Original Research Article

# Long-term grazing removal increased invasion and reduced native plant abundance and diversity in a sagebrush grassland

Lauren M. Porensky [a], [*], Rachel McGee [b], David W. Pellatz [c]

[a] Rangeland Resources and Systems Research Unit, USDA Agricultural Research Service, 1701 Centre Ave, Fort Collins, CO, 80526, USA
[b] Douglas Ranger District, 2250 E Richards St, Douglas, WY, 82633, USA
[c] Thunder Basin Grasslands Prairie Ecosystem Association, 671 Steinle Road, Douglas, WY, 82633, USA

## ARTICLE INFO

## ABSTRACT

Effects of long-term grazing removal on vegetation are highly variable across ecosystems and grazing contexts. In some cases, long-term exclosures can be used to enhance vegetation production, plant diversity, or wildlife habitat. In other situations, exclosures can become more invaded by undesirable species, less drought-tolerant, or less diverse than grazed sites. Grasslands in North America's semi-arid Great Plains prairies can tolerate large herbivore grazing and resist invasion, while cold desert shrublands of the Intermountain West are more invisible and sensitive to grazing. These major ecoregions intersect in northeast Wyoming, where a diverse ecotonal plant community supports a wide array of sensitive wildlife. The effects of grazing removal on vegetation and invasive species in this ecotone are poorly understood, despite clear implications for conservation and management. In 2016, we measured effects of long-term (>49 year-old) livestock exclosures on vegetation and soil properties in the ecotone. Compared to adjacent grazed sites, exclosures had 72% less foliar cover of drought-resistant, warm-season perennial grasses, fewer native species, and nearly three times as much invasive annual grass cover. Long-term livestock removal did not affect live sagebrush shrub cover, density or size, but led to taller herbaceous vegetation structure. Findings suggest that although long-term grazing removal may be useful for achieving taller structure, light to moderate levels of large herbivore grazing may be necessary to resist invasion and maintain ecosystem integrity in this ecotone. In the context of ongoing global change, it will be critical to maintain natural disturbance regimes such as grazing in ecosystems that evolved with disturbance. In these systems, a total lack of natural disturbance does not represent a reasonable target or reference state. Instead, management for a range of disturbance frequencies and intensities across the landscape will likely support high vegetation heterogeneity, which in turn will help conserve high biodiversity and ecosystem function.

Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

## 1. Introduction

Grazing exclosures have a long history in ecology, conservation and management. Exclosures have been used to learn about the effects of grazing (Bakker et al., 2006; Forbes et al., 2019; Goheen et al., 2018; Koerner et al., 2018; Lezama et al.,

* Corresponding author.
  E-mail address: lauren.porensky@usda.gov (L.M. Porensky).

2014; Milchunas and Lauenroth, 1993; Young et al., 2018), to passively restore plant production or diversity (e.g., Al-Rowaily et al., 2015; Bock et al., 1984; Pei et al., 2008; Valone et al., 2002; Yayneshet et al., 2009), or to enhance habitat for sensitive wildlife (e.g., Bock et al., 1984; Schulz and Leininger, 1990; Yeo, 2005). The effects of long-term grazing removal on vegetation vary across ecological and biogeographic contexts. At broad scales, vegetation responses are shaped by factors such as ecosystem-level productivity (Bakker et al., 2006; Lezama et al., 2014; Milchunas and Lauenroth, 1993), evolutionary history of grazing (Milchunas and Lauenroth, 1993), herbivore type (Bakker et al., 2006; Parker et al., 2006; Veblen et al., 2015; but see Veblen et al., 2016), herbivore selectivity (Augustine and McNaughton, 1998), and the sensitivity or tolerance of dominant plant species to grazing (Augustine and McNaughton, 1998; Koerner et al., 2018). Impacts of exclosures on shrubs are particularly variable, with strong evidence that the removal of grazing can either promote shrubs (e.g., Cipriotti and Aguiar, 2012; Manier and Hobbs, 2006) or reduce shrubs (e.g., Roques et al., 2001; Van Auken, 2000) depending on ecosystem context and herbivore type (Veblen et al., 2015).

Relationships between grazing removal and plant invasion are less well studied. Exclosures can suppress invasion by increasing the abundance of native plants (Al-Rowaily et al., 2015; Anderson and Inouye, 2001; Reisner et al., 2013; Veblen et al., 2015; Yeo, 2005) or biocrusts (Anderson et al., 1982; Root et al., 2020; Slate et al., 2019; Yeo, 2005) that are themselves able to resist invaders (e.g., via competitive exclusion). However, exclosures can also become more invaded than grazed sites (Augustine et al., 2017; Loeser et al., 2007; Milchunas et al., 1990; Porensky et al., 2017), particularly if the native plants that compete most effectively with invaders are lost (Milchunas et al., 1992). In some cases, grazed sites support higher abundance or diversity of both native and non-native plants than ungrazed sites (Chaneton et al., 2002; Stahlheber and DAntonio, 2013). Both across and within systems, attempts to quantify the effects of grazing removal are complicated by the fact that grazing is not a binomial process (i.e. grazed vs. ungrazed, Davies and Boyd, 2019). Multivariate factors including grazing intensity, timing, duration, and animal type will impact both long-term trajectories within exclosures (due to legacies of pre-exclosure grazing) and the potential for divergence between exclosures and adjacent grazed areas.

In western North America, ecoregions with different plant communities and evolutionary histories of grazing are juxtaposed. In cold desert shrublands of the Intermountain West (EPA Level II ecoregion 10.1, Omernik, 1987), grazing exclosures tend to enhance the cover or height of dominant shrub species (Courtois et al., 2004; Manier and Hobbs, 2006; Stohlgren et al., 1999; Veblen et al., 2015). Effects of exclosure on herbaceous plant community composition and diversity tend to be weak in cold desert shrublands (Coughenour, 1991; Courtois et al., 2004; Davies et al., 2009; Manier and Hobbs, 2006; Stohlgren et al., 1999; Veblen et al., 2015; Yeo, 2005), though there is evidence that exclosures can reduce bare ground and indicators of erosion (Veblen et al., 2015; Yeo, 2005) while increasing litter cover (Coughenour, 1991; Davies et al., 2009; Stohlgren et al., 1999) and shifting the abundances of common bunchgrasses (Veblen et al., 2015; Yeo, 2005). Some cold desert studies document more invasion in grazed areas (Veblen et al., 2015; Williamson et al., 2019), while others report minimal effects of exclosure on invasion (Courtois et al., 2004), or more invasion in ungrazed and burned sites than other site types (Davies et al., 2009). In some areas, the removal of grazing can enhance biocrust cover and diversity, which in turn can inhibit invasion (Anderson et al., 1982; Brummer et al., 2016; Ponzetti and McCune, 2001; Root et al., 2020; Slate et al., 2019; Yeo, 2005).

In semi-arid prairies of the Great Plains (EPA Level II ecoregions 9.3 and 9.4), the removal of grazing causes a slow, predictable and reversible plant community shift from dominance by $C_4$ (warm-season) to $C_3$ (cool-season) native perennial grasses (Augustine et al., 2017; Fuhlendorf et al., 2001; Irisarri et al., 2016; Porensky et al. 2016, 2017; Vermeire et al., 2018). Exclosures in semi-arid prairies can be associated with higher (Milchunas and Lauenroth, 1993; Porensky et al., 2017) or lower (Koerner et al., 2014; Vermeire et al., 2018) species diversity than grazed sites. These exclosures can also be associated with increased presence of weedy, ruderal, or invasive species (Augustine et al., 2017; Milchunas et al., 1990; Porensky et al., 2017; but see Vermeire et al., 2018). As in the Intermountain West, Great Plains exclosures are associated with increases in litter or standing dead plant cover (Porensky et al. 2016, 2017; Vermeire et al., 2018), but unlike the Intermountain West, grazed areas in the Great Plains can have more lichen and moss cover than ungrazed areas (Porensky et al., 2017). Impacts of exclosure on shrubs in semi-arid prairies are weak and variable depending on shrub identity (Augustine et al., 2017) and the presence of other, interacting disturbances (Connell et al., 2018; Fuhlendorf et al., 2009; Ratajczak et al., 2016). In both systems, there is some evidence that long-term exclosure leads to increases in vegetation structure or biomass, which could have important management implications for both livestock and wildlife (Irisarri et al., 2016; Veblen et al., 2015; Yeo, 2005).

The North American cold deserts meet the semi-arid prairies in northeast Wyoming. The ecotone, or transition zone, between these two major ecoregions supports a diverse plant community where dominant plants from both regions coexist (Porensky et al., 2018). The area also supports a wide array of sensitive wildlife, including greater sage-grouse (*Centrocercus urophasianus*), black-tailed prairie dogs (*Cynomys ludovicianus*), and associated species (Duchardt et al. 2018, 2019; Parker et al., 2019). The ecotone's plant community is poorly understood, though previous work suggests that it displays a hybrid response to disturbance drivers such as wildfire, in that the response includes characteristics typical of the Great Plains as well as characteristics typical of the Intermountain West (Porensky and Blumenthal, 2016; Porensky et al., 2018). Effects of large herbivore grazing on vegetation in this ecotone are relatively unknown, though recent work suggests short-term (2-yr) grazing removal has little impact on vegetation structure (Connell et al., 2018).

We surveyed long-term livestock exclosures in northeast Wyoming to determine how grazing removal altered vegetation and soil characteristics in this ecotonal system. We predicted that impacts of exclosure on the herbaceous plant community would parallel findings from semi-arid prairies, including a shift from $C_4$ to $C_3$ perennial grass dominance, increased

herbaceous vegetation structure, and increased non-native species abundance. We expected impacts of exclosure on the shrub layer to follow trends observed in cold deserts, including increased shrub cover or size.

## 2. Methods

### 2.1. Study region

The study took place in 2016 on the United States Forest Service (USFS) managed Thunder Basin National Grassland in northeast Wyoming, USA (43°15′16″- 43°46′25″ N; 104°53′6″- 105°23′31″ W). Long-term mean annual precipitation (1981−2010) was 320 mm (PRISM Climate Group, 2004), and most precipitation falls during the spring and summer. Precipitation in the 2016 water year (October 2015 through September 2016) was 82% of average. Mean monthly temperature ranges from −5 °C in December to 22 °C in July. Vegetation includes a shrub layer dominated by *Artemisia tridentata* subsp. *wyomingensis* and an understory characteristic of northern mixed-grass prairie. Common graminoids include the $C_4$ (warm-season) perennial grass *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths, the $C_3$ (cool-season) perennial graminoids *Hesperostipa comata* (Trin. & Rupr.) Barkworth and *Pascopyrum smithii* (Rydb.) Á. Löve, and the annual grasses *Bromus tectorum* L., *Bromus arvensis* L., and *Vulpia octoflora* (Walter) Rydb. Common forbs include *Plantago patagonica* Jacq., *Sphaeralcea coccinea* (Nutt.) Rydb, *Logfia arvensis* (L.) Holub, and *Alyssum desertorum* Stapf. The cactus *Opuntia polyacantha* Haw. is also common.

### 2.2. Study design

The study used a paired sampling design. From the USFS we obtained the locations of 34 exclosures within the focal study area. We surveyed each exclosure and rejected those that had unsound fences or evidence of livestock use (19 exclosures), access limitations (2 exclosures), or dense trees (2 exclosures). This process left us with 11 candidate exclosures. For nine of these, USFS records indicated that they had been maintained as long-term study plots and were intended to quantify the ecological effects of grazing removal on upland vegetation (Fig. 1). The other two intact exclosures were much younger and located in riparian areas, and these were not included in the current analysis.

Most of the nine long-term exclosures were established in 1940−1942, and all were in place before 1967, though exact dates of establishment were uncertain in some cases. Exclosures ranged from 0.28 to 1.17 ha in size (mean = 0.52, SD = 0.27) and were located on flat or gently sloping uplands with loamy or clayey soils (R058BY122WY or R058BY104WY ecological sites) (Soil Survey Staff, 2015). Exclosures were constructed using barbed wire fence (typically 5 strand). Fences excluded livestock and pronghorn (*Antilocapra americana*), but likely allowed access by deer and elk (*Odocoileus hemionus*, *Cervus canadensis*, and *Odocoileus virginianus*) (Connell et al., 2018) as well as small mammals and insects. Areas outside of exclosures were managed as grazing allotments by the USFS; over the 50+ years of the study, these areas typically experienced moderate grazing intensities by domestic sheep and/or cattle, with variable seasons of use. Historical records indicate that grazing intensities may have been heavier during World War II.

Within each exclosure we used GIS to randomly place a 30 m-long transect. All interior transects were >2 and < 55 m from the exclosure fence. Each interior transect was paired with an exterior transect located outside of the exclosure. For each exterior transect, we identified areas >5 and < 55 m from the exclosure fence that were within the same pasture and soil survey polygon, and that were well-matched with the interior transect in terms of slope, aspect, and topographic wetness index (TWI) values derived from a Digital Elevation Model (DEM) (Gesch, 2007; Soil Survey Staff, 2015). Within these suitable areas, we randomly placed a 30 m-long transect oriented in the same direction as the interior transect. We sampled the 18 paired transects from June 21 − August 10, 2016. Paired transects were always sampled within a 5-day period.

During preparation of the manuscript, we discovered that six of the exclosures had been sampled by the USFS at irregular intervals between 1957 and 1990. One additional exclosure sampled during this timeframe was removed before 2016. Due to differences in methods, these historical data were not directly comparable to 2016 data. However, we include them to illustrate historical context and trend. Historical data were typically collected at two transects inside and two transects outside of each exclosure. Inside and outside transects were located >5 and < 55 m from the exclosure fence.

### 2.3. Data collection

In 2016, we measured surface soil aggregate stability at 18 locations per transect using the methods described by Herrick et al. (2005). For each transect, we also recorded the dominant pedoderm class, resource retention class, and soil redistribution class (Burkett et al., 2011).

At every third meter along each transect we visually estimated vascular plant cover by species to the nearest percent in 20 × 50 cm quadrats (10 per transect). We estimated canopy cover as plant material that would intercept a raindrop. For portions of the quadrat with no foliar or basal vascular plant cover, we estimated cover of lichen, moss, litter, and bare ground. At the same locations used for canopy cover, we tallied all species rooted within a 0.5 × 1 m quadrat to generate an estimate of species richness. We also calculated and analyzed Shannon diversity, but since results were very similar to those for species richness, we report only richness here.
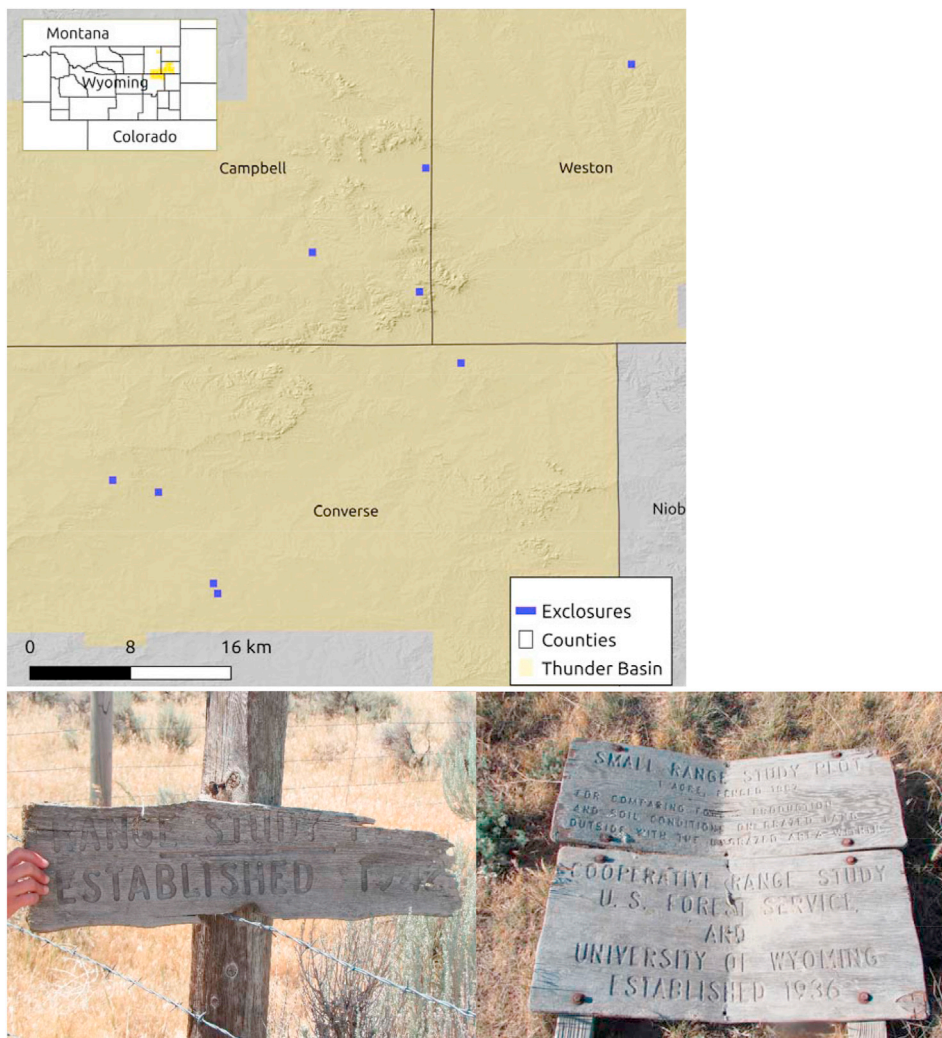
**Fig. 1.** Nine historical exclosures and paired areas outside exclosures were sampled in northeast Wyoming in 2016. All historical exclosures had been maintained for at least 49 years by the US Forest Service.

We used the line point intercept method to record basal cover by species (Herrick et al., 2005), dropping a pin every 50 cm along the transect from 0 to 25 m (51 locations per transect). For *A. tridentata* shrubs we estimated canopy cover along the 30 m transect using the gap intercept method (Herrick et al., 2005). We measured live and dead shrub densities by counting all individuals rooted within a 2 × 30 m belt transect. For the first ten live *A. tridentata* encountered in the 2 m wide belt, we measured height, length and width. We used the standard equation for the volume of an ellipsoid to calculate shrub volume as (4/3)*π*(length/2)*(width/2)*(height/2).

We assessed structural responses of herbaceous vegetation by measuring maximum vegetation height and vegetation visual obstruction. 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. We placed the visual obstruction pole at 1.5 m intervals on each side of the 30 m transect (40 readings per transect), and recorded vegetation structure to the centimeter increment, from 4 m away and at a height of 1 m. Within each of the 10 quadrats used for foliar cover, we also measured the droop height of the grass and forb individuals rooted closest to the southwest corner of each frame. Without straightening the plant, we measured vertically from the ground to the tallest current year's growth (leaf or inflorescence) on each plant.

Historical plant cover data were collected using a Parker 3-Step method (Parker and Harris, 1959). At each of 100 evenly spaced points along each 30.5 m-long (100 ft-long) transect, observers recorded the plant species (or occasionally, multiple species) present at that location. For some sampling periods, annual plants were recorded as litter, while during other periods they were recorded as plants. In cases where multiple plant species were recorded at a given point, we assigned equal proportional cover to each species (e.g. 0.5% cover for each of 2 species). For points with no plant cover, observers assigned the

point to bare ground, litter, and occasionally to moss, lichen, rock, or erosion pavement, though these latter categories were not recorded consistently across sampling periods.

### 2.4. Data analysis

All response variables were aggregated to the transect scale ($N = 18$) before analysis. For most response variables, we used linear mixed models (LMMs) with grazing (inside vs. outside exclosure) as a fixed factor and Exclosure ID (pairing factor) as a random factor. We used this LMM structure to examine relationships between long-term exclosures and a) soil stability; b) absolute foliar cover of 12 functional groups, including all vascular plants, all perennial graminoids, $C_3$ perennial graminoids, $C_4$ perennial grasses, native annual grasses (*V. octoflora*), non-native annual grasses (*B. tectorum + B. arvensis*), forbs, woody plants (mostly *A. tridentata* and *Artemisia frigida*), cactus, litter, lichen and moss, and bare ground; c) basal cover of all vascular plants, all perennial graminoids, $C_4$ perennial grasses, litter, and bare ground; d) species richness; e) *A. tridentata* density and volume; and f) plant height and visual obstruction. For basal cover of lichen and moss, $C_3$ perennial graminoids, native annual grasses, non-native annual grasses, forbs, woody plants, and cactus, and for *A. tridentata* canopy cover, we used non-parametric Wilcoxon signed rank tests on matched pairs due to non-normally distributed data. For soil surface descriptors, we used Chi square analysis of contingency tables to compare class distributions between transects inside and outside of exclosures.

For plant species composition, we performed a detrended correspondence analysis on relative foliar plant cover using a Bray-Curtis dissimilarity matrix. For this analysis, we included all recorded vascular plant species ($N = 45$, Supplemental Table 1) and excluded entities such as bare, lichen, moss, and litter. We ran a PerMANOVA on the dissimilarity matrix with grazing (inside vs. outside exclosure) and Exclosure ID as predictors. We also extracted DCA axis scores and used Linear Mixed Models (LMMs) as described above to evaluate the effects of exclosure on plant community composition while correcting for our paired sampling design.

We analyzed historical Parker 3-step data using LMMs with grazing (inside vs. outside exclosure), year (continuous), and grazing × year as fixed factors. Random factors included Exclosure ID ($N = 7$) and Transect ID nested within Exclosure ID. Response variables included percent cover of all vascular plants, all perennial graminoids, $C_3$ perennial graminoids, $C_4$ perennial grasses, woody plants, cactus, litter, and bare ground. Due to inconsistent sampling methods across time, we were unable to statistically analyze historical data for forbs, annual grasses, moss and lichen, rock, or erosion pavement.

Ordination analyses were conducted in R 3.4.0 using the vegan package (Oksanen et al., 2013), and all other analyses were conducted in JMP (JMP®, Version 12. SAS Institute Inc., Cary, NC, 1989−2007). Data were transformed or variance-weighted when necessary to meet model assumptions. All results were considered significant at $p < 0.05$, marginally significant at $0.05 < p < 0.10$, and are reported as means ± standard error except where noted.

## 3. Results

### 3.1. Soil stability

Soil aggregate stability rankings were high and did not differ between ungrazed exclosures ($5.22 \pm 0.26$) and grazed areas outside exclosures ($5.23 \pm 0.16\%$; $F_{1,8} = 0.07$, $P = 0.8$). Pedoderm class, resource retention class, and soil redistribution class values were similar between exclosures and adjacent grazed areas (Chi square $P$-values >0.5, Supplemental Fig. 1).

### 3.2. Foliar cover

Compared to grazed areas outside exclosures, ungrazed areas inside exclosures had 28% as much $C_4$ perennial grass cover ($F_{1,8} = 31.5$, $P = 0.0005$), 29% as much native annual grass cover ($F_{1,8} = 5.55$, $P = 0.046$), 46% as much bare ground ($F_{1,8} = 7.63$, $P = 0.02$), and nearly 300% as much annual brome cover ($F_{1,8} = 13.4$, $P = 0.006$; Fig. 2a). Cover of other functional groups did not differ significantly between exclosures and adjacent grazed areas ($P$-values > 0.10; Supplemental Fig. 2a).

### 3.3. Basal cover

Compared to grazed areas, ground surfaces in ungrazed exclosures had 135% as much litter cover ($F_{1,8} = 18.4$, $P = 0.003$), 59% as much basal plant cover ($F_{1,8} = 8.3$, $P = 0.02$), 15% as much lichen and moss cover (Wilcoxon $S = 17.5$, $P = 0.03$), and 59% as much bare ground ($F_{1,8} = 4.54$, $P = 0.066$; Fig. 2b). Differences in total plant cover were driven by perennial graminoids ($F_{1,8} = 18.0$, $P = 0.003$) and specifically $C_4$ perennial grasses ($F_{1,8} = 20.1$, $P = 0.002$; Fig. 2b). Basal cover values of other functional groups were very low (< 5%) and did not differ significantly between exclosures and adjacent areas ($P$-values > 0.6; Supplemental Fig. 2b), though median cover of annual bromes was slightly higher inside of exclosures (1% inside vs. 0% outside).
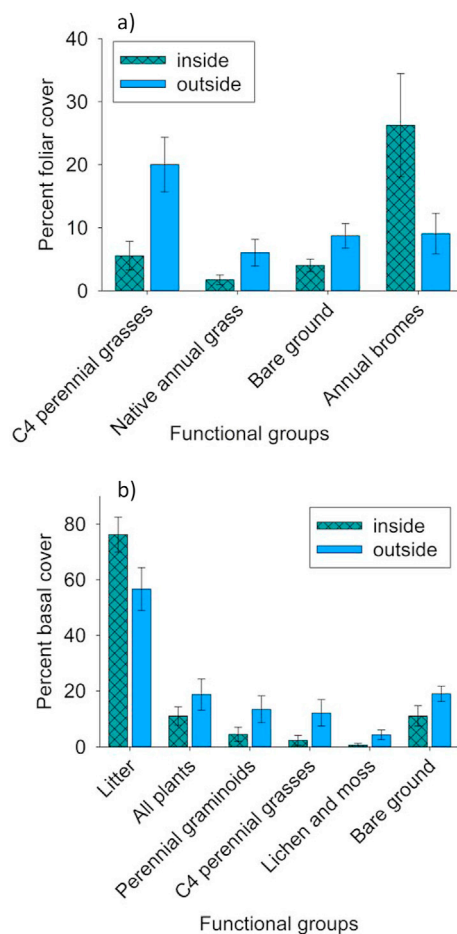
**Fig. 2.** Percent foliar cover (a) and basal cover (b) of functional groups for which historical exclosure had a significant or marginally significant effect on cover. For other functional groups, see Supplemental Fig. 2.

### 3.4. Plant community composition

PerMANOVA results indicated that both grazing treatment (inside vs. outside exclosure) and Exclosure ID significantly influenced plant community composition (grazing $R^2 = 0.11$, $F_{1,17} = 6.03$, $P < 0.001$; Exclosure ID $R^2 = 0.74$, $F_{8,17} = 4.91$, $P < 0.001$). DCA axes 1 through 4 explained 52%, 26%, 11%, and 4% of the variation in plant compositional data, respectively. The first two axes were significantly associated with grazing treatment (DCA 1 $F_{1,8} = 12.6$, $P = 0.008$; DCA 2 $F_{1,8} = 13.4$, $P = 0.006$; DCA 3 $F_{1,8} = 0.06$, $P = 0.8$; DCA 4 $F_{1,8} = 0.55$, $P = 0.5$). DCA Axis 1 separated *B. tectorum* (associated with exclosures) from *B. gracilis, P. patagonica, B. arvensis, Vicia americana* Muhl. ex Willd., *A. desertorum,* and *Schedonnardus paniculatus* (Nutt.) Trel. (associated with areas outside of exclosures; Table 1; Fig. 3). DCA Axis 2 separated *P. smithii, A. desertorum, Cerastium arvense* L., *Draba nemorosa* L., *Picradeniopsis oppositifolia* (Nutt.) Rydb. ex Britton, *Camelina microcarpa* Andrz. ex DC., *B. arvensis,* and *Lappula occidentalis* (S. Watson) Greene (associated with exclosures) from *O. polyacantha, V. octoflora, B. gracilis, Aristida purpurea* Nutt., and *Lepidium densiflorum* Schrad. (associated with areas outside of exclosures; Table 1; Fig. 3).

### 3.5. Species richness

The mean number of species observed per 0.5 m$^2$ quadrat was similar between ungrazed exclosures and grazed areas outside exclosures ($F_{1,8} = 1.97$, $P = 0.2$; Fig. 4a). However, native species richness was 31% higher in grazed areas outside of exclosures ($F_{1,8} = 6.95$, $P = 0.03$; Fig. 4a), while non-native species richness was 38% higher inside of exclosures ($F_{1,8} = 10.1$, $P = 0.01$; Fig. 4a).

**Table 1**

Pairwise correlations between species relative cover and DCA axis scores by transect ($N = 18$). Grazing exclosures were associated with positive values on DCA axes 1 and 2.

**Table 1.** Pairwise correlations between species relative cover and DCA axis scores by transect ($N$=18). Grazing exclosures were associated with positive values on DCA axes 1 and 2.

| Axis | Species | Species Code | Pearson's r | P |
|---|---|---|---|---|
| DCA1 | *Bouteloua gracilis* | BOGR | -0.71 | 0.0009 |
| DCA1 | *Plantago patagonica* | PLPA | -0.7 | 0.001 |
| DCA1 | *Bromus arvensis* | BRAR | -0.55 | 0.02 |
| DCA1 | *Vicia americana* | VIAM | -0.51 | 0.03 |
| DCA1 | *Alyssum desertorum* | ALDE | -0.49 | 0.04 |
| DCA1 | *Schedonnardus paniculatus* | SCPA | -0.48 | 0.046 |
| DCA1 | *Draba reptans* | DRRE | -0.43 | 0.07 |
| DCA1 | *Poa secunda* | POSE | -0.4 | 0.098 |
| DCA1 | *Artemisia frigida* | ARFR | 0.46 | 0.055 |
| DCA1 | *Chenopodium pratericola* | CHPR | 0.47 | 0.05 |
| DCA1 | *Bromus tectorum* | BRTE | 0.89 | <.0001 |
| DCA2 | *Opuntia polyacantha* | OPPO | -0.67 | 0.002 |
| DCA2 | *Vulpia octoflora* | VUOC | -0.65 | 0.003 |
| DCA2 | *Bouteloua gracilis* | BOGR | -0.59 | 0.01 |
| DCA2 | *Aristida purpurea* | ARPU | -0.56 | 0.02 |
| DCA2 | *Lepidium densiflorum* | LEDE | -0.53 | 0.02 |
| DCA2 | *Carex duriuscula* | CADU | -0.42 | 0.08 |
| DCA2 | *Hesperostipa comata* | HECO | -0.41 | 0.09 |
| DCA2 | *Lappula occidentalis* | LAOC | 0.68 | 0.002 |
| DCA2 | *Bromus arvensis* | BRAR | 0.69 | 0.002 |
| DCA2 | *Camelina microcarpa* | CAMI | 0.71 | 0.001 |
| DCA2 | *Picradeniopsis oppositifolia* | PIOP | 0.71 | 0.001 |
| DCA2 | *Draba nemorosa* | DRNE | 0.71 | 0.001 |
| DCA2 | *Cerastium arvense* | CEAR | 0.71 | 0.001 |
| DCA2 | *Alyssum desertorum* | ALDE | 0.72 | 0.0008 |
| DCA2 | *Pascopyrum smithii* | PASM | 0.75 | 0.0003 |

### 3.6. Sagebrush

Densities of live *A. tridentata* shrubs were similar inside and outside of exclosures (Fig. 4b; $F_{1,8} = 0.04, P = 0.9$). Exclosures had three times as many standing dead *A. tridentata* shrubs per hectare as areas outside exclosures (Fig. 4b; $F_{1,8} = 5.66$, $P = 0.045$). Canopy cover of live *A. tridentata* was similar inside and outside of exclosures (median values were 3.6% inside vs. 2.9% outside; Wilcoxon $S = -8.5, P = 0.3$), as were average volumes of live *A. tridentata* ($0.088 \pm 0.045$ m$^3$ inside vs. $0.049 \pm 0.022$ m$^3$ outside; $F_{1,5.5} = 2.17, P = 0.2$).

### 3.7. Vegetation structure

Maximum vegetation height was 35% taller ($F_{1,8} = 10.6, P = 0.01$) and visual obstruction height was 117% taller ($F_{1,8} = 14.2$, $P = 0.006$) inside of exclosures than outside (Fig. 4c). These results were not sensitive to whether the obstructing species was native or non-native. Grass droop height was 44% taller inside of exclosures than outside ($F_{1,8} = 14.6, P = 0.005$), and forb droop height also showed a trend towards taller plants inside exclosures ($F_{1,8} = 4.35, P = 0.07$; Fig. 4c).

### 3.8. Historical cover data

The earliest sampling records we found were from 1957; to the best of our knowledge, most of the sampled exclosures were installed at least 15 years earlier. Although the intensity and temporal scale of sampling varied widely across sites, we were able to detect main effects of exclosure on several functional groups (Supplemental Fig. 3). Across sampling periods, exclosures had 71% as much bare ground (32% outside vs. 23% inside; $F_{1,22} = 9.53, P = 0.005$), 145% as much litter (24% outside vs. 34% inside; $F_{1,20} = 10.6, P = 0.004$), 78% as much perennial graminoid cover (27% outside vs. 21% inside; $F_{1,15} = 21.0$,
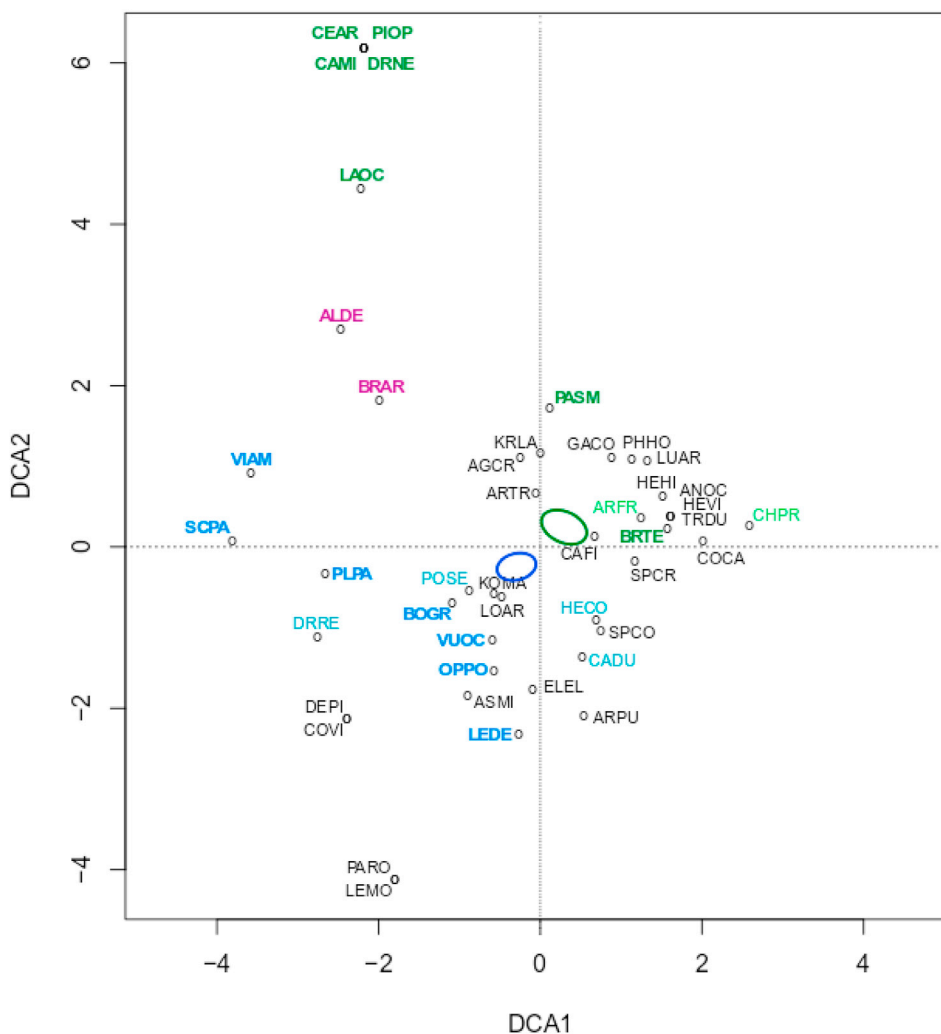
**Fig. 3.** DCA ordination of plant community composition from transects inside and outside of historical exclosures. Ellipses display centroids ± SE for transects inside (green) and outside (blue) of exclosures. Species in green were significantly (dark green) or marginally (light green) associated with exclosures, while species in blue were significantly (dark blue) or marginally (light blue) associated with areas outside of exclosures. Species in purple were positively associated with exclosures along one DCA axis but negatively associated with exclosures along a second DCA axis. For species names, see Table 1 and Supplemental Table 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

$P = 0.0004$), 67% as much $C_4$ perennial grass cover (17.6% outside vs. 11.8% inside; $F_{1,22} = 19.2$, $P = 0.0002$), 132% as much cactus (4.3% outside vs. 5.7% inside; $F_{1,12} = 6.49$, $P = 0.03$), and 159% as much woody plant cover (7.1% outside vs. 11.3% inside; $F_{1,15} = 7.09$, $P = 0.02$) as adjacent grazed areas. In all these cases, the effect of exclosure did not vary significantly over time (exclosure × year $P$-values >0.15). Total plant cover and $C_3$ perennial graminoid cover were not impacted by exclosure (exclosure and exclosure × year $P$-values > 0.15). Annual bromes were not consistently recorded across sampling periods, though species lists indicated that *Bromus tectorum* has been present at most sites since the earliest sampling date. Annual bromes were recorded most consistently in the 1980s; during this decade, *B. tectorum* was slightly more abundant inside exclosures than outside (3.15 ± 1.66% vs. 1.38 ± 1.10%).

## 4. Discussion

We investigated impacts of long-term livestock removal on vegetation and soils in a diverse shrubland-grassland ecotone. Ungrazed exclosures were associated with less native perennial grass cover, fewer native species, and more invasive annual grass cover than grazed sites. Long-term exclosures did not strongly affect sagebrush shrub cover, density or size, but had higher vegetation structure than grazed sites. Our findings suggest that some level of grazing is necessary to resist invasion and maintain ecosystem integrity in this system over the long-term. At the same time, exclosures may be useful for achieving certain objectives, such as plant communities with taller structure.
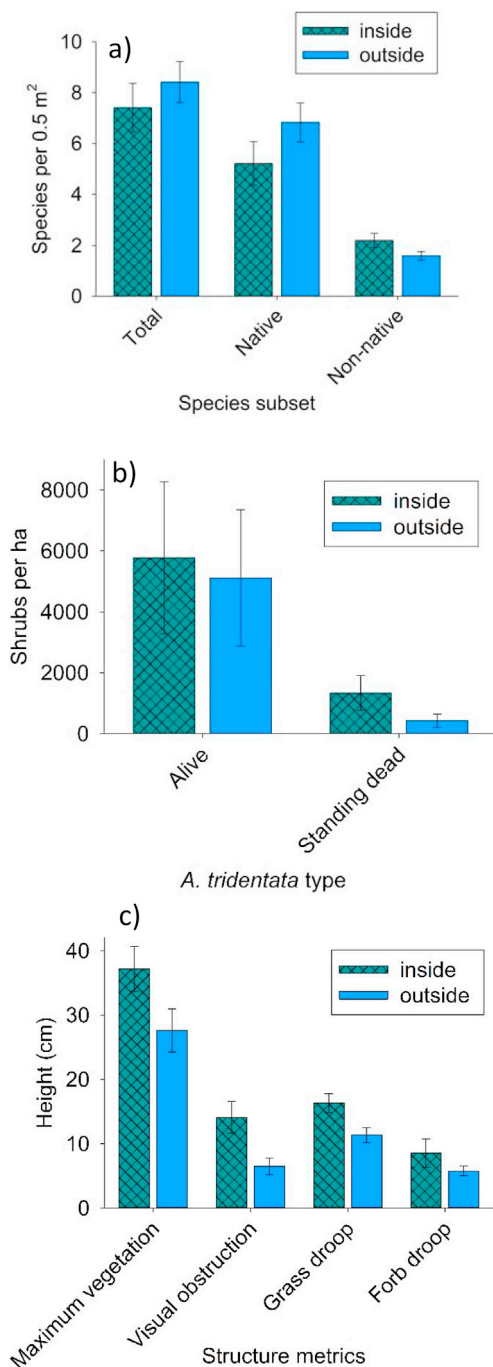
**Fig. 4.** Species richness (a), *A. tridentata* densities (b), and vegetation structure metrics (c) inside and outside of historical exclosures. Total species richness and live *A. tridentata* density were similar inside and outside of exclosures. However, native species richness, non-native species richness, and standing dead *A. tridentata* density varied significantly based on exclosure presence. All metrics of vegetation structure were higher inside of historical exclosures than outside.

The effects of livestock grazing are highly variable based on stocking rate, stock density, and the timing and duration of grazing treatments. Here, we compared the total lack of livestock grazing to a typical public lands grazing scenario in which pastures experience moderate stocking rates and variable seasons of use, usually in the context of an extensive rotational grazing system (Roche et al., 2015). Our results do not provide any information about the effects of higher grazing intensities; in fact, previous studies suggest that heavy grazing can be associated with more brome invasion (e.g., Reisner et al., 2013; Root et al., 2020), less native diversity (e.g., Milchunas and Lauenroth, 1993; Porensky et al., 2017), or both (Loeser et al., 2007). We

also note that our study only investigated upland exclosures, rather than exclosures in riparian areas, which may respond differently (e.g., Schulz and Leininger, 1990).

We hypothesized that herbaceous plant communities inside of exclosures would follow trends typical of semi-arid prairies in the Great Plains, including a shift in dominance from $C_4$ to $C_3$ perennial grasses (Augustine et al., 2017; Fuhlendorf et al., 2001; Irisarri et al., 2016; Porensky et al. 2016, 2017; Vermeire et al., 2018). Our results only partially supported this hypothesis. Plant communities inside exclosures did have fewer $C_4$ perennial grasses, and the relative abundance of *Pascopyrum smithii*, a native $C_3$ perennial grass, responded positively to exclosure. However, exclosures did not significantly increase the cover of $C_3$ perennial grasses as a whole; instead, exclosures had high cover of invasive annual brome species (*B. arvensis* and *B. tectorum*), which varied from 9% cover outside to 26% cover inside exclosures. An increase in non-native species abundance inside exclosures supports our hypotheses as well as several previous studies in semi-arid Great Plains prairies; in those studies, long-term exclosures were associated with weedy or invasive species (Augustine et al., 2017; Milchunas et al., 1990; Porensky et al., 2017; but see Vermeire et al., 2018), but such species remained relatively rare compared to native perennials. Annual brome invasion inside exclosures is likely related to shifts in the competitive environment driven by the loss of invasion-resistant $C_4$ perennials such as *Bouteloua gracilis* (Milchunas et al., 1992; Porensky et al., 2017). It is also possible that exclosure fences, taller-structured $C_3$ perennials and standing dead shrubs contributed to invasion by capturing brome seeds. However, we did not observe corresponding increases in tumble mustards or other species typically associated with seed capture due to fencelines and taller structured vegetation. Future research is needed using larger exclosures in order to rule out the potential effects of fencelines and species movement between treatments (i.e. species pool effects) (Forbes et al., 2019).

Previous studies from Great Plains prairies have found support for both higher species diversity inside exclosures (Milchunas and Lauenroth, 1993; Porensky et al., 2017) and lower species diversity inside exclosures (Koerner et al., 2014; Vermeire et al., 2018). In our study, we found no change in total species richness, but reduced native species richness and increased non-native species richness inside of exclosures. Although our results differ in important ways from previous studies in the central Great Plains, they match up surprisingly well with a study from northern Arizona, also in an ecotone, which found higher cheatgrass abundance, lower native species richness, and higher non-native species richness inside of exclosures (Loeser et al., 2007; Souther et al., 2019). A study of exclosures across Montana, western Wyoming and western Colorado also found fewer native species inside of exclosures than in grazed areas (Stohlgren et al., 1999).

In terms of ground cover, previous work from Intermountain West cold desert shrublands suggested that exclosures tend to increase the abundance of litter and biocrust, while reducing bare ground and indicators of erosion (Anderson et al., 1982; Coughenour, 1991; Ponzetti and McCune, 2001; Root et al., 2020; Stohlgren et al., 1999; Veblen et al., 2015; Yeo, 2005). We found that exclosures had less bare ground and more litter than grazed sites, but exclosures also had less lichen and moss, and indicators of erosion did not differ between exclosures and grazed sites. These results match patterns found elsewhere in the semi-arid Great Plains prairies (Porensky et al. 2016, 2017). Litter can enhance *B. tectorum* by creating safe sites for seedling establishment (Jones et al., 2015), while biocrusts tend to inhibit non-native annual grass establishment (Root et al., 2020; Slate et al., 2019). Thus, in addition to shifts in the biotic competitive environment, the combination of high litter and low biocrust cover inside of exclosures may promote higher levels of non-native annual grasses in this environment. Importantly, and in contrast to previous work from the Intermountain West (Ponzetti and McCune, 2001; Yeo, 2005), typical grazing management on these public lands (moderate intensity, variable season of use) was not associated with lower soil stability or reduced biocrust cover, compared to long-term exclosures. These findings support the idea that the eastern edge of the sagebrush steppe is more resistant to livestock grazing than sites farther west.

Our findings failed to support the hypothesis that exclosures would increase shrub cover or size. Rather, in line with ground cover results, data on sagebrush cover, density, and size suggested the ecotone behaves more similarly to semi-arid prairies than sagebrush steppe. In particular, unlike previous studies from Intermountain sites (Courtois et al., 2004; Manier and Hobbs, 2006; Stohlgren et al., 1999), we detected little evidence of shifts in shrub abundance due to exclosure. Historical data suggested a slight shift in woody plant cover (from ~7% outside exclosures to ~11% inside exclosures), but this difference was not statistically significant in 2016. Live sagebrush densities and sizes did not respond to livestock removal. Differences between this study and previous studies may be related to the types of large herbivores that were excluded; in Utah, cattle removal did not affect shrub metrics, but total ungulate removal led to increases in shrub size and biomass (Veblen et al., 2015). Similar to an elk removal study from western Wyoming (Coughenour, 1991), we found that exclosure led to an increase in the abundance of standing dead shrubs. These increases may simply reflect a lack of large herbivore trampling and subsequent decomposition in the litter layer.

Supporting our hypotheses as well as previous studies from both ecoregions (e.g., Irisarri et al., 2016; Yeo, 2005), we found that long-term exclosures supported taller vegetation structure than grazed sites. This finding contrasts with data from short-term (2-yr) exclosures in the same ecosystem (Connell et al., 2018), suggesting that the effects of livestock removal on vegetation structure are due to long-term changes in species composition rather than short-term utilization effects. In our study, dominant species in grazed areas included $C_4$ grasses and native annual grasses, both of which are short-statured. The replacement of these plants by species such as *Pascopyrum smithii, Bromus* spp., and standing dead shrubs would naturally lead to taller structure inside exclosures. Taller vegetation structure can have positive impacts on some grassland birds (e.g., grasshopper sparrows and lark buntings), but may also lead to declines in species that prefer shorter structure (e.g., horned larks, Duchardt et al., 2019; Duchardt et al., 2018).

Historical data offered some information on the rate of change for different variables in this study. Many differences were already apparent by 1957, 15 years after exclosures were installed. In most cases, the magnitude of exclosure effects grew between sampling in the 1980s and 2016. In particular, the effects of livestock removal on $C_4$ perennial grasses and annual bromes appear to have intensified over the past 30 years.

## 5. Conservation and management implications

Long-term livestock removal can be useful to achieve certain goals in the ecotone between the North American cold deserts and the semi-arid prairies. Exclosures create areas of taller structure, which may be beneficial for certain birds and insects (Duchardt et al., 2019). However, our work emphasizes that these sites may require some level of grazing in order to achieve other goals, including resisting invasion and maintaining ecosystem integrity. Invasive annual grasses are predicted to become a greater threat in this region as a result of climate change (Blumenthal et al., 2016; Bradley, 2009). Moreover, the $C_4$ perennial grasses whose cover declined inside exclosures are highly drought-tolerant (Morgan et al., 1998) and serve as critical sources of forage for livestock and wildlife during droughts. Thus, to maximize invasion resistance and drought tolerance it will be critical to maintain natural disturbance regimes such as grazing in ecosystems that evolved with disturbance (Fuhlendorf et al., 2012; Milchunas and Lauenroth, 1993). In Great Plains prairies, and apparently also in the ecotone separating these ecosystems from the sagebrush steppe, plant communities appear well-adapted to grazing by large herbivores. The lack of this natural disturbance does not represent a reasonable target or reference state. Instead, management for a range of disturbance frequencies and intensities across the landscape will likely support high levels of vegetation heterogeneity, which in turn will help conserve high biodiversity and ecosystem function in this unique ecotone (Duchardt et al., 2018; Fuhlendorf et al., 2012).

## Author contributions

LMP: conceptualization, methodology, data collection and analysis, wrote original draft. RAM: conceptualization, data collection, validation, writing - review & editing. DWP: conceptualization, data collection, validation, writing - review & editing.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgements

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2020.e01267.

## References

Al-Rowaily, S.L., El-Bana, M.I., Al-Bakre, D.A., Assaeed, A.M., Hegazy, A.K., Ali, M.B., 2015. Effects of open grazing and livestock exclusion on floristic composition and diversity in natural ecosystem of Western Saudi Arabia. Saudi J. Biol. Sci. 22, 430–437.

Anderson, D.C., Harper, K., Rushforth, S., 1982. Recovery of cryptogamic soil crusts from grazing on Utah winter ranges. Rangeland Ecology & Management/ Journal of Range Management Archives 35, 355–359.

Anderson, J.E., Inouye, R.S., 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. Ecol. Monogr. 71, 531–556.

Augustine, D.J., Derner, J.D., Milchunas, D., Blumenthal, D., Porensky, L.M., 2017. Grazing moderates increases in C3 grass abundance over seven decades across a soil texture gradient in shortgrass steppe. J. Veg. Sci. 28, 562–572.

Augustine, D.J., McNaughton, S.J., 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. J. Wildl. Manag. 62, 1165–1183.

Bakker, E.S., Ritchie, M.E., Olff, H., Milchunas, D.G., Knops, J.M., 2006. Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. Ecol. Lett. 9, 780–788.

Blumenthal, D.M., Kray, J.A., Ortmans, W., Ziska, L.H., Pendall, E.J.G.C.B., 2016. Cheatgrass is favored by warming but not CO2 enrichment in a semi-arid grassland, 22, 3026–3038.

Bock, C.E., Bock, J.H., Kenney, W.R., Hawthorne, V.M., 1984. Responses of birds, rodents, and vegetation to livestock exclosure in a semidesert grassland site. Rangeland Ecology & Management/Journal of Range Management Archives 37, 239–242.

Bradley, B.A., 2009. Regional analysis of the impacts of climate change on cheatgrass invasion shows potential risk and opportunity. Global Change Biol. 15, 196–208.

Brummer, T.J., Taylor, K.T., Rotella, J., Maxwell, B.D., Rew, L.J., Lavin, M., 2016. Drivers of *Bromus tectorum* abundance in the western North American sagebrush steppe. Ecosystems 19, 986–1000.

Burkett, L.M., Bestelmeyer, B.T., Tugel, A.J., 2011. A field guide to pedoderm and pattern classes. Agriculture handbook 1. ISBN tag 0-9755552-4-3.

Chaneton, E.J., Perelman, S.B., Omacini, M., León, R.J., 2002. Grazing, environmental heterogeneity, and alien plant invasions in temperate Pampa grasslands. Biol. Invasions 4, 7–24.

Cipriotti, P.A., Aguiar, M.R., 2012. Direct and indirect effects of grazing constrain shrub encroachment in semi-arid Patagonian steppes. Appl. Veg. Sci. 15, 35–47.

Connell, L., Scasta, J., Porensky, L., 2018. Prairie dogs and wildfires shape vegetation structure in a sagebrush grassland more than does rest from ungulate grazing. Ecosphere 9, e02390.

Coughenour, M.B., 1991. Biomass and nitrogen responses to grazing of upland steppe on Yellowstone's northern winter range. J. Appl. Ecol. 71–82.

Courtois, D.R., Perryman, B.L., Hussein, H.S., 2004. Vegetation change after 65 years of grazing and grazing exclusion. J. Range Manag. 57, 574–582.

Davies, K.W., Boyd, C.S., 2019. Grazing is not binomial (i.e., grazed or not grazed): a reply to Herman. Bioscience 70, 6–7.

Davies, K.W., Svejcar, T.J., Bates, J.D., 2009. Interaction of historical and nonhistorical disturbances maintains native plant communities. Ecol. Appl. 19, 1536–1545.

Duchardt, C.J., Augustine, D.J., Beck, J.L., 2019. Threshold responses of grassland and sagebrush birds to patterns of disturbance created by an ecosystem engineer. Landsc. Ecol. 34, 895–909.

Duchardt, C.J., Porensky, L.M., Augustine, D.J., Beck, J.L., 2018. Disturbance shapes avian communities on a grassland–sagebrush ecotone. Ecosphere 9, e02483.

Forbes, E.S., Cushman, J.H., Burkepile, D.E., Young, T.P., Klope, M., Young, H.S.J.F.e., 2019. Synthesizing the effects of large. wild herbivore exclusion on ecosystem function 33, 1597–1610.

Fuhlendorf, S.D., Briske, D.D., Smeins, F.E., 2001. Herbaceous vegetation change in variable rangeland environments: the relative contribution of grazing and climatic variability. Appl. Veg. Sci. 4, 177–188.

Fuhlendorf, S.D., Engle, D.M., Elmore, R.D., Limb, R.F., Bidwell, T.G., 2012. Conservation of pattern and process: developing an alternative paradigm of rangeland management. Rangel. Ecol. Manag. 65, 579–589.

Fuhlendorf, S.D., Engle, D.M., Kerby, J., Hamilton, R., 2009. Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing. Conserv. Biol. 23, 588–598.

Gesch, D.B., 2007. The national elevation dataset. In: Maune, D. (Ed.), Digital Elevation Model Technologies and Applications: the DEM Users Manual, second ed. American Society for Photogrammetry and Remote Sensing, Bethesda, Maryland, pp. 99–118.

Goheen, J.R., Augustine, D.J., Veblen, K.E., Kimuyu, D.M., Palmer, T.M., Porensky, L.M., Pringle, R.M., Ratnam, J., Riginos, C., Sankaran, M., 2018. Conservation lessons from large-mammal manipulations in East African savannas: the KLEE, UHURU, and GLADE experiments. Ann. N. Y. Acad. Sci. 1429, 31–49.

Herrick, J.E., Zee, J.W.V., Havstad, K.M., Whitford, W.G., 2005. quick start. Monitoring Manual for Grassland, Shrubland and Savanna Ecosystems, vol. 1. University of Arizona Press, Tucson, AZ, USA.

Irisarri, J.G.N., Derner, J.D., Porensky, L.M., Augustine, D.J., Reeves, J.L., Mueller, K.E., 2016. Grazing intensity differentially regulates ANPP response to precipitation in North American semiarid grasslands. Ecol. Appl. 26, 1370–1380.

Jones, R.O., et al., 2015. The role of resource limitation in restoration of sagebrush ecosystems dominated by cheatgrass (Bromus tectorum). Ecosphere 6 (7), 1–21.

Koerner, S.E., Burkepile, D.E., Fynn, R.W., Burns, C.E., Eby, S., Govender, N., Hagenah, N., Matchett, K.J., Thompson, D.I., Wilcox, K.R.J.E., 2014. Plant community response to loss of large herbivores differs between North American and South African savanna grasslands, 95, 808–816.

Koerner, S.E., Smith, M.D., Burkepile, D.E., Hanan, N.P., Avolio, M.L., Collins, S.L., Knapp, A.K., Lemoine, N.P., Forrestel, E.J., Eby, S., Thompson, D.I., Aguado-Santacruz, G.A., Anderson, J.P., Anderson, T.M., Angassa, A., Bagchi, S., Bakker, E.S., Bastin, G., Baur, L.E., Beard, K.H., Beever, E.A., Bohlen, P.J., Boughton, E.H., Canestro, D., Cesa, A., Chaneton, E., Cheng, J., D'Antonio, C.M., Deleglise, C., Dembélé, F., Dorrough, J., Eldridge, D.J., Fernandez-Going, B., Fernández-Lugo, S., Fraser, L.H., Freedman, B., García-Salgado, G., Goheen, J.R., Guo, L., Husheer, S., Karembé, M., Knops, J.M.H., Kraaij, T., Kulmatiski, A., Kytöviita, M.-M., Lezama, F., Loucougaray, G., Loydi, A., Milchunas, D.G., Milton, S.J., Morgan, J.W., Moxham, C., Nehring, K.C., Olff, H., Palmer, T.M., Rebollo, S., Riginos, C., Risch, A.C., Rueda, M., Sankaran, M., Sasaki, T., Schoenecker, K.A., Schultz, N.L., Schütz, M., Schwabe, A., Siebert, F., Smit, C., Stahlheber, K.A., Storm, C., Strong, D.J., Su, J., Tiruvaimozhi, Y.V., Tyler, C., Val, J., Vandegehuchte, M.L., Veblen, K.E., Vermeire, L.T., Ward, D., Wu, J., Young, T.P., Yu, Q., Zelikova, T.J., 2018. Change in dominance determines herbivore effects on plant biodiversity. Nature Ecology & Evolution 2, 1925–1932.

Lezama, F., Baeza, S., Altesor, A., Cesa, A., Chaneton, E.J., Paruelo, J.M., 2014. Variation of grazing-induced vegetation changes across a large-scale productivity gradient. J. Veg. Sci. 25, 8–21.

Loeser, M.R.R., Sisk, T.D., Crews, T.E., 2007. Impact of grazing intensity during drought in an Arizona grassland. Conserv. Biol. 21, 87–97.

Manier, D.J., Hobbs, N.T., 2006. Large herbivores influence the composition and diversity of shrub-steppe communities in the Rocky Mountains, USA. Oecologia 146, 641–651.

Milchunas, D.G., Lauenroth, W.K., 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecol. Monogr. 63, 327–366.

Milchunas, D.G., Lauenroth, W.K., Chapman, P.L., 1992. Plant competition, abiotic, and long- and short-term effects of large herbivores on demography of opportunistic species in a semiarid grassland. Oecologia 92, 520–531.

Milchunas, D.G., Lauenroth, W.K., Chapman, P.L., Kazempour, M.K., 1990. Community attributes along a perturbation gradient in a shortgrass steppe. J. Veg. Sci. 1, 375–384.

Morgan, J.A., LeCain, D.R., Read, J.J., Hunt, H.W., Knight, W.G., 1998. Photosynthetic pathway and ontogeny affect water relations and the impact of CO2 on Bouteloua gracilis (C4) and Pascopyrum smithii (C3). Oecologia 114, 483–493.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2013. vegan: community Ecology Package. R package version 2.0-10. http://CRAN.R-project.org/package=vegan.

Omernik, J.M., 1987. Ecoregions of the conterminous United States. Map (scale 1:7,500,000). Ann. Assoc. Am. Geogr. 77, 118–125.

Parker, J.D., Burkepile, D.E., Hay, M.E., 2006. Opposing effects of native and exotic herbivores on plant invasions. Science 311, 1459–1461.

Parker, K.W., Harris, R.W., 1959. The 3-step method for measuring condition and trend of forest ranges. In: Proceedings of the Symposium at Tifton, Georgia Techniques and Methods of Measuring Understory Vegetation. USDA, Southern and Southeastern Forest Experiment Stations, Tifton, Georgia, pp. 55–69.

Parker, R.A., Duchardt, C.J., Dwyer, A.M., Painter, C., Pierce, A.K., Michels, T.J., Wunder, M.B., 2019. Trophic Ecology Warrants Multispecies Management in a Grassland Setting: Proposed Species Interactions on Black-Tailed Prairie Dog Colonies (Rangelands).

Pei, S., Fu, H., Wan, C., 2008. Changes in soil properties and vegetation following exclosure and grazing in degraded Alxa desert steppe of Inner Mongolia, China. Agric. Ecosyst. Environ. 124, 33–39.

Ponzetti, J.M., McCune, B.P., 2001. Biotic soil crusts of Oregon's shrub steppe: community composition in relation to soil chemistry, climate, and livestock activity. Bryol. 104, 212–225, 214.

Porensky, L.M., Blumenthal, D.M., 2016. Historical wildfires do not promote cheatgrass invasion in a western Great Plains steppe. Biol. Invasions 18, 3333–3349.

Porensky, L.M., Derner, J.D., Augustine, D.J., Milchunas, D.G., 2017. Plant community composition after 75 yr of sustained grazing intensity treatments in shortgrass steppe. Rangel. Ecol. Manag. 70, 456–464.

Porensky, L.M., Derner, J.D., Pellatz, D.W., 2018. Plant community responses to historical wildfire in a shrubland−grassland ecotone reveal hybrid disturbance response. Ecosphere 9, e02363.

Porensky, L.M., Mueller, K.E., Augustine, D.J., Derner, J.D., 2016. Thresholds and gradients in a semi-arid grassland: long-term grazing treatments induce slow, continuous and reversible vegetation change. J. Appl. Ecol. 53, 1013–1022.

PRISM Climate Group, 2004. Oregon State University. http://prism.oregonstate.edu created 4 Feb.

Ratajczak, Z., Briggs, J.M., Goodin, D.G., Luo, L., Mohler, R.L., Nippert, J.B., Obermeyer, B., 2016. Assessing the potential for transitions from tallgrass prairie to woodlands: are we operating beyond critical fire thresholds? Rangel. Ecol. Manag. 69, 280–287.

Reisner, M.D., Grace, J.B., Pyke, D.A., Doescher, P.S., 2013. Conditions favouring *Bromus tectorum* dominance of endangered sagebrush steppe ecosystems. J. Appl. Ecol. 50, 1039–1049.

Robel, R., Briggs, J., Dayton, A., Hulbert, L., 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. J. Range Manag. 295–297.

Roche, L.M., Cutts, B.B., Derner, J.D., Lubell, M.N., Tate, K.W., 2015. On-Ranch grazing strategies: context for the rotational grazing dilemma. Rangel. Ecol. Manag. 68, 248–256.

Root, H.T., Miller, J.E., Rosentreter, R., 2020. Grazing disturbance promotes exotic annual grasses by degrading soil biocrust communities. Ecol. Appl. 30, e02016.

Roques, K.G., O'Connor, T.G., Watkinson, A.R., 2001. Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. J. Appl. Ecol. 38, 268–280.

Schulz, T.T., Leininger, W.C., 1990. Differences in riparian vegetation structure between grazed areas and exclosures. J. Range Manag. 43, 295–299.

Slate, M.L., Callaway, R.M., Pearson, D.E., 2019. Life in interstitial space: biocrusts inhibit exotic but not native plant establishment in semi-arid grasslands. J. Ecol. 107, 1317–1327.

USDA Soil Survey Staff, N.R.C.S., 2015. Soil survey geographic (SSURGO) database, Available online at: http://sdmdataaccess.nrcs.usda.gov/.

Souther, S., Loeser, M., Crews, T.E., Sisk, T., 2019. Drought exacerbates negative consequences of high-intensity cattle grazing in a semiarid grassland. Ecological Applications n/a e02048.

Stahlheber, K.A., DAntonio, C.M., 2013. Using livestock to manage plant composition: a meta-analysis of grazing in California Mediterranean grasslands. Biol. Conserv. 157, 300–308.

Stohlgren, T.J., Schell, L.D., Vanden Heuvel, B., 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. Ecol. Appl. 9, 45–64.

Valone, T.J., Meyer, M., Brown, J.H., Chew, R.M., 2002. Timescale of perennial grass recovery in desertified arid grasslands following livestock removal. Conserv. Biol. 16, 995–1002.

Van Auken, O.W., 2000. Shrub invasions of North American semiarid grasslands. Annu. Rev. Ecol. Systemat. 31, 197–215.

Veblen, K.E., Nehring, K.C., McGlone, C.M., Ritchie, M.E., 2015. Contrasting effects of different mammalian herbivores on sagebrush plant communities. PloS One 10, e0118016.

Veblen, K.E., Porensky, L.M., Riginos, C., Young, T.P., 2016. Are cattle surrogate wildlife? Savanna plant community composition explained by total herbivory, not herbivore identity. Ecol. Appl. 26, 1610–1623.

Vermeire, L.T., Strong, D.J., Waterman, R.C.J.R.E., Management, 2018. Grazing History Effects on Rangeland Biomass, Cover and Diversity Responses to Fire and Grazing Utilization, vol. 71, pp. 770–775.

Williamson, M.A., Fleishman, E., Mac Nally, R.C., Chambers, J.C., Bradley, B.A., Dobkin, D.S., Board, D.I., Fogarty, F.A., Horning, N., Leu, M., Wohlfeil Zillig, M., 2019. Fire, Livestock Grazing, Topography, and Precipitation Affect Occurrence and Prevalence of Cheatgrass (Bromus Tectorum) in the Central Great Basin. Biological Invasions, USA.

Yayneshet, T., Eik, L., Moe, S., 2009. The effects of exclosures in restoring degraded semi-arid vegetation in communal grazing lands in northern Ethiopia. J. Arid Environ. 73, 542–549.

Yeo, J.J., 2005. Effects of grazing exclusion on rangeland vegetation and soils, East Central Idaho. Western North American Naturalist 65, 11.

Young, T.P., Porensky, L.M., Riginos, C., Veblen, K.E., Odadi, W.O., Kimuyu, D.M., Charles, G.K., Young, H.S., 2018. Relationships between cattle and biodiversity in multiuse landscape revealed by Kenya Long-Term Exclosure Experiment. Rangel. Ecol. Manag. 71, 281–291.