

RESEARCH ARTICLE

Contrasting Effects of Different Mammalian Herbivores on Sagebrush Plant Communities

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OPEN ACCESS

Citation: Veblen KE, Nehring KC, McGlone CM, Ritchie ME (2015) Contrasting Effects of Different Mammalian Herbivores on Sagebrush Plant Communities. PLoS ONE 10(2): e0118016. doi:10.1371/journal.pone.0118016

Academic Editor: Martin Schädler, Helmholtz Centre for Environmental Research (UFZ), GERMANY

Received: October 13, 2014

Accepted: January 7, 2015

Published: February 11, 2015

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Data Availability Statement: All relevant data are within the paper and its Supporting Information files.

Funding: This work was supported by the Deseret Land and Livestock <http://www.deseretlandandlivestock.com/> (MER); Utah Agricultural Experiment Station <http://uaes.usu.edu/> (KEV); Utah Agricultural Experiment Station Mineral Lease Funds (MER); USDA-ARS Pollinating Insect Research Unit [http://www.ars.usda.gov/main/site_main.htm?modecode=20-80-05-00\(CMM\)](http://www.ars.usda.gov/main/site_main.htm?modecode=20-80-05-00(CMM)); and the National Science Foundation DEB grants 0087201 and 0244247 (MER). The funders had no role in data collection and analysis, decision to publish, or

Abstract

Herbivory by both grazing and browsing ungulates shapes the structure and functioning of terrestrial ecosystems worldwide, and both types of herbivory have been implicated in major ecosystem state changes. Despite the ecological consequences of differences in diets and feeding habits among herbivores, studies that experimentally distinguish effects of grazing from spatially co-occurring, but temporally segregated browsing are extremely rare. Here we use a set of long-term exclosures in northern Utah, USA, to determine how domestic grazers vs. wild ungulate herbivores (including browsers and mixed feeders) affect sagebrush-dominated plant communities that historically covered ~62 million ha in North America. We sampled plant community properties and found that after 22 years grazing and browsing elicited perceptible changes in overall plant community composition and distinct responses by individual plant species. In the woody layer of the plant community, release from winter and spring wild ungulate herbivory increased densities of larger Wyoming big sagebrush (*Artemisia tridentata*, ssp. *wyomingensis*) at the expense of small sagebrush, while disturbance associated with either cattle or wild ungulate activity alone was sufficient to increase bare ground and reduce cover of biological soil crusts. The perennial bunchgrass, bottlebrush squirreltail (*Elymus elymoides*), responded positively to release from summer cattle grazing, and in turn appeared to competitively suppress another more grazing tolerant perennial grass, Sandberg's blue grass (*Poa secunda*). Grazing by domestic cattle also was associated with increased non-native species biomass. Together, these results illustrate that ungulate herbivory has not caused sagebrush plant communities to undergo dramatic state shifts; however clear, herbivore-driven shifts are evident. In a dry, perennial-dominated system where plant community changes can occur very slowly, our results provide insights into potential long-term trajectories of these plant communities under different large herbivore regimes. Our results can be used to guide long-term management strategies for sagebrush systems and improve habitat for endemic wildlife species such as sage-grouse (*Centrocercus* spp.).

preparation of the manuscript. With the exception of Deseret Land and Livestock, the funders had no role in study design. Deseret Land and Livestock identified general locations for the exclosures so we could focus the study on known winter ungulate range. However, the specific locations of different treatments were chosen by the authors.

Competing Interests: Deseret Land and Livestock provided funding for the building of exclosures. This does not alter the authors' adherence to PLOS ONE policies on sharing data and materials.

Introduction

Large ungulate herbivory shapes the physiognomy and functioning of terrestrial ecosystems worldwide. Both grazing and browsing can profoundly influence the structure and composition of plant communities [1–6] with far-reaching consequences for multiple taxa [7–11], including other ungulate herbivores [12–15]. The presence of grazers, such as cattle, has been implicated in major ecosystem state shifts, including woody plant encroachment and apparently permanent conversions from native to non-native plant communities [16–19] (but see [20–22]). Yet despite the potential for additive or antagonistic effects among different ungulates on plant communities (e.g., [23]), the effects of browsing have been underemphasized in the scientific grazing literature and often times completely ignored.

Large herbivores can have contrasting effects on plant community composition and dynamics through their behavior and diet preferences [24, 25], both of which can vary seasonally [26, 27]. Cattle are globally distributed domestic grazers that efficiently digest herbaceous material (i.e., mostly grasses and some forbs). Heavy use by grazers such as cattle can reduce or eliminate perennial grasses, thereby shifting plants towards dominance by woody species (Fig. 1) [28–30] or less palatable herbaceous species [31, 32]. While some wild ungulate grazers (e.g., equids and Bovini) may have effects on plant communities very similar to domestic cattle, other wild ungulates are browsers (e.g., North American mule deer [*Odocoileus hemionus*]) that feed primarily on woody species and forbs [33] or mixed feeders (e.g., elk [*Cervus elaphus*]) that both graze and browse and show a variable and broad diet range [34–36]. In highly seasonal systems the feeding behavior of ungulate herbivores varies temporally whereby animals browse woody plants more in winter or spring when herbaceous forage is unavailable [27, 37]. Browsing can exert major controls over woody plant dynamics and may directly oppose the effects of grazing on state changes between woody- and grass-dominated states (Fig. 1) [38–40]. Large ungulate herbivores also have the potential to reduce plant community resistance to disturbance and invasion by undesirable plant species, for instance by preferentially foraging on the most palatable plants, increasing bare ground or damaging biological soil crusts via hoof action [41–44]. The relative roles of different types of large herbivores in invasion dynamics, however, have received little attention in the scientific literature [43].

Rarely are the effects of grazing and browsing herbivores distinguished within a single study [45–50] (but see [51]). An abundance of studies focus on the experimental effects of livestock grazing (e.g., [2, 20, 52–54]). Of those that use controlled replication, most make comparisons between treatments to which livestock grazers do vs. do not have access. Typically wild ungulates are allowed access to both treatment types, thereby controlling for, but not exploring the potentially important role of wild ungulates (which can include grazers, browsers, and/or mixed feeders) in plant community dynamics. Other studies experimentally test the effects of wild ungulates in the absence of domestic grazers [55–59] (but see [15, 54]), a land management scenario which is becoming increasingly uncommon. Experimentally investigating the roles of large herbivores with contrasting feeding habits within a single system in a controlled setting will provide insights into the mechanisms behind plant-herbivore dynamics and management options for multi-use landscapes.

Here we use a set of long-term exclosures to determine how cattle (which in our study are grazers that use the site primarily in summer) vs. wild ungulates (which in our study are browsers and mixed feeders that use the study site mainly in winter and spring) affect sagebrush-dominated plant communities. These plant communities provide critical ecological services and habitat for endemic plant and wildlife species, but presently cover less than half of their original 60 million ha in the Intermountain West of North America [60–63]. We focus on communities dominated by Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), for

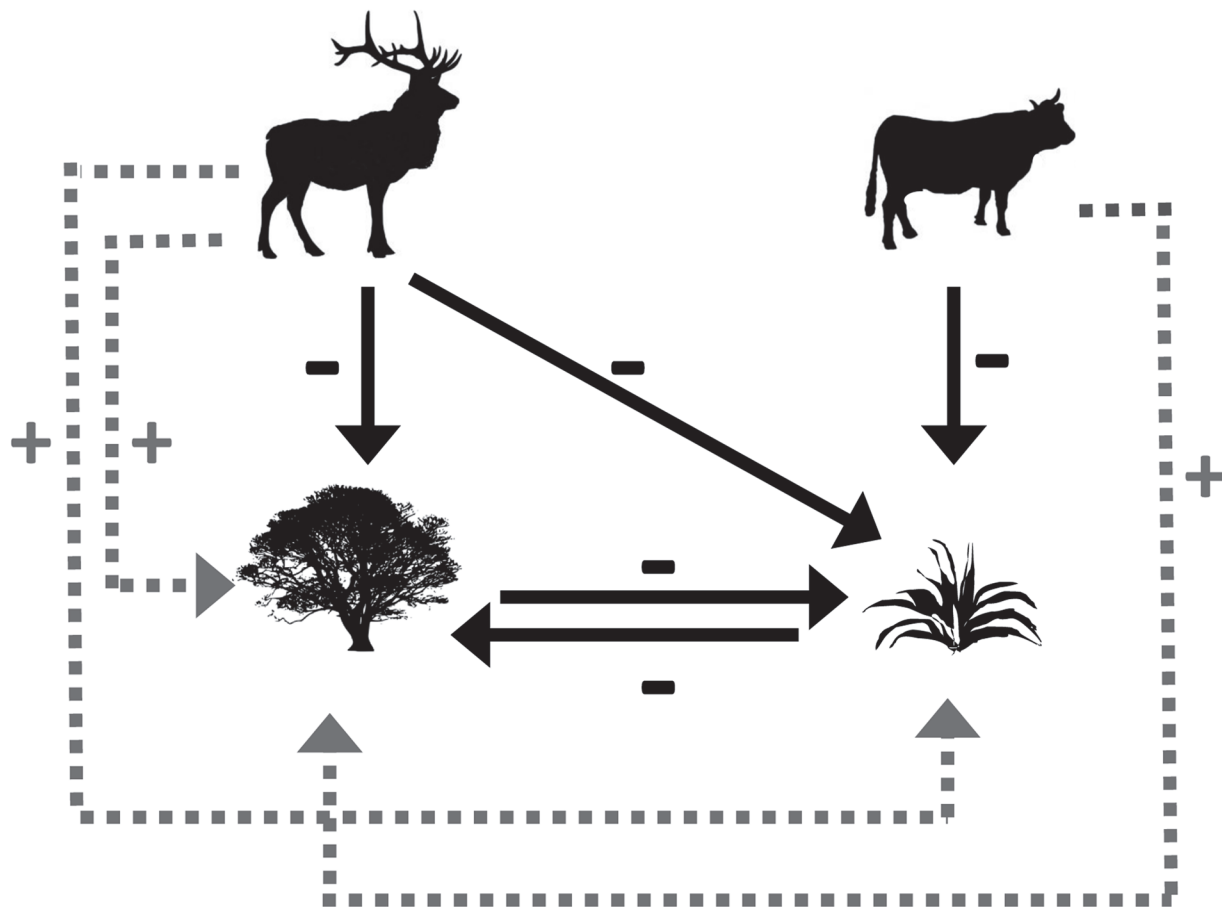


Fig 1. Conceptual model. Conceptual model of interactions among browsing, grazing, woody plants, and perennial grasses. Model assumes that wild ungulates (top left) will both browse and graze, while cattle (top right) will primarily graze. Solid arrows indicate direct effects and assume net negative effects of herbivory and competition on plant biomass. Dashed arrows indicate indirect effects of browsing and grazing mediated through competition between woody plants (bottom left) and perennial grasses (bottom right). Browsing and grazing, depending on their timing, intensities, interactions, and net effects, can shift plant communities between woody- and grass-dominated states.

doi:10.1371/journal.pone.0118016.g001

which there are no published studies that use controlled experimentation to distinguish domestic grazer and wild ungulate (primarily Rocky mountain elk and mule deer) effects on plant community dynamics. In particular we test how different types of herbivory influence a) shrubs and grasses, the dominant components of the plant community (Fig. 1), and b) non-native species and ground cover (including biological soil crusts) that can further influence plant community dynamics.

Materials and Methods

Site Description

This study was conducted at Deseret Land and Livestock (DLL), a private ranch headquartered 13 km south of Woodruff, UT, USA (41° 24' N; 111° 13' W). Our experimental sites are dominated by Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) and were

intentionally located in lower elevation areas that are used by cattle in the spring and summer (May–September) and by wild ungulates predominantly in the winter and early spring (November–March). The primary native ungulates on DLL are elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and to a lesser extent, pronghorn (*Antilocarpa americana*). Both elk and deer migrate to higher elevations during the summer and descend to lower elevations in the winter. Elk are considered mixed feeders, and the proportion of their diets made up of browse increases in the winter, particularly under snowier conditions [27]. Deer, considered browsers, rely heavily on woody material in the winter [27]. The main grass species at the study site are bluebunch wheatgrass (*Pseudoroegneria spicata*), Indian ricegrass (*Achnatherum hymenoides*), Sandberg's bluegrass (*Poa secunda*), needle and thread (*Hesperostipa comata*) and bottlebrush squirreltail (*Elymus elymoides*). The main forbs are spiny phlox (*Phlox hoodii*), pussytoes (*Antennaria* spp.), and milk vetch (*Astragalus* spp.). The primary non-natives are bur buttercup (*Ceratocephala testiculata*), desert alyssum (*Alyssum desertorum*), and cheatgrass (*Bromus tectorum*). Plant species nomenclature and nativity are based on the USDA PLANTS database [64].

Our study focused on three livestock pastures (Dip, Neponset, and Kate) ranging in size from 567–1200 ha. Neponset (1980 m, 6–10% slopes, sandy loam soils) and Kate (2010 m, 4–10% slopes, fine sandy loam soils) pastures are typically grazed on a 5 year rest-rotation schedule. These pastures are grazed by cattle in May or June for three years and in October or November for one year, and then are rested for the fifth year. Dip pasture (2010 m, 6–15% slopes, loam soils) typically is grazed in both the early (May) and late (September) growing season and is rarely rested. The average duration for grazing on each pasture is 10 days to three weeks, depending on forage production and herd size; average cattle herd size per pasture is 1000–1500 head of cattle (Mike Meek, DLL Ranch Manager, *Pers. Comm.*). Rainfall for the year (July–June) preceding our sample periods was 70.1% of the 20-year average for 2012 and 85.2% for 2013. Rainfall for the 4 months (March–June) preceding our sample periods was 25.7% of the 20-year average for 2012 and 37.8% for 2013.

Study design

In 1991 and 1992, we established a set of three 90 m x 90 m plots in each of the three study pastures. Within each pasture, one 90 m x 90 m plot was assigned to each of the following treatment types: 1) Total enclosure (no large ungulates allowed), 2) Cattle enclosure (access by wild ungulates only), and 3) Control (access by wild ungulates and cattle). Total enclosures were constructed with 2.5 m high barbwire fencing (20 strand spaced 20 cm vertically) to fence out all ungulates. Cattle enclosures were constructed with low (1.5 m) barbwire fencing (three strands spaced 50 cm vertically) to allow wild ungulates to traverse the fence; additionally one entire side of each cattle enclosure was opened during the majority of the year (when livestock were not in the pasture) to facilitate wild ungulate access. Wild ungulate use of our study pastures is highest during November–March when wild ungulates focus their foraging activity in these lower elevation areas. Control plots were unfenced.

In July of 2012 and 2013, we sampled vegetation, ground cover, and ungulate use along five 50 m transects in the central 60 m x 60 m study area of each 90 m x 90 m plot. The five transects were ten meters apart, oriented perpendicular to the overall slope of the plot. Vegetation frequency data were collected in five evenly spaced 1 m x 1 m quadrats per transect ($n = 25$ per plot). We recorded densities of live and dead shrubs by height class (<15 cm, 15–50 cm, 50–100 cm, 100–200 cm) in 4 m wide belts along each transect. Densities of perennial bunchgrasses (identified to species) and cattle, elk, deer, pronghorn and lagomorph pellet groups (identified to species by shape and size) were recorded along 2 m wide belt transects. To assess

water runoff and erosion potential we measured gap size between the basal growth of perennial plants along a 50 m transect (sensu [65]). We sampled ground cover (below any vegetation) in twenty-pin 25 cm² pin frames. Pin frames were placed every 5 m along each transect (n = 50 per plot). We classified pin hits into five class types: biological soil crust (non-moss), biological soil crust (moss), litter, bare ground and physical (non-biological) crust.

Plant biomass data were collected from late June to mid-July in 1992 (baseline data) and again in 2012 and 2013 in the core 60 m x 60 m study areas of each plot. This core study area was subdivided into nine 20 m x 20 m subplots. In each sampling year, one of the nine subplots per enclosure was randomly selected for biomass harvesting. Within the selected subplots, all live aboveground biomass of rooted and overhanging plants was harvested per species within three randomly located 10 cm x 5 m biomass transects. The harvested biomass was sorted to only include the current year's growth which was then dried for 48 hours at 50°C and weighed.

Statistical Analyses

Plant community level analyses were based on frequency data which were summarized by first determining a frequency value for each transect (occurrence in 0–5 quadrats) and then averaging the five transect values to determine a plot level value. Species that occurred in <5% of the 225 plots were removed from the analyses. We used nonmetric multidimensional scaling (NMDS) to ordinate average frequency values for plant species in our 9 plots (3 treatments x 3 pastures) (S1 File). We then performed individual NMDS analyses for each pasture (3 treatments x 5 transects, in this case averaging by transect rather than plot) (S2 File). NMDS is a robust unconstrained ordination method that uses plant occurrence data alone to identify ordination axes and explain plant community variation [66]. We used the metaMDS function in the Vegan library (version 2.0–8) for R (version 3.0.1). This function produces ordinations based on multiple random starts to avoid local minima and rotates axes to maximize variance along the first axis. We also used the Adonis function to perform a permutational multivariate analysis of variance (perMANOVA) testing simultaneous response of all plant species to a) the effects of Pasture and Treatment and b) the effects of Treatment within each Pasture (permutations = 999). We set alpha values of 0.1 and used Bray-Curtis (Sorenson) dissimilarity matrices for all analyses.

Plant biomass data were organized into five growth forms: Shrubs, Grasses, Forbs, Non-native annuals, and Total (i.e., all growth forms combined). These data were analyzed with generalized linear mixed models (GLMMs) [67]. Fixed effects included herbivore treatment (Total enclosure, Cattle enclosure, or Control), year (2012 or 2013), treatment*year interaction, baseline biomass (measured in 1992), and treatment*baseline biomass interaction. Non-significant (p > 0.1) treatment*baseline biomass interactions were removed from models. Random factors included pasture and plot nested within pasture, and we used an autoregressive AR(1) covariance structure to address the non-independence of repeated surveys within the same subplot. Response variables were variance-weighted when necessary to meet model assumptions, and Tukey post-hoc tests were used. Analyses were run in R 3.0.1 (package nlme [67]). Results are reported as untransformed means ± 1 S.E. We then performed Cohen's *d* effect size analyses (described below) for each growth form in each year.

We used Cohen's *d* (also known as Hedges' *g*) effect size analysis [68, 69] for analysis of all other data. A *d* statistic was calculated separately for Cattle vs. Control and Total vs. Control comparisons within each pasture. We calculated *d* statistics using the following equation:

$$d = \frac{m_2 - m_1}{s_{\text{pooled}}}, \quad 1$$

where the pooled standard deviation (s_{pooled}) is calculated as:

$$s_{\text{pooled}} = \sqrt{\frac{(n_2 - 1)s_2^2 + (n_1 - 1)s_1^2}{n_1 + n_2 - 2}}, \quad 2$$

where m_i is the transect mean, n_i is the number of transects, s_i^2 is the plot variance; subscripts 1 and 2, respectively, are values from the Control plot and treatment enclosure plot (in this case, either Cattle or Total) [68, 69]. We then calculated a mean d statistic across pastures for 1) Cattle vs. Control and 2) Total vs. Control comparisons, and calculated a 90% confidence interval (CI) for each mean [70]. Effect size analyses are widely used to combine results from multiple studies, which is conceptually similar to combining results from multiple sites or blocks as we have done here [71].

Ethics statement

This study took place on privately owned land. The owner, Deseret Land and Livestock, approved all field activities. No protected species were sampled.

Results

Pellet counts (Table 1) and effect sizes analyses of pellet densities indicate that Total enclosure treatments were effective at excluding deer ($CI_{90} = -14.7$ to -0.516), elk ($CI_{90} = -46.72$ to -10.17), pronghorn ($CI_{90} = -8.59$ to -1.81), and cattle ($CI_{90} = -8.3$ to -5.65). Cattle enclosure treatments successfully excluded cattle ($CI_{90} = -6.58$ to -5.08), but allowed pronghorn ($CI_{90} = -2.66$ to 0.51); deer and elk use of Cattle enclosure plots were not as high as in Control plots but were still significantly greater than in Total enclosures (deer $CI_{90} = -2.43$ to -0.04 ; elk $CI_{90} = -8.26$ to -1.96). Lagomorphs were not excluded from Total ($CI_{90} = -2.90$ to 3.25) or Cattle ($CI_{90} = 0.26$ to 2.65) enclosure treatments. Overall use of the site by pronghorn was low relative to deer and elk (Table 1).

Community level analyses

Plant community composition varied more among pastures than herbivore treatments, as indicated by a two-dimensional NMDS solution of plant frequency data that produced a good fit after one iteration (Fig. 2; stress = 0.08; $R^2 = 0.97$). PerMANOVA results further support these results, indicating a significant effect of “pasture” (pseudo- $F_{2,4} = 0.01$; Fig. 2b) and non-significant “herbivore treatment” effect (pseudo- $F_{2,4} = 0.65$; Fig. 2a).

NMDS plant community analyses for individual pastures, however, revealed distinctions among different herbivore treatments. Three-dimensional NMDS solutions for Kate and Dip pastures indicated that Total enclosure plots were distinct from Cattle and Control plots (Fig. 2c,e); distinctions were less clear for Neponset (Fig. 2d). Fits were good to fair (Kate stress = 0.11, $R^2 = 0.99$; Neponset stress = 0.096, $R^2 = 0.91$; Dip stress = 0.098; $R^2 = 0.91$). Results of perMANOVA indicated highly significant treatment effects in Kate (pseudo- $F_{2,12} = 0.001$) and Dip (pseudo- $F_{2,12} = 0.001$) pastures (Fig. 2c,e), and less significant treatment effects in Neponset (pseudo- $F_{2,12} = 0.07$) pasture (Fig. 2d).

Examination of species richness data (derived from frequency plots) across all pastures indicate that cattle reduced plant species richness. Cattle enclosure treatments reduced richness relative to Control plots ($CI_{90} = -1.33$ to -0.61), whereas Total enclosure treatments did not significantly alter species richness relative to Control plots ($CI_{90} = -3.13$ to 1.59).

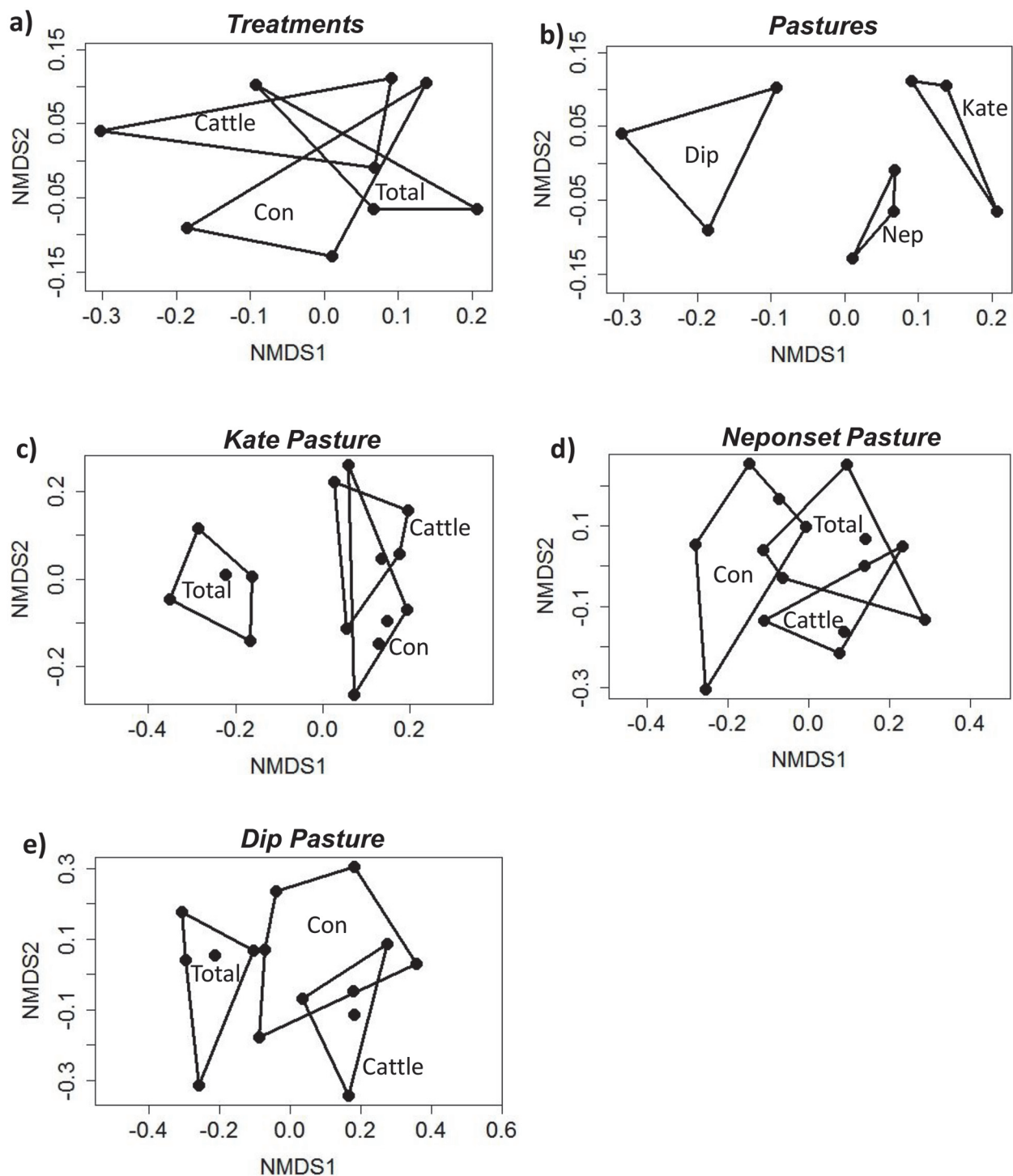


Fig 2. NMDS results. Non-metric Multidimensional Scaling (NMDS) results depicting sample points and convex hulls for (a) three herbivore treatments and (b) three pastures in relation to plant species community composition ($n = 125$ frequency frames per sample point); and (c-e) treatments within individual pastures ($n = 25$ frequency frames per sample point). Total, Cattle, and Control treatments exclude, respectively, all large herbivores, cattle only, and no large herbivores.

doi:10.1371/journal.pone.0118016.g002

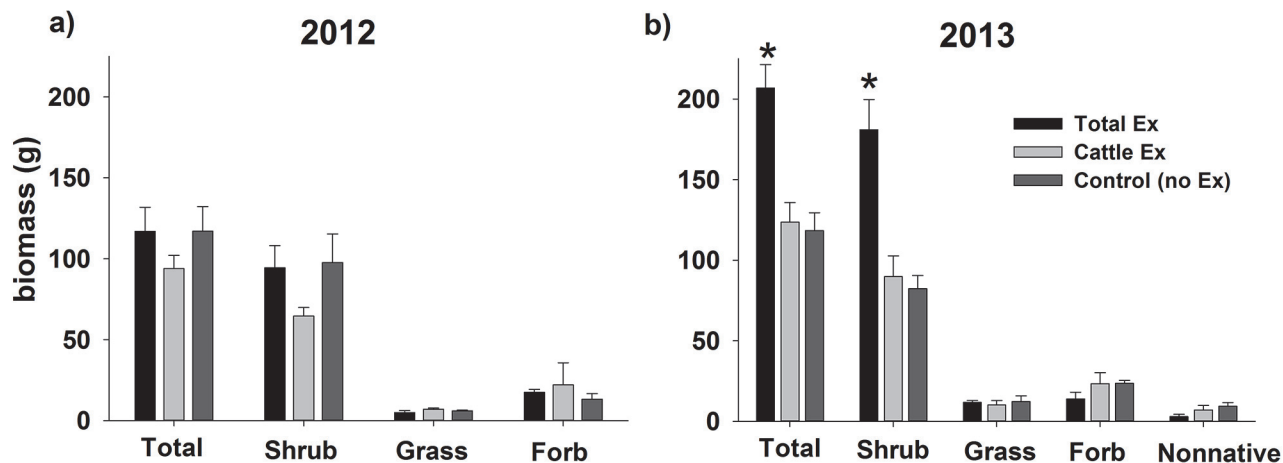


Fig 3. Plant Biomass. Mean biomass $\pm$ 1 S.E. in (a) 2012 and (b) 2013 of different plant growth forms (Total [i.e., all groups combined], Shrubs, Grasses, Forbs, and Non-natives) across three herbivore treatments. “Total Ex” denotes exclusion of large herbivore wildlife and cattle, “Cattle Ex” denotes exclusion of only cattle (but not wild herbivores), and “Control” denotes no exclusion i.e., access by both types of herbivore. Asterisks indicate treatment-year combinations that are significantly different ($p < 0.10$) than all other treatment-year combinations within a given plant growth form.

doi:10.1371/journal.pone.0118016.g003

Biomass

Shrub, Grass, Forb and Total biomass were significantly lower in the drier year, 2012 (Fig. 3; Shrubs $F_{1,6} = 136.91$, $p < .0001$; Grass $F_{1,6} = 24.81$, $p = 0.003$; Forbs $F_{1,6} = 3.80$, $p = 0.099$; Total biomass $F_{1,6} = 17.34$, $p = 0.006$), and Non-native biomass was too low for analysis during this year. Effect size analyses also revealed significant effects of Cattle, but not Total exclusion treatments in 2012 (Table 2). In particular, Cattle exclusion significantly increased Grass biomass relative to Controls. Cattle exclusion also decreased Total biomass, a pattern most likely driven by non-significant treatment effects on Shrub biomass (Table 2), which made up 78% of Total biomass.

The wetter year (2013) revealed significant effects of Total exclusion that were not evident in 2012. In 2013, both Total biomass and Shrub biomass were higher in Total exclusion plots than in all other treatment-year combinations (Fig. 3; Total biomass $F_{2,6} = 7.27$, $p = 0.03$; Shrubs $F_{2,6} = 17.38$, $p = 0.003$). Effect size analyses of 2013 biomass also indicate lower forb biomass in Total relative to Control plots (Table 2). The wetter year also revealed patterns in non-native species (that had been too low in biomass to analyze in the drier year). In particular,

Table 1. Dung pellet groups.

	TOTAL	CATTLE	CONTROL
Deer	1.33 $\pm$ 1.33	116 $\pm$ 36.3	142.67 $\pm$ 47.68
Elk	0 $\pm$ 0	137.33 $\pm$ 9.61	265.33 $\pm$ 51.24
Pronghorn	0 $\pm$ 0	32 $\pm$ 12.86	46.67 $\pm$ 25.96
Cattle	0 $\pm$ 0	18.67 $\pm$ 5.33	130.67 $\pm$ 6.67
Lagomorphs	1120 $\pm$ 269.59	1188 $\pm$ 124.00	1086.67 $\pm$ 124.71

Mean densities (# per ha) $\pm$ 1 SE for pellet groups by species across three herbivore treatments: 1) Total exclusion plots that exclude both cattle and wild ungulates, 2) Cattle exclusion plots that exclude only cattle, and 3) Control plots where no large herbivores are excluded.

doi:10.1371/journal.pone.0118016.t001

in 2013, non-native biomass (comprised of 51% *C. testiculata*, 47% *A. desertorum*, and 2% *B. tectorum*) was significantly lower in Cattle and Total enclosure plots relative to Control plots (Table 2). The overall effect size was greatest for Total treatments, but the variability was too great to be significantly different than Cattle enclosure treatments.

Species and growth form analyses

Densities of three perennial grasses varied with respect to herbivore treatment (Fig. 4a, Table 3). Effect size analyses indicate that densities of the perennial bunchgrass *E. elymoides* increased in both Cattle and Total enclosure plots compared to controls (Fig. 4a). The most common grass, *P. secunda*, showed the opposite pattern and was lower in the two enclosure treatments than in the controls (Fig. 4a). The grass *P. spicata* was reduced by cattle exclusion. *Achnatherum hymenoides* and *H. comata* did not respond significantly to herbivore treatment.

Densities of *A. tridentata* ssp. *wyomingensis* varied across herbivore treatments and shrub size classes (Fig. 4b, Table 3). The Total herbivore exclusion treatment, the only treatment to exclude wildlife, was characterized by a higher number of mid-sized (50–100 cm) individuals and lower number of small (<15 cm) individuals relative to control plots. The Cattle exclusion treatment (to which wildlife did have access), did not significantly differ from Control. There were no significant effect size differences for the 15–50 cm and 100–200 cm size classes, though they followed similar trends to <15 cm and 50–100 cm size classes, respectively.

Gap size analyses indicate that plots where both cattle and wildlife were excluded (i.e., Total exclusion plots) had a significantly higher proportion of 50–100 gaps, but lower proportion of very large (200 cm+) gaps (Fig. 4c). The infilling of very large gaps (and resulting increase in smaller gaps) is consistent with the absolute increases in densities of 50–100 cm *A. tridentata* ssp. *wyomingensis* shrubs (Table 3) and the grass *E. elymoides* (Table 3) in Total enclosure plots relative to control plots.

Effect size analyses indicated that cover of all biological soil crust groups combined was increased by Total exclusion plots, likely driven by moss, the only group with cover high enough for individual analysis (Fig. 4d). Amount of bare soil was significantly lower in both treatments that excluded cattle (Fig. 4d). There were no significant effect size differences for either litter or physical crust (Fig. 4d).

Discussion

Grazing and browsing ungulates co-habit rangelands worldwide and can have distinct and sometimes contrasting effects on plant community trajectories [45, 48, 49, 72, 73]. This is the first published study to experimentally address and demonstrate, within a single study, the effects of long-term manipulation of both wild ungulates (including browsers and mixed feeders) and domestic grazers on Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), a dominant land cover type of conservation concern [60–63] in the western U.S.A. Here we have revealed, after only twenty-two years, distinct effects of a domestic grazer and native ungulates on major plant species and growth forms, including long-lived native perennial species, annual invasive species, and biological soil crusts. These changes to specific plant functional groups and soil crusts were accompanied by perceptible effects of wild ungulate exclusion on overall plant community composition (as assessed by NMDS) in this sagebrush community. At two of three sites, overall plant community composition differed in the one treatment that excluded vs. two treatments that allowed wild ungulate access (Fig. 2c,e), illustrating a clear wild ungulate effect and a relatively small domestic grazer effect. Distinctions among the three herbivore treatments were weaker (but still significant to the 0.1 level) for the third site (Fig. 2d), possibly

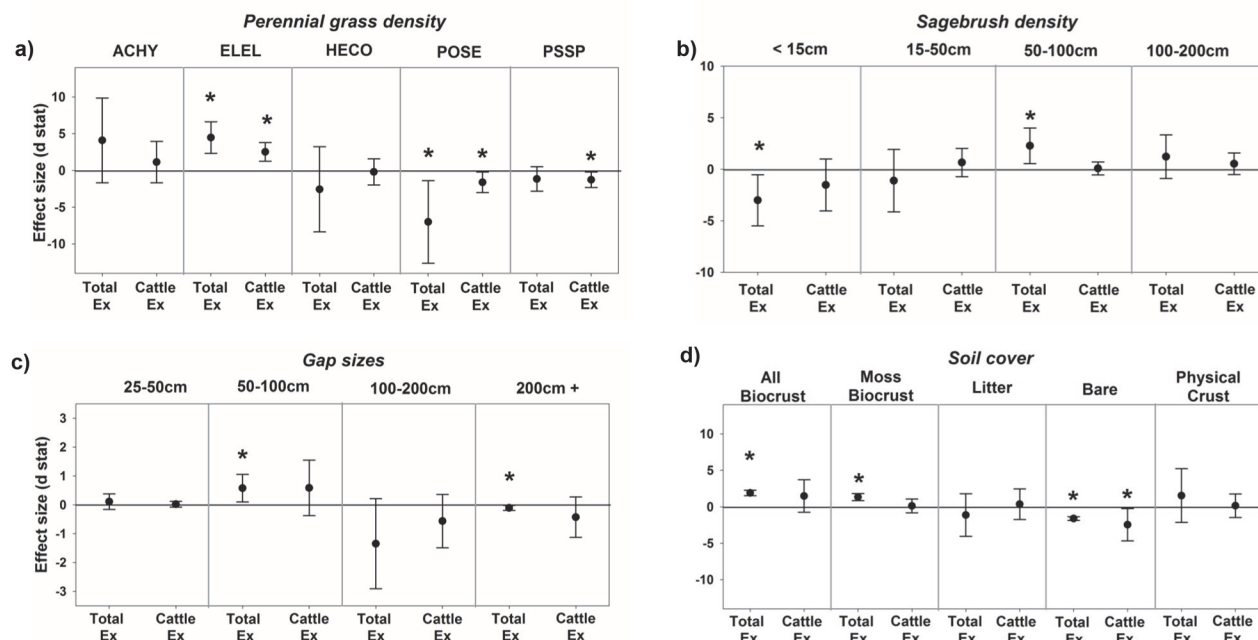


Fig 4. Effect size analyses. Effect size analyses of (a) perennial grass (*Achnatherum hymenoides* [ACHY], *Elymus elymoides* [ELEL], *Hesperostipa comata* [HECO], *Poa secunda* [POSE], *Pseudoroegneria spicata* [PSSP]) density, (b) sagebrush (*A. tridentata* ssp. *wyomingensis*) density, (c) inter-plant gap size, and (d) soil cover across herbivore treatments. “Total Ex” denotes exclusion of all large herbivores, and “Cattle Ex” denotes exclusion of only cattle (but not wild herbivores). If symbol is above the zero line, then magnitude of response is greater in the treatment enclosure than in the control. If symbol is below the zero line, then response is less than in the control. Error bars show 90% CI. If error bars do not equal or cross zero line, then difference is considered significant.

doi:10.1371/journal.pone.0118016.g004

Table 2. Biomass effect sizes.

	YEAR	2012	2013
TOTAL BIOMASS	Total	-0.32 ± 1.56	3.81 ± 3.64
	Cattle	-0.68 ± 0.56	0.59 ± 1.83
SHRUBS	Total	-0.53 ± 1.84	4.23 ± 4.48
	Cattle	-1.16 ± 1.24	0.06 ± 1.49
GRASSES	Total	-0.18 ± 1.80	-0.01 ± 0.90
	Cattle	1.51 ± 1.48	-0.007 ± 0.1.91
FORBS	Total	0.42 ± 0.58	-1.52 ± 1.04
	Cattle	-0.31 ± 2.39	-0.50 ± 1.02
NON-NATIVES	Total	—	-2.54 ± 2.41
	Cattle	—	-1.21 ± 0.91

Means and 90% confidence intervals for Cohen’s *d* effect size analyses of annual biomass in 2012 and 2013. “Total” denotes effect of exclusion of all large herbivores relative to Control plots (where no large herbivores are excluded), and “Cattle” denotes effects of exclusion of only cattle (but not wild herbivores) relative to Control plots. Bold values indicate treatments with confidence intervals that do not overlap zero and are considered significantly different from control.

doi:10.1371/journal.pone.0118016.t002

Table 3. Plant densities, gaps, and soil cover.

	TOTAL	CATTLE	CONTROL
Perennial grass density ^a			
ACHY	497.4 ± 229.6	297.4 ± 155.4	248 ± 123.6
ELEL	500 ± 69.4	364 ± 37.2	201.4 ± 60.2
HECO	553.4 ± 268.2	1036 ± 544.6	1208 ± 548
POSE	1898.6 ± 368.6	2462.6 ± 436	2758.6 ± 379.2
PSSP	259 ± 188.6	147.8 ± 61.6	301.6 ± 119.6
Sagebrush density ^a			
<15 cm	42 ± 4.2	90.7 ± 2.4	458.7 ± 366.5
15–50 cm	821.3 ± 178	1098 ± 349.9	952.7 ± 260.5
50–100 cm	1253.3 ± 142.2	993.3 ± 138.6	994.7 ± 95.5
100–200 cm	44.7 ± 31.7	54.7 ± 47.8	51.3 ± 49.3
Inter-plant gaps ^b			
25–50 cm	74.12 ± 3.88	72.7 ± 1.53	78.13 ± 1.42
50–100 cm	64.8 ± 6.31	62.32 ± 3.08	65.96 ± 3.89
100–200 cm	43.18 ± 7.53	37.58 ± 5.24	44.63 ± 5.57
200+ cm	19.6 ± 5.81	15.3 ± 4.41	18.31 ± 5.86
Soil cover ^c			
All biocrust	2.66 ± 0.25	2.16 ± 0.25	1.62 ± 0.15
Moss biocrust	1.84 ± 0.27	1.27 ± 0.13	1.27 ± 0.12
Litter	11.75 ± 0.94	13.36 ± 0.67	12.69 ± 0.94
Bare	1.44 ± 0.22	1.31 ± 0.22	2.06 ± 0.15
Physical crust	4.59 ± 1.11	3.67 ± 0.28	3.89 ± 0.98

Means ± 1 SE for perennial grass densities by species, sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) densities by size class, inter-plant gaps by total length in each gap size class, and soil cover types across three herbivore treatments: 1) Total enclosure plots that exclude both cattle and wild ungulates, 2) Cattle enclosure plots that exclude only cattle, and 3) Control plots where no large herbivores are excluded.

^a #/ha

^b total cm

^c # pin hits (of 20)

doi:10.1371/journal.pone.0118016.t003

because of greater heterogeneity in soil type and landscape position among plots, or because of lower overall plant productivity (pers. obs) and herbivore use (Table 1) at the site.

Specific wildlife effects

Wildlife effects on plant community composition appeared to be driven at least partially by browsing of woody species. Wild ungulates showed size-class-specific effects on Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis*) densities across all sites. The dominant herbivores in the study area that browse on woody species in the winter are elk and mule deer. As might be expected from examples of browsing effects in a variety of ecosystems [38–40, 74], release from browsing increased densities of the most common adult-sized sagebrush (50–100 cm) in our study. This coincided with lower relative densities of small sagebrush (<15 cm). Small sagebrush in wildlife exclusion plots likely represent mostly new recruits that were suppressed by either a) adult shrubs or b) grasses (sensu [75]) that were also released from herbivory in wildlife exclusion plots. Small sagebrush in wildlife accessible plots on the other hand likely represent a combination of new recruits and older individuals maintained in short stature by recurrent browsing [38, 76]. Regardless, our results reveal that removal of browsing animals—a

phenomenon that could occur due to unintentional species losses or intentional management decisions—increases dominance by larger-statured woody species and presumably competition for resources (e.g., light) necessary for establishment and growth of smaller individuals. This pattern is typical of “bush encroachment” which is often (but not always) associated with rangeland degradation regionally and globally [19, 77, 78], and in this system could negatively affect endemic wildlife species such as sage-grouse [79].

Release from wild ungulate herbivory also increased annual biomass of shrubs (Fig. 3b), of which the majority (78–79%) were Wyoming big sagebrush. These results suggest a suppressive effect of browsing in the wildlife-accessible plots. This pattern was only evident during the wetter year (2013), perhaps because both production and browsing were lower across all treatments during the drier year. Although it is not possible to parse out the relative contributions of long-term changes in shrub density (described above) vs. short-term browsing effects on annual shrub biomass patterns, it is clear that shrub biomass is greater in the absence of browsers.

Interestingly, although woody species can suppress grasses [19, 77, 78], in this case grass production was not reduced by increased shrub production. This result provides further evidence that some perennial grasses—at least when they are ungrazed—are not necessarily out-competed by woody species [80, 81], particularly under favorable moisture conditions. Alternatively, release from grazing (by cattle, elk, or both) may have compensated for any shrub-driven reductions in grass production. Forb production, on the other hand, appeared to be reduced by shrubs, though sagebrush effects on forbs have been reported to range from neutral [80] to facilitative elsewhere [82, 83]. Forbs are especially important to management of sagebrush systems due to their potential to offer resistance against undesirable invasive annual plants such as cheatgrass (*B. tectorum*) [84] and to their role in the diets of species of concern such as sage-grouse [79]. Our results provide evidence that managing for sufficient wild ungulate populations may be a critical component of maintaining productive and structurally diverse sagebrush stands and key habitat characteristics for native species conservation.

Specific cattle effects

Cattle grazing influenced individual species and certain plant growth forms within the herbaceous plant community. Although these effects were not yet associated with significant differences in overall plant community composition, they provide insights into potential plant community trajectories and future communities. The early successional shallow-rooted bunchgrass, bottlebrush squirreltail (*E. elymoides*), showed a positive response to release from cattle grazing and in turn appeared to competitively suppress the more common shallow-rooted grass, Sandberg’s blue grass (*P. secunda*). Increased *P. secunda* dominance under grazed conditions is a regionally common pattern for this abundant, grazing-tolerant grass [85] (but see [41]). Another bunchgrass, needle and thread (*H. comata*), did not respond significantly to grazing exclusion, likely because it is only a moderately preferred forage species for livestock [64]. Although densities of the more grazing-sensitive perennial bunchgrass, bluebunch wheatgrass (*P. spicata*) would have been expected to increase under grazing release in both herbivore exclusion plot types [85], densities did not increase in Total exclusion plots, likely due to increased shrub competition. Most surprising was that densities of *P. spicata* were significantly reduced in Cattle exclusion plots relative to grazed Control plots. Historically, elk (mixed feeders) may have preferentially grazed in Cattle exclusion plots (compared to Controls) to avoid competition with cattle, thereby increasing grazing pressure on highly palatable *P. spicata*. Cattle-wildlife competition and compensatory increases in wildlife habitat use have been shown in other exclosure studies [14, 73]. In the case of our study, historic compensatory responses by elk (and the consequent reduction in desirable *P. spicata* forage) may help explain the slight

present-day aversion elk showed to our cattle exclusion plots (Table 1). These types of patterns can only be revealed by study designs that explicitly distinguish effects of different types of herbivory.

Our study also revealed year-dependent effects of cattle grazing. Release from cattle grazing increased grass biomass during the drier year, 2012, when forage would have been most limiting and grazing pressure highest across the landscape. In the same plots, however, total biomass decreased (relative to Control plots), likely reflecting a (non-significant) decrease in shrub production associated with increased grass competition [86].

Additive and synergistic cattle-wildlife effects

Due to our experimental design and because Total and Cattle exclusion effect sizes did not differ significantly from each other, we cannot rule out the possibility that the effects of “wild ungulate” removal discussed above are actually additive or synergistic effects of removing both cattle and wild ungulates from Total enclosure plots. For example, although cattle are considered “grazers” they can browse on woody material [87], and perhaps shrubs only respond positively when they are released from both wild and domestic herbivore browsing. Plant community responses in Cattle exclusion plots also may reflect more than the direct effects of removing cattle. Plant community responses in these plots may be the product of synergistic cattle-wild ungulate effects. For example, as described above for *P. spicata*, the plant community effects of cattle removal may elicit compensatory behavioral responses by wild ungulates.

Different seasonal use patterns by wild ungulates vs. cattle also can result in apparent non-additivity of herbivory effects. Whereas cattle grazing occurred during active growing periods, grazing effects of the mixed feeder at our study site, elk, would have occurred during winter and early spring when grasses and are forbs are dormant. This timing would have mitigated negative wild ungulate effects on herbaceous plants. Likewise, winter (dormant season) use of the study area by wild ungulates may have amplified negative effects of browsing on shrubs by inhibiting shrub regrowth [38] or compensatory responses like secondary chemical defenses against herbivory [88]. In addition, winter herbivory can result in net nutrient inputs to soils that stimulate grass production or quality and improve grass compensatory response to grazing later in the growing season [89]. The seasonal dichotomy in range use by wild vs. domestic livestock is widespread across western North America and in other systems dominated by *Artemisia* [90], suggesting that the overall browsing and grazing impacts we observed may be typical for sagebrush communities.

Invasive species, inter-plant gap sizes, and biological soil crusts

One potential source of concern for land managers is that non-native species biomass was higher in plots accessible by domestic grazers during the wetter year. Exotic species invasions are arguably the primary threat to sagebrush-dominated systems in the Intermountain West of North America [91], and inappropriate livestock management practices as well as overabundance of wild herbivores are cited as contributing to invasions by undesirable species in ecosystems worldwide [5, 16, 43, 44, 92, 93]. In the present study we have not shown evidence of widespread invasion attributable to grazing; rather we have shown evidence of Wyoming big sagebrush plant communities with a small non-native species component that is more strongly expressed during wetter years—but most strongly in the presence of domestic grazers. However, even low levels of invasion can become more problematic following major disturbance (e.g., extended drought), and those species that are limited by elevation or moisture [42] may increase in prevalence in warmer climate conditions predicted for this area [94]. Moreover, cattle grazing had a negative effect on *E. elymoides*, a species that is a strong competitor with

invasive *B. tectorum*. A populous and more diverse native plant community is a potential form of resistance against invasive species [95] (but see [93]) and we did find lower overall plant species richness in plots accessible by cattle.

Smaller inter-plant gap sizes between perennial plants often are associated with increased biotic resistance to disturbance and invasive species [41, 96]. We found that gap sizes were smaller in plots where wildlife were excluded, consistent with our result of higher shrub cover in these plots. Despite the potential for small inter-plant gaps to provide resistance against non-native species [41], increased invasive biomass in our study was associated with cattle rather than wild ungulate activity. This suggests that, when wild herbivores are present, and/or when the plant community is relatively uninvaded, gap size may not be an ideal early indicator or correlate of invasion risk.

Cover of biological soil crusts, an indicator of soil condition [97, 98], was higher in the Total herbivore exclusion treatment. Crusts create microsites for germination of a diversity of native plants that are typically desired for their conservation value and resistance against exotic species [41, 99, 100]. Our results suggest that the presence of wild ungulates alone (i.e., even in the absence of cattle) creates sufficient disturbance to limit biological soil crust cover. Given that the site likely evolved under wildlife herbivory (including grazers, browsers and mixed feeders), however, the level of soil crust disturbance we detected likely falls within the natural range of variability for the area. Cattle exclusion plots, on the other hand, did not significantly increase soil crust cover (relative to Control plots). But we cannot rule out cattle activity as an important driver of biological soil crust cover because cattle accessible plots showed significantly higher bare ground, which would have been driven at least in part by non-significant loss of soil crust cover. Cattle activity in other ecosystems has been shown to decrease biological soil crust cover and increase safe sites for establishment of one pervasive invader, *B. tectorum* [41, 85, 101], though it is possible that our study area is more resilient to crust disturbance because it is wetter and more productive. Nonetheless, our results suggest an important consideration in managing for biological soil crusts is total large herbivore pressure, particularly livestock which are more readily managed than wildlife. Continued efforts to untangle the effects of large ungulates on biological soil crusts are important throughout sagebrush-dominated systems that typically support both free-roaming wild ungulate herbivores and domestic livestock.

Conclusions

Although twenty-two years of herbivore treatments did not cause dramatic state shifts in this sagebrush community, they did reveal distinctive domestic grazer vs. wild ungulate effects on plant communities and insights into potential future trajectories of these plant and soil crust communities. Our results point to the importance of wild ungulate suppression of woody plant densities and sizes. Combined with the positive wildlife effects on forbs, these results suggest that long-term conservation of Wyoming big sagebrush plant communities may require sufficient wildlife browsing to maintain productive sagebrush stands. Also of note are the positive effects of cattle activity on non-native biomass and negative effects on the native bunchgrass, *E. elymoides*. This native species and its congeners are relatively good competitors against the widespread invasive annual *B. tectorum* in sagebrush systems [102, 103].

Our results also provide evidence that herbivore effects on plant communities, including invasive species, can vary considerably across superficially similar site conditions in Wyoming big sagebrush plant communities [1, 20, 104]. Our experimental approach allowed us to identify a role of wild ungulates (which often is conflated with cattle) in shrub-grass dynamics. Valuable future work would entail using a similar approach to examine sagebrush sites across a

broad range of environmental conditions and identify mechanisms for cross-site variability of herbivory effects.

Supporting Information

S1 File. Plant frequency by treatment. Mean plant frequencies for each of three treatments (DX = no large ungulates allowed, LX = cattle excluded, accessible by wild ungulates only, OX = accessible by cattle and wild ungulates) for each of three sites (Kate, Dip, Neponset). Each treatment plot had five transects with five 1 m x 1 m quadrats per transect. Species codes follow USDA Plant Database codes (<http://plants.usda.gov/>); AF53 is an unidentified annual forb. (DOCX)

S2 File. Plant frequency by transect. Plant frequencies for five transects (n = five 1 m x 1 m quadrats per transect) at each of three treatments (DX = no large ungulates allowed, LX = cattle excluded, accessible by wild ungulates only, OX = accessible by cattle and wild ungulates) for each of three sites (Kate, Dip, Neponset). Species codes follow USDA Plant Database codes (<http://plants.usda.gov/>); AF53 is an unidentified annual forb. (DOCX)

Acknowledgments

We received field and lab assistance from Hope Braithwaite, Corey Sample, Seth Nafziger, Chelan Rogers, Bethany Unger, James Cane, Brendan Knowles, Brittany Duncan, and Sara Germain. We wish to thank Deseret Land and Livestock for hosting this study and for the logistical support provided by Rick Danvir, Todd Black, and Mike Meek. We thank L.M. Porensky, T.P. Young, and two anonymous reviewers for readings of previous versions of the manuscript. This research was supported by the Utah Agricultural Experimentation Station, Utah State University and approved as journal paper number #8736.

Author Contributions

Conceived and designed the experiments: MER KEV CMM. Performed the experiments: KEV KCN CMM MER. Analyzed the data: KEV CMM. Wrote the paper: KEV KCN CMM MER.

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