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Prairie dogs and wildfires shape vegetation structure in a sagebrush grassland more than does rest from ungulate grazing

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Abstract. Understanding drivers of vegetation structure has direct implications for wildlife conservation and livestock management, but the relative importance of multiple disturbances interacting within the same system to shape vegetation structure remains unclear. We investigated the separate and interactive effects of multiple disturbance drivers on vegetation structure through a three-tiered, large-scale manipulative experiment in northeast Wyoming, USA. We used nested grazing exclosures to isolate the effects of herbivory from livestock, wild ungulates, or small mammals within areas affected by either historical wildfire, black-tailed prairie dog (*Cynomys ludovicianus*) colonies, or neither disturbance. We analyzed the interactive effects of disturbance history and contemporary herbivory by either small mammals alone, small mammals + native ungulates, or small mammals + native ungulates + livestock on vegetation structure by quantifying vegetation height, visual obstruction, shrub density, shrub canopy, and shrub leader growth. The exclusion of wild ungulates and lightly to moderately stocked livestock for two years did not significantly affect herbaceous vegetation structure, shrub density, or shrub canopy cover. Maximum vegetation height, visual obstruction, and heights of grasses and forbs were ~50% lower on black-tailed prairie dog colonies than in undisturbed areas. Prairie dog colonies contained 71% lower shrub densities than undisturbed sites. Sites with wildfire or black-tailed prairie dogs had 89% lower canopy cover of shrubs and Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), when compared to undisturbed sites. Shrub leaders experienced over 4.5 times more browsing on prairie dog colonies, when compared to undisturbed areas. For most metrics, disturbance history did not modify the effects of contemporary herbivory on vegetation structure. However, shrubs on prairie dog colonies experienced significantly more leader browsing in the combined presence of livestock, native ungulates, and small mammals than in treatments where livestock were excluded. Our research has direct implications for wildlife conservation and rangeland management by demonstrating that short-term (1–2 yr) rest from large ungulate grazing may not substantially alter vegetation structure in this system. Instead, structural variation is strongly driven by black-tailed prairie dog colonization and historical wildfire. Understanding and managing multiple, potentially interacting disturbances is critical for maximizing wildlife conservation and livestock production in heterogeneous landscapes.

Key words: black-tailed prairie dogs; ecosystem engineer; ecotone; habitat mosaics; habitat structure; interactive effects; keystone species; livestock; northern mixed-grass prairie; sagebrush steppe.

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INTRODUCTION

Vegetation structure, or the way vegetation is spatio-temporally arranged in three-dimensional space (including vegetation height, visual obstruction, shrub density, and shrub canopy), serves as a fundamental link between pattern and process in landscape ecology and is often sensitive to disturbance (Turner 1989). Habitat patch type, scale, and structure influence wildlife utilization, movement, and forage intake (MacArthur and Pianka 1966, Simpson et al. 2004, van Beest et al. 2010). Vegetation structure provides microhabitats for small mammals and spiders (Brown and Kotler 2004, Warui et al. 2005, Doherty et al. 2015, Ceradini and Chalfoun 2017), influences the navigation and utilization of a landscape by livestock (Clark et al. 2017) and wild ungulates (Van Dyke and Darragh 2006, Allen et al. 2014, Riginos 2015), and provides a suite of habitat resources for birds ranging from nesting to screening cover (Chalfoun and Martin 2009, Doherty et al. 2014). Moreover, natural disturbance can alter vegetation structure and lead to shifts in foraging space-use patterns in response to newly available resources (Thompson et al. 2008, Nkwabi et al. 2011, Augustine and Derner 2015). Natural disturbance can also elicit settlement or nesting in newly disturbed areas (Augustine et al. 2007, Derner et al. 2009, Augustine and Derner 2015). Despite the importance of vegetation structure for the conservation of biodiversity and ecosystem function, relatively little is known about how multiple forms of disturbance operate and interact within the same ecosystem to shape vegetation structure within variable temporal and spatial scales.

Globally, vegetation structure and patch variability in grasslands and savannas are strongly driven by natural disturbance regimes (Fuhlendorf et al. 2006, McGranahan et al. 2012, Ondei et al. 2017). These disturbances influence height and cover of herbaceous and woody plants, often within variable spatio-temporal regimes that result in heterogeneous landscapes (Fuhlendorf and Engle 2001). In North America, semi-arid rangelands include deserts, shrublands, grasslands, and forests that evolved with spatially and temporally variable disturbance regimes of wildfire, large ungulate herbivory, and the ecosystem engineering activities of colonial burrowing mammals (Beetle 1960, Stebbins 1981, Anderson 2006). Moreover, interactions among multiple disturbances, including wildfire, herbivory by native megafauna, and colonial burrowing mammals, are driving forces of plant community structure and composition in these ecosystems (Knapp et al. 1999, Fuhlendorf and Engle 2004, Gordon et al. 2004). The interactive effects of disturbance across space and time can serve to broaden the suite of plant functional groups and their structural features on the landscape (Fahnestock and Detling 2002, Fuhlendorf and Engle 2004, Augustine et al. 2007, Augustine and Derner 2015). Ecological disturbances can also promote diversity in vegetation communities and their structure (West 1993, Baker et al. 2013), thus optimizing wildlife habitat and forage quality and quantity (Derner et al. 2009, Augustine and Baker 2013, Hovick et al. 2015), ecosystem function (Sousa 1984), and associated services (Fuhlendorf and Engle 2001).

Not all rangelands, however, have similar disturbance dependence or function, and intentionally managing for optimal disturbance regimes, especially in disturbance-sensitive plant communities such as big sagebrush (*Artemisia tridentata* [Beetle & Young])-dominated shrublands, continues to be challenging (Beck et al. 2009, Davies et al. 2011, Chambers et al. 2014). Much research on vegetation community response to multiple disturbances has focused on the interactive effects of two drivers, such as fire and herbivory by livestock (Fuhlendorf and Engle 2004, Limb et al. 2011, Scasta et al. 2016*b*), herbivory by native colonial mammals and livestock (Sierra-Corona et al. 2015, Ponce-Guevara et al. 2016), fire and native colonial mammals (Augustine et al. 2007), fire and native ungulates (Larson et al. 2013, Breland et al. 2014, Augustine and Derner 2015), and native ungulates and livestock (Veblen et al. 2016). These studies convincingly demonstrate that the interactive effects of two disturbances often differ both quantitatively and qualitatively from the effects of isolated disturbances. For example, Ponce-Guevara et al. (2016) demonstrated interactive herbivory effects by cattle and black-tailed prairie dogs decreased height of mesquite (*Prosopis glandulosa*) bushes twice as much, when compared to areas where cattle and prairie dogs occurred alone or were absent. Despite this recognition that multiple disturbances can interact, ecological research has only recently begun to investigate the interactive effects of more than two distinct disturbance drivers operating in the same system (e.g., Royo et al. 2010, Odadi et al. 2017). Nonetheless, most grasslands and shrublands frequently experience three or more simultaneous and interactive disturbances (e.g., fire, drought, grazing by livestock, grazing by native ungulates, small mammal disturbances, and insect and disease outbreaks).

A better understanding of the interactive effects of multiple disturbances on vegetation structure is critical for effective management of complex landscapes. In western North America, land managers are often responsible for meeting multiple, diverse rangeland management objectives including productive and sustainable livestock grazing, energy development, and the maintenance or restoration of ecosystem biodiversity and wildlife habitat (West 1993, Davies et al. 2011). In this region, population declines of sensitive wildlife associated with specific habitat structure, such as the greater sage-grouse (*Centrocercus urophasianus*), black-footed ferret (*Mustela nigripes*), and pygmy rabbit (*Brachylagus idahoensis*), create an urgency to better understand how natural and anthropogenic disturbances influence vegetation structure and wildlife habitat for diverse species assemblages. The effects of multiple, interactive disturbances on vegetation structure are particularly poorly understood in shrubland–grassland ecotone regions where divergent climate regimes, disturbance-sensitive vegetation communities, and historic disturbance regimes are juxtaposed and interact to create unique ecosystem responses (Porensky et al. 2016*b*).

We sought to better understanding the interactive effects of historic wildfire and herbivory by domestic and wild ungulates, as well as black-tailed prairie dogs (*Cynomys ludovicianus*), on vegetation structure in a sagebrush steppe–mixed-grass prairie ecotone. We used a large-scale manipulative experiment to ask: In a sagebrush–grassland ecotone, how does the structure of vegetation respond to (1) disturbance history (undisturbed, burned, or colonized by prairie dogs), (2) native ungulate herbivory, (3) livestock herbivory, (4) small mammal herbivory, and (5) interactions among these multiple disturbances? We predicted ungulate exclusion would increase herbaceous vegetation (maximum height and visual obstruction) and shrub (density, canopy, and leader growth) structure and that these metrics would respond differently to the exclusion of livestock vs. native herbivores, with the greatest effects resulting from the exclusion of livestock. We further predicted that metrics of herbaceous vegetation structure would be greater in areas with historic wildfire and lower on prairie dog colonies, and expected metrics of shrub structure to be reduced on both disturbance types, when compared to undisturbed sites. Finally, we predicted the interaction of herbivory by multiple herbivore types and historical disturbance from wildfire and prairie dogs would further reduce these metrics of vegetation structure when compared to areas experimentally excluded from herbivory and without a legacy of historical disturbance.

MATERIALS AND METHODS

Study site

Our study was carried out in the Thunder Basin National Grassland (hereafter Thunder Basin), a 6,880 km^2 landscape in northeastern Wyoming, USA (497013, 4830298 m, UTM Zone 13N; Fig. 1). Mean annual precipitation was 320 mm (1981–2010; PRISM Climate Group 2017), and mean spring precipitation, which drives plant production in this system, was 177 mm (April–June 1981–2010; Derner and Hart 2007, Western Regional Climate Center). Mean spring precipitation at our sampling sites during the study period 2015–2017 was 308, 125, and 171 mm, respectively (PRISM Climate Group 2017; Table 1). Sampling sites were located on loamy soils, which cover 38% of the study region (Ecological Site R058BY122WY, NRCS) and elevation ranged from 1328 to 1511 m a.s.l. (PRISM Climate Group 2017). Sampling sites included both private land and public land managed by the U.S. Forest Service (USFS). Domestic livestock grazing practices reflected typical management in the region and included a broad range of animal types, classes, and timing of use (Appendix S1: Table S1). Stocking rates were light to moderate (Appendix S1: Table S1). Variation in grazing management practices was part of the experimental design, and we treated domestic livestock grazing as a categorical factor (present/absent) to compare the effects of typical livestock grazing practices to the effects of

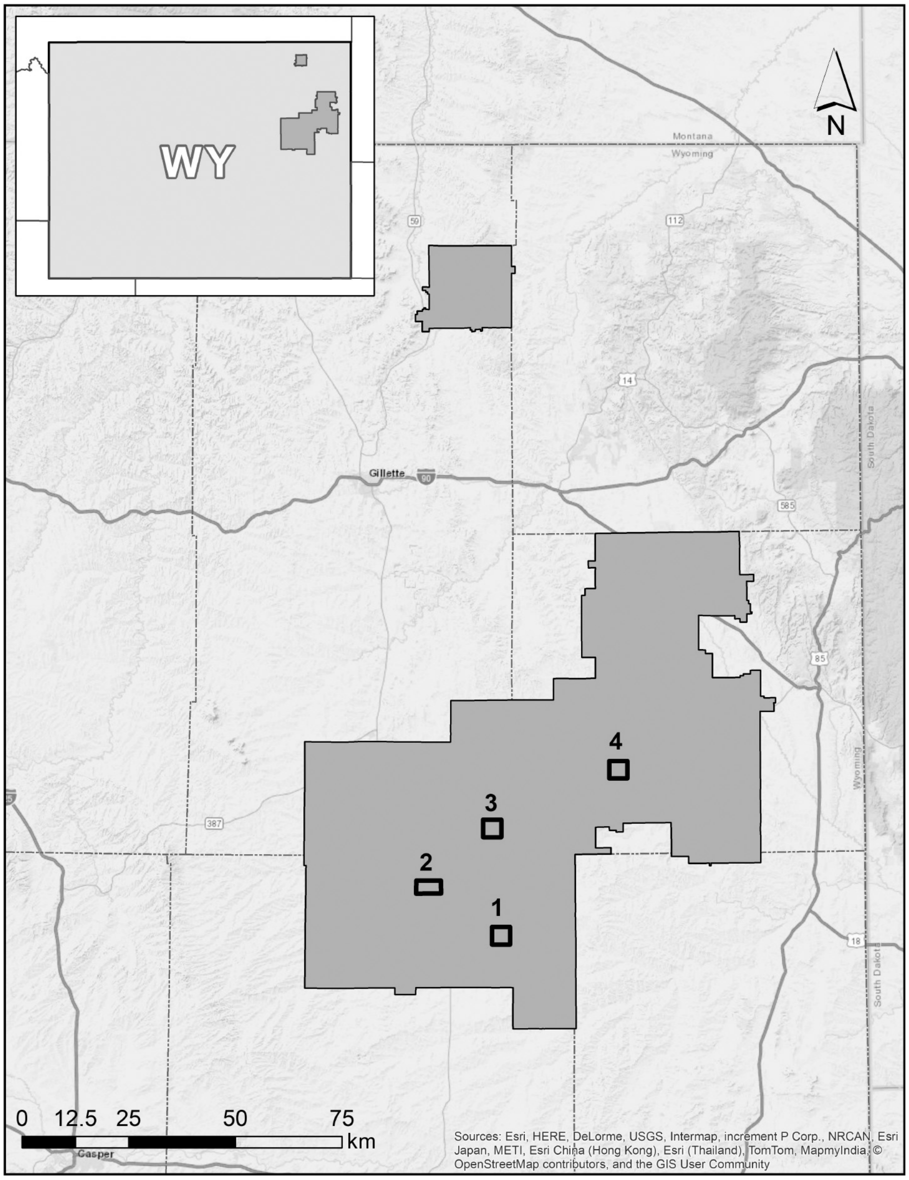

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Fig. 1. The nested exclosure study occurred across four sites in Thunder Basin National Grassland, a 688,000 ha landscape including mixed-grass prairie and sagebrush grasslands in northeastern Wyoming, USA (basemap by ESRI 2018).

other variable disturbances (ungulate herbivory, prairie dog herbivory, and historic wildfire) within this landscape.

Vegetation in undisturbed areas (e.g., control sites) included a northern mixed-grass prairie understory coupled with a sparse, sagebrush-dominated overstory. Common perennial grasses included blue grama (*Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths), western wheatgrass (*Pascopyrum smithii* (Rydb.) Á. Löve), prairie Junegrass (*Koeleria macrantha*; (Ledeb.) Schult.), threadleaf sedge (*Carex filifolia* Nutt.), Sandberg bluegrass (*Poa secunda* J. Presl), and needle-and-thread (*Hesperostipa comata* (Trin. & Rupr.) Barkworth). Annual grasses included two exotic brome species (*Bromus arvensis* L. and *Bromus tectorum* L.) and the native sixweeks fescue (*Vulpia octoflora* Walter Rydb) (Porensky and Blumenthal

Table 1. Site characteristics of nested exclosure study examining interactive effects of disturbance and grazing in northeast Wyoming, USA.

Site	Prairie dogs/ha	Colony size in ha†	Year of fire	No. ha burned	Precipitation 2015‡ (pre-treatment)	Precipitation 2016‡ (year 1)	Precipitation 2017‡ (year 2)	Easting (X)§	Northing (Y)
1	25	47.6	2003	415	296	133	176	490768	4797199
2	12	20.3	2011	183	280	146	173	473778	4808713
3	24	68.6	2004	127	317	124	174	488636	4822578
4	7	34.7	2003	703	338	96	159	518293	4836281

Note: Each 1600-ha site included three sets of nested exclosures (one set on a prairie dog colony, one on a historically burned area, and one on an undisturbed area), each of which was 1 ha in size.

† Colonies at sites 1, 2, and 3 were mapped in 2016, while the colony at Site 4 was last mapped in 2014. Values represent a conservative estimate of colony size.

‡ Growing season precipitation (April–June [mm]).

§ Transverse Mercator projection, NAD 1983 datum UTM Zone 13.

2016). Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beetle & Young) and plains pricklypear cactus *Opuntia polyacantha* (Haw.) were also common throughout the landscape. Vegetation nomenclature adheres to USDA Plants Database (USDA NRCS 2017).

Native ungulates present in the study region (listed approximately in order from most to least abundant) included pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), elk (*Cervus canadensis*), and white-tailed deer (*Odocoileus virginianus*). Black-tailed prairie dogs, rabbits (*Sylvilagus* spp.), and hares (*Lepus* spp.) were also abundant.

Experimental design

We randomly selected four 16 km^2 sites in Thunder Basin. All sites included three distinct types of disturbance history (hereafter disturbance): a black-tailed prairie dog colony, a historic wildfire, and an undisturbed control (unburned, absent of prairie dogs; see Table 1 for disturbance characteristics). The experiment had a blocked design with each of the three distinct disturbance classes present in each of the four sites (n = 12). Within each site, large candidate areas were selected within each disturbance so that sampling areas would be matched in terms of soil type, slope, aspect, and topographic wetness index (an indicator of landscape position). In a random location within each candidate area, we permanently established nested grazing exclosures in fall 2015. Each set of nested exclosures was wholly contained within each disturbance type. Livestock grazing exclosures were 100 × 100 m (1 ha) and constructed with three smooth, high tensile wire strands. We installed the top wire 107 cm and the bottom wire 41 cm above the ground to allow native ungulates unobstructed access inside the livestock exclosure. Nested inside each livestock exclosure, we randomly located and permanently established a native ungulate grazing exclosure 20 × 20 m in size with woven wire field fencing that was 120 cm tall. We permanently installed three 20-m sampling stations at random locations (standardized by distance to fence) within each disturbance type (total n = 36): one outside of each livestock grazing exclosure and accessible to livestock, wild ungulates, and small mammal herbivory (hereafter "Out"); a second inside the livestock grazing exclosure and accessible to wild ungulates and small mammals (hereafter "Livestock Ex"); and the third inside the native ungulate grazing exclosure and accessible only to small mammals, (hereafter "Ungulate Ex"; Fig. 2).

The exclusion fences largely functioned as planned. We used motion-activated game cameras to continuously document ungulate use at each sampling station from November 2016 to November 2017. Camera data indicated fences were largely successful in achieving treatment objectives. Livestock were repeatedly observed at all Out stations except for Site 2 Fire Out, which was un-grazed during the timeframe of our sampling and excluded from analysis (see Appendix S1: Table S1). Cameras recorded native ungulate visits at all Out stations and 11 out of 12 Livestock Ex stations. Cameras documented several cases of calf or lamb presence at Livestock Ex stations for short periods. Although the Ungulate Ex fencing was originally designed to

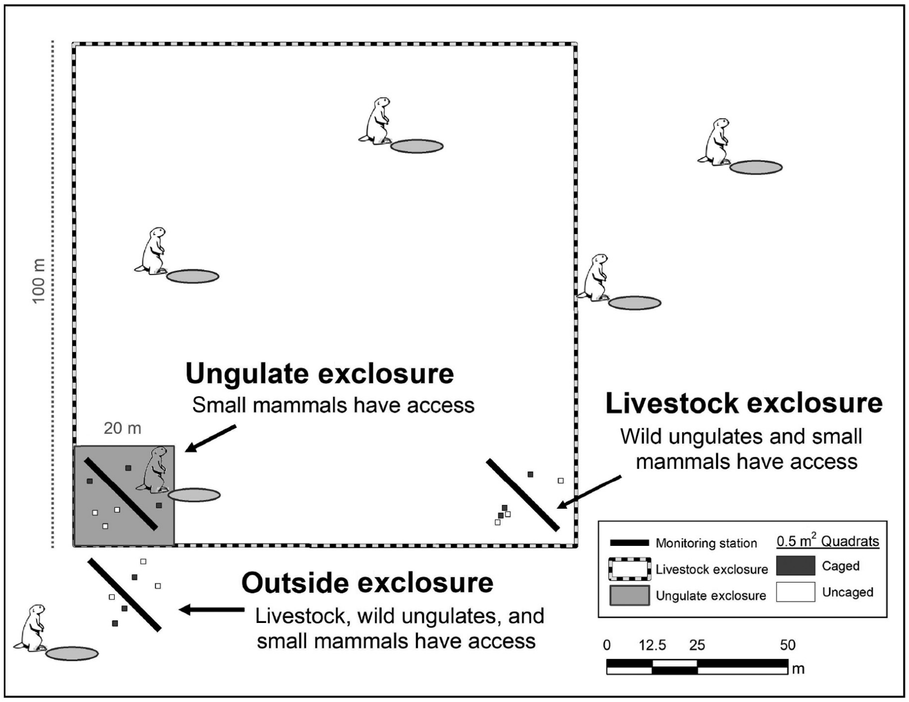

Fig. 2. Diagram of nested exclosure experimental design installed at each combination of site and disturbance history (prairie dog disturbance pictured here). We permanently installed three, 20-m sampling stations at random locations (standardized for distance from fence corners) within each disturbance type (total *n* = 36): one outside of each livestock grazing exclosure and accessible to livestock, wild ungulates, and small mammal herbivory (Out); a second inside the livestock grazing exclosure and accessible to wild ungulates and small mammals (Livestock Ex); and the third inside the native ungulate grazing exclosure and accessible only to small mammals (Ungulate Ex).

exclude pronghorn, it also eliminated most deer and elk use. We documented only three cases of native ungulate presence at Ungulate Ex stations over 12 months of camera trapping. A deer was observed for four minutes at Site 3 Prairie Dog in December 2016, two elk spent 3 h at Site 2 Fire in December 2016, and one elk spent five minutes at Site 2 Fire in October 2017.

Within each 20 × 20 m sampling station, we randomly located six 0.5-m^2 quadrats. Lagomorphs and prairie dogs were excluded from three randomly selected quadrats per sampling station using six-sided, 0.75 × 0.75 × 1 m cages made of 2.5-cm chicken wire. Cages were present throughout the 2016 and 2017 growing seasons but were removed during the winter (November–April) to avoid snow drift effects. The bottom of each cage (i.e., the floor) remained in place year-round and plants grew unimpaired through the mesh floor. Although very small mammals (e.g., mice) could access vegetation inside of these cages, we hereafter refer to them as “small mammal exclusion cages” to distinguish between ungulate and lagomorph/prairie dog exclusion. This design allowed us to experimentally manipulate the interactive effects of historic disturbance and herbivory by livestock, wild ungulates, and small mammals.

Data collection

Estimating prairie dog densities and spring precipitation.—In July 2017, we counted the density of prairie dog burrow entrances in a 20 × 20 m area at each sampling station as a surrogate for estimating prairie dog populations (Biggins et al. in Fish and Wildlife Service 1993). We assessed burrow entrance activity based on signs of activity during the current growing season. Signs of active burrows included fresh scat, vegetation clipping near burrow, and pathways worn in vegetation, whereas signs of inactive burrows included multiple layers of spider webs and vegetation overgrowth near burrow entrances (Andelt and Hopper 2016). We used the count of active burrows to estimate prairie dog population (Biggins et al. 1993; Table 1). We used the parameter–elevation relationships on independent slopes model to calculate spring precipitation, received 1 April–30 June, separately for each year and site by averaging precipitation estimates for the four corners of each site (Table 1; Derner and Hart 2007, PRISM Climate Group 2017).

*Vegetation structure, shrub canopy, and shrub density.—*We measured vegetation structure, shrub density, and shrub cover at each sampling station during peak vegetation growth (late June–early July for vegetation structure; July–August for shrubs). Baseline sampling occurred in 2015 prior to the establishment of the nested grazing exclosures, and stations were resampled in 2016 and 2017 following treatment installation.

We assessed structural responses of herbaceous vegetation to disturbance and herbivory by measuring maximum vegetation height and vegetation visual obstruction (Scasta et al. 2016*b*). For both metrics, we used a visual obstruction pole (modified from Robel et al. 1970) with alternating black and white bands modified to a 1-cm increment, a method with application in grasslands broadly (Ganguli et al. 2000). We placed the modified Robel pole at 1-m intervals on each side of the 20-m sampling station (40 readings per station) and recorded vegetation structure to the centimeter increment, from 4 m away and at a height of 1 m. We calculated mean readings for each station and sampling event for analysis.

We measured shrub canopy using the canopy gap intercept (i.e., line intercept) method. Along each 20-m transect (one per station), we recorded the vertical projection of shrub canopy segments by species. We recorded either gap (>5 cm of non-canopy) or length of canopy vertical projection (Herrick et al. 2005). We measured shrub density by counting all adult shrub species rooted in a 2 × 20 m belt transect. In 2015, we did not record adult and seedling shrubs separately. To estimate and exclude seedlings from 2015 shrub data, we examined how shrub size metrics (height, length, width, and basal diameter, measured for the first ten shrubs encountered in the 2-m belt) differed for seedlings vs. adults in subsequent surveys. Based on this exercise, we determined seedlings to have a basal diameter <1.5 cm and height <15 cm tall. We applied this ruleset to 2015 shrub volume data to determine percent of seedlings, for each sampling station, across all sites and disturbance types. We used this percentage to adjust 2015 shrub density data and removed estimated shrub seedlings from the shrub density dataset.

*Shrub browse.—*We evaluated shrub browsing by measuring the change in length of marked leaders at each sampling station in November 2015, July–August 2016, November 2016, and July–August 2017 (four sampling events). In July–August 2015, we marked the first five shrubs encountered with a height of $\geq$20 cm within a 2-m belt. If necessary, we extended these protocols to a 20 × 20 m area until we identified and permanently marked five shrubs. At each shrub, we installed four uniquely colored zip-ties on leader branches, excluding inflorescences, at either 10 cm or 5 cm from the leader tip. We recorded installation length, color, and shrub number. At each subsequent monitoring event, we measured the length of the shrub leader from zip-tie to leader tip. If a zip-tie could not be located or was found unattached and on the ground, we assumed complete herbivory of the leader and recorded a leader length of zero. We re-established zip-ties as necessary on the same five shrubs to maintain four leaders unless there were no leaders available on the shrub for new zip-ties. If a shrub was completely missing, we assumed complete herbivory of all leaders. For each sampling event, we first calculated proportional change in leader length per month by individual shrub (([(measurement 2 − measurement 1)/measurement 1] ÷ number of days between measurement events) × 30.5 d = change in leader length per month) and then averaged measurements across all shrubs at a given sampling station.

*Droop height.—*In June 2017, we added measurements of grass and forb height at the quadrat scale. For a single individual of grass and forb located closest to the northwest corner of each quadrat (six per sampling station), we measured maximum vertical height without straightening (droop height, a structural metric suggested for use in sage-grouse habitat monitoring; Stiver et al. 2015). If the grass was an annual, we repeated this process for the closest perennial grass. For rhizomatous species, we measured the closest shoot. This metric provides height data at the scale of individual plants, while the visual obstruction pole-based maximum height measurement described above provides data at a patch scale (over 4 m).

*Prairie dog considerations.—*During the growing season of 2016, prairie dogs invaded one of our Fire sites located on private land and impacted the herbaceous vegetation structure at all three sampling stations, and we therefore omitted maximum height and visual obstruction data collected from that site in 2016 from the model. Prairie dogs were lethally controlled in adherence to all legal stipulations in fall 2016 and did not recolonize during the 2017 growing season. Prior to 2017, the USFS restricted recreational shooting of prairie dogs to designated parcels which did not include our study sites; however, beginning in 2017, the ban was lifted and we witnessed recreational shooting of prairie dogs at several of our sites on several occasions. Recreational shooting has been shown to be an ineffective means of controlling prairie dog populations (Hoogland 2006), and we do not believe shooting influenced prairie dog herbivory pressures.

Beginning in mid-summer 2017, black-tailed prairie dogs began to experience fatality and colony collapse from sylvatic plague, a disease which causes nearly 100% mortality in affected colonies (Luce 2001). Two of our four sites with prairie dog disturbance experienced population collapse during this time, but herbaceous vegetation was surveyed at least 2–3 weeks before collapse, and therefore, we feel results remain representative of vegetation structure on active prairie dog colonies.

Statistical analyses

We used linear mixed-effects models to evaluate whether disturbance type (Control, Fire or Prairie Dog), exclosure type (Out, Livestock Ex or Ungulate Ex), or disturbance × exclosure interactions affected metrics of vegetation structure (visual obstruction, vegetation height, shrub density, shrub cover, and shrub browsing). To account for variability across sites, we included site, which was our blocking effect, as a random effect. To account for our hierarchical stratified sampling design with repeated measurements, we included sampling station nested within site and disturbance type ($n = 36$) as a second random effect. To account for precipitation variability among years and sites, we included spring precipitation received per site and year as an additional random effect. Fixed effects include disturbance, exclosure type, disturbance × exclosure, time since experimental treatment, imposed as a continuous variable (for canopy cover and density: 2015 = 0, 2016 = 1, 2017 = 2; for shrub leader data: November 2015 = 1, August 2016 = 2, November 2016 = 3, August 2017 = 4), exclosure × time, and disturbance × exclosure × time. Disturbance × time was not included in the model because we did not experimentally manipulate disturbance types. We constructed models addressing shrub density, cover, and browsing similarly, except we removed spring precipitation from the model because we did not expect it to heavily influence shrub measurements on a year to year basis. For 2017 droop height analyses, we removed spring precipitation and fixed effects related to time since treatment initiation and added fixed effects related to small mammal exclusion cages (main effect and interactions with disturbance and ungulate exclosure). We calculated the percent relative change to summarize metrics of vegetation structure as [(Control − Disturbance1)/Disturbance1] × 100. All linear mixed-effects models were executed in JMP (JMP, version 12.0.1, Cary, North Carolina, USA). Data were transformed when necessary to meet model assumptions of normality and homoscedasticity, and results are presented as means ± SE.

RESULTS

Vegetation structure, shrub canopy, and shrub density

Maximum vegetation height at the patch scale was reduced by at least 54% on sites colonized by prairie dogs compared to fire and undisturbed sites (prairie dog mean = 13.1 cm ± 0.9, fire mean = 32.0 ± 1.5, control mean = 28.3 ± 1.4; $F_{2,23} = 32.41$, $P < 0.0001$; Fig. 3). Similarly, height of vegetation causing visual obstruction was reduced by more than 55% on prairie dog colonies compared to fire and undisturbed sites (prairie dog mean = 3.6 ± 0.4 cm, fire mean = 8.7 ± 0.9,

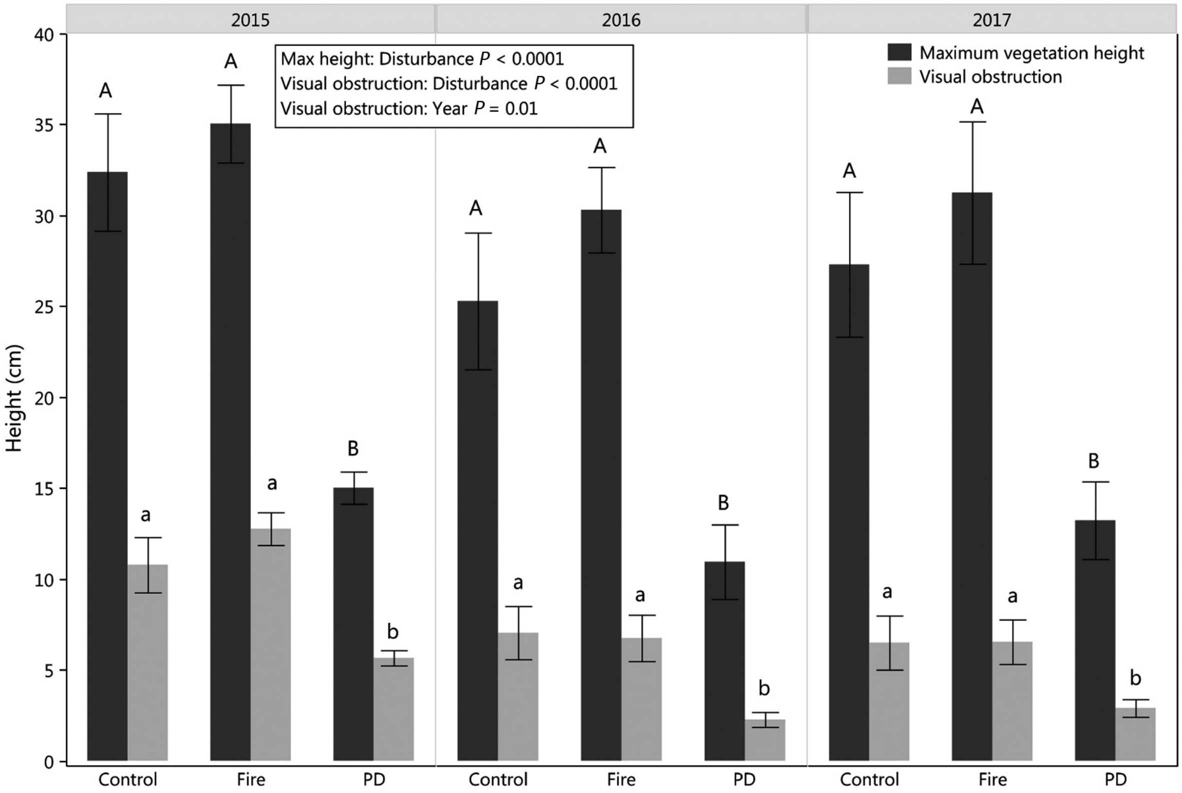

Fig. 3. Maximum vegetation height and height of vegetation causing visual obstruction on control (undisturbed), fire, and prairie dog colony (PD) sites. For a given response, disturbances sharing letters did not differ significantly (Tukey's HSD for main effect of disturbance across years) and capitalization of letters indicates differences for either maximum vegetation height (capitalized) or visual obstruction (lower case). Grazing exclosures had no significant effects and are therefore omitted from the figure. Error bars are calculated based on $n = 4$ site replicates per year.

control mean = 8.1 ± 0.7; $F_{2,23} = 16.21$, $P < 0.0001$; Fig. 3). Visual obstruction significantly varied by treatment year ($P = 0.01$); obstruction heights were greatest during the year of greatest precipitation (2015) and lower in subsequent years. Maximum vegetation height and height of visual obstruction were not significantly explained by exclosure, disturbance × exclosure, treatment year × exclosure, or treatment year × exclosure × disturbance (all P-values > 0.34).

Shrub density, canopy, and leader growth

Average shrub density of all species was reduced by 71% and 78% on prairie dog and fire sites, respectively, when compared to undisturbed sites, regardless of herbivory treatment (prairie dog mean = 7.9 ± 2.4 shrubs/40 m^2, fire mean = 5.9 ± 2.1, control mean = 27.0 ± 5.1; $F_{2,24} = 3.96$, $P = 0.03$; Fig. 4). No other model effects (exclosure, disturbance × exclosure, year of grazing exclosure treatment, treatment year × exclosure, or treatment year × exclosure × disturbance) were significant (all P-values > 0.18). Average shrub density of the dominant shrub, *Artemisia tridentata,* was also significantly explained by disturbance history. *Artemisia tridentata* density was reduced by 76 and 81% on sites with prairie dogs and fires, respectively, when compared to undisturbed sites (prairie dog mean = 4.9 ± 1.5 shrubs/40 m^2, fire mean = 3.8 ± 1.7, and control mean = 20.4 ± 4.3; $F_{2,23} = 5.08$, $P = 0.02$; Fig. 4). Density of *A. tridentata* shrubs declined slightly over time across all treatments (treatment year $P = 0.046$), and no other model effects were significant (all P-values > 0.55).

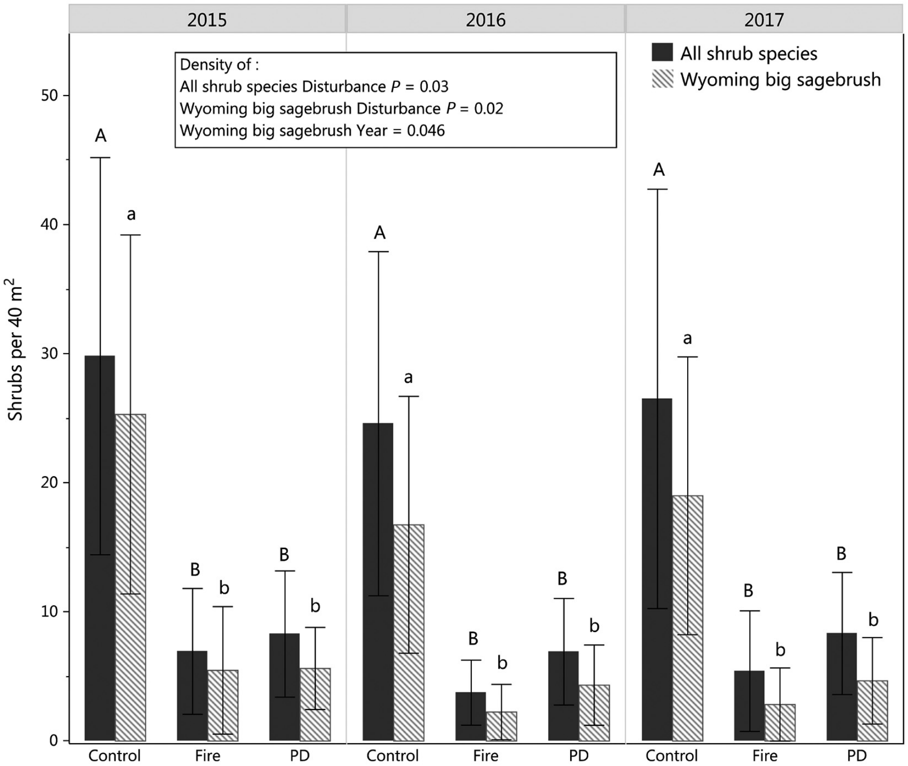

Fig. 4. Density of all adult shrub species and adult Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) shrubs at undisturbed (control), fire, or prairie dog colony (PD) sites. For a given response, disturbances sharing letters did not differ significantly (Student's *t*-test for main effect of disturbance across years for all shrub species and Tukey's HSD for main effect of disturbance across years) and capitalization of letters indicates differences for either all shrub species combined (capitalized) or Wyoming big sagebrush only (lower case). Grazing exclosures had no significant effects and are therefore omitted from figure. Error bars are calculated based on $n = 4$ site replicates per year.

Average percent shrub canopy of all shrub species was reduced by 90% and 89% on sites with prairie dogs and fire, respectively, when compared to undisturbed sites, regardless of herbivory treatment (prairie dog mean = 0.7 ± 0.2%, fire mean = 0.6 ± 0.3, and control mean = 6.1 ± 1.5; $F_{2,22} = 5.07$, $P = 0.02$; Fig. 5). No other model effects were significant (all P-values > 0.09). Similarly, percent shrub canopy of *A. tridentata* was reduced by 90% on sites with prairie dogs and fire, when compared to undisturbed sites (prairie dog mean = 0.6 ± 0.2%, fire mean = 0.6 ± 0.3, control mean = 5.8 ± 1.4; $F_{2,22} = 5.2$, $P = 0.01$; Fig. 5). No other model effects significantly explained *A. tridentata* canopy cover (all P-values > 0.08).

Average leader length of all shrub species was reduced by 369% and 158% on sites with prairie dogs or fire, respectively, when compared to undisturbed sites (prairie dog mean = −12.2 ± 1.5%, fire mean = −6.7 ± 1.9%, and control mean = −2.6 ± 0.6% per month; disturbance $F_{2,55} = 25.51$, $P < 0.0001$; Fig. 6). Disturbance significantly interacted with exclosure ($F_{4,29} = 2.76$, $P = 0.046$; Fig. 6): Prairie dog sites with all grazers (Out station) had significantly more browsing than those with livestock excluded (Livestock Ex stations). Shrub leaders on all prairie dog stations experienced significantly more browsing than undisturbed areas, while leaders at stations with fire had an intermediate level of browsing (Fig. 6). No other model effects (exclosure, month of grazing, exclosure treatment, treatment month × exclosure, or treatment month × exclosure × disturbance) were significant (all P-values > 0.18). For *A. tridentata*, average leader length was

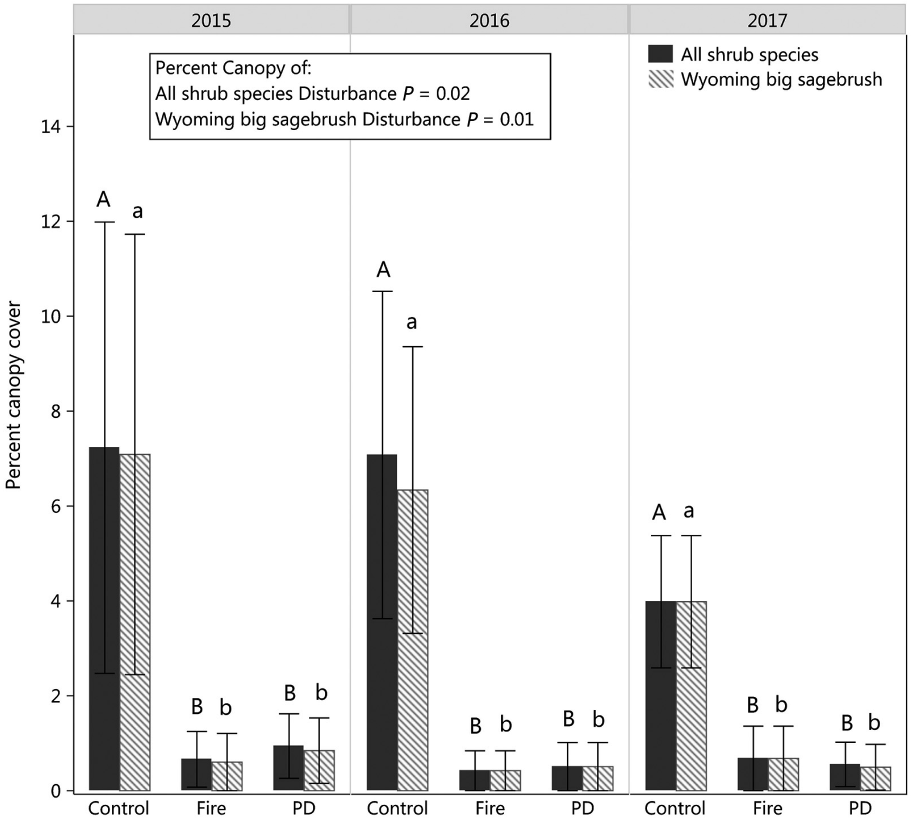

Fig. 5. Canopy cover of all adult shrub species and adult Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) shrubs at undisturbed (control), fire, or prairie dog colony (PD) sites. For a given response, disturbances sharing letters did not differ significantly (Student's *t*-test for main effect of disturbance across years for all shrub species and Tukey's HSD for main effect of disturbance across years) and capitalization of letters indicates differences for either all shrub species combined (capitalized) or Wyoming big sagebrush only (lower case). Grazing exclosures had no significant effects and are therefore omitted from figure. Error bars are calculated based on $n = 4$ site replicates per year.

reduced by 346% at sites with prairie dogs but increased by 62% at sites with fire, when compared to undisturbed sites (prairie dog mean = −11.6 ± 1.4% per month, fire mean = −1.0 ± 0.8% per month, and control mean = −2.6 ± 0.6% per month; $F_{2,13} = 27.17$, $P < 0.0001$; Fig. 7). No other model effects were significant (all P-values > 0.06).

Droop height

For both perennial grasses and all grasses, the effect of small mammal exclosure cages depended on disturbance history (disturbance × cage for perennial grass: $F_{2,167} = 5.58$, $P = 0.005$; all grass $F_{2,166} = 8.71$, $P = 0.0003$). On prairie dog colonies, perennial grasses in small mammal exclosures were 70% taller than grasses exposed to any combination of mammalian herbivory (caged mean = 17.8 ± 1.2 cm, uncaged mean = 10.4 ± 1.1), but cages had no significant effects on perennial grass height on undisturbed or burned sites (Fig. 8). For all grasses, results were similar except that small mammal exclusion significantly influenced grass height at both prairie dog and control sites (Fig. 8; control caged mean = 19.9 ± 2.0 cm, uncaged mean = 12.5 ± 1.3, prairie dog caged mean = 17.6 ± 1.2, uncaged mean = 10.4 ± 1.1). Finally, both small mammal exclusion and disturbance history affected forb heights (Fig. 8, cage $F_{1,140} = 16.17$, $P < 0.0001$, disturbance $F_{2,19} = 8.74$, $P = 0.002$), but disturbance history did not influence the effect of small mammal exclusion (cage × disturbance $F_{2,139} = 0.64$,

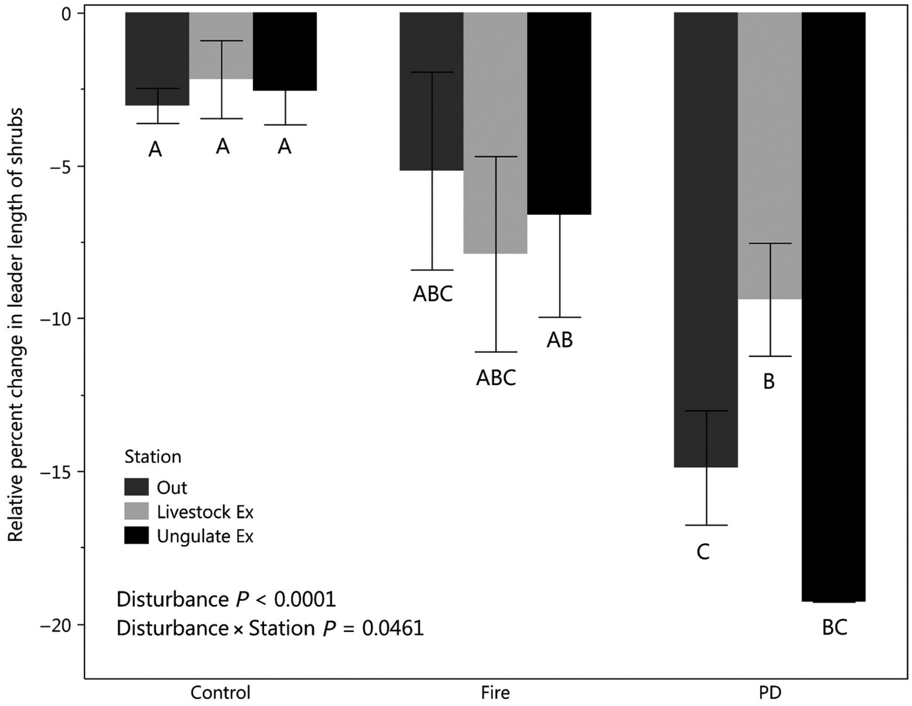

Fig. 6. Relative percent browse of all shrub species at each station (Out, Livestock Ex, Ungulate Ex) and disturbance type (control [undisturbed], fire, and prairie dog colony [PD] sites). Treatments sharing letters did not differ significantly (Tukey's HSD for main effect of disturbance across measurement months).

$P = 0.5$). Forbs on burned sites were at least 40% taller than forbs on undisturbed sites or prairie dog colonies, and small mammal exclusion increased forb height by 38% (Fig. 8). Ungulate exclosure, disturbance × exclosure, exclosure × cage, and disturbance × exclosure × cage did not significantly influence droop heights (all P-values > 0.10).

Discussion

Our research demonstrates that within a sagebrush steppe–mixed-grass prairie ecotone experiencing light-to-moderate livestock grazing pressure, prairie dogs are critical mechanistic drivers of variation in vegetation structure, with historic wildfires contributing to a lesser extent with respect to shrub characteristics and vegetation height. At this grazing pressure and study duration (2 yr), we detected few interactive effects of herbivore exclusion and historic disturbance. However, we did observe that the effects of livestock and small mammal herbivory were more pronounced on prairie dog colonies than on sites with other disturbance histories. This research has applied ecological implications because vegetation structure drives habitat suitability and resource availability for both domestic and wild animals (Lwiwski et al. 2015, Veblen et al. 2016, Ondei et al. 2017). Moreover, abiotic factors such as precipitation, slope, soil, and temperature can further modify vegetation heterogeneity and structure (Davies et al. 2007, Reed et al. 2009). Our study demonstrates that at sites with similar abiotic conditions, historic disturbance shapes vegetation structure more strongly than short-term release from herbivory by different types of ungulates.

Effects of grazing by livestock and wild ungulates

Two years of livestock and wild ungulate exclusion, in the presence or absence of longer term disturbances, had few significant main effects or interactive effects on multiple metrics of vegetation structure measured in our study. This was somewhat surprising, given that large ungulate herbivory can often create structural heterogeneity by removing herbaceous biomass (Holechek et al. 2006, Valeix et al. 2007, Veblen

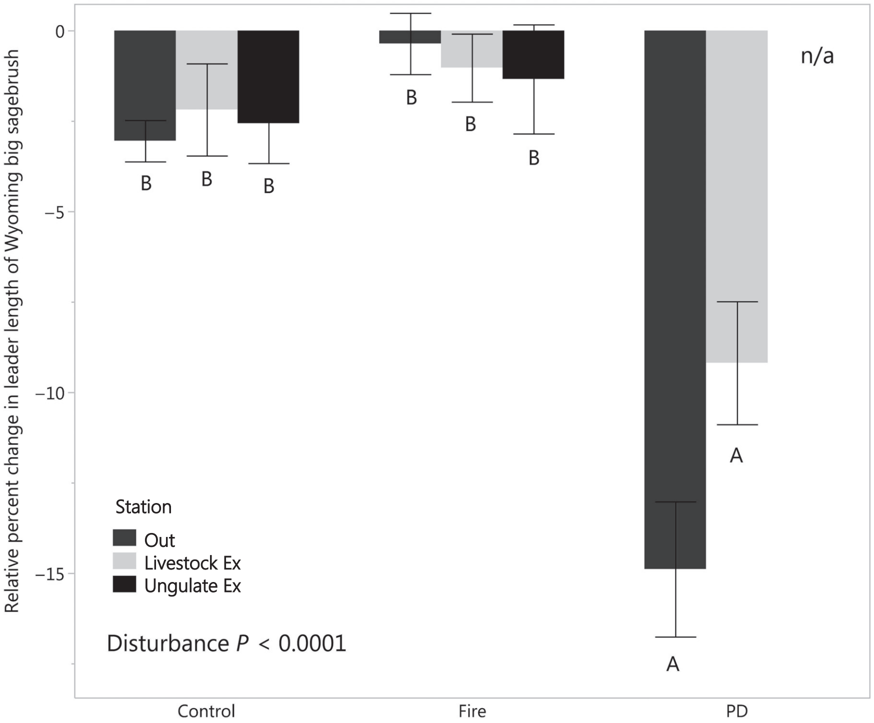

Fig. 7. Relative percent browse of Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) at each station and disturbance type except for Ungulate Ex on Prairie Dog colonies, for which there were no shrubs (denoted with n/a). Disturbances sharing letters did not differ significantly (Tukey's HSD for main effect of disturbance across measurement months). Grazing exclosures had no significant effects.

et al. 2016). We hypothesize that effects of livestock exclusion on vegetation structure may become more apparent over longer time periods. For example, longer term effects of exclosure were demonstrated in an 80-yr study from eastern Oregon, USA (notably, in an area outside of the historic or current range of black-tailed prairie dogs), and included alterations to sagebrush height, sagebrush canopy diameter and gap, and height of sagebrush canopy from ground surface (Davies et al. 2018). Other studies have also demonstrated delayed or slow shifts in plant community composition in response to shifts in grazing pressure (Irisarri et al. 2016, Porensky et al. 2016*a*, Veblen et al. 2016). We note that livestock utilization levels and grazing timing were not experimentally manipulated in our study. Instead, they were determined independently by agricultural producers or federal agencies (depending on land ownership) and were found to be generally light to moderate (Appendix S1: Table S1). We expect that two years of imposed rest might have resulted in stronger structural effects if stocking rates had been heavier (Lwiwski et al. 2015).

Similarly, neither shrub density nor shrub canopy were significantly affected by two years of rest from livestock or wild ungulate browsing, whereas 20+-yr-long studies suggest the exclusion of livestock and wild ungulates can result in greater shrub biomass (Veblen et al. 2015). Although the contribution of shrubs to livestock diet is greatest in the winter (beef cattle, 11–19%, and domestic sheep, 13–23%), shrubs comprise a larger portion of winter diet for wild ungulates (mule deer [*Odocoileus hemionus*], 70–78%; elk [*Cervus canadensis*], 34–44%; pronghorn, 44–62%; Scasta et al. 2016*a*). Despite shifts by livestock and native ungulates to a higher browse diet in wintertime, neither shrub density nor canopy were significantly affected by herbivory or interactive effects of herbivory and historic disturbance.

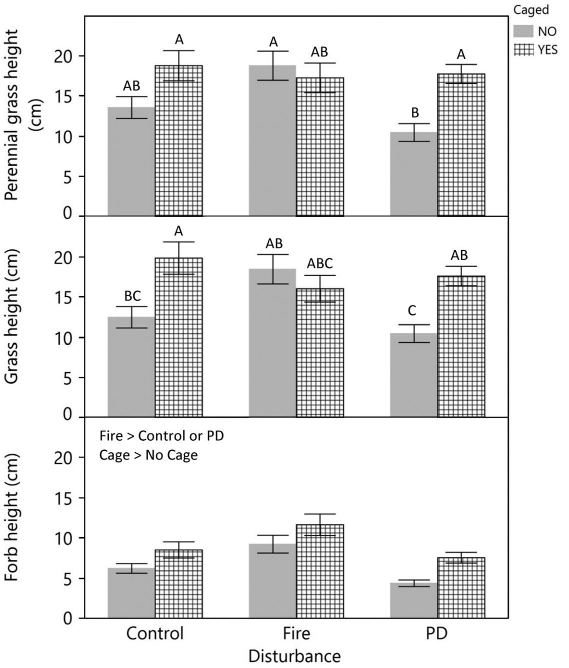

Fig. 8. Droop height of forbs, all grasses, and perennial grasses in the presence and absence of small mammal herbivory (caged vs. uncaged) at control (undisturbed), fire, and prairie dog colony (PD) sites in 2017. For a given response, treatments sharing letters did not differ significantly (Tukey's HSD for main effect of disturbance across years). Ungulate exclosures had no significant effects and are therefore omitted from figure.

However, shrub browsing, as examined through leader browsing, revealed an interactive effect of livestock grazing on prairie dog colonies. Effects of livestock on shrub leader growth within prairie dog colonies may be caused by concentrated herbivory, in which many herbivores (livestock + native ungulates + prairie dogs) browsed on the relatively few shrubs present on colonies and therefore caused larger impacts per shrub (Ponce-Guevara et al. 2016). Additionally, or alternatively, because this interaction was observed for all shrub species but not for sagebrush alone, it is possible that livestock were selectively browsing on non-sagebrush shrubs present at our sites, which include saltbush (*Atriplex canescens* [Pursh] Nutt.) and winterfat (*Krascheninnikovia lanata* [Pursh] A. Meeuse & Smit). Finally, it is possible that we simply had more power to detect a livestock browsing effect for all shrubs than for *Artemisia tridentata* alone. Shrub density also declined slightly over time, likely due to mortality of shrubs during or after the dry year of 2016. We expected that the effects of ungulate herbivores on vegetation structure might differ more among sites with different disturbance histories. However, we found few significant interactions between ungulate exclosures and disturbance type. From a shrub perspective, long-term study of this system is prudent to assess response to livestock and ungulate grazing pressures and their interactive effects with disturbance.

Effects of historic disturbance

Our data revealed historic disturbance from wildfire and prairie dogs are major drivers of structural variation of habitat on loamy soils in a sagebrush steppe–mixed-grass prairie landscape. Vegetation structure and shrub dynamics in this system appear to be engineered by disturbance regimes, with the greatest engineering effects caused by prairie dogs. We found significant differences in maximum vegetation height, visual obstruction, and leader browse of *A. tridentata* on prairie dog colonies when compared to undisturbed sites, while density and canopy of all shrub species, as well as *A. tridentata,* were similarly affected by disturbance. The effects of prairie dog herbivory on herbaceous vegetation are widely documented (Whicker and Detling 1988, Augustine and Springer 2013) and were supported by our droop height analyses, which showed that herbivory by small mammals on prairie dog colonies (i.e., prairie dog herbivory) tended to reduce perennial grass heights more than herbivory by small mammals at burned or undisturbed sites (Fig. 8). Our droop height analyses also suggested that over a two-year period, small mammal herbivory is a more important driver of herbaceous structure than ungulate herbivory or their combination, in this system (Whicker and Detling 1988). Little is known regarding the direct effect of prairie dogs on shrubs in a sagebrush ecosystem (but see Baker et al. 2013). We observed substantial shrub browsing inside and outside of ungulate exclosures, but only on prairie dog colonies (Figs. 6–7). This suggests that shrub herbivory within prairie dog colonies was at least in part due to the prairie dogs themselves and not solely due to preferential browsing of rare forage resources by ungulates. It is also possible, but we believe highly unlikely, that other small mammals co-occurring with prairie dogs were responsible for observed shrub browsing. Although prairie dogs also select habitat with low visual obstruction, including small or low-density shrubs (Roe and Roe 2003), our data are the first to directly demonstrate a reduction in shrub leader growth due to prairie dog herbivory, which further emphasizes their role as ecosystem engineers.

The short- and long-term effects of wildfire on sagebrush and herbaceous vegetation are widely documented (Sankaran et al. 2005, Davies et al. 2011, Scasta et al. 2015). Wyoming big sagebrush require 20 + yr for post-fire recovery (Beetle 1960, Harvey 1981). Although the majority of shrubs observed at our sites were Wyoming big sagebrush, other observed shrub species included silver sagebrush (*Artemisia cana* [Pursh] ssp. *viscidula* (Osterh.) Beetle) and winterfat, and both are well suited for re-establishment via root sprouting post-fire (Woodmansee and Potter 1971, Harvey 1981). Despite the presence of resprouting shrub species, we found that shrub densities on historic wildfires were significantly lower than densities on undisturbed sites. In areas of historic wildfire, increased droop height of forbs, grasses, and perennial grasses may reflect advantageous growth by the herbaceous community after the removal of shrubs by wildfire (Harniss and Murray 1973, Uresk et al. 1976, Lett and Knapp 2003).

Implications for management and conservation

Contemporary management and conservation challenges require robust, experimental research on vegetation responses to the interactive effects of fire and herbivory by livestock, native ungulates, and small mammals. Our study demonstrates that two years of rest from herbivory by livestock (with a light-to-moderate stocking rate) and wild ungulates may not cause major structural shifts in a sagebrush steppe–mixed-grass prairie ecotone. Instead, natural disturbance regimes proved to be the main driver of short-term structural variation in this landscape. Understanding the influential role of natural disturbance regimes may inform the appropriate use of surrogates, such as prescribed fire, herbivory by livestock (Veblen et al. 2016), or a combination of the two (Fuhlendorf and Engle 2004). In contrast, no surrogate exists to replicate the colonial effects of black-tailed prairie dogs (Kotliar et al. 1999), and yet the co-occurrence of prairie dogs and disturbance-sensitive sagebrush shrubs and sagebrush-obligate species such as sage-grouse is an emerging issue of complexity and concern on working landscapes.

Prairie dogs engineer habitat to maintain short vegetation height, and this type of habitat alteration could be counter-productive to habitat maintenance for sage-grouse and other sagebrush-obligate species (Miller and Eddleman 2001, Davies et al. 2011, Beck et al. 2012). Similarly, wildfires appear to alter structure by removing shrub canopy for multiple decades in this ecosystem. Conversely, currently undisturbed areas may provide ideal habitat for sagebrush associated species, but less suitable habitat for prairie dogs and their associates. Current management for sage-grouse habitat often focuses on anthropogenic disturbance (livestock grazing) and natural disturbances such as wildfire, but should also consider habitat structure alterations from co-occurring species of concern such as prairie dogs. Our findings suggest that spatial prioritization based on disturbance history may help managers achieve multiple management objectives in landscapes where sagebrush and prairie dogs coexist. For example, managers could implement management mosaics that match existing landscape mosaics, in which sagebrush conservation efforts are prioritized for sites without a history of repeated prairie dog colonization, and vice versa. Further research on overlap and co-occurrence between these two types of habitat and their associated wildlife assemblages would help land managers and wildlife biologists move from single-species management to approaches based on multi-species assemblages and existing landscape patterns. Our research highlights the importance of direct comparisons among multiple disturbance drivers that coexist and interact within the same system and has global implications for the management of grassland and shrubland systems where multiple herbivores, including ecosystem engineers and livestock, co-occur and interact.

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