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ARTICLE

Small effects of livestock grazing intensification on diversity, abundance, and composition in a dryland plant community

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Abstract

Livestock grazing is a globally important land use and has the potential to significantly influence plant community structure and ecosystem function, yet several critical knowledge gaps remain on the direction and magnitude of grazing impacts. Furthermore, much of our understanding of the long-term effects on plant community composition and structure are based on grazer exclusion experiments, which explicitly avoid characterizing effects along grazing intensity gradients. We sampled big sagebrush plant communities using 68 plots located along grazing intensity gradients to determine how grazing intensity influences multiple aspects of plant community structure over time. This was accomplished by sampling plant communities at different distances from 17 artificial watering sources, using distance from water and cow dung density as proxies for grazing intensity at individual plots. Total vegetation cover and total grass cover were negatively related to grazing intensity, and cover of annual forbs, exotic cover, and exotic richness were positively related to grazing intensity. In contrast, species richness and composition, bunchgrass biomass, shrub density and size, percentage cover of bare ground, litter, and biological soil crusts did not vary along our grazing intensity gradients, in spite of our expectations to the contrary. Our results suggest that the effects of livestock grazing over multiple decades (mean = 46 years) in our sites are relatively small, especially for native perennial species, and that the big sagebrush plant communities we sampled are somewhat resistant to livestock grazing. Collectively, our findings are consistent with existing evidence that indicates the stability of the big sagebrush plant functional type composition under current grazing management regimes.

KEYWORDS
Artemisia tridentata, big sagebrush, grazing, grazing gradient, piosphere, species richness, water sources

INTRODUCTION

Livestock grazing is a globally important and widespread land use (Milchunas & Lauenroth, 1993), and by some estimates there are almost 2.4 billion grazing livestock (cattle, sheep, and goats) distributed across the planet today (Robinson et al., 2014). Human population and the demand for meat and animal products are increasing, and the intensity and scale of grazing is likely to continue to increase (Bouwman et al., 2005; Thornton, 2010), with sustained or increased impacts for plant communities.

Consensus on the effects of livestock grazing on plant community structure has remained elusive, with the most consistent finding being that livestock grazing often has negative effects on plant communities in the driest locations (Eldridge et al., 2016; Herrero-Jáuregui & Oesterheld, 2018). Livestock grazing can have divergent effects depending on ecosystem type, site characteristics, plant community composition and evolutionary history, plant traits and adaptations to grazing, herbivore type (e.g., sheep or cattle), grazing intensity, or the combination of grazing duration and herbivore abundance (Eldridge et al., 2016; Hobbs, 1996; Milchunas & Lauenroth, 1993; Titcomb et al., 2021). Across ecosystem types, grazing at a moderate intensity can increase or decrease aboveground net primary production (Li et al., 2017; Milchunas & Lauenroth, 1993), increase or decrease diversity (Cingolani et al., 2005; Milchunas et al., 1988), and have little to large effects on species composition and species abundances (Augustine & McNaughton, 1998; Davies et al., 2018). In studies comparing low grazing intensity or grazing exclusion, results are similarly mixed across ecosystem types with positive, negative, and no effects on plant communities reported in the literature (Filazzola et al., 2020; Gao & Carmel, 2020; Herrero-Jáuregui & Oesterheld, 2018). Clarifying the way in which grazing affects plant community structure over long time periods is important to inform management activities and best practices to support the sustainability of natural resources now and in the future.

Livestock move across landscapes in response to abiotic and biotic factors, which vary at a variety of spatial and temporal scales (Bailey et al., 1996; Cheleuitte-Nieves et al., 2020), therefore the severity of grazing effects may vary over time (Pastor et al., 1997) or in response to spatial movements of grazers (Briske et al., 2008). Available water, forage quality, disturbance, and topography influence livestock distribution and subsequently, grazing effects, even when the number of animals and timing of grazing is the same (Bailey, 2004; Bailey et al., 1996; Belsky et al., 1999). Managers use water and other attractants to influence the spatial and temporal distribution of livestock across the landscape (Andrew, 1988; Bailey, 2004; Porath et al., 2002). The number and complexity of factors that affect livestock behavior makes understanding grazing effects difficult (Cheleuitte-Nieves et al., 2020; Stohlgren et al., 1999), especially when simplistic approaches (i.e., grazed vs. ungrazed treatments) are used that do not account for external influences on animal behavior (Bailey et al., 1996). Therefore, studying the effects of livestock grazing requires careful attention to and even utilization of the factors that influence grazer movements and behavior.

Opportunities for ecological discovery regarding grazing impacts lie in exploiting known gradients of grazing intensity that occur around and extend from watering sources, especially in ecosystems that are water limited (Andrew, 1988). Distance from water represents a gradient in cumulative grazing intensity that is replicable (Adler & Hall, 2005; Andrew, 1988; Pickup et al., 1998; Titcomb et al., 2021; Turner, 1998), and in combination with grazer dung density, distance from water can be an accurate measure of local grazing pressure on the plot scale (Eldridge et al., 2017; Fensham et al., 2010; Oñatibia & Aguiar, 2018).

Indeed, distance from water studies have been used to document grazing-induced changes in ecosystem properties in water-limited grazing systems around the world. Increased grazer concentration around watering points affects plant community structure in the Patagonian steppe (Oñatibia & Aguiar, 2018; Oñatibia et al., 2018), Mongolian grasslands (Cheng et al., 2011), African savannas (Egeru et al., 2015; Jawuoro et al., 2017; Titcomb et al., 2021), North American deserts (Brooks et al., 2006), Irano-Turanian steppe (Shahriary et al., 2012), and Australian rangelands (Eldridge et al., 2017; Fensham et al., 2010). Despite these efforts, there are often unclear or conflicting results on the direction and magnitude of grazer effects on plant communities. For example, studies in the Patagonian steppe suggest that grazing effects increase with more annual precipitation (Oñatibia et al., 2018), while work in Australia suggests that grazing impacts increase as annual precipitation decreases (Eldridge et al., 2016), and in Spanish Mediterranean grazing systems, grazing impacts showed divergent responses across moisture gradients (Carmona et al., 2012; de Bello et al., 2007). The impacts of grazing intensity on plant diversity showed mixed effects on diversity and composition in southern African rangelands (Hanke et al., 2014) and savanna systems (Titcomb et al., 2021), North American shrub-steppe (Tueller & Platou, 1991), and Irano-Turanian steppe (Rahmanian et al., 2020).

The diversity of effects observed across these grazing systems suggests that controlling for environmental covariates could improve our understanding. One practical approach is to use artificial, opposed to naturally occurring, watering points to observe grazing impacts.

Artificial watering points are widespread and can offer insight into long-term changes in vegetation in response to grazing intensity, as watering sources are often placed in otherwise uniform vegetation and remain in place for decades (Belsky et al., 1999; Landsberg et al., 2003). Furthermore, the extent to which artificial watering sources have changed upland vegetation is often unknown, and understanding the magnitude and extent of those changes can inform management and conservation decision-making.

In big sagebrush (*Artemisia tridentata*) ecosystems of western North America, which occupy ~76 million hectares (Rigge et al., 2020), livestock grazing is a ubiquitous land use, yet, as with rangelands globally, analyses of grazing effects on composition and species richness are often inconclusive (Camp et al., 2014; Courtois et al., 2004; Herrero et al., 2015; Knick et al., 2003). Comparisons of moderate rotational grazing versus exclusion of grazing suggest that grazing can decrease perennial grass standing crop (Rickard et al., 1975; West et al., 1984), aboveground production (Rickard et al., 1975), forb production and cover (Davies et al., 2010), species richness (Veblen et al., 2015), and shrub cover (Manier & Hobbs, 2007). Other studies have found that grazing can increase species richness (Manier & Hobbs, 2006), forb cover (Manier & Hobbs, 2006), and shrub cover (Veblen et al., 2015) or have little or no effects on big sagebrush plant community structure and composition (Courtois et al., 2004; Holechek & Stephenson, 1983; Stohlgren et al., 1999). Recent studies have shown that grazing exclusion over multiple decades produces only minor differences from moderate grazing (Copeland et al., 2021), or even decrease diversity and increase exotic species abundance (Porensky et al., 2020). Far fewer studies have examined plant community responses along grazing intensity gradients in these systems (but please refer to Adler et al., 2005; Tueller & Platou, 1991). The variability of outcomes from these grazing studies probably results from: (1) experimental design issues related to low replication and length of grazing cessation in studies relying on grazed/ungrazed comparisons; and (2) differences in the effects of timing and amount of precipitation on productivity and functional type abundance (Anderson & Inouye, 2001; Stohlgren et al., 1999).

Our goal was to determine how grazing intensity influences key components of big sagebrush plant community structure, which we accomplished by sampling along grazing intensity gradients associated with artificial watering sources on level uplands. We drew upon current models of grazing effects (Cingolani et al., 2005; Milchunas et al., 1988) to address the following hypotheses:

1. Plant species richness, functional type richness, and Shannon's diversity index increase from the areas closest to the watering source to those farthest away due to decreases in grazing intensity.
2. Plant communities in heavily grazed locations near watering sources are more similar in species and functional type composition to one another, while plant communities located farthest away from watering sources are less similar because of differential animal preference and differential sensitivity of plant species to grazing, resulting in plant community homogenization under high grazing intensity.
3. Cover and biomass of bunchgrasses are lowest near water and increase with distance from watering source as grazing intensity declines because of cattle preferences for bunchgrass species.

An improved understanding of the extent and severity of grazing effects around artificial watering sources and the cumulative impact of grazing intensity will help to inform land management in an ecosystem that provides habitat to many species of conservation concern that is likely to experience substantial challenges in the coming century (Knick et al., 2003; Palmquist et al., 2021).

METHODS

Study area

We conducted this study in big sagebrush-dominated plant communities in the upper Green River Basin of Wyoming, USA, in a ~4000 km^2 area. Big sagebrush plant communities exhibit considerable variability in both functional type and total species richness across their geographic extent in Wyoming (Jordan et al., 2020). Therefore, we constrained the geographic extent of our study area to maximize homogeneity in plant community composition, and soils, while representing variability in precipitation and temperature at the basin scale. All of the study sites are currently grazed by cattle during the summer, and are also grazed by mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), and feral horses (*Equus caballus*).

All sites have a semiarid climate with a mean annual temperature ranging from 1.6°C to 3.7°C and mean annual precipitation between 191 and 349 mm. Sites ranged from 2040 to 2284 m in elevation. Soil texture was similar across sites (Appendix S1: Figure S1).

In addition to big sagebrush, the dominant plant functional types are perennial bunchgrasses and perennial forbs. The dominant perennial bunchgrass species in the study area are Sandberg's bluegrass (*Poa secunda*), Indian ricegrass (*Achnatherum hymenoides*), needle and thread (*Hesperostipa comata*), and bottlebrush squirreltail

(*Elymus elymoides*). The most common perennial forbs are Hood's phlox (*Phlox hoodii*), pussytoes (*Antennaria* spp.), and milk vetch (*Astragalus* spp.). The most common non-native species was desert alyssum (*Alyssum desertorum*). We identified plants that did not possess adequate identifiable species characteristics to genus or functional type. Plant species nomenclature and nativity are based on the USDA PLANTS database (USDA, NRCS, 2017).

Sampling design and site selection

To identify the location of livestock watering sources, we obtained a database of artificial watering locations on Bureau of Land Management lands from BLM Field Offices within the study area. Our use of artificial watering points that were consistent in size allowed us to (1) control for the total area of livestock concentration around water relative to natural water bodies that are more variable in size and shape, (2) avoid confounding from topographically mediated vegetation gradients that often exist around natural watering sources, and (3) obtain records of how long each artificial watering source had been in place. We chose 17 watering sources (from this point forward "sites") on level uplands (slope $< 2^{\circ}$) with similar soil types and vegetation dominated by big sagebrush. In these areas, stocking rates ranged between 0.09 and 0.5 animal unit months (AUMs) per hectare with the average stocking rate of 0.26 AUMs per hectare (Appendix S1: Table S1; Allen et al., 2011). Because distance from water studies captures historical grazing pressure, we determined how long each watering point had been in place. Our artificial watering sources had an average age of 46 years ($SD = 16$) and 88% of watering sources were in place for at least two decades. The exceptions were one watering source for which we were unable to obtain a construction date and a second that had been in place for 8 years.

We sampled plant communities along the grazing intensity gradient within each site by randomly selecting plot locations within each of four distance bins that radiated outward from each watering source: 30–75, 75–300, 300–500, and 500–700 m (Adler & Hall, 2005; Adler et al., 2005). Other studies using distance from water gradients have used distances comparable with ours (Eldridge & Whitford, 2009; Manthey & Peper, 2010; Sasaki et al., 2011; Sternberg, 2012). We established a 100 m^2 plot in each of these distance bins by randomly choosing a distance within each bin, resulting in four plots per site and a total of 68 plots across all sites. We avoided the denuded, trampled area immediately adjacent to the watering source (<30 m). All field data were collected between May and June 2017 during peak phenological activity for most species.

Vegetation data

In each plot, we recorded the presence of and estimated percentage cover for each plant species using cover class codes outlined in Peet et al. (1998). We also recorded estimates for other cover groups: dead shrubs, woody debris, lichen, animal dung, litter, biotic soil crusts, bare ground, and rocks. Additionally, we recorded aspect, elevation, and slope at the plot origin.

Because previous studies have found that bunchgrasses can be sensitive to grazing (Anderson & Holte, 1981; Rickard et al., 1975), we characterized the grazing effects on perennial bunchgrasses. We collected 40 randomly selected bunchgrass individuals within each plot and recorded their identity, measured their basal diameter and height, and collected all aboveground biomass, excluding aboveground crowns. We dried samples in an oven set to 40°C until they reached a constant mass, and recorded mass to the nearest tenth of a gram for each individual. Notably, our drying temperatures were lower than those used in other studies (Matthews, 2010).

Soils

We collected three soil samples with an auger at 10 cm increments to a depth of 30 cm in each plot for a total 12 samples per site. We used a gravimetric method modified from Bouyoucos (1935) to quantify soil texture. We measured soil salinity using the NRCS 2009 protocols (Burt, 2009) with an Oakton Waterproof EcoTestr EC High Conductivity Tester Pocket Meter.

Presence of cattle and feral horses

We estimated dung density at each plot as a second measurement of grazing intensity among plots (Tate et al., 2003). We recorded dung density by counting all dung pats within our 100 m^2 plots, separately for cattle and feral horses.

Analysis

We conducted all analyses in R v.4.1.1 (R Core Team, 2021). To determine the relationship between our two proxies for grazing intensity—dung density and distance from water—we modeled dung density versus distance from water with a nonlinear model using generalized least squares. To aid interpretation of this relationship, we calculated the pseudo-R^2 for the model as the summed square of residuals divided by the summed squared difference to the mean.

For plant communities, we quantified total species and functional type richness in each plot. To evaluate functional type richness, we assigned each species to a functional type: bunchgrass, rhizomatous grass, annual forb, perennial forb, or shrub. We excluded succulents (represented by a single species) from the analysis, as this species was not abundant at any site. To quantify diversity in each of our plots, we calculated Shannon's diversity index and evenness. To calculate evenness, we used a modified Pielou's index (exp[Shannon Diversity]/richness), using percentage cover as our metric for abundance (Jost, 2010).

To quantify similarity in species composition across plots, we calculated Jaccard's coefficient on square root transformed species percentage cover data, which resulted in a larger contribution of low abundance plant species (that are common in big sagebrush plant communities) to the similarity index than untransformed cover (McCune et al., 2002). To visualize the differences between plots, we used nonmetric multidimensional scaling (NMDS), the most appropriate indirect ordination technique for plant community data (McCune et al., 2002). We used the "metaMDS" function in the *vegan* package (Oksanen et al., 2020), for an ordination solution with five dimensions and 100 random starts. To identify how species compositional changes differed among sites and with grazing intensity, we overlaid convex hulls for both sites and distance from water bins using the "ordihull" function in the *vegan* package (Oksanen et al., 2020). We followed the same procedure to determine the similarity of bunchgrass species composition within plots across distance from water sampling bins. For each plot, we summed biomass for all bunchgrass individuals belonging to the same species, which served as the measure of abundance. We then calculated Jaccard's coefficient based on the biomass for bunchgrass species.

To test for significant differences in species composition in plots across grazing intensity gradients, we used the multiresponse permutation procedure (MRPP; McCune et al., 2002). MRPP tests the null hypothesis of no difference between two or more defined groups, either by differences in the mean or the spread of variables and is a nonparametric analog to multivariate analysis of variance (MANOVA). We implemented MRPP using the function "mrpp" in the *vegan* package (Oksanen et al., 2020) based on Jaccard's coefficient calculated using square root transformed cover values for each species to test for differences in species composition between distance from water bins.

To evaluate the effects of grazing intensity on species richness, diversity, evenness, functional type richness, total vegetation cover, total grass cover, bunchgrass biomass, bunchgrass height, and bunchgrass basal area, we fitted linear mixed effects models using the function "lmer" in the *lme4* package (Bates et al., 2015; Zuur et al., 2009) to examine changes in these variables over the distance from water and dung density gradients. In these models, we included random intercepts to account for site-level effects and for non-independence of samples within each site, and treated either distance from watering source or cow dung density (proxies for grazing intensity) as a fixed effect.

RESULTS

We collected data on dung density along the distance from water gradients to evaluate whether grazing intensity changed along the gradient. Dung density decreased exponentially as distance from water increased (Figure 1). Nonplant canopy cover class elements (litter, vagrant lichen, bare ground, dead shrubs, rock, woody debris, and biotic crusts) had no relationship with grazing intensity (Appendix S2: Table S1).

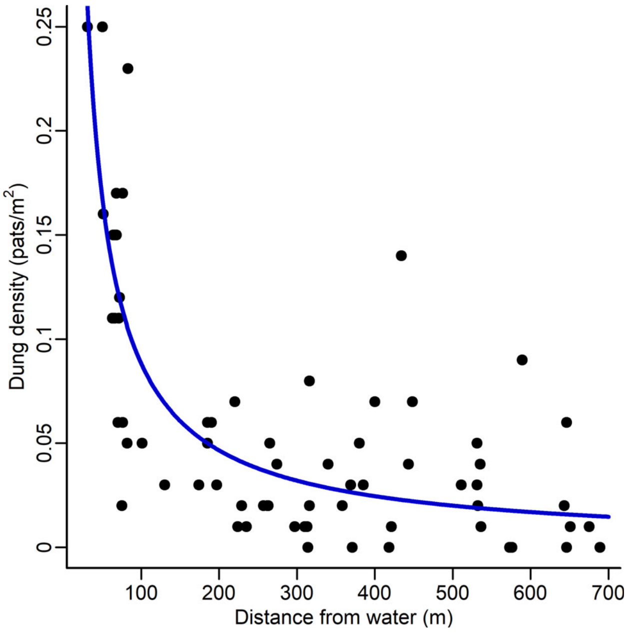

FIGURE 1 Dung density (dung pats/m^2) versus distance from water (m) (RMSE = 3.7 and pseudo-R^2 = 0.63) along 17 grazing intensity gradients in big sagebrush ecosystems in central Wyoming.

Species richness, composition, and diversity

We found 150 plant species across the 17 sites. Species richness per 100 m^2 plot ranged from 8 to 46 (Appendix S2: Table S2). Most species were perennial forbs, followed by bunchgrasses, shrubs, annual forbs, and rhizomatous grasses (Appendix S2: Figure S1). 83% of the species were perennials, and 96% of all species were native (Appendix S2: Table S2). Among 4% that were exotics, 75% were annual forbs, accounting for 89% of exotic cover.

Species richness did not vary with either distance from water or dung density, and we found nearly identical richness across the distance from water sampling bins (Tables 1 and 2). However, species diversity decreased under higher grazing intensity, measured both by distance from water and dung density, whereas evenness was not related to grazing intensity (Figure 2; Appendix S2: Table S3). Across functional types, only annual forbs had a significant negative relationship with distance from water ($p = 0.02$), whereas richness of all other functional types had no relationship with the grazing intensity metrics (Table 2). Native species richness had no relationship with distance from water or dung density, but exotic richness decreased significantly with distance from water ($p = 0.02$), but not with dung density (Table 2).

Species composition did not change with distance from water and was more similar within sites than among distance from water bins at a site (Figure 3). Within sites, species composition in the most heavily grazed plots was 54% to 58% similar to plots with lower grazing pressure (Figure 4a). Within each of the four distance from water sampling bins, species were between 26% to 33% similar to plots within the same sampling bin at other sites. MRPP indicated that species composition was not significantly different between plots located at different distances from water (chance-corrected within-group agreement $[A] = -0.02$, $p = 1$).

Functional type cover and bunchgrass biomass

Total vegetation cover was negatively related to dung density ($p = 0.02$; Figure 5a), but not related to distance from water (Table 3). Grass cover decreased consistently but not significantly with dung density ($p = 0.05$) and increased with distance from water ($p < 0.01$; Figure 5b,c). Annual forb cover had no relationship with dung density, but decreased with distance from water ($p = 0.03$; Appendix S2: Table S4). Perennial forb cover, shrub cover, cover of exotic species, and cover of bare ground, litter, and biological soil crusts did not vary over the distance from watering source or dung density gradients (Appendix S2: Table S1, S4, S5).

Our measurements of individual bunchgrass allometric variables (height, mass, and basal diameter) were not significantly related to dung density or distance from water (Appendix S3: Table S1). Jaccard's similarity based on total bunchgrass biomass by species was more similar within sites than among distance from water bins across sites, and did not vary significantly between distance from water sampling bins (Figure 4b). Bunchgrass biomass in the most heavily grazed plots was 44%–51% similar to plots with lower grazing pressure (Figure 4b).

TABLE 1 Mean (1 standard error in parentheses) total number of plant species, number of species by functional type, and mean number of exotic species in 100 m^2 for each distance from water bin (A–D) along grazing gradients at 17 big sagebrush ecosystem sites in Wyoming (upper panel), and percentage cover at 100 m^2 (1 standard error in parentheses) for all species, functional types, and all exotic species for each distance from water bin (lower panel).

Distance from water	Total richness	Total cover	Perennial forbs	Annual forbs	Grasses	Shrubs	Exotics
Richness							
A (0–75 m)	22.4 (1.0)	…	11.2 (0.8)	2.9 (0.3)	5.1 (0.2)	2.8 (0.1)	1.1 (0.1)
B (75–300 m)	20.9 (0.9)	…	11.0 (0.7)	1.9 (0.2)	4.8 (0.1)	2.9 (0.1)	0.7 (0.1)
C (300–500 m)	21.3 (1.0)	…	11.4 (0.7)	2.1 (0.3)	4.8 (0.2)	2.8 (0.1)	0.8 (0.1)
D (500–700 m)	21.5 (0.9)	…	11.5 (0.7)	1.8 (0.2)	5.1 (0.2)	2.8 (0.1)	0.5 (0.1)
Cover							
A (0–75 m)	…	53.0 (1.6)	6.3 (0.6)	1.8 (0.2)	8.9 (0.3)	35.9 (1.4)	1.0 (0.2)
B (75–300 m)	…	53.4 (1.6)	6.7 (0.8)	1.0 (0.1)	10.5 (0.4)	35.2 (1.0)	0.4 (0.1)
C (300–500 m)	…	57.2 (1.5)	6.5 (0.5)	1.0 (0.1)	11.0 (0.5)	38.6 (1.1)	0.4 (<0.1)
D (500–700 m)	…	59.4 (1.6)	6.8 (0.6)	0.8 (0.1)	11.9 (0.5)	39.8 (1.0)	0.3 (<0.1)

TABLE 2 Results of the linear mixed effects models for species richness, grass richness, perennial forb richness, annual forb richness, shrub richness, and exotic richness responses at 100 m^2 to grazing intensity over distance from water and cow dung density gradients across 17 sites in big sagebrush ecosystems in Central Wyoming.

	Fixed effects					**Random effects**	
						Variance	
Response and predictor	**Est.**	**SE**	***df***	***t* value**	***p***	**Site**	**Residual**
Species richness							
Intercept	21.992	1.977	17.122	11.12	<0.01	1.28e−5 ± 0.003	10.6 ± 3.251
Distance from water	−0.001	0.002	15.017	−0.75	0.46		
Intercept	21.355	1.880	16.173	11.36	<0.01	0.006 ± 0.077	11.05 ± 3.325
Cow Dung Density	0.023	0.073	35.545	0.32	0.75		
Intercept	15.531	2.014	0.408	7.71	0.29	0.023 ± 0.154	8.883 ± 2.981
Age of water source	0.116	0.631	1.745	1.85	0.22		
Grass richness							
Intercept	5.030	0.317	11.288	15.86	<0.01	1.28e−5 ± 0.001	0.536 ± 0.732
Distance from water	−0.0001	0.0005	14.099	−0.37	0.72		
Intercept	4.911	0.309	15.384	15.88	<0.01	6.97e−4 ± 0.026	0.623 ± 0.789
Cow dung density	0.008	0.017	20.244	0.48	0.64		
Intercept	4.207	0.647	7.791	6.5	<0.01	0.001 ± 0.033	0.639 ± 0.033
Age of water source	0.017	0.015	18.249	1.1	0.28		
Perennial forb richness							
Intercept	11	1.49	18.3	7.39	<0.01	2.62e−5 ± 0.005	6.06 ± 2.460
Distance from water	0.0006	0.001	15	0.31	0.76		
Intercept	11.584	1.360	16.137	8.51	<0.01	0.0002 ± 0.004	7.044 ± 2.654
Cow dung density	−0.055	0.057	50.788	−0.96	0.34		
Intercept	4.207	0.647	7.791	6.5	<0.01	0.001 ± 0.033	0.639 ± 0.033
Age of water source	0.017	0.015	18.249	1.1	0.28		
Annual forb richness							
Intercept	2.795	0.503	16.387	5.5	<0.01	05.45e−7 ± 0.001	1.14 ± 1.067
Distance from water	**−0.002**	**0.0006**	**36.436**	**−2.93**	**<0.01**		
Intercept	1.812	0.479	15.120	3.78	<0.01	0.009 ± 0.097	0.804 ± 0.897
Cow dung density	0.071	0.034	11.603	2.1	0.06		
Intercept	0.363	0.651	9.224	0.56	0.59	0.002 ± 0.053	1.113 ± 1.055
Age of water source	0.038	0.018	7.556	2.04	0.08		
Shrub richness							
Intercept	2.857	0.304	8.737	9.38	<0.01	1.52e−07 ± 0.0003	0.026 ± 0.517
Distance from water	−0.0001	0.0003	31.129	−0.46	0.65		
Intercept	2.8	0.207	13.5	13.51	<0.01	2.57e−4 ± 0.016	0.290 ± 0.539
Cow dung density	7.18e−04	1.26e−02	18.8	0.06	0.96		
Intercept	2.906	0.446	0.704	6.51	0.17	1.8e−4 ± 0.013	0.291 ± 0.540
Age of water source	−0.003	0.01	2.128	−0.31	0.78		
Exotic richness							
Intercept	1.075	0.21	10.285	5.11	<0.01	6.62e−07 ± 0.001	0.199 ± 0.445
Distance from water	**−0.001**	**0.0003**	**6.755**	**−2.99**	**0.02**		

(Continues)

TABLE 2 (Continued)

	Fixed effects					Random effects	
						Variance	
Response and predictor	Est.	SE	*df*	*t* value	*p*	Site	Residual
Intercept	2.8	0.207	13.5	13.5	<0.01	2.57e−4 ± 0.016	0.290 ± 0.539
Cow dung density	7.18e−04	1.26e−03	18.8	0.06	0.96		
Intercept	0.376	0.398	8.122	0.95	0.37	6.18e−06 ± 0.002	0.0281 ± 0.529
Age of water source	0.007	0.007	13.221	0.98	0.34		

Note: In the site column of variance of random effects, the values listed are either distance from watering source (m) or cow dung pat density in pats/m^2. Significant predictors are highlighted in bold. *df*, degrees of freedom; SE, standard error.

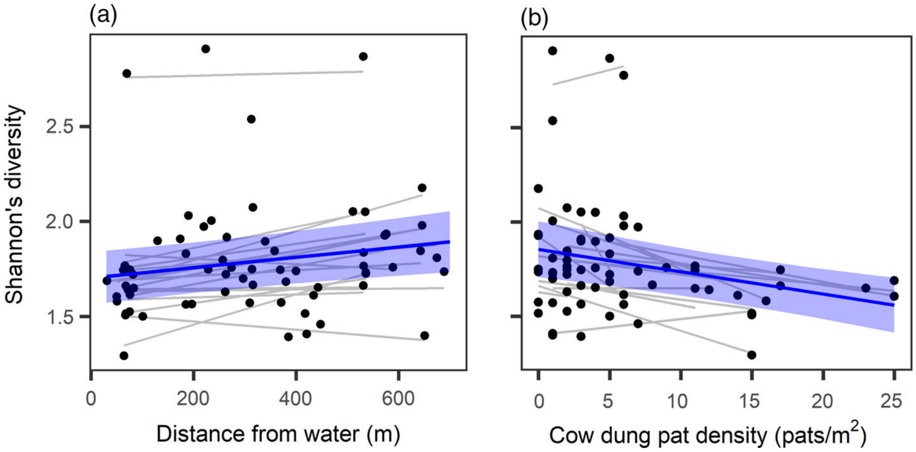

FIGURE 2 Shannon's diversity index over distance from water (a) and over cow dung pat density (b) grazing intensity gradients at 17 sites in big sagebrush ecosystems in Wyoming. In each panel, site-level relationships are shown as light gray lines. The linear mixed effects models are shown as blue lines with the 95% confidence interval shown as a blue polygon.

Among each of the four distance from water sampling bins, bunchgrass biomass was 10%–32% similar, from highest to lowest grazing pressure.

DISCUSSION

We examined how livestock grazing intensity influences multiple aspects of plant community structure in a widespread dryland ecosystem to determine the specific plant community characteristics most affected by livestock grazing. Grazing intensity—estimated by either distance from water or dung density—did not affect plant species composition or native species richness in the big sagebrush plant communities we sampled. However, we found that total vegetation cover, grass cover, and species diversity decreased as grazing intensity increased, but the magnitude of the effects was small for most sites. Collectively, these results suggested that within the climatic range our sites occupy, the big sagebrush plant communities are somewhat resistant to grazing.

Grazing intensity gradients

Grazing intensity decreased along our distance from the water gradient, as exemplified by dung density. Distance from water was more often related to plant community metrics than dung density. However, the relationships between plant community metrics and dung density suggested that dung density could be used to capture relative grazing pressure at a particular site independent of that site's proximity to water, as suggested in other grazing effects research (Lange, 1969; Tate et al., 2000). Furthermore, the comparison of plant community responses across dung density and distance from water gradients has often led to consistent conclusions, supporting the use of both metrics as proxies for grazing intensity (Stumpp et al., 2005; Turner, 1998).

Patterns of plant richness and diversity

We hypothesized that species richness would be lowest under the highest grazing intensities (i.e., closest to the

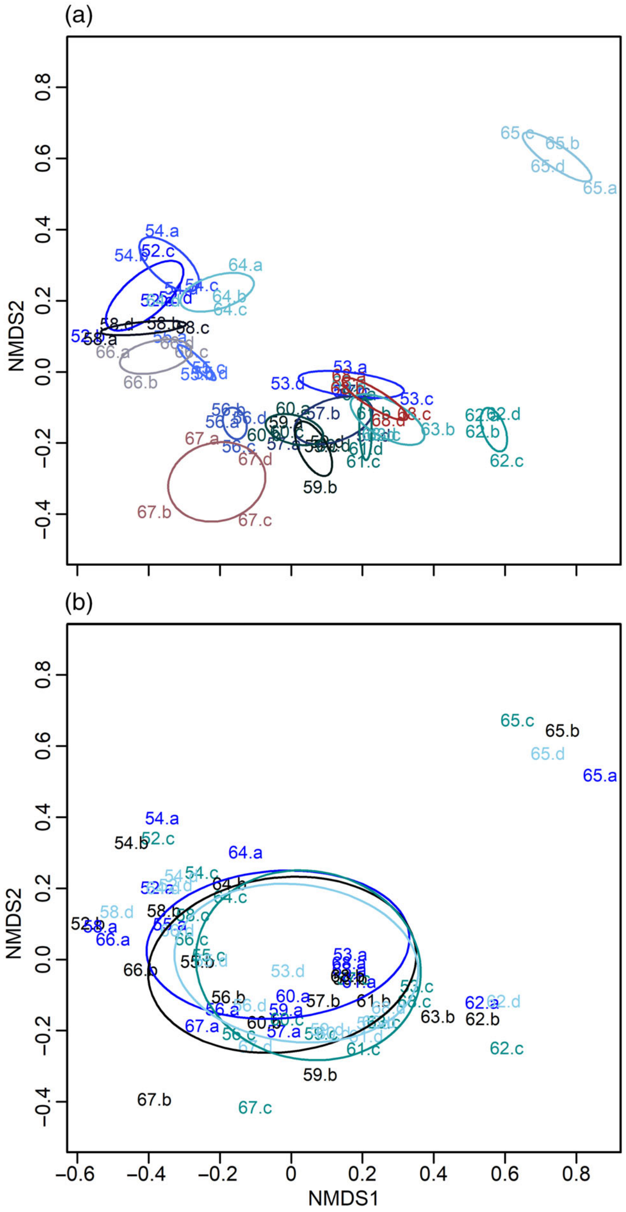

FIGURE 3 Nonmetric Multidimensional Scaling (NMDS; stress = 0.08) ordination of square root transformed species percentage cover showing differences in plant species composition across sites (a) and across distance from water sampling bins (b) along grazing intensity gradients in big sagebrush ecosystems in central Wyoming. Plots within sites have the same color in (a) and plots within distance from water sampling bins have the same color in (b).

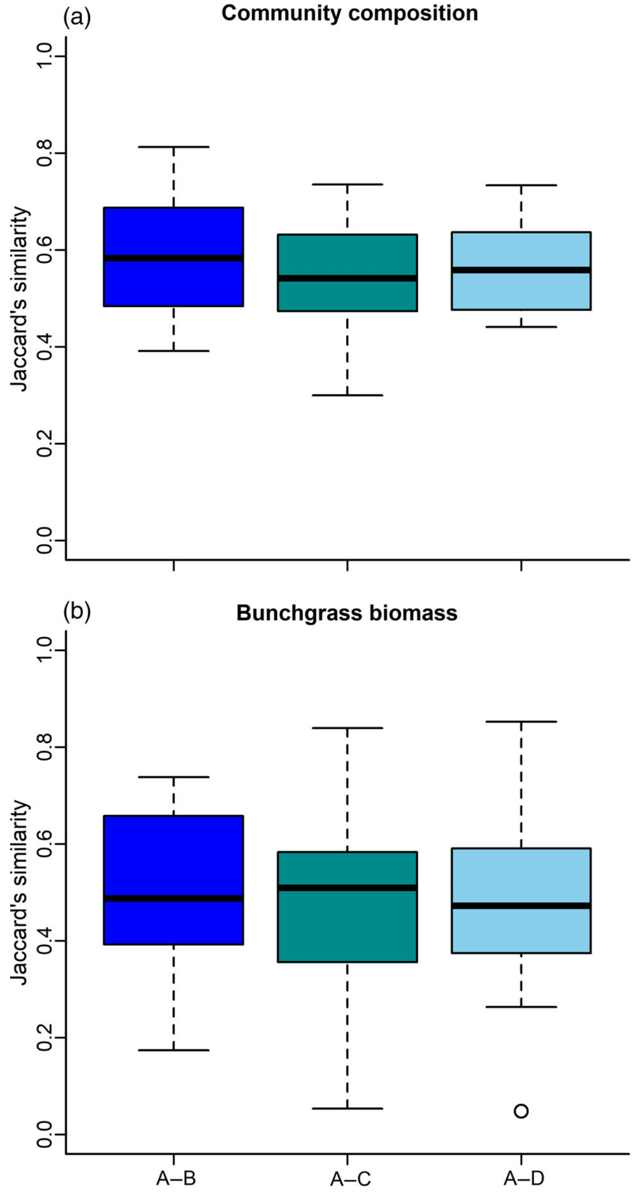

FIGURE 4 Jaccard's coefficient comparing the most proximate distance from water bin (A) to the other three distance from water categories (B–D) for plant species composition (a) and bunchgrass biomass composition by species collected in plots (b) across 17 sites in big sagebrush ecosystems in central Wyoming.

watering source), but we detected no changes in richness with grazing intensity. Despite no detectable changes in richness, we did find that increased grazing pressure reduced species diversity, although the effect was small. We compared the data from our sampling effort to a previous vegetation survey contained within our study area, and found that our richness values were statistically indistinguishable from the previous survey (Appendix S2: Table S6; Jordan et al., 2020). Therefore, we did not detect a grazing effect on richness, and a comparison of our data with sites with relatively low grazing pressure within the same geographic region supported this finding. A long-standing theoretical model of grazing effects on richness predicted decreases in species richness with increasing grazing intensity, with the rate of decline closely tied to aridity and evolutionary history of grazing (Milchunas et al., 1988); our data do not support the

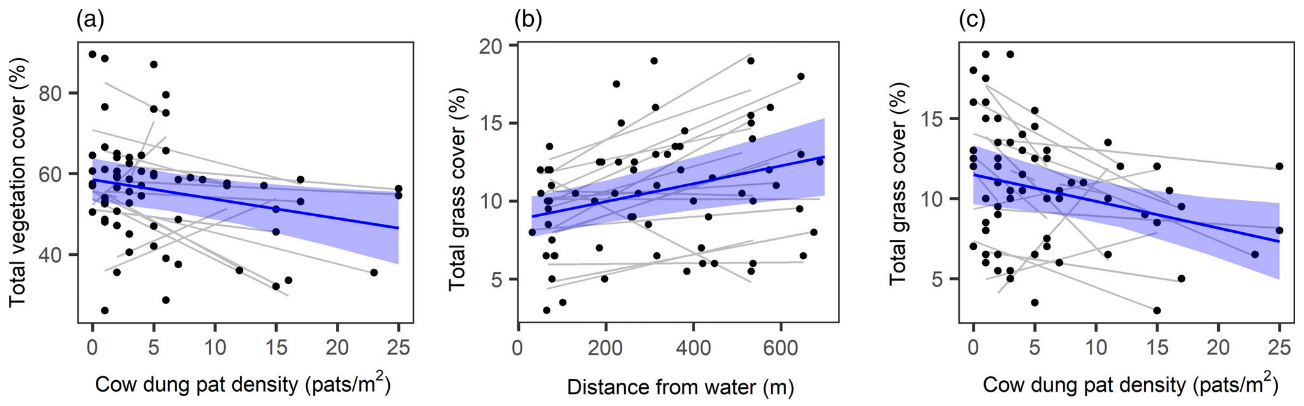

FIGURE 5 Total vegetation cover (a) and total grass cover (b, c) over cow dung pat density and distance from water grazing intensity gradients at 17 sites in big sagebrush ecosystems in Wyoming. In each panel, site-level relationships are shown as light gray lines. The linear mixed effects models are shown as blue lines with the 95% confidence interval shown as a blue polygon.

TABLE 3 Results of the linear mixed effects models assessing total vegetation and total grass cover responses to grazing intensity over distance from water and cow dung density gradients in big sagebrush ecosystems in Central Wyoming.

	Fixed effects					Random effects	
						Variance	
Response and predictor	Est.	SE	*df*	*t* value	*p*	Site	Residual
Total vegetation cover							
Intercept	51.721	3.693	14.073	14	<0.01	6.07e−04 ± 0.024	61 ± 7.809
Distance from water	0.013	0.007	15.213	1.68	0.11		
Intercept	58.496	2.661	16.7	21.98	<0.01	8.87e−04 ± 0.029	92.1 ± 9.595
Cow dung density	**−0.478**	**0.204**	**52.527**	**−2.35**	**0.02**		
Total grass cover							
Intercept	8.830	0.659	13.311	13.39	<0.01	1.98e−05 ± 0.004	4.67 ± 0.004
Distance from water	**0.005**	**0.001**	**13.617**	**3.32**	**<0.01**		
Intercept	11.491	0.919	14.331	12.49	<0.01	0.0865 ± 0.294	39.024 ± 6.247
Cow dung density	−0.166	0.067	5.520	−2.47	0.052		

Note: In the site column of variance of random effects, the values listed are either distance from watering source (m) or cow dung pat density in pats/m^2. Significant predictors are highlighted in bold. *df*, degrees of freedom; SE, standard error.

theoretical model. Other field studies in big sagebrush ecosystems and in other water-limited ecosystems have also found richness to be unaffected by grazing, consistent with our study (Adler et al., 2005; Eldridge et al., 2016; Stohlgren et al., 1999; Yeo, 2005), and resulting in a call for consistent reporting of other metrics of plant communities (i.e., diversity and evenness) alongside richness (Hanke et al., 2014).

Explanations for why grazing can have little effect on species richness include different responses of species to grazing (i.e., grazing-resistant vs. grazing-sensitive species) and resulting compensatory dynamics, reductions in the relative abundance of the dominant species thereby promoting species coexistence, and greater belowground competition than aboveground competition (Eldridge et al., 2016; Stohlgren et al., 1999). In contrast, other studies have documented effects consistent with the theoretical model: species richness declines with grazing in system-specific studies conducted in big sagebrush (Veblen et al., 2015), Australian rangelands (Eldridge et al., 2017; Landsberg et al., 2003), and these results have been supported by meta-analyses across grazing systems in Australia (Eldridge et al., 2016) and across the globe (Herrero-Jáuregui & Oesterheld, 2018). We propose that across the grazing gradients we studied, the ability of many forb and grass species to persist at low abundance made species richness relatively insensitive to grazing intensity, along with subtle turnover toward more exotic species under the highest grazing intensities. Similar to our diversity findings, studies have found a small but detectable decline in vegetation diversity metrics as grazing pressure increases in other grazing systems: Australian rangelands (Ludwig et al., 1999), African montane forests (Kikoti & Mligo, 2015) and rangeland systems (Jawuoro et al., 2017; Shezi et al., 2021), Middle Eastern grazing systems (Rahmanian et al., 2020), and South American semideserts (Cesa & Paruelo, 2011).

We found that exotic richness increased slightly with grazing intensity, as indicated by distance from water. Higher exotic richness near water is likely to have occurred because of soil surface disturbance created by the high level of livestock activity and the generally higher tolerance of exotic species to disturbance, relative to native counterparts (Brooks et al., 2006; Todd, 2006). Total vegetation cover decreased slightly with grazing intensity, possibly additionally facilitating the establishment of exotic species (Anderson & Inouye, 2001). Livestock grazing has been implicated in increasing the spread of exotic species on the landscape scale in other big sagebrush studies (Adler et al., 2005; Mack, 1981), namely through the processes explained above, as well as grazing-induced reductions in biological soil crust cover, increases in gap size, and the reduction in native species abundances. Our findings offer some support that increased livestock abundance reduces plant cover and in turn facilitates increases in the abundance of exotic species.

Composition

We hypothesized that grazing would cause changes in plant community composition, but we found no significant changes in species composition across our grazing intensity gradients. In some studies, heavy grazing intensities have been shown to homogenize vegetation through selective pressure (Adler & Lauenroth, 2000; Adler et al., 2001; Anderson & Briske, 1995), and we expected that we would find greater similarity in species composition between plots at the heavily grazed end of our gradient. However, other grazing studies in semiarid rangelands have reported small or no effects of grazing on species composition, consistent with our study (Copeland et al., 2021; Courtois et al., 2004; Davies et al., 2016; Fernandez-Gimenez & Allen-Diaz, 2001). In addition, a global meta-analysis of grazing effects on plant community composition showed little difference in composition when grazing pressure switched from moderate to low levels or even to no grazing (Herrero-Jáuregui & Oesterheld, 2018). Because the rangelands we sampled are grazed only at moderate levels (0.09–0.5 AUMs/ha), our grazing intensity gradients may not capture an intensity high enough to cause changes in plant composition. Furthermore, these areas probably experienced widespread overgrazing by sheep prior to the passage of the Taylor Grazing Act in 1934 (Morris & Rowe, 2014) and, as a result of this history of heavy grazing, the composition of the modern plant communities we sampled may have changed over time and now have a low sensitivity to modern cattle grazing practices (Copeland et al., 2021).

Total and functional type cover and biomass

We predicted that livestock grazing would reduce the cover and biomass of bunchgrasses, for which we found partial support. Our data indicated that increasing grazing intensity slightly reduced total vegetation and grass cover, which is consistent with other studies in semiarid rangelands globally that documented reductions in total vegetation cover with increases in grazing intensity (Eldridge et al., 2017; Oñatibia et al., 2018; Valenta et al., 2020). However, we found no relationship between grazing and bunchgrass biomass. Consistent with our study, Davies et al. (2016) found that winter grazing at a moderate intensity reduced bunchgrass cover, but did not reduce bunchgrass biomass compared with ungrazed controls, although grazing took place in the summer season in our study. The changes in grass cover we observed over the grazing gradients we sampled were small and may not represent a reduction in bunchgrass resource use, especially given the lack of relationships between grazing intensity and bunchgrass height, mass, and basal diameter (Appendix S3: Table S1; Davies et al., 2016). We did not measure bunchgrass density (individuals/unit area), which could have changed independently of our other measured variables. Further studies could incorporate bunchgrass density as a potential response variable. Therefore, the bunchgrass component of big sagebrush ecosystems may be more sensitive to multiyear precipitation patterns or the relative abundance of exotic species than modern grazing practices (Maurer et al., 2020; Porensky et al., 2020), as other grazing studies have found no or mixed relationships between grazing and total bunchgrass cover (Courtois et al., 2004; Holthuijzen & Veblen, 2016; Yeo, 2005).

Previous work in big sagebrush ecosystems has found that cattle grazing can reduce the cover of bunchgrasses (Adler et al., 2005; Camp et al., 2014; Rickard et al., 1975), which is consistent with our findings. Some exclosure studies in big sagebrush ecosystems have found more consistent responses across sites: total bunchgrass cover increased in the absence of grazing (Anderson & Inouye, 2001) and grazing decreased total bunchgrass cover or the cover of certain bunchgrass species (Rickard et al., 1975; Veblen et al., 2015). Collectively, these results indicated that bunchgrasses are the preferred forage for livestock in big sagebrush plant communities and even moderate grazing intensities can reduce the cover of bunchgrasses via consumption of aboveground net primary productivity.

Implications

Livestock grazing did not dramatically alter plant community structure of the big sagebrush stands we sampled. Cattle grazing can modify dryland plant community structure (Davies et al., 2018; Eldridge et al., 2016; Veblen et al., 2015), but over the range of big sagebrush there is varying sensitivity to modern grazing practices, which are likely to be driven by the interactions of climate, historical grazing pressure, and modern plant community composition (Copeland et al., 2021; Davies et al., 2018). Collectively, our findings support existing evidence that the balance between grasses and shrubs in big sagebrush ecosystems is relatively stable with current grazing practices (Davies et al., 2018). Our results are most applicable to areas that contain a big sagebrush overstory, a relatively intact perennial understory of forbs and grasses, and a low abundance of exotic species. Our work contributes to the knowledge on the effects of livestock grazing intensity in big sagebrush ecosystems, which are likely to experience increasing conservation challenges over the coming decades (Knick et al., 2003; Palmquist et al., 2016; Schlaepfer et al., 2017).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Jordan, 2021) are available in Zenodo at https://doi.org/10.5281/zenodo.5705665.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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