitation is 340 mm, and mean annual precipitation during the growing season (April–August) is 242 mm. During 2004–2011, annual precipitation was 293, 370, 301, 350, 330, 436, 360, and 356 mm, respectively, and growing season precipitation was 169, 250, 158, 216, 240, 352, 285, and 245 mm, respectively.

Soils consist of very deep, well-drained, fine sandy loams to loamy sands on convex alluvial flats and upland plains. Two C_4 grasses (*Bouteloua gracilis* [Willd. Ex Kunth] Lag. ex Steud and *B. dactyloides* [Nutt.] J. T. Columbus) dominate the vegetation (> 80% of aboveground net primary production); *Opuntia polyacantha* Haw. is an important succulent plant, and *Sphaeralcea coccinia* [Nutt] Rydb. is the dominant forb (Milchunas et al. 2008). Plant nomenclature follows the USDA

PLANTS database (USDA-NRCS 2014). All research occurred in pastures with no known history of crop cultivation. Pastures were grazed by cattle at moderate stocking rates (~ 0.60 animal unit months $\cdot$ ha^{-1}) each year from 15 May to 1 October, where an animal unit month was defined as the equivalent of a 454-kg livestock unit grazing for 30 d. Previous work showed that cattle at this site graze on prairie dog colonies in proportion to their availability within the landscape (Guenther and Detling 2003).

Study Design
We used a natural experiment created by the annual expansion of prairie dog colonies in our study area during 1997–2006 followed by rapid extirpation of prairie dogs from the colonies due to epizootic plague during the fall and winter of 2006–2007. We studied four prairie dog colony sites. The outermost boundaries of these colonies were mapped annually using global positioning system technology beginning in 1997 and continuing until 2011, with the exception that colonies were not mapped in 1998, 1999, or 2001. Mapping of colony boundaries followed methods described by Sidle et al. (2012). Colony expansion primarily occurred during 2000–2006; sizes were 8, 12, 18, and 31 ha in 2000 and expanded to 129, 200, 244, and 245 ha, respectively, in 2006. During September 2006–April 2007, the area occupied by prairie dogs at these four colonies declined rapidly by > 95%, indicative of an epizootic outbreak of plague caused by the bacterium *Yersinia pestis*. Plague is the only disease known to cause such contractions in colony size over such a short time period, and past research in our study areas has documented that such rapid, extensive colony contractions are the result of plague (Stapp et al. 2004; Antolin et al. 2006; Savage et al. 2011).

During May and June 2007, we used the annual maps of colony boundaries to identify five prairie dog occupancy history categories in each pasture: 1) areas occupied by prairie dogs prior to 2000 (7–10 yr of occupancy prior to plague), 2) areas colonized by prairie dogs between 2000 and 2002 (5–6 yr of occupancy prior to plague), 3) areas colonized between 2002 and 2004 (3–4 yr of occupancy prior to plague), 4) areas colonized between 2004 and 2006 (1–2 yr of occupancy prior to plague), and 5) areas with no recent (past 10 yr) history of prairie dog occupancy. Within these five occupancy categories in each pasture, we then identified those portions of the areas occurring on similar soils and randomly selected a location for a 40×40 m plot. See Appendix A (available online at http://dx. doi.org/10.2111/REM-D-14-00032.s1) for an example of plot layout relative to soils and prairie dog occupancy history in one block of the experiment. The first block was on soils of the Ulm-Renohill complex (fine sandy loam; correlated to the Loamy Plains ecological site), the second on soils of the Ulm-Cushman complex (fine sandy loam; correlated to the Loamy Plains ecological site), the third on soils of the Zigweid series (sandy loam; correlated to the Sandy Plains ecological site), and the fourth on soils of the Edgar series (loam; correlated to the Overflow ecological site; USDA-NRCS 2007).

Vegetation Sampling
At each 40×40 m plot, we established a nested grid of quadrats where we measured vegetation foliar cover. At each quadrat,
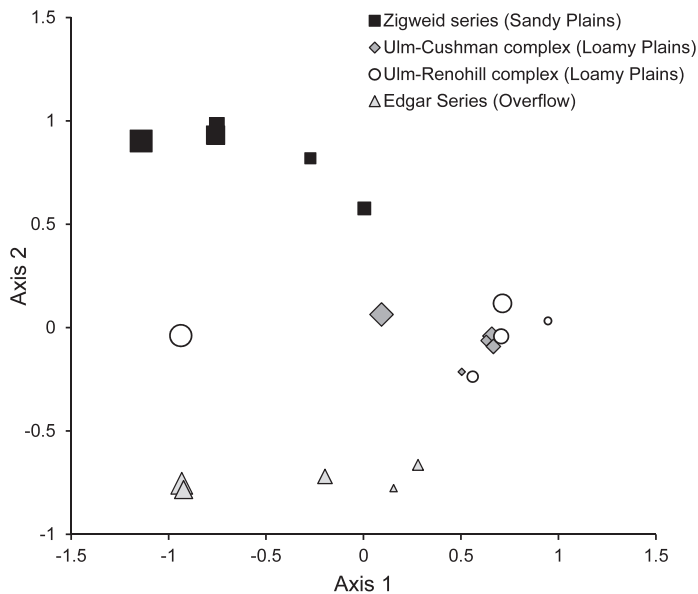
Figure 1. Nonmetric multidimensional scaling ordination of plant species composition at 20 sites (five sites in each of four soil types) in the shortgrass steppe of northeastern Colorado measured in June 2007. Within each soil type, the five sites represented a gradient of prairie dog occupancy history. The largest symbols in each soil type represent sites occupied for 7–10 yr prior to 2007. Symbols of decreasing size represent sites occupied for 5–6 yr, 3–4 yr, and 1–2 yr, respectively, and the smallest symbols represent sites with no history of prairie dog occupation. Axes 1 and 2 explained 75% of the variation in the original species matrix. Variation associated with occupancy history occurs primarily along axis 1, whereas variation associated with soils was orthogonal to the effects of prairie dogs and occurs primarily along axis 2.

we visually estimated foliar cover of each plant species and additionally estimated the bare soil exposure. Cover was recorded by classes consisting of 0–1%, 2–5%, 6–15%, 16–25%, 26–40%, 41–60%, and >60%, and cover class midpoints were used in all statistical analyses (Hickman and Derner 2007). The grid consisted of 17 sampling locations; at each location, we measured vegetation cover in three 50×20 cm quadrats placed 20 cm apart such that the three quadrats combined occurred within a 50×100 cm area (Appendix B; available online at http://dx.doi.org/10.2111/REM-D-14-00032.s1). This grid design allowed for analyses of spatial variation among quadrats across scales of 0.2–20 m. With this design, we sampled 51 quadrats (17 locations $\times$ 3 quadrats per location) within each of the 20 40×40 m plots. Quadrat locations were permanently marked with a 10-cm-long nail and 3-cm-diameter washer placed in the northeast and southwest corners to facilitate annual remeasurement at the same location. Vegetation measurements occurred during 20 June–10 July, 2007, 2008, 2009, and 2011. When the first measurements occurred in 2007, vegetation on the plots had been growing in the absence of prairie dog activity for ~ 2 mo.

None of the study plots were recolonized by prairie dogs during 2007–2010. When vegetation measurements began in June 2011, two of four plots in the 7–10-yr occupancy category, one of four plots in the 5–6-yr occupancy category, and two of four plots in the 3–4-yr occupancy category had been partially recolonized by prairie dogs (one or more burrow

mounds in the plot with signs of recent excavation and prairie dog scat). Measurements from 2011 must therefore be interpreted with recognition that plots were beginning to experience recolonization by prairie dogs at that time.

Statistical Analyses

To examine variation in plant species composition in relation to prairie dog occupancy history and among the four blocks of study sites at the beginning of the study, we conducted a nonmetric multidimensional scaling (NMS) ordination of the species $\times$ site matrix. We used NMS ordination because it does not make assumptions regarding normality of the data and has been shown to perform well with simulated gradients (McCune and Grace 2002). We performed preliminary analyses of the relationship between number of ordination axes and stress. Based on the rate of reduction in stress with increasing number of axes (McCune and Grace 2002), we performed a three-axis NMS ordination using the Sorenson distance measure in PC-ORD (v6.0; MjM Software Design, Gleneden Beach, OR).

We used repeated measures analysis of variance (ANOVA) to examine how foliar cover of four plant functional groups and bare soil exposure changed over time within the different prairie dog occupancy history categories. Functional groups consisted of C_4 perennial grasses (dominated by *Bouteloua gracilis*; includes *B. dactyloides*, *Sporobolus cryptandrus* [Torr.] A. Greay, *A. purpurea*, and *Muhlenbergia torreyi* [Kunth] Hitchc. ex Bush), C_3 perennial grasses and sedges (dominated by *Pascopyrum smithii* [Rydb.] A. Love and *Carex duriuscula* C.A. Mey; includes *Hesperostipa comata* [Trin. & Rupr.] Barkworth and *Elymus elymoides* [Raf] Swezey), perennial forbs (dominated by *S. coccinia*; includes 27 other species), and annual forbs (dominated by *Cryptantha minima* Rydb. and *Machaeranthera tanacetifolia* [Kunth] Nees; includes 21 other species). Nomenclature follows USDA-NRCS (2014). In addition to analyzing patterns for mean bare soil exposure at each site, we also calculated the within-grid variance in bare soil at each site (a nonspatially explicit measure of variation in bare soil) and examined how this variation was related to site occupancy history and year. All ANOVAs were performed using the Mixed procedure in SAS (v9.2; SAS Institute, Cary, NC).

Finally, we used Moran's I (Sokal and Oden 1978), calculated at three spatial scales within each sampling grid, to examine spatially explicit variation in the distribution of bare soil (i.e., areas lacking plant or litter cover). Moran's I measures local spatial autocorrelation in bare soil for quadrats separated by a specified distance class, where values near 0 indicate a lack of spatial autocorrelation and values approaching 1 or −1 indicate strong positive or negative spatial autocorrelation respectively. We calculated Moran's I using the statistical package GS+ (v7.0; Gamma Design Software, Plainwell, MI).

RESULTS

Vegetation Composition Relative to Prairie Dog Occupancy History

Vegetation measurements in June 2007, when plants had grown for 2 mo (from mid-April to mid-June 2007) in the absence of
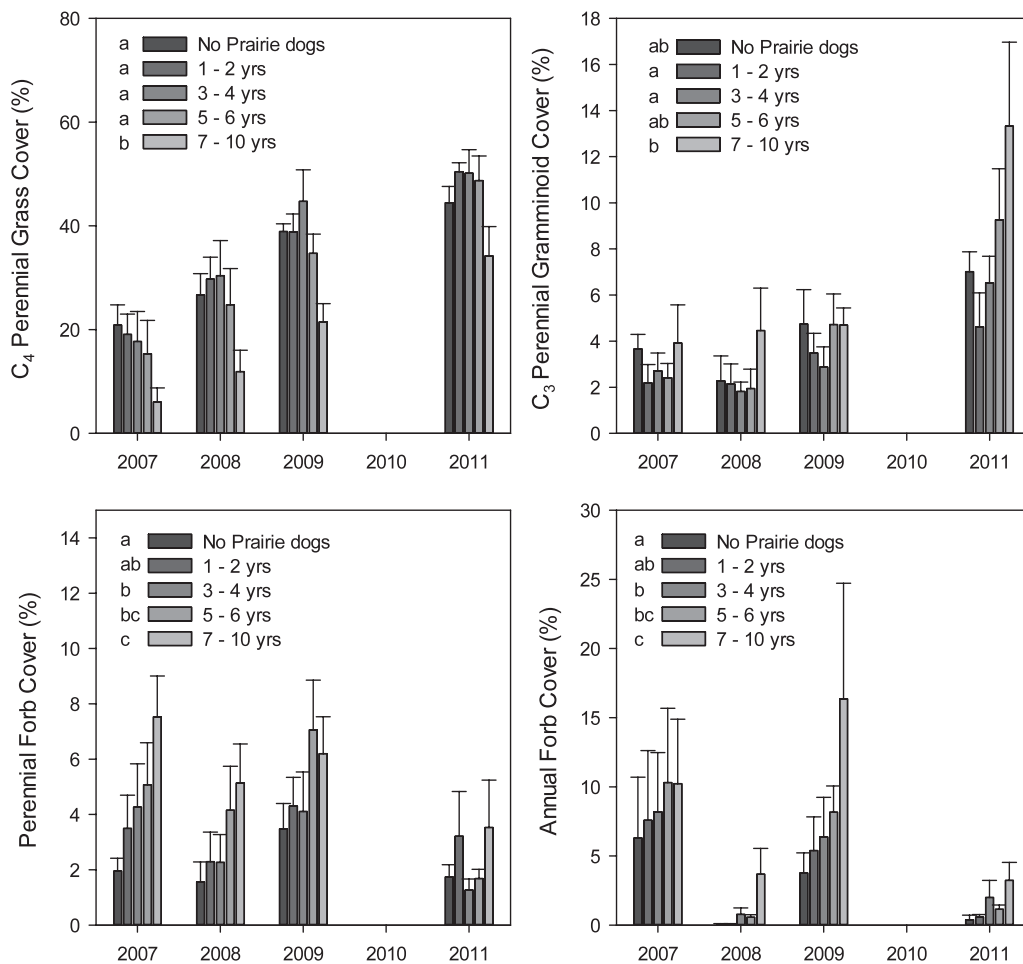
Figure 2. Cover of four plant functional groups in relation to prairie dog occupancy history in the shortgrass steppe of northeastern Colorado during 2007–2011. Bars with different shades refer to sites with varying number of years of prairie dog occupancy prior to a plague epizootic that removed prairie dogs before the 2007 growing season. The label "1–2 years" refers to sites occupied by prairie dogs for 1–2 yr prior to 2007 and so on. For all four plant functional groups, we did not detect significant interactions between prairie dog occupancy history and year (Table 1). Letters next to occupancy category legends and below years indicate which categories and years differ significantly at the $P < 0.05$ level.

prairie dog activity, revealed a clear gradient in plant species composition (Fig. 1) and cover of plant functional groups (Fig. 2) related to the length of prior occupancy by prairie dogs. First, the NMS ordination of species composition showed that sites occupied 7–10 yr were consistently located more negatively on axis 1 compared to sites with no history of occupancy, while sites with 1–6 yr of prairie dog occupancy were generally located in between these extremes (Fig. 1). Within each for the four replicate sets of sites (i.e., blocks), variation associated with prairie dog occupancy history was consistently distributed along axis 1 (Fig. 1). Variation associated with the history of prairie dog occupancy was orthogonal to differences among sites on different soils (occurring primarily along axis 2), showing that prairie dog occupancy history generally altered plant species composition in a manner that was consistent within each soil type but substantially different than variation among soil types (Fig. 1). The ordination also suggests greater similarity in plant community composition across soil types in the absence of prairie dogs and greater divergence in composition across soil types with 7–10 yr of prairie dog occupancy (Fig. 1).

In the first postplague growing season, most large differences in functional group cover were evident only between sites occupied for 7–10 yr prior to plague vs. sites with no history of prairie dog occupancy (Fig. 2). For C_4 perennial grasses, cover in 2007 declined linearly from unoccupied sites (21% cover) up to sites occupied for 5–6 yr (15% cover), but significant differences were not detected among these colony age classes. Cover was significantly lower (6%) at sites occupied 7–10 yr (Fig. 2A). *Aristida purpurea* comprised only a minor portion of the total C_4 perennial grass cover at all sites, and its abundance was not influenced by prairie dog occupancy history ($F_{4,12}=2.04$, $P=0.152$). Minimum *A. purpurea* cover was recorded in 2007 (mean of 0.1% cover on sites with 7–10 yr of prairie dog occupancy and 0.5% cover on sites with no prairie dogs), and maximum *A. purpurea* cover was recorded in 2009 (mean of 0.8% cover with 7–10 yr of prairie dog occupancy and 1.9% cover with no prairie dogs).

In the first growing season following prairie dog extirpation (2007), perennial C_3 graminoids did not exhibit a clear trend related to the occupancy gradient but were significantly greater on 7–10 yr compared to 1–4 yr (Fig. 2B). Trends for annual and perennial forb cover among sites were opposite that for C_4
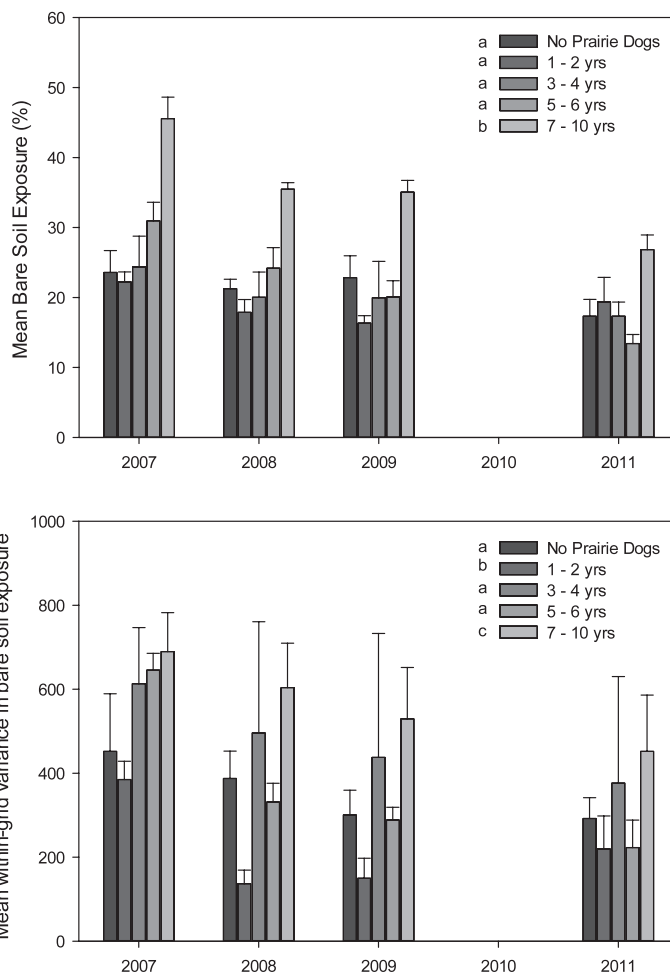
Table 1. Results of repeated measures analysis of variance testing how the abundance of four plant functional groups varies among years (2007–2011) and in relation the history of prairie dog occupancy in the shortgrass steppe of northeastern Colorado. For tests for all response variables, the degrees of freedom in the numerator and denominator were, respectively, 4 and 12 for occupancy history, 3 and 9 for year, and 12 and 36 for the occupancy history × year interaction.

Functional group	Factor	F	P
C_4 perennial grasses	Occupancy history	14.9	0.000
	Year	65.66	< 0.0001
	Occupancy × year	0.46	0.924
C_3 perennial gramminoids	Occupancy history	3.69	0.035
	Year	16.41	0.001
	Occupancy × year	1.05	0.430
Perennial forbs	Occupancy history	5.48	0.010
	Year	6	0.016
	Occupancy × year	0.67	0.764
Annual forbs	Occupancy history	8.83	0.002
	Year	44.98	< 0.0001
	Occupancy × year	0.3	0.985
Bare soil exposure	Occupancy history	23.57	< 0.0001
	Year	11.8	0.002
	Occupancy × year	1.32	0.249
Variance in bare soil	Occupancy history	8.32	0.002
	Year	6.69	0.0114
	Occupancy × year	0.83	0.6204

Figure 3. Mean bare soil exposure and within-site variation in bare soil exposure in relation to prairie dog occupancy history in the shortgrass steppe of northeastern Colorado during 2007–2011. Bars with different shades refer to sites with varying number of years of prairie dog occupancy prior to a plague epizootic that removed prairie dogs before the 2007 growing season. The label "1–2 years" refers to sites occupied by prairie dogs for 1–2 yr prior to 2007, and "7–10 years" refers to sites occupied by prairie dogs for 7–10 yr prior to 2007. Letters next to occupancy category legends and below years indicate which categories and years differ significantly at the $P < 0.05$ level.

grasses, as forb cover increased linearly from unoccupied sites to sites occupied 7–10 yr (Figs. 2C and 2D). In general, cover of all functional groups was similar on sites occupied for 1–4 yr prior to plague compared to sites with no history of prairie dogs, indicating that plant cover on sites occupied for 4 or fewer years recovered to unoccupied levels in a single growing season.

## Vegetation Dynamics Following Prairie Dog Extirpation

We used repeated measures ANOVA to test whether variation among occupancy categories varied across the 4 yr of measurements and assess whether and how dynamics on sites with the longest history of occupancy differed from other occupancy categories. For all four functional groups, we detected significant differences in cover among occupancy history categories and among years but no significant year × occupancy interactions (Table 1). In general, cover of all functional groups on sites occupied for 1–4 yr prior to plague was similar to cover on sites with no history of prairie dogs. C_4 grass cover increased substantially and at the same rate in all five occupancy categories over time (Fig. 2A), reflecting the fact that the study was initiated following a drought year in 2006 and continued through a series of average and above-average precipitation years during 2008–2010. Where prairie dogs occupied the site for 7–10 yr prior to plague, C_4 grass cover still had not recovered to the same level as unoccupied sites by 2011. However, even though C_4 cover had been reduced to extremely low levels on these sites in 2007 (mean cover of 6%), C_4 grass cover recovered rapidly, reaching mean cover of 34% by 2011. C_3 perennial graminoid cover was

stable during 2007–2009 and then increased notably between 2009 and 2011 following above-average precipitation in 2009. Trends suggested a greater increase in C_3 graminoids in 2011 on sites occupied 7–10 yr compared to all other occupancy categories (Fig. 2B), but the year × occupancy class interaction was not significant (Table 1). Patterns for C_3 graminoids show that long-term prairie dog occupancy did not suppress cover in the short term or reduce the capacity for C_3 graminoids to increase in abundance once prairie dogs were removed.

Perennial forb cover declined from 2007 to 2011 and remained significantly greater on sites occupied 7–10 yr relative to unoccupied sites throughout the study (Fig. 2C). Annual forb cover varied widely among years, possibly in response to spring precipitation patterns. Across the 4 yr, annual forb cover was significantly greater on sites occupied
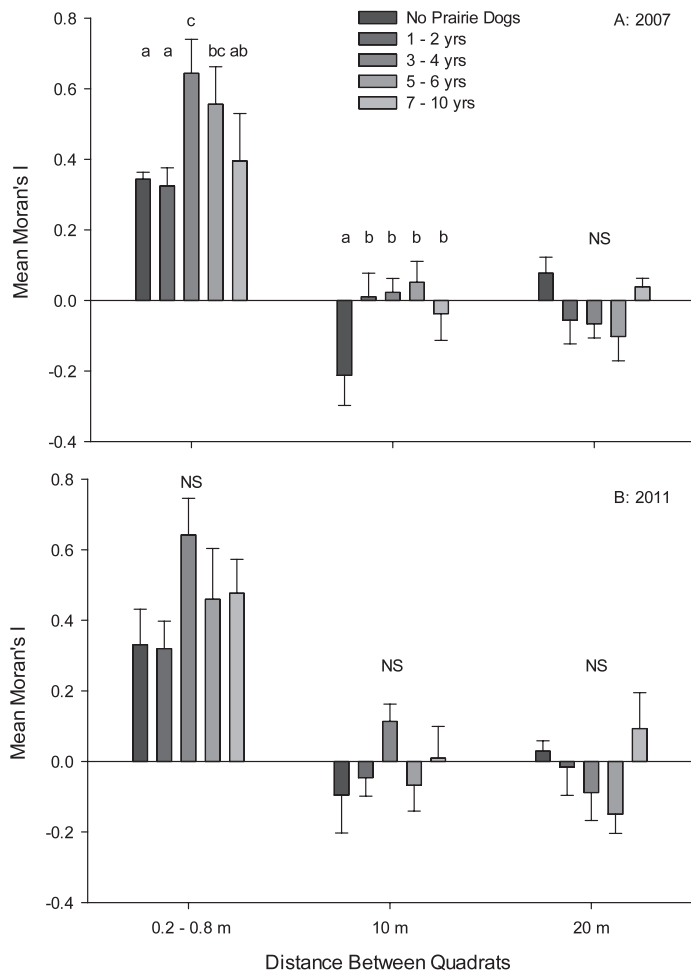
Figure 4. Mean Moran's I for bare soil exposure in relation to prairie dog occupancy history in the shortgrass steppe of northeastern Colorado during 2007–2011. Bars with different shades refer to sites with varying number of years of prairie dog occupancy prior to a plague epizootic that removed prairie dogs before the 2007 growing season. Moran's I is a measure of spatial autocorrelation with values approaching 1 or −1 indicating strong positive or negative autocorrelation and values near zero indicating a random spatial pattern. For 2007, bars with the same letter above them indicate occupancy categories with similar levels of spatial autocorrelation for a given spatial scale. NS indicates spatial scales for which there were no differences in spatial pattern among occupancy categories. In both 2007 and 2011, spatial autocorrelation for all occupancy categories was significantly greater ($P < 0.05$) at the submeter spatial scale compared to the 10-m and 20-m scales.

for 7–10 yr compared to sites occupied < 6 yr as well as unoccupied sites (Fig. 2D).

Patterns for bare soil exposure were generally the inverse of our findings for C_4 perennial grasses, with significant differences among occupancy classes and years (Table 1; Fig. 3A). In 2007, bare soil exposure was substantially greater on sites occupied 7–10 yr compared to all other sites (Fig. 3A). Mean bare soil exposure declined monotonically across years during the study on all occupancy categories. In 2009 and 2011, bare soil was consistently less than 25% at sites in all occupancy categories, except sites that were occupied 7–10 yr (mean bare soil of 35% in 2009 and 27% in 2011; Fig. 3A). Bare soil on

sites occupied 7–10 yr prior to prairie dog extirpation declined from a mean of 46% in 2007 to 27% in 2011 but did not decline to the levels occurring in any of the other occupancy categories.

Vegetation Spatial Patterns Following Prairie Dog Extirpation

To assess changes in the spatial pattern of vegetation cover, we used bare soil exposure as our response variable because it represents the distribution of areas lacking any form of vegetation cover. We examined whether prairie dogs altered spatial patterns in bare soil by creating more frequent and/or larger bare patches and whether such patch formation may be associated with rates of vegetation recovery after prairie dog extirpation. Variability in bare soil within a site generally showed similar patterns as mean bare soil exposure. Variability was significantly greater at sites occupied 7–10 yr compared to all other occupancy classes, and variability declined in all occupancy categories over time (Fig. 3B).

We used Moran's I to evaluate patchiness (i.e., spatial autocorrelation) in bare soil at submeter, 10-m, and 20-m spatial scales. During the first growing season following prairie dog extirpation (2007), spatial autocorrelation in bare soil at the submeter scale was significantly greater at sites occupied 3–6 yr compared to sites occupied both for longer (7–10 yr) and shorter (1–2 yr and unoccupied) time periods (Fig. 4A). At the 10-m scale, we found significant negative spatial autocorrelation at unoccupied sites (test for difference from 0: $P = 0.005$) but no spatial autocorrelation in any other occupancy classes. At the 20-m scale, we found no significant negative or positive spatial autocorrelation in any occupancy category (Fig. 4A). In 2011, at each of the three spatial scales we found no differences among occupancy categories in the degree of spatial autocorrelation (Fig. 4B). In both 2007 and 2011, spatial autocorrelation for all occupancy categories was significantly greater ($P < 0.05$) at the submeter scale compared to the 10-m and 20-m scales (Fig. 4).

DISCUSSION

The spatial distribution and temporal persistence of black-tailed prairie dog colonies in grasslands of the western Great Plains, primarily west of the 102nd meridian (Cully et al. 2006), are highly influenced by epizootic plague. Where complexes of prairie dog colonies persist on the landscape, periodic outbreaks of epizootic plague often affect colonies at intervals of once every 12 yr or less (Augustine et al. 2008; Hartley et al. 2009; Cully et al. 2010). Areas affected by prairie dogs continuously for longer than a decade are extremely rare in landscapes that harbor plague. For example, in Colorado and Montana, areas continuously occupied by prairie dogs for a period of > 10 yr accounted for only 0.16% and 0.27% of the landscape, respectively (Augustine et al. 2008).

Based on a chronosequence approach, Hartley et al. (2009) found that periodic extirpation of prairie dogs due to plague dampens their effects on shortgrass steppe vegetation, suggesting that prairie dogs do not induce irreversible changes in vegetation composition. Our direct measurements of post-plague vegetation dynamics provide clear support for this conclusion. First, we found that sites occupied by prairie dogs

1–4 yr prior to extirpation exhibit recovery in plant cover and composition to levels in unoccupied (control) sites within a single growing season, at least in the absence of drought. Furthermore, sites that were occupied by prairie dogs for 7–10 yr prior to extirpation did experience significant reductions in C_4 perennial grass cover compared to sites with shorter occupancy histories, but cover of these C_4 perennial grasses recovered rapidly over 5 yr following extirpation of the prairie dogs, demonstrating that irreversible shifts in vegetation state did not occur. We note that our findings regarding C_4 perennial grass recovery occurred during a 5-yr period that did not encompass a drought year, but we did observe similar rates of increase in C4 perennials during 2007–2008 (years of average and slightly below-average precipitation) as during 2009–2011 (years of above-average precipitation).

Our findings, combined with those of Hartley et al. (2009), suggest incorporating significant revisions regarding the effects of prairie dogs on vegetation dynamics and associated state transitions for the shortgrass steppe. Current models (USDA-NRCS 2007) include a transition from a state dominated by a mixture of perennial C_4 shortgrasses and C_3 graminoids (state 1) to a state characterized by high bare soil exposure and increased abundance of A. purpurea and annual forbs (state 2), with the transition resulting from the presence of prairie dogs. These models suggest that ≥40 yr of prairie dog absence is required to transition back from state 2 to state 1. Furthermore, current models suggest that such recovery may be possible only with the implementation of a prescriptive livestock grazing plan that allows for rest from grazing for portions of the growing season each year (USDA-NRCS 2007). In contrast, our findings indicate that where epizootic plague outbreaks periodically affect colonies at intervals of 10 yr or shorter, vegetation on those colonies represents a phase characterized by increased bare soil (up to 30–50%), reduced cover of perennial C_4 grasses, and increased cover of perennial C_3 forbs and graminoids (i.e., phase 1 within state 1 described above). In addition, neither our study nor Stapp (2007) found increased abundance of A. purpurea in active prairie dog colonies. The vegetation phase on active colonies can transition back to a phase dominated by C_4 perennial shortgrasses and C_3 perennial graminoids (phase 2 within state 1) within 1–5 yr after prairie dog extirpation and can do so with continuous, season-long (May–October) cattle grazing at moderate stocking rates. Furthermore, our findings indicate that prairie dog effects on vegetation composition were consistent across the soil types we studied (Fig. 1) and that the general trajectory and rate of recovery after prairie dog extirpation was consistent across soil types.

Previous meta-analyses indicate that the shortgrass steppe is one of the most grazing-resistant grasslands in the world, which has been attributed to the long coevolutionary history of grazing by large ungulates (Milchunas and Lauenroth 1993; Milchunas et al. 2008). The four dominant graminoid species in our study (Bouteloua gracilis, Bouteloua dactyloides, Carex dursicola, and Pascopyrum smithii) exhibit a suite of adaptations to defoliation. The first three species are all characterized by a prostrate growth form and high rates of biomass allocation belowground (B. gracilis and C. durisicola) or to stolons (B. dactyloides; Milchunas et al. 2008). The rhizomatous growth form of P. smithii facilitates rapid spread into patches where grazing has suppressed bunchgrasses and thereby generated microsites with reduced intensity of interspecific competition. We suggest that, collectively, these traits allow these perennial graminoids to maintain dominance in areas affected by continuous prairie dog occupation for 1–6 yr. With longer continuous prairie dog occupancy (7–10 yr), C_4 perennial grasses decline notably in abundance but retain the capacity to recover quickly once prairie dogs are removed.

Finally, we suggest that the capacity for these perennial graminoids to recover is related to their spatial distribution on long-term occupied sites. In particular, we found that 7–10 yr of prairie dog occupancy did not increase patchiness in bare soil at the submeter scale or the 10-m scale (Fig. 4). Variance in bare soil was greater with increasing length of prairie dog occupancy (Fig. 3B), reflecting increasing exposure of bare soil within some quadrats. However, the finding that small areas (quadrats) with high bare soil exposure were not more spatially aggregated on sites with 7–10 yr of prairie dog occupancy indicates that plants were still widely dispersed within each square meter on the site. This fine-scale pattern of plant persistence may be one factor allowing perennials to recolonize most plant interspaces during the first 1–3 yr after extirpation of prairie dogs. These findings support the contention of Bestelmeyer et al. (2006) that assessing rangeland vegetation at multiple scales can provide insight to vegetation resilience and the potential presence of thresholds.

Because prairie dogs consume large quantities of many of the same plant species that livestock consume (Detling 2006), they are considered by many to be competitors with livestock. Depending on weather conditions, site productivity, and the proportion of pastures they occupy, prairie dogs can suppress livestock weight gains in semiarid rangelands, particularly if they occupy 30% or more of the area of a pasture (Derner et al. 2006; Augustine and Springer 2013). However, controlling prairie dog populations through poisoning can be expensive and in some cases cost ineffective (Collins et al. 1984). Our findings suggest that vegetation recovery following prairie dog extirpation, either by plague or by poisoning, is likely to vary spatially within a given colony site, and impacts to livestock weight gains will depend on the prior recent history of prairie dog occupancy. The capacity for vegetation on shortgrass steppe to rapidly recover after prairie dog removal suggests that removal via poisoning could provide short-term returns for livestock production. Conversely, the periodic recurrence of plague in this region (and hence extirpation without associated costs to livestock managers) suggests that over longer time frames, poisoning may have limited economic value. Clearly, these predictions are based on the assumption that plague will continue to exert similar effects on prairie dog populations in the future. Should prairie dog resistance to plague or effective vaccination or other plague control strategies develop, consequences for vegetation dynamics will need additional long-term study.

MANAGEMENT IMPLICATIONS

Our results support the idea that arid and semiarid grasslands can be surprisingly resilient to disturbance associated with multiple years of intense grazing pressure (Bestelmeyer et al.

2013). We found no evidence that occupation of sites by prairie dogs over time frames of 1–10 yr caused irreversible shifts in the state of the vegetation. Our finding of high vegetation resilience to the intense grazing regime imposed by prairie dogs, which may consume 70% or more of the annual aboveground net primary production on their colonies (Detling 2006), is also consistent with many previous studies reporting strong resistance of the shortgrass steppe plant community to less intense disturbance imposed by livestock grazing (Milchunas et al. 2008). We suggest that STMs for vegetation of the shortgrass steppe should explicitly incorporate the time frame over which prairie dogs occupy a site and recognize that vegetation changes currently induced by prairie dogs represent a phase shift rather than an alternate stable state. Given that colonial, burrowing herbivores are native to most semiarid grasslands worldwide (Davidson et al. 2012), we suggest their effects on vegetation dynamics be examined with explicit consideration of those factors, such as disease, that control the distribution and abundance of their colonies in space and time.

LITERATURE CITED

Ansley, R. J., and M. J. Castellano. 2006. Strategies for savanna restoration in the southern Great Plains: effects of fire and herbicides. *Restoration Ecology* 14:420–428.

Antolin, M., L. Savage, and R. Eisen. 2006. Landscape features influence genetic structure of black-tailed prairie dogs (*Cynomys ludovicianus*). *Landscape Ecology* 21:867–875.

Archer, S., M. Garrett, and J. Detling. 1987. Rates of vegetation change associated with prairie dog (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie. *Vegetatio* 72:159–166.

Augustine, D. J., and B. Baker. 2013. Associations of grassland bird communities with black-tailed prairie dog colonies in the North American Great Plains. *Conservation Biology* 27:324–334.

Augustine, D. J., M. R. Matchett, T. P. Toombs, J. F. Cully, Jr., T. L. Johnson, and J. G. Sidle. 2008. Spatiotemporal dynamics of black-tailed prairie dog colonies affected by plague. *Landscape Ecology* 23:255–267.

Augustine, D. J., and T. Springer. 2013. Competition and facilitation between a native and a domestic herbivore: trade-offs between forage quantity and quality. *Ecological Applications* 23:850–863.

Bagchi, S., D. D. Briske, X. B. Wu, M. P. McClaran, B. T. Bestelmeyer, and M. E. Fernández-Giménez. 2012. Empirical assessment of state-and-transition models with a long-term vegetation record from the Sonoran Desert. *Ecological Applications* 22:400–411.

Baker, B., D. Augustine, J. Sedgwick, and B. Lubow. 2013. Ecosystem engineering varies spatially: a test of the vegetation modification paradigm for prairie dogs. *Ecography* 36:230–239.

Bestelmeyer, B. T., M. C. Duniway, D. K. James, L. M. Burkett, and K. M. Havstad. 2013. A test of critical thresholds and their indicators in a desertification-prone ecosystem: more resilience than we thought. *Ecology Letters* 16:339–345.

Bestelmeyer, B. T., D. A. Trujillo, A. J. Tugel, and K. M. Havstad. 2006. A multi-scale classification of vegetation dynamics in arid lands: what is the right scale for models, monitoring, and restoration? *Journal of Arid Environments* 65:296–318.

Bestelmeyer, B. T., A. J. Tugel, G. L. Peacock, Jr., D. G. Robinett, P. L. Shaver, J. R. Brown, J. E. Herrick, H. Sanchez, and K. M. Havstad. 2009. State-and-transition models for heterogeneous landscapes: a strategy for development and application. *Rangeland Ecology & Management* 62:1–15.

Briske, D. D., B. T. Bestelmeyer, T. K. Stringham, and P. L. Shaver. 2008. Recommendations for development of resilience-based state-and-transition models. *Rangeland Ecology & Management* 61:359–367.

Briske, D. D., S. D. Fuhlendorf, and F. E. Smeins. 2005. State-and-transition models, thresholds, and rangeland health: a synthesis of ecological concepts and perspectives. *Rangeland Ecology & Management* 58:1–10.

Chartier, M., and C. Rostagno. 2006. Soil erosion thresholds and alternative states in northeastern Patagonian rangelands. *Rangeland Ecology & Management* 59:616–624.

Cid, M. S., J. K. Detling, A. D. Whicker, and M. A. Brizuela. 1991. Vegetational responses of a mixed-grass prairie site following exclusion of prairie dogs and bison. *Journal of Range Management* 44:100–105.

Collins, A. R., J. P. Workman, and D. W. Uresk. 1984. An economic analysis of black-tailed prairie dog (*Cynomys ludovicianus*) control. *Journal of Range Management* 37:358–361.

Coppock, D. L., J. E. Ellis, J. K. Detling, and M. I. Dyer. 1983. Plant-herbivore interactions in a North American mixed-grass prairie. I. Effects of black-tailed prairie dogs on intrasesonal aboveground plant biomass and nutrient dynamics. *Oecologia* 56:1–9.

Cully, J. F., D. E. Biggins, and D. B. Seery. 2006. Conservation of prairie dogs in areas with plague. *In:* J. L. Hoogland [ed.]. Conservation of the black-tailed prairie dog: saving North America's western grasslands. Washington, DC, USA: Island Press. p. 157–168.

Cully, J. F., Jr., T. L. Johnson, S. K. Collinge, and C. Ray. 2010. Disease limits populations: plague and black-tailed prairie dogs. *Vector-Borne and Zoonotic Diseases* 10:7–15.

Davidson, A. D., J. K. Detling, and J. H. Brown. 2012. Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands. *Frontiers in Ecology and the Environment* 10:477–486.

Derner, J., J. Detling, and M. Antolin. 2006. Are livestock weight gains affected by black-tailed prairie dogs? *Frontiers in Ecology and the Environment* 4:459–464.

Detling, J. K. 2006. Do prairie dogs compete with livestock? *In:* J. L. Hoogland [ed.]. Conservation of the black-tailed prairie dog: saving North America's western grasslands. Washington, DC, USA: Island Press. p. 65–88.

Guenther, D. A., and J. K. Detling. 2003. Observations of cattle use of prairie dog towns. *Journal of Range Management* 56:410–417.

Hartley, A. E., J. K. Detling, and L. T. Savage. 2009. Introduced plague lessens the effects of an herbivorous rodent on grassland vegetation. *Journal of Applied Ecology* 46:861–869.

Hickman, K. R., and J. D. Derner. 2007. Blackland tallgrass prairie vegetation dynamics following cessation of herbicide application. *Rangeland Ecology & Management* 60:186–190.

Knowles, C. J., J. D. Proctor, and S. C. Forrest. 2002. Black-tailed prairie dog abundance and distribution in the Great Plains based on historic and contemporary information. *Great Plains Research* 12:219–254.

Kotliar, N. B., B. W. Baker, A. D. Whicker, and G. E. Plumb. 1999. A critical review of assumptions about the prairie dog as a keystone species. *Environmental Management* 24:177–192.

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. Geneden Beach, OR, USA: MjM Software Design. 300 p.

Milchunas, D., and W. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* 63:327–366.

Milchunas, D., W. Lauenroth, I. Burke, and J. K. Detling. 2008. Effects of grazing on vegetation. *In:* W. Lauenroth and I. C. Burke [eds.]. Ecology of the shortgrass steppe: a long-term perspective. New York, NY, USA: Oxford University Press. p. 389–446.

Savage, L. T., R. Reich, L. Hartley, P. Stapp, and M. F. Antolin. 2011. Climate, soils and connectivity predict plague epizootics in black-tailed prairie dogs. *Ecological Applications* 21:2933–2943.

Sidle, J. G., D. J. Augustine, D. H. Johnson, S. D. Miller, J. F. Cully, Jr., and R. P. Reading. 2012. Aerial surveys adjusted by ground surveys to estimate area

occupied by black-tailed prairie dog colonies. *Wildlife Society Bulletin* 36:248–256.

SOKAL, R., AND N. ODEN. 1978. Spatial autocorrelation in biology 2. Some biological implications and four applications of evolutionary and ecological interest. *Biological Journal of the Linnean Society* 10:229–249.

STAPP, P. 2007. Rodent communities in active and inactive colonies of black-tailed prairie dogs in shortgrass steppe. *Journal of Mammalogy* 88:241–249.

STAPP, P., M. F. ANTOLIN, AND M. BALL. 2004. Patterns of extinction in prairie dog metapopulations: plague outbreaks follow El Nino events. *Frontiers in Ecology Environment* 2:235–240.

STRINGHAM, T., K. KRUEGER, AND P. L. SHAVER. 2003. State and transition modeling: an ecological process approach. *Journal of Range Management* 56:106–113.

SUDING, K. N., K. L. GROSS, AND G. R. HOUSEMAN. 2004. Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology and Evolution* 19:46–53.

TWIDWELL, D., B. W. ALLRED, AND S. D. FUHLENDORF. 2013. National-scale assessment of ecological content in the world's largest land management framework. *Ecosphere* 4(8): Article 94.

[USDA-NRCS] US DEPARTMENT OF AGRICULTURE–NATURAL RESOURCES CONSERVATION SERVICE. 2007. Ecological site descriptions for: Loamy Plains (R067BY002CO), Overflow (R067BY036CO) and Sandy Plains (R067BY024CO), MLRA 067B—Central High Plains, Southern Part. Available at: https://esis.sc.egov.usda.gov/ESDReport/fsReport.aspx?id=R067BY002CO, https://esis.sc.egov.usda.gov/ESDReport/fsReport.aspx?id=R067BY036CO, and https://esis.sc.egov.usda.gov/ESDReport/fsReport.aspx?id=R067BY024CO. Accessed 12 May 2014.

[USDA-NRCS] US DEPARTMENT OF AGRICULTURE–NATURAL RESOURCES CONSERVATION SERVICE. 2014. The PLANTS database. Available at: http://plants.usda.gov. Accessed 4 October 2014.

VAN DE KOPPEL, J., AND M. RIETKERK. 2004. Spatial interactions and resilience in arid ecosystems. *The American Naturalist* 163:113–121.

VAN LANGEVELDE, F., C. A. D. M. VAN DE VIJVER, L. KUMAR, J. VAN DE KOPPEL, N. DE RIDDER, J. VAN ANDEL, A. K. SKIDMORE, J. W. HEARNE, L. STROOSNIJDER, W. J. BOND, H. H. T. PRINS, AND M. RIETKERK. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* 84:337–350.

WESTOBY, M., B. WALKER, AND I. NOY-MEIR. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* 42:266–274.

WHICKER, A., AND J. DETLING. 1988. Ecological consequences of prairie dog disturbances. *BioScience* 38:778–785.