

Recovery of the herbaceous component of degraded sagebrush steppe is unimpeded by 75 years of moderate cattle grazing

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Abstract. Understanding the effects of contemporary cattle grazing on herbaceous perennial communities in big sagebrush steppe is important for managing for wildlife habitat, plant diversity, and productivity, yet potentially complicated by legacy impacts of historic, often higher intensity, livestock grazing. Here, we evaluate whether recovery of herbaceous communities in eastern Oregon, USA, after the cessation of intense spring sheep grazing (1935) was affected by moderate cattle grazing in paired plots with or without grazing over the past 75 yr (1936–2011). We tested for the effects of cattle grazing on herbaceous community recovery, as indicated by changes over time in plant density, and composition, as measured by Bray–Curtis dissimilarity. We also included current and prior to sampling year precipitation anomalies, to account for the weather effects, and a random term for pasture location of plot pairs to include potential subtle differences in abiotic environment and grazing management. We further tested whether time since cessation of intense sheep grazing and moderate cattle grazing were associated with convergence or divergence in community composition indicated by changes in evenness, richness, species relative abundance (rank order), and turnover or species appearance or disappearance. Total perennial herbaceous, forb, and grass density increased over time in sites grazed and ungrazed by cattle, though species varied in the direction of their response to contemporary cattle grazing. Community composition metrics indicated convergence over time including increasing evenness, decreasing Bray–Curtis dissimilarity, decreasing shifts in species relative abundance (rank order), and lower rates of species turnover (and gain and loss). Contemporary cattle grazing was not associated with convergence or divergence in composition. Precipitation anomalies for the current or prior water year were only occasionally significant in herbaceous density and community composition change models. Our results indicate similar long-term recovery trajectories occurred in sites with moderate cattle grazing or removal of all livestock following cessation of intense sheep grazing. Management planning and resource assessment focused on herbaceous perennial communities in sagebrush steppe should seek to separate the impacts of historic from contemporary livestock grazing practices.

Key words: Great Basin; livestock grazing; plant community; plant diversity; rangeland.

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INTRODUCTION

Livestock grazing is widespread in arid and semi-arid ecosystems globally and can significantly affect plant community composition (Milchunas and Lauenroth 1993, Hendricks et al. 2005, Eldridge et al. 2016). In the Great Basin, a dryland region with expansive rangelands in the western USA, declines in plant diversity and compositional changes over time may occur with livestock grazing due to differences between the historic abundance and behavior of native herbivores vs. historic and current livestock grazing practices (Platou and Tueller 1985, Milchunas et al. 1988, Rook et al. 2004). Evidence from long-term studies in the region is needed to distinguish between the effects of contemporary modern cattle grazing and the impacts of higher intensity grazing practiced in the early 20th century, as well as to account for the effects of variable weather on plant community dynamics (Anderson and Inouye 2001).

While some attributes of Great Basin plant communities, especially sagebrush (*Artemisia* L.) steppe, may predispose them to negative impacts of grazing on productivity and diversity, observations of responses to livestock grazing in sagebrush steppe range from positive or neutral (Rice and Westoby 1978, Bates and Davies 2014, Dittel et al. 2018) to negative (Pickford 1932, Laycock 1967, Austin and Urness 1998, Yeo 2005, Rickart et al. 2013). The relative lack of grazing resilient traits among the dominant herbaceous species in sagebrush steppe (Mack and Thompson 1982, Adler et al. 2004, Diaz et al. 2007) suggests sensitivity to livestock grazing (Milchunas and Lauenroth 1993). However, sagebrush dominated plant communities date from at least the mid-Miocene, 12 million years ago (Davis and Ellis 2010), and therefore co-occurred and persisted alongside a diverse assemblage of grazers and browsers (Janis et al. 2000), including bison as recently as the last few hundred years (Grayson 2006). Additionally, several characteristics of plant communities other than traits may influence their responses to livestock grazing. For example, grazing may increase species richness in systems where grazing suppresses dominant plant species, resulting in increases in non-preferred species (Koerner et al. 2018). In sagebrush steppe, dominant grass species are generally palatable

and occur with various densities of less palatable dominant shrubs, such as sagebrush, suggesting that the effects of high-intensity grazing may differ with subtle gradations like the ratio of shrubs to grasses in a particular site.

Variability in the outcomes of livestock grazing studies in the sagebrush steppe may be partially attributed to differences between livestock species (i.e., sheep vs. cattle) combined with grazing regime, including intensity, timing, and frequency of use, yet these variables are not necessarily considered in many livestock grazing studies (Davies and Boyd 2020). For instance, high-intensity sheep grazing in the spring has much greater negative impacts on perennial herbaceous species than high-intensity grazing in the fall (Laycock 1967). The effects of grazing differ by livestock species due to a myriad of differences in selectivity and consumption of various plant species (Rook et al. 2004). Livestock grazing intensity, as opposed to the presence or absence of livestock, affects multiple aspects of vegetation composition and abundance, both directly and indirectly, such as via impacts on biological soil crusts (Reisner et al. 2013).

Livestock grazing practices have varied widely in the Great Basin. Historic intense grazing in the late 1800s to the early 1900s led to rangeland degradation in the region (Griffiths 1902, Wagner 1978, Morris and Rowe 2014), and these legacy effects are difficult to distinguish from the effects of recent grazing management. Successional dynamics in plant communities formerly exposed to heavy grazing pressure are commonly observed in exclosure studies dating from the mid-20th century in the region (Gardner 1950, Anderson and Holte 1981, Austin and Urness 1998, Courtois et al. 2004). Recovery in areas outside exclosures is associated with the implementation of moderate grazing practices, such as decreased grazing intensity and frequency (Yorks et al. 1992), due to rangeland grazing regulations in the mid-1900s (i.e., Taylor Grazing Act, 73rd U.S. Congress 1934).

The effects of livestock grazing on Great Basin plant communities could also be contingent on environmental factors affecting plant community productivity and dynamics, such as weather patterns, climate, and soil fertility, which impact ecosystem responses to livestock grazing (Milchunas and Lauenroth 1993, Lunt et al. 2007)

including the effects of grazing intensity (Irisarri et al. 2016). For instance, species responses to grazing intensity are altered by precipitation zones across the Great Basin (Holthuijzen and Veblen 2016) and grazing intensity interacts with weather to affect herbaceous production across functional groups (Bates and Davies 2014). Plant community response to livestock grazing may also be related to indirect effects, such as changes in soil properties. For example, long-lasting declines in plant productivity are likely where livestock grazing leads to increased erosion and associated reductions in soil nutrients or water holding capacity (Neff et al. 2005, Duniway et al. 2018).

Mechanisms for divergence in plant community composition in sites with and without cattle grazing are likely to vary with historical grazing practices and landscape context (Lunt et al. 2007). Species turnover associated with local extinction and colonization via seed dispersal of long-lived perennial species is more likely in sites where grazing has been excluded for longer time periods (O'Connor 1991, Purschke et al. 2014). However, change in plant communities in sites removed from grazing following a long period of landscape-scale high-intensity grazing may be limited by the abundance and composition of the existing plant community. For example, in a sagebrush steppe area with low herbaceous cover previously exposed to historic intense grazing, herbaceous cover did not recover after 5–6 yr of grazing removal (Davies et al. 2016a). In another sagebrush steppe site removed from livestock grazing, recovery trends in herbaceous cover and diversity appeared to be largely driven by slow-growing populations of residual species rather than dispersal of new species into the site (Anderson and Holte 1981, Anderson and Inouye 2001).

We addressed two major types of livestock grazing impacts common across the Great Basin in this study: recovery from historically relatively high-intensity sheep grazing and the ongoing effects of contemporary moderate cattle grazing. Our overall question was how moderate grazing (i.e., contemporary grazing) would affect changes in abundance and composition of herbaceous communities following historic intense livestock grazing. To address this question, we tested several hypotheses. First, we anticipated

that communities would change over time in response to the removal of historic intense grazing, largely due to increases in density of perennial species, particularly recovery of grazing sensitive species. Second, we expected that plant communities exposed to long-term moderate livestock grazing would diverge from those protected from contemporary livestock grazing. Third, we expected divergence due to moderate livestock grazing to increase over time, because communities exposed to moderate cattle grazing would remain more similar to the historic, intensely grazed state.

To test general hypotheses related to recovery patterns, we asked how time since cessation of high-intensity grazing, contemporary moderate cattle grazing or grazing exclusion, and relatively high or low precipitation and pasture location (associated with subtle site differences in environmental characteristics) were associated with changes in perennial herbaceous community density. We also tested whether time since cessation of high-intensity grazing and contemporary moderate cattle grazing were associated with overall shifts in community composition associated with increasing divergence, indicated by dissimilarity, and heterogeneity as indicated by multivariate dispersion. We further investigated the potential for community divergence or convergence by testing for associations with trends in specific elements of community dynamics, such as shifts in evenness and rates of species turnover.

METHODS

Study area

Study sites were located at the Northern Great Basin Experimental Range (NGBER) in eastern Oregon (119°42' W, 43°29' N, Fig. 1). Lower elevations at the NGBER are big sagebrush steppe with woody vegetation dominated by Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) and higher elevation areas dominated by western juniper (*Juniperus occidentalis* Hook.) and mountain big sagebrush (*A. tridentata* Nutt. spp. *vaseyana* [Rydb.] Beetle). Understory herbaceous vegetation are mainly mixtures of native perennial cool-season bunchgrasses and forbs. Elevation ranges from 1350 to 1676 m (~10 m resolution

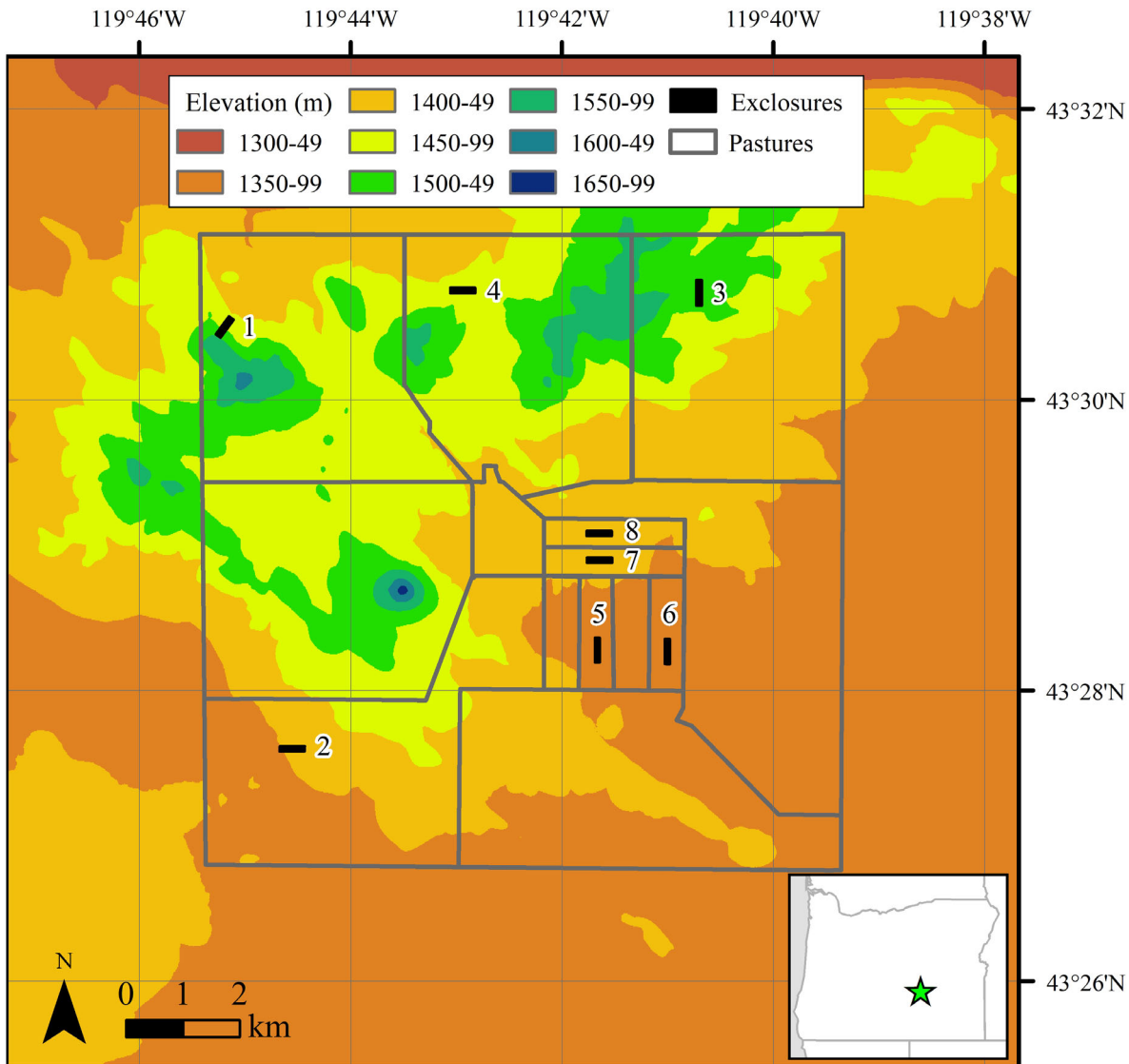


Fig. 1. Map of the Northern Great Basin Experimental Range with the locations of the 2-ha exclosures included in the analysis along with the pasture unit boundaries and elevation in meters. The inset map shows the location (star) within the state of Oregon (map projection: WGS 1984/Web Mercator EPSG 3857).

digital elevation model, U.S. Geological Survey 2019). Dominant soils are derived from Pliocene extrusive volcanic parent material (Lentz and Simonson 1986, SSURGO Database, U.S. Department of Agriculture 2017).

The research area is within the northern Great Basin, characterized as cold desert, with freezing temperatures and snow common in the winter, and high temperatures with relatively lower precipitation during the summer. Mean daily

temperatures for the coldest month are $-3.7\text{ }^{\circ}\text{C} \pm 2.0\text{ SD}$ and $20.2\text{ }^{\circ}\text{C} \pm 1.4\text{ SD}$ for the warmest month (1938–2011, NOAA Daily Global Historical Climatology Network, Station USC00358029, Menne et al. 2012a, b). Mean annual precipitation is $267\text{ mm} \pm 76\text{ SD}$ (range 102–474 mm). Most precipitation falls as snow in the winter months (November–February) with mean values of $834\text{ mm} \pm 385\text{ SD}$ (range 143–1672 mm).

The study area as well as much of the sagebrush steppe in eastern Oregon was heavily grazed by sheep in the spring (March–May) in the early 1920s until 1935 and described as overgrazed by the mid-1930s when the experimental range was established (Sneva et al. 1984). Some sheep as well as cattle grazing occurred from 1936 to 1939 (Sneva et al. 1984). Grazing pressure associated with both livestock numbers and season length was lower in the late 1940s–1950s to allow for vegetation recovery (Sneva et al. 1984). From 1940 through present, the area was grazed by cattle for various intervals from mid-April through November (unpublished NGBER records, Sneva et al. 1984). From the 1960s to the present, cattle grazing has been maintained at moderate levels with occasional rest years in different pastures and variation in cattle numbers between years (1946–1974, mean 0.24, range 0.14–0.40 Animal Unit Months [454 kg mature cow consuming 12 kg dry mass per day, or equivalent, for 30 d]/ha, Sneva et al. 1984; 1976–2011, mean 0.27, range 0.14–0.40 AUMs/ha, unpublished NGBER records).

Thirteen rectangular 2 ha (67×134 m) enclosures were set up in 1936 and paired with adjacent areas grazed by livestock, with one pair located within each of the NGBER pastures (Sneva et al. 1984). The locations of the pairs of grazed and ungrazed (enclosure) sampling sites within each pasture were likely chosen to represent the vegetation within their respective pastures, particularly in larger pastures, but details on original site selection are not available (Sneva et al. 1984). We included eight pairs ($N = 16$) in analyses; the remaining five pairs were excluded due to inconsistent monitoring across years or differences in grazing regime (Fig. 1). Paired sites span 1390–1540 m in elevation (Appendix S1: Table S1, U.S. Geological Survey 2019) and are on either cobbly loam (three of eight pairs), sandy to clay cobbly loam (three pairs), or gravelly fine sandy loam (two pairs, Lentz and Simonson 1986, U.S. Department of Agriculture 2017).

Perennial herbaceous (grass and forb) species density was sampled between 1937 and 2011 in eight years (across two years in 1939–1940) at one time point in late spring through summer (May–August): 1937, 1939/1940, 1960, 1974, 1997, 2003, 2008, and 2011. Sampling methods varied

across the time periods. Single large 37.16 m^2 square areas (6.096×6.096 m, 20×20 ft) per grazed or ungrazed site were monitored in 1937, 1939/1940, 1960, and 1974 in the same locations. The square areas in the enclosures were located approximately 25–30 m from the enclosure fence and generally 30–80 m from the enclosure corner. The comparison (grazed) square sampling areas were established across from the enclosure sampling areas across the closest fence line at 25–30 m from the enclosure fence and within 10–20 m of the same distance from the enclosure corner. In 1997, the location of the sampling areas and the sampling design changed with grazed or ungrazed sites monitored with ten 0.2-m^2 quadrats (0.4×0.5 m) along five 30-m transects 15 m apart (10 m^2 area sampled in total). With this new sampling design, comparison grazed areas were located within 10–15 m of the enclosure fence and not necessarily on the same side of the enclosure as the original 1937–1974 square sampling areas. In 2003, 2008, and 2011, grazed or ungrazed sites were monitored with ten 0.2-m^2 quadrats (0.4×0.5 m) along seven 30-m transects (14 m^2 area sampled in total) 15 m apart. One grazed and ungrazed pasture pair (number 2) included two dominant sagebrush subspecies, which were monitored separately in 2003–2011 with two sets of transects (one set in each area of dominant sagebrush subspecies) with ten 0.2-m^2 quadrats along five 30-m transects approximately 15 m apart, arranged to remain within the area of the dominant sagebrush subspecies. Sampling areas from 1997 to 2011 were generally in the same areas, but the exact transect locations were not identical because they were not permanently marked. The earlier sampling strategy with the square design (1937–1974) included a greater area, but the sampling only included a small proportion of the enclosure and comparison adjacent grazed area, whereas the more recent transect design (1997–2011) included a smaller area for density sampling, but was dispersed across most of the enclosure and comparison adjacent area. Density values were averaged across all grazed or ungrazed transects regardless of sagebrush subspecies for those years. Species were combined into genera groups in many cases due to inconsistent identification between monitoring years (see Appendix S1: Table S2 for species and species groups aggregated to the

genus level). Species and genera group richness increased with the decrease in sample area and altered sampling design (square to transects, species/genera groups: 1937–1974, mean 13.7 ± 0.4 standard error (SE), 1997–2011, mean 19.2 ± 0.4 SE). Sedges (*Carex* L. spp.) were also removed due to differences across monitoring years in density estimation; the most common species is rhizomatous and stem number and frequency were measured for density in different years. However, the genus was encountered infrequently and in low abundance throughout the sampling years. Species or genus abundance was calculated with mean density (mean number of plants per square meter) across all transects or for the single square plot for each pasture and cattle grazing unit.

We calculated precipitation anomalies for each sampling year to estimate relatively favorable or unfavorable weather affecting perennial herbaceous communities. Precipitation anomalies were calculated as the percentage of mean precipitation (October 1936–May 2011) for the current (sampling) year and the year prior by water years to emphasize precipitation influencing the summer growing season (October–September used for year prior to sampling and October–May for the current year). Weather data were acquired from the same local weather station as the averages described above for 1938–2011 and from a different weather station for 1936–1937, which was located ~65 km east of the research site at a slightly lower elevation (1250 m). Precipitation anomalies (percentage of the mean) ranged from 39% to 128% between October and May for sampling years (Appendix S1: Table S3).

Statistical analysis

We tested whether plant communities recovered since cessation of intense grazing and whether moderate cattle grazing affected the recovery rate with linear mixed models for herbaceous perennial density (R package lme4, Bates et al. 2015). Models included time since cessation of high-intensity grazing, cattle grazing exclusion, their interaction, and precipitation anomalies for the current and previous water year as predictors. We also included a random effect for each pasture, in other words, each pair of cattle removal and grazed plots, due the combination of unmeasured environmental and

management variables potentially associated with each pasture location. We constructed models for perennial herbaceous total density as well as the following groups: forbs, large bunchgrasses (*Poaceae*, excluding Sandberg bluegrass, *Poa secunda*, J. Presl), and *P. secunda*. We separated *P. secunda* from other grasses based on observations that it responds positively to higher grazing pressure compared to other co-occurring perennial bunchgrasses (Yeo 2005, Veblen et al. 2015), perhaps because it is shallow-rooted and initiates growth and matures earlier in the spring (U.S. Forest Service 1937, Passey et al. 1982). Non-significant fixed effect terms ($P > 0.05$) were removed sequentially with model comparison (Zuur et al. 2009) with Kenward-Roger degrees of freedom for mixed models (R package pbkrtest, Kenward and Roger 1997, Halekoh and Højsgaard 2014). We refit final models with restricted maximum likelihood and calculated the significance of final model terms with *F* tests (type III sum of squares, Kenward-Roger df, R package car, Fox and Weisberg 2011).

We tested whether time since cessation of historic intense sheep grazing and contemporary cattle grazing were associated with changes in plant community composition aside from their effects on overall density patterns with permutational multivariate analyses of variances (perMANOVAs) for dissimilarity in plant community composition (measured with Bray–Curtis distance matrices, R package vegan, function adonis2, $N = 999$ permutations, Oksanen et al. 2019). We conducted separate perMANOVAs for total perennial herbaceous, perennial forb, and perennial grass density and constrained permutations by grazing and enclosure plot pair (strata for pasture in the adonis2 model, $N = 8$). We tested whether year since removal of intense sheep grazing affected perennial herbaceous community variation between sites grazed and ungrazed by cattle by including the interaction between sampling year and grazing in the perMANOVA models. Where the interaction term was not significant, we tested for the main (individual) effects of cattle grazing and year since removal of intense sheep grazing. We also included precipitation anomalies for the current (October–May) and prior water years' precipitation (October–September) in perMANOVA models to test the effects of relatively high or low

precipitation on community dissimilarity. We also constructed perMANOVA models with and without the years 1937 and 1939/1940 because differences associated with moderate cattle grazing might be slight in early sampling years (1937 and 1939/1940) due to the length of time required for plant populations to respond to removal of all livestock grazing.

In addition to separation between communities in multivariate space tested by the perMANOVAs, changes in multivariate dispersion (a measure of variance) might indicate whether communities were becoming more heterogeneous (higher dispersion) or homogeneous (lower dispersion) with time since historic intense grazing and/or due to moderate cattle grazing. We tested for differences in community dispersion between all sites sampled in each time point since cessation of high-intensity grazing (irrespective of cattle grazing, $N = 8$), between all ungrazed and moderate cattle grazed sites (irrespective of time point, $N = 1$), and between each combination of cattle grazing or exclusion and time point since intense grazing and ($N = 16$, R package `vegan`, `betadisper`, and `permutest` functions, $N = 999$, Tukey's test for pairwise differences, Anderson 2006, Oksanen et al. 2019). We conducted separate analyses for the total perennial herbaceous community as well as for perennial grasses and perennial forbs. Finally, we visually explored the perMANOVA tests with an ordination approach with non-metric multidimensional scaling (NMDS) based on Bray–Curtis distances and fit year since cessation of historic grazing and moderate cattle grazing (R package `vegan`, `metaMDS` and `envfit` functions, $k = 3$, $N = 999$ permutations, Minchin 1987).

While shifts in community dissimilarity and multivariate dispersion indicate convergence or divergence in composition and homogeneity, they do not indicate the types of patterns, such as changes in species number or relative abundance, which might be underlying these trends. Therefore, we tested whether specific metrics of community change, related to divergence, were affected by contemporary moderate cattle grazing and time since cessation of historic intense grazing. Our metrics included species richness, occurrence difference (number of different species divided by total unique species, range 0–1, across grazing categories only), evenness (Evar

index, range 0–1, Smith and Wilson 1996), rank order (species rank based on relative abundance), and species gain and loss (across time points only, R package `codyn`, Avolio et al. 2019, Hallett et al. 2019). Community divergence is indicated by increases in differences for species richness (across time points or between grazing groups), rank order, species gain and loss rates (across time points) or occurrence (between groups), and decreases in differences in evenness (time points or groups). Opposite patterns suggest convergence with cattle grazing or across time points. We used linear models to test whether time since cessation of intense sheep grazing affected convergence or divergence in compositional change due to contemporary grazing, as indicated by differences in community change metrics (richness, evenness, rank order, and occurrence) between plots with and without moderate cattle grazing. We included the pasture (plot pair) and interaction between pasture and time since cessation of intense grazing in models to test for differences associated with the pasture locations. Separately, we used linear mixed models (following the procedures describe for the density analyses) to test whether differences in compositional change metrics (richness, evenness, rank order, and species gain and loss) across time points was associated with time since cessation of intense grazing, moderate cattle grazing, and their interaction.

We also tested for differences in results associated with sampling strategy, between large squares (1937–1974) and transects (1997–2011), with separate linear mixed models for density and perMANOVA analyses for dissimilarity with time since experiment establishment and cattle grazing for the early sampling period (1937–1974). All analyses were conducted in R version 3.5.3 (R Core Team 2019).

RESULTS

Total perennial herbaceous density recovered after cessation of sheep grazing, from an initial density of 11.1 ± 2.0 SE (all results are means ± 1 SE plants/m²) in 1937 across both grazing treatments, to higher values with moderate cattle grazing, hereafter “grazed,” 53.0 ± 4.2 , compared to ungrazed areas 42.3 ± 3.0 during the last four sampling periods (1997–2011,

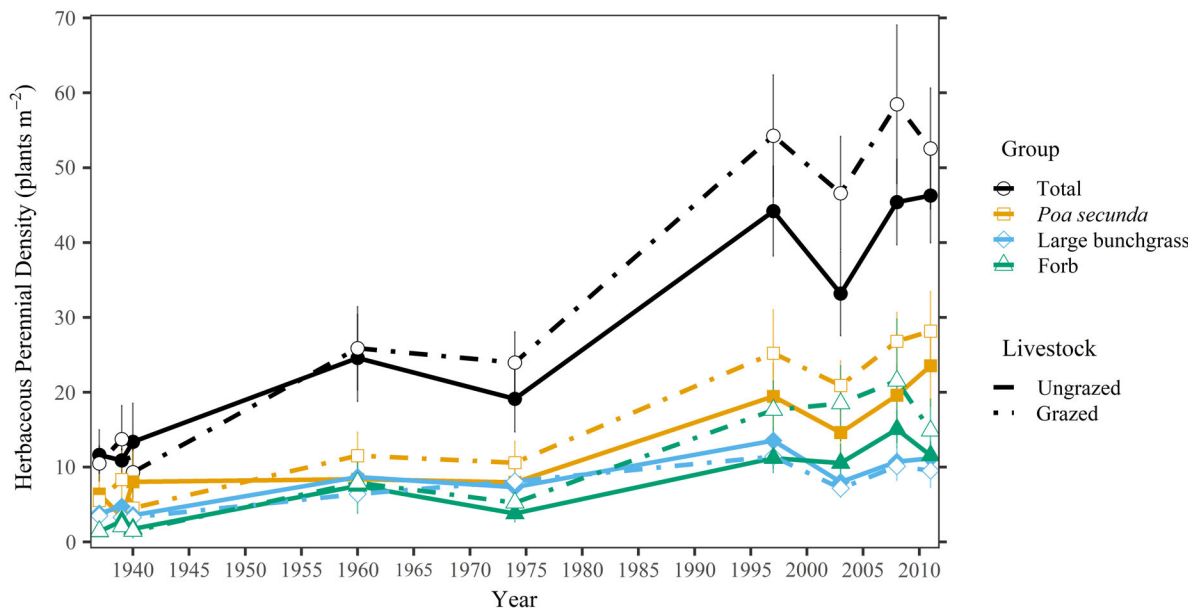


Fig. 2. Perennial density (plants/m²) by year and cattle grazing for total herbaceous, *Poa secunda*, large bunchgrass, and forb groups.

Fig. 2). Perennial grass density was greater than perennial forb density across all sampling periods (Fig. 2). Mean perennial grass density also increased over time (9.6 ± 1.8 in 1937) and was higher in grazed (34.8 ± 2.4) than ungrazed sites (30.2 ± 2.4) by the 1997–2011 sampling periods. The majority of the perennial grass density across all sampling periods was *P. secunda*, a low stature grazing tolerant species, that consistently occurred in higher densities with cattle grazing and increased from initial values (1937, 6.0 ± 1.5 ; 1997–2011, 19.3 ± 2.1 without grazing and 25.3 ± 2.3 with grazing, Fig. 2). Large bunchgrass species were less numerous than *P. secunda* overall, and their density increased over time, but was lower with grazing (1937, 3.7 ± 0.5 ; 1997–2011, 10.9 ± 1.0 without grazing and 9.6 ± 0.9 with grazing, Fig. 2). Perennial forb density increased over time and was higher with grazing (1937, 1.4 ± 0.4 ; 1997–2011, 12.1 ± 1.1 without grazing and 18.1 ± 2.7 with grazing, Fig. 2).

Total perennial herbaceous density increased with time since cessation of intense sheep grazing and this trend interacted with the effect of moderate cattle grazing, with higher density in grazed sites in recent decades (interaction,

Kenward-Roger [KR] $df = 117$, $F = 4.6$, $P = 0.034$; time, $df = 117$, $F = 189.2$, $P < 0.001$; cattle grazing effect. KR $df = 117$, $F = 4.4$, $P = 0.038$, Fig. 2). Prior (October–September) and current (October–May) water year precipitation anomalies did not have significant effects ($P \leq 0.05$) on total herbaceous density (not retained in final model). Large perennial bunchgrass density increased with time since cessation of intense grazing (KR $df = 117$, $F = 125.0$, $P < 0.001$), was lower in areas with cattle grazing (KR $df = 117$, $F = 4.2$, $P = 0.043$), and increased with relative high prior water year precipitation anomaly (KR $df = 117$, $F = 21.0$, $P < 0.001$) but was not significantly related to current water year precipitation anomaly or interactions between time since cessation of intense grazing and cattle grazing. *P. secunda* density also increased with time since cessation of intense grazing (KR $df = 118$, $F = 111.4$, $P < 0.001$) and was higher in areas with cattle grazing (KR $df = 118$, $F = 7.8$, $P = 0.006$) but was not affected by interactions between time since cessation of intense grazing and cattle grazing or precipitation anomaly in the current or prior water year. Perennial forb density increased over time since cessation of intense grazing (KR $df = 117$,

$F = 65.8$, $P < 0.001$) and was higher with cattle grazing (KR $df = 117$, $F = 3.7$, $P = 0.06$), and sites with cattle grazing had higher density in later years (significant interaction, KR $df = 117$, $F = 3.8$, $P = 0.05$). Neither precipitation anomaly was significant in final models for perennial forb density.

Models for time since cessation of intense grazing and cattle grazing and their interaction for years sampled with large squares only (1937–1974) and transects and large squares in different years (1937–2011) showed similar significant ($P < 0.05$) effects of time since cessation of intense grazing on density for all categories of perennial herbaceous density (total, forb, large bunchgrass, and *P. secunda*, Appendix S1: Table S4). However, only models with all sampling years and including both sampling methods supported the effects of cattle grazing (Appendix S1: Table S4).

Some species appeared to respond consistently to contemporary grazing practices (1960–2011). Two grass species had higher densities in grazed areas across all years (≥ 0 minimum mean difference, grazed—ungrazed density, *P. secunda* and Thurber's needlegrass, *Achnatherum thurberianum* [Piper] Barkworth) while four species had lower densities in grazed areas (≤ 0 maximum mean difference, grazed—ungrazed density, Idaho fescue, *Festuca idahoensis* Elmer; Cusick's bluegrass, *Poa cusickii* Vasey, basin wildrye, *Leymus cinereus* [Scribn. & Merr.] Á. Löve; and beardless wildrye *Leymus triticooides* [Buckley] Pilg., Appendix S1: Table S5, Fig. S1). Several forb species or genera groups had consistently higher densities in grazed areas (clover, *Trifolium* L. spp.; desert parsley, *Lomatium* Raf. spp.; narrowleaf mock goldenweed, *Nestotus stenophyllus* [A. Gray] R.P. Roberts, Urbatsch & Neubig, Indian paintbrush, *Castilleja Mutis ex L. f. spp.*; foothill death camas, *Zigadenus paniculatus* [Nutt.] S. Watson; and hoary tansyaster, *Machaeranthera canescens* [Pursh] A. Gray, Appendix S1: Table S5, Fig. S2). In contrast, other forb species or genera groups had lower densities in grazed areas (hawkbeard, *Crepis* L. spp.; ragwort, *Senecio* L. spp.; rockcress, *Arabis* L. spp.; common yarrow, *Achillea millefolium* L., oneflowered broomrape *Orobanche uniflora* L., Douglas's catchfly, *Silene douglasii* Hook., and bitter root, *Lewisia rediviva* Pursh, Appendix S1: Fig. S2). Among forbs and

grasses, several species or genera groups did not respond consistently negatively or positively to grazing, and a few tended to have positive or negative responses to grazing based on mean density differences, but not consistently across all years (Appendix S1: Table S5, Figs. S1, S2).

We found that Bray–Curtis dissimilarity, an indicator of community change, was affected by both time since cessation of intense sheep grazing and cattle grazing, but time consistently explained more variability (as measured by R^2) than cattle grazing for total perennial herbaceous, forb, and grass components (Table 1; Appendix S1: Table S6). Current (October–May) and prior (October–September) water year precipitation anomalies were only significant ($P < 0.05$) to marginally significant ($P < 0.10$) in models including 1937 and 1939/1940 for total perennial herbaceous, forb, and grass density (Table 1; Appendix S1: Table S6). Dissimilarity between grazed and ungrazed paired plots generally declined over time, indicating community convergence, with the highest values observed in 1937–1974 (non-metric multidimensional scaling plots, Fig. 3; Appendix S1: Fig. S3; Fig. 4). Time since cessation of intense grazing significantly affected total perennial herbaceous community variability (Bray–Curtis dissimilarity) for sampling time points with large square sampling

Table 1. Results for permutational analysis of variance for total herbaceous density with year since cessation of intense sheep grazing (year) and cattle grazing (grazing) and current (October–May) and prior water year (October–September) precipitation anomalies (Bray–Curtis dissimilarity, full model with interaction between year and grazing, removed if $P \geq 0.10$, marginal test of terms, permutations constrained by enclosure pair within each pasture).

Predictor variables	R^2	F	P value
All years (1937–2011)			
Year	0.13	19.6	0.001
Grazing	0.01	2.2	0.044
Current year precipitation anomaly	0.01	2.0	0.066
Prior year precipitation anomaly	0.01	1.9	0.076
Post-1940 (1960–2011)			
Year	0.07	7.3	0.001
Grazing	0.02	2.4	0.027
Current year precipitation anomaly	<0.01	0.3	0.985
Prior year precipitation anomaly	<0.01	0.7	0.638

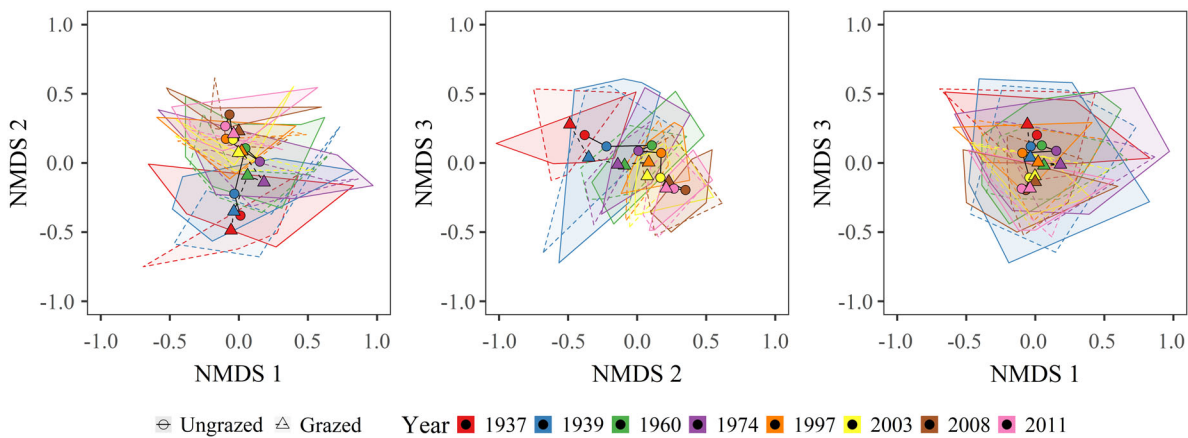


Fig. 3. Non-metric multidimensional scaling (NMDS) plots for perennial herbaceous community by sampling year and cattle grazing with convex hull polygons for scores for each year and grazing combination and trajectories for the centroids of ungrazed and grazed scores across sampling years. Model fit: year, $R^2 = 0.66$, $P = 0.001$, livestock grazing, $R^2 = 0.02$, $P = 0.101$ (stress 0.17, metaMDS, Bray–Curtis distance, envfit for factor and vectors, $k = 3$, $N = 999$ permutations, vegan package, Minchin 1987).

methods (1937–1974, $R^2 = 0.07$, $F = 4.6$, $P < 0.002$), but cattle grazing, current, or previous water year precipitation anomalies were not significant. For perennial forb and grass components, dissimilarity was significantly affected by year regardless of sampling method, whereas contemporary cattle grazing was not significant for large square monitoring plots (Appendix S1: Table S6).

We tested whether community composition was becoming more heterogeneous or homogeneous with multivariate dispersion, a measure of the distance between communities and their group centroid. We found that dispersion for the total perennial herbaceous community was not significantly different across combinations of sampling year and moderate cattle grazing ($df = 15$, $F = 1.4$, $P = 0.178$) or for grazed vs. ungrazed sites ($df = 1$, $F = 0.2$, $P = 0.641$). Dispersion was significantly different across sampling years ($df = 7$, $F = 2.8$, $P = 0.012$, Fig. 5) though pairwise tests did not indicate differences between individual pairs of years (Appendix S1: Table S7). Dispersion for the perennial forb component of the community differed between combinations of sampling year and grazed or ungrazed status ($df = 15$, $F = 3.3$, $P = 0.001$) and across years ($df = 7$, $F = 8.4$, $P = 0.001$) but not between grazed and ungrazed sites ($df = 1$, $F = 0.2$, $P = 0.704$). Pairwise tests indicated

declining multivariate dispersion, or increasing homogeneity, for the forb component of the plant community between the 1930s and 2000s sampling periods (Appendix S1: Table S7). Dispersion for the perennial grass portion of the plant community was not significantly different across combinations of sampling year and grazed or ungrazed status ($df = 15$, $F = 1.4$, $P = 0.134$) or between grazed and ungrazed sites ($df = 1$, $F = 1.0$, $P = 0.299$). Dispersion for the grass component was significantly different between years ($df = 7$, $F = 2.5$, $P = 0.022$); however, pairwise tests between year pairs were not significant (Appendix S1: Table S7).

Some community composition change metrics suggested convergence between paired sites grazed and ungrazed by cattle over time since cessation of intense grazing, contrary to expectations. Differences between ungrazed and grazed sites as measured by species rank order and species occurrence difference (species unique to grazed and ungrazed sites divided by the total number of species) declined with time since cessation of intense sheep grazing, indicating convergence in community composition, while species richness differences due to grazing did not change with time and evenness differences increased (Table 2, Figs. 6–8). Evenness differences did not indicate consistently higher or lower evenness with grazing over time (values

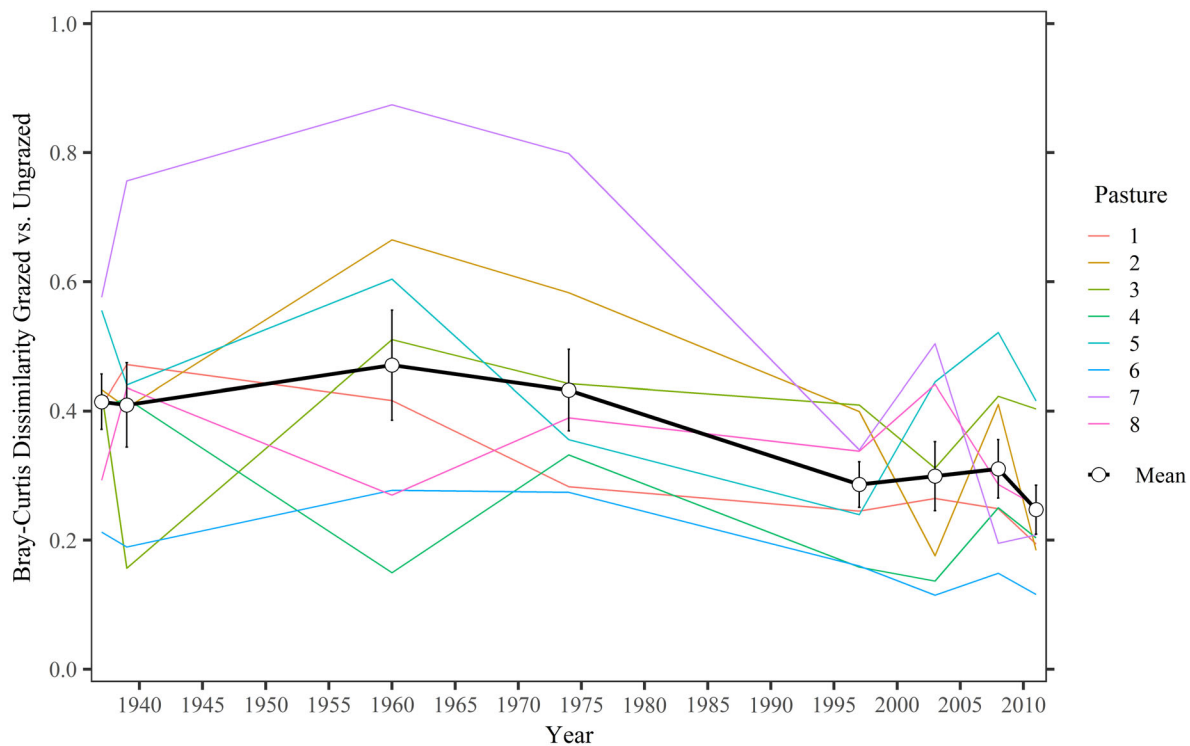


Fig. 4. Bray–Curtis dissimilarity associated with cattle grazing by pasture (paired plots) with means (open circles) and standard errors.

above or below the 0). Pasture location significantly interacted with time since intense grazing for both species rank order and evenness, suggesting a lack of consistency for these temporal trends across spatial units within the study area (Table 2, Figs. 6–8).

We also found that time since cessation of intense grazing was associated with convergence in composition between time points according to multiple community change metrics, whereas no significant differences were associated with grazing (Table 3). Specifically, species richness, species rank order, and rates of species gain and loss all declined over time, while evenness increased (Table 3).

DISCUSSION

Results of this study point to convergence in plant community composition between moderately grazed and ungrazed areas over time, contrary to expectations. This trend occurred along with increases in perennial herbaceous density,

suggesting recovery from intensive sheep grazing in the early 1900s, which coincided with both the beginning of the livestock removal experiment and a shift to moderate cattle grazing. Multiple metrics of community change suggest increasing plant community similarity over time since the end of intensive sheep grazing across temporal and spatial gradients within the study (between sampling years and pastures). In contrast, contemporary moderate cattle grazing was not strongly linked to plant community divergence as expected nor was there was a trend for increasing divergence from ungrazed plots with cattle grazing over time. This indicates that successional processes led to similar recovery in sites moderately grazed by cattle and sites removed from livestock grazing.

Livestock management following historic unrestricted livestock grazing in the late 1800s and early 1900s resulted in improved rangeland conditions across the western United States (Holechek 1981, Box 1990), but it remained unclear if recovery would have been more

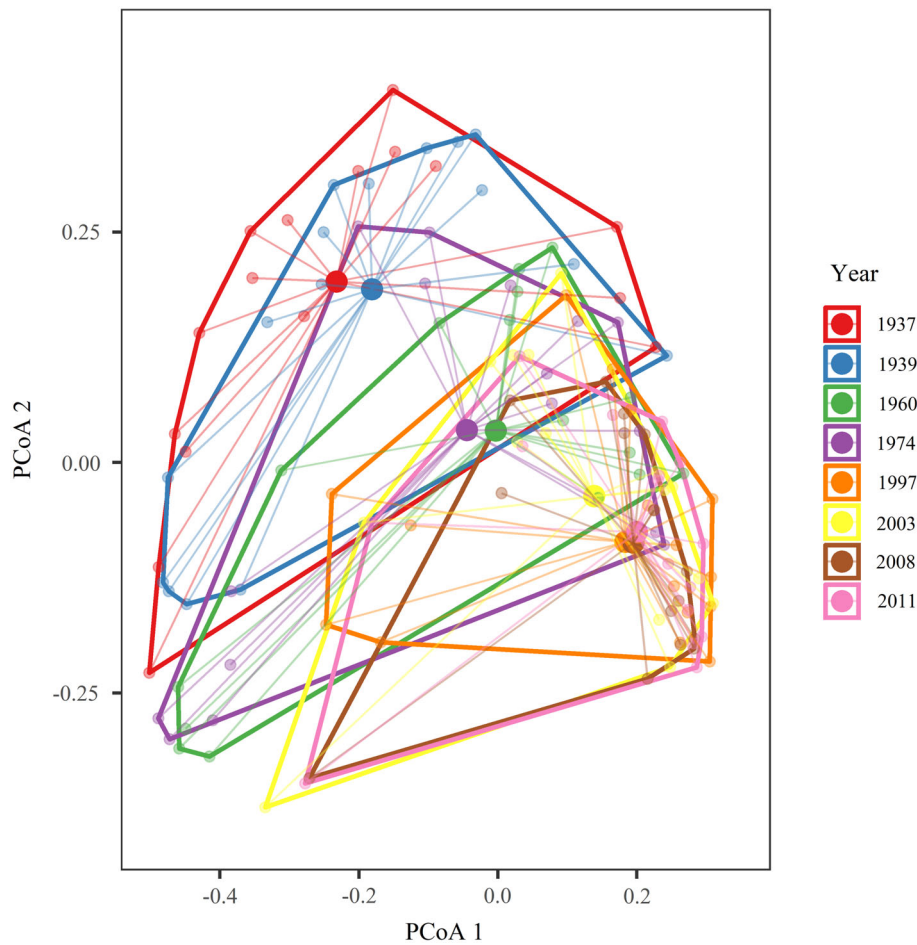


Fig. 5. Multivariate dispersion with principal components analysis (PCoA) by sampling years (indicated by color) with convex hulls and lines from small points (all plots, grazed and ungrazed by cattle) illustrated the distance to centroid (spatial median, larger points, Bray–Curtis distances, R package *vegan*, *betadisper*, and *permutest* functions, $N = 999$).

successful with grazing exclusion. Similar increases in native perennial bunchgrasses and forbs in moderately grazed and ungrazed areas in our study, even in earlier decades, demonstrate that improved grazing management did not markedly differ from the effects of livestock exclusion. In Nevada, similar vegetation characteristics between long-term (65 yr) livestock removal exclosures and moderately grazed areas also suggested that recovery was ultimately similar with grazing exclusion and moderate grazing (Courtois et al. 2004), though no data were available from the time of exclosure establishment.

Livestock grazing can affect plant communities by favoring species with grazing tolerant traits

(Adler et al. 2004). Many species in the Great Basin may not be highly grazing tolerant, which could lead to higher grazing sensitivity for communities in the region (Platou and Tueller 1985). However, in this study we saw few indications of herbaceous community divergence associated with contemporary cattle grazing. This is likely a function of the moderate grazing intensity as well as seasonal rotation currently implemented at the study location (NGBER) which allowed for rangeland recovery to take place over several decades. Weak relationships between grazing and most vegetation characteristics in similar Wyoming big sagebrush communities have been observed in the same location (Davies et al. 2009)

Table 2. Results for linear models testing the effects of year since cessation of intense sheep grazing (year) and pasture (location) on differences between grazed and ungrazed community compositional change metrics: species richness, rank order, evenness, species difference (type III sum of squares, bolded for $P < 0.05$).

Response variables	Predictor variables	df	F	P value
Species richness	Year	1	0.1	0.740
	Pasture	7	0.9	0.528
	Year × pasture	7	0.9	0.526
Rank order	Year	1	17.0	<0.001
	Pasture	7	3.0	0.011
	Year × pasture	7	3.0	0.011
Evenness	Year	1	0.8	0.380
	Pasture	7	2.3	0.044
	Year × pasture	7	2.2	0.048
Species occurrence difference	Year	1	8.5	0.005
	Pasture	7	1.5	0.180
	Year × pasture	7	1.5	0.188

and elsewhere (Condon et al. 2019). While overall community composition was quite similar between sites with and without cattle grazing, grazing was associated with higher perennial herbaceous species density in recent decades, mostly associated with increases in particular species such as Sandberg bluegrass (*Poa secunda*). Herbaceous species density, when different, was also generally greater outside compared with inside grazing exclosures in Nevada (Courtois et al. 2004). This may be due to grazing disturbance increasing the amount of bare ground or otherwise creating microsite conditions favorable to recruitment (Oesterheld and Sala 1990, Bullock et al. 1994, Kladivova and Munzbergova 2016).

In contrast to the weak effects of contemporary livestock grazing practices, years since exclosure establishment consistently exerted strong effects on community composition. Similar to other studies in sagebrush systems (Robertson 1971), the legacy effect of intense grazing prior to the

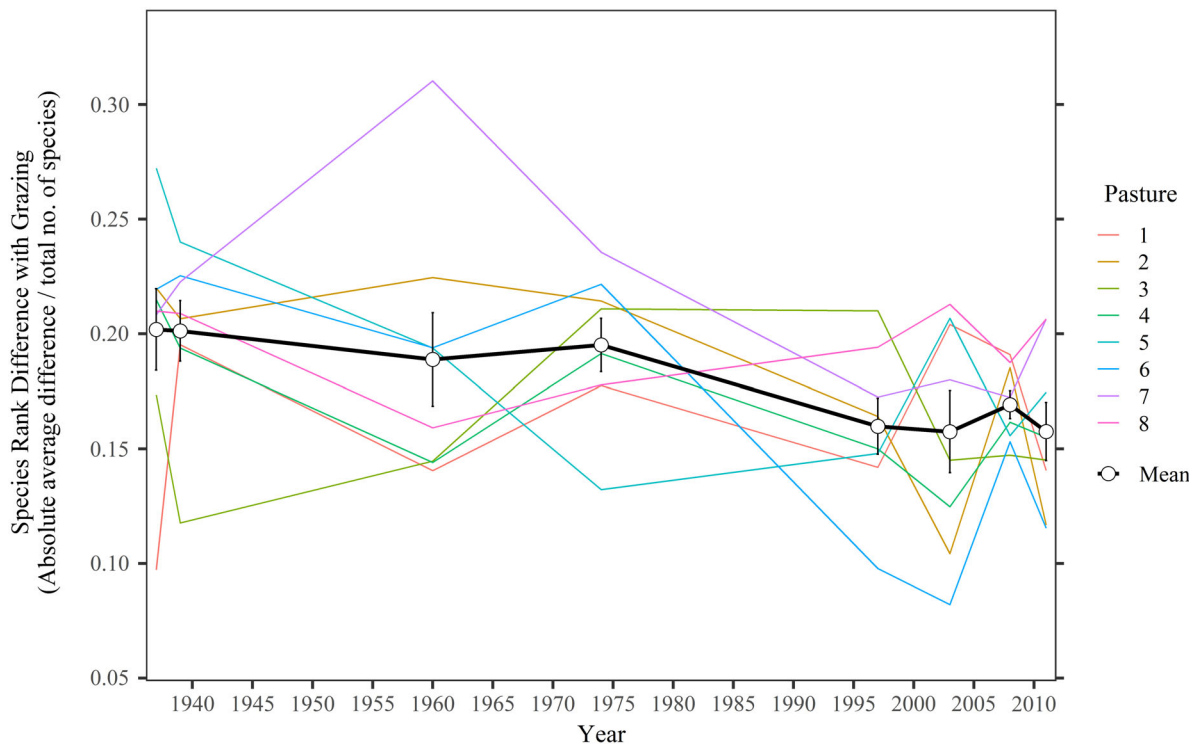


Fig. 6. Species rank differences associated with cattle grazing (absolute value of average difference divided by total number of unique species) by pasture (paired plots) with means (open circles) and standard errors.

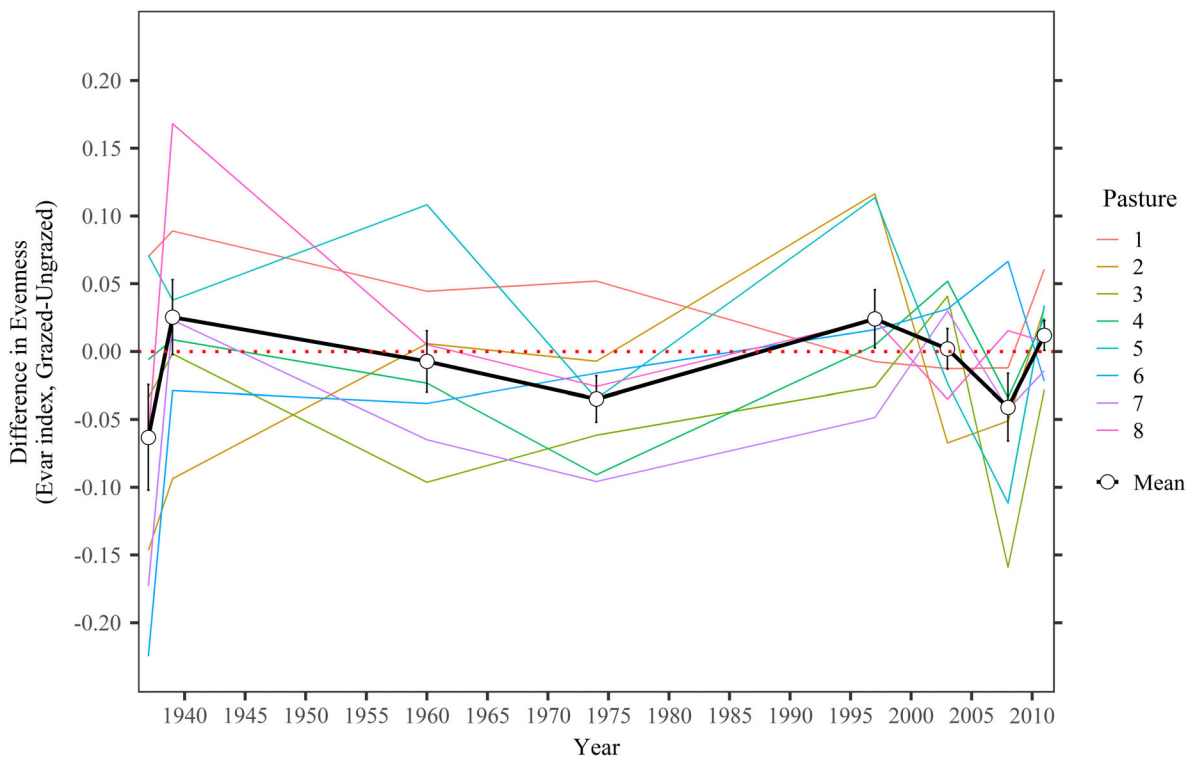


Fig. 7. Difference in evenness (Evar index, Smith and Wilson 1996) associated with cattle grazing by pasture (paired plots) with means (open circles) and standard errors. The red dotted line indicates whether evenness is greater in grazed plots (positive values) or ungrazed plots (negative values).

beginning of the experiment appeared to have long-lasting effects on plant community composition. Reports of sheep grazing in the early 1900s in our study area indicate heavy spring utilization (Griffiths 1902, Sneva et al. 1984), which has been implicated in decreasing herbaceous vegetation in sagebrush steppe (Laycock 1967). Because this study did not include sheep and/or high-intensity grazing over the last several decades, we cannot identify the exact nature of the differences between prolonged sheep and cattle grazing that may be associated with the observed patterns, such as intensity, timing, or livestock behavior (Laycock 1967, Rook et al. 2004, Tóth et al. 2018). Overall, these results highlight the need for considering grazing intensity both seasonally and across years in assessing the potential for long-lasting effects on plant communities.

This study occurred in the absence of fire or high cover of invasive annual grasses, which are interacting disturbances affecting plant communities across much of the sagebrush steppe

(Mitchell et al. 2017) and can interact with livestock exclusion and grazing intensity. Though the most common invasive annual grass, cheatgrass (*Bromus tectorum* L.) is generally in low abundance within and outside exclosures in this study (0–5% canopy cover in the most recent sampling year, 2011), research on portions of the same exclosure sites has shown that fire with long-term grazing exclusion can lead to a several-fold increase in cheatgrass cover (Davies et al. 2009) which persists for decades post-fire (Davies et al. 2016b). Livestock grazing effects on fuel characteristics pre-fire may decrease bunchgrass mortality when fire does occur, leading to greater resilience to cheatgrass invasion post-fire (Davies et al. 2016b, 2018). On the other hand, higher grazing intensity following fire may (Condon and Pyke 2018), or may not (Bates and Davies 2014), lead to reduced perennial vegetation and increased cheatgrass abundance. Even in the absence of fire, high-intensity cattle grazing in arid sagebrush plant communities can lead

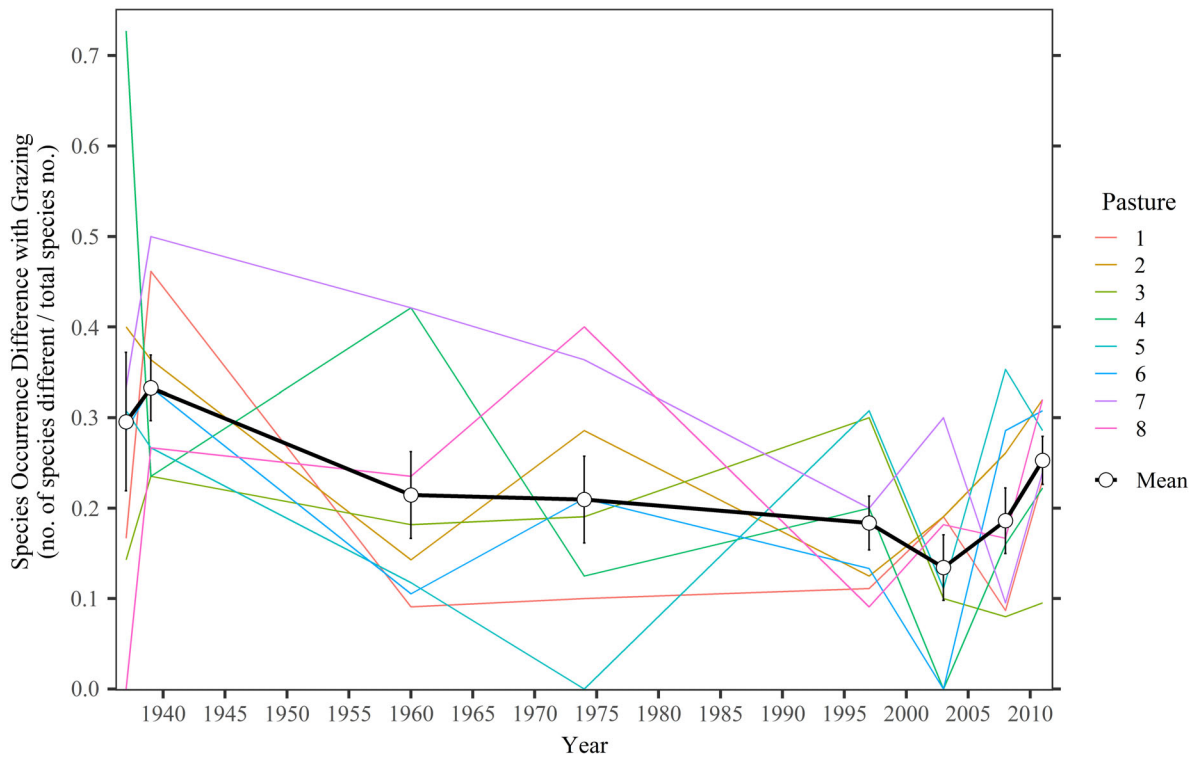


Fig. 8. Species occurrence difference (number of species different divided by the total number of unique species) associated with cattle grazing by pasture (paired plots) with means (open circles) and standard errors.

Table 3. Results for final linear mixed models (random effect for plot pair) testing for the effects of year since cessation of intense sheep grazing (year) and cattle grazing (grazing) on difference between sampling points in elements of community composition change (species richness, rank order, evenness, species gain, or loss between monitoring time points, Kenward-Roger degrees of freedom = 103 for all models, type III sum of squares). Grazing was not significant ($P \geq 0.10$) alone or interacting with year for any response variable.

Response variables	Final predictor variables	F	P value
Species richness	Year	3.6	0.059
Rank order	Year	8.7	0.004
Evenness	Year	3.8	0.054
Species gain	Year	21.8	<0.001
Species loss	Year	7.4	0.006

to increased cheatgrass abundance by negatively affecting biocrust abundance (Root et al. 2020). Overall, these previous studies suggest that

interpreting the effects of cattle grazing on plant community dynamics in sagebrush steppe is particularly complex when abundant annual grasses and fire are involved, and our results are more relevant to relatively intact sites where these two drivers of change are not highly influential.

Documentation for this long-running experiment was insufficient to identify specific management practices associated with slight differences in composition observed between contemporary grazed and ungrazed areas over time or space. However, utilization in the study area did vary over time, as managers decreased stocking rates in the early decades to allow for vegetation to recover, and generally varied grazing timing and intensity in response to vegetative production in recent decades (unpublished NGBER records, Sneva et al. 1984). Similarly, differences over time in particular pastures could be due to changes in grazing intensity associated with water placement or grazing timing (on and off dates relative to plant phenology or rest years) across sampling years.

Several aspects of this study were limited by the type and quality of monitoring information collected across the different sampling time periods. For instance, lack of consistent plant identification between time periods required bulking several species within diverse genera that may have responded differentially to grazing exclusion, pasture, and year since cessation of higher intensity sheep grazing. Including these species in the analyses might have led to greater differences due to contemporary cattle grazing or over time. We also suspect that the inconsistent seasonal timing (May–August) of monitoring in earlier sampling periods (1937–1974) may have affected species detection, particularly for perennial forbs, because of phenological variation in general, rapid senescence of some early season species, and lack of persistent or emergent vegetation across years for some late season species. In latter years (1997–2011), sampling occurred around approximately peak biomass in May–June, and therefore, species detection and abundance estimates were likely similar across those sampling years. While the combination of species identification and detection issues could have affected trends over time since cessation of sheep grazing, they are less likely to have impacted estimates of the differences between concurrently sampled sites with and without moderate cattle grazing. This analysis was also limited to density as a response metric because it was the only herbaceous community data consistently collected across all sampling time periods. However, individual species might vary in size, indicated by changes in cover and biomass, with recovery from intense grazed by sheep or contemporary cattle grazing (Eckert and Spencer 1987) and these changes may or may not parallel density differences. Indeed, another study at the same site (NGBER) demonstrated that dominant perennial bunchgrasses tend to be smaller in areas with cattle grazing compared with ungrazed areas (Davies et al. 2018). Perennial herbaceous cover and biomass, which are related to growth, are likely to be more dynamic in response to precipitation or short-term changes in management than density, which is related to recruitment and mortality. The sampling design and methodology also changed over the time frame of the study, with earlier time points comprehensively surveying one large plot and latter

time points sampling many small plots dispersed over multiple transects across a broader spatial extent per grazing/pasture unit. The location of the grazed sampling area also changed for some pastures between 1974 and 1997 along with the sampling design shift from large squares to dispersed transects. This set of sampling design changes could have led to greater turnover between the 1974 and 1997 time points. Models with only years prior to 1974 (square sampling designs) demonstrated similar recovery trends with year since cessation of intense grazing as models with all time points (all sampling designs), suggesting the effect of year on compositional changes was robust with respect to sampling design changes. In contrast, models for the older sampling periods (and sampling design) did not support the effects of grazing observed in models with all time points (all sampling designs). However, that lack of result for contemporary cattle grazing with the earlier sampling method could be due to the slow emergence of cattle grazing effects with additional time points and/or in recent years, rather than a result of changes in sampling design. More frequent monitoring throughout the 1936–2011 period would have allowed for more sophisticated analyses to address the potential effects of variable weather conditions (e.g., precipitation) on vegetation trajectories in response to grazing.

While our results generally document recovery from intense sheep grazing and low sensitivity of plant density to moderate cattle grazing, features of both the study site and design may not be applicable to areas which differ substantially in environmental characteristics known to influence vegetation. For example, our study area soils may be relatively robust to grazing associated soil erosion observed in drier sites in the Colorado Plateau (Duniway et al. 2019, Fick et al. 2020), a factor which could have accelerated plant recovery after intense grazing. Ungrazed enclosure areas are also relatively small and surrounded by grazed areas, leading to significant connectivity between grazed and ungrazed plant populations (Liston et al. 2003), with grazed plant populations in higher relative abundance than ungrazed populations. This could affect our results due to seed dispersal and establishment of species common outside enclosures to adjacent areas inside enclosures, and vice versa, potentially reducing the

effects of the grazing treatment on community composition. However, the long-term nature of the experiment would still be expected to eventually lead to shifts in relative abundance if contemporary moderate cattle grazing practices were impacting plant populations in a similar manner as the historic sheep grazing, or leading to long-term degradation of soil productivity.

There was little difference between the response of perennial forb and grass components to moderate grazing or time since intense grazing. We also did not observe evidence of species completely restricted to either grazed or ungrazed sites. However, several grass and forb species or genera did occur in greater abundance with or without grazing. This suggests that moderate livestock grazing or exclusion could impact particular species even in the absence of strong plant community divergence or effects on functional groups (forbs vs. grasses). In some cases, the response of individual species is likely related to grazing-associated traits. For instance, Sandberg bluegrass (*P. secunda*) is a low stature species with earlier phenology than many other co-occurring perennial grasses, traits which likely enable it to proliferate in sites with moderate cattle grazing in our study area and elsewhere (Yeo 2005, Veblen et al. 2015). However, the species positive response to moderate cattle grazing contrasts with the apparent negative impacts of the historic intense sheep grazing, indicated by increasing densities since the 1930s, perhaps due to differences between sheep and cattle grazing behavior.

Our results emphasize that sagebrush steppe community recovery after prolonged and intense grazing can take decades and that impacts of historical intensive grazing fundamentally differ from effects of seasonally implemented moderate grazing. Even within a relatively small study area, differences due to environmental heterogeneity (associated with pasture) interacted with, and were more significant, than the effects of moderate grazing in general. Studies which do not explicitly include effects of past intense grazing, relevant to much of the Great Basin (Morris and Rowe 2014) and much of the western USA (Holechek 1981), or major environmental gradients such as low soil fertility (Harrison et al. 2003) or weather (Vermeire et al. 2008, Morris et al. 2016), are likely to arrive at different conclusions regarding the effects of contemporary grazing on plant

communities. Furthermore, documenting the nuanced differences between contemporary cattle grazing and past, less regulated practices may be critical for sustainably managing grazing in dryland systems to avoid potential negative effects from increases in invasive species (Williamson et al. 2020) or greater soil erosion (Fick et al. 2020). Identifying the relative impacts of contemporary livestock grazing practices, historic intense grazing, and environmental variation on plant community structure could help develop the predictive framework necessary to manage for plant composition goals in sagebrush steppe, such as those associated with wildlife habitat, or ecosystem services associated with greater density and diversity of native species.

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