

Large herbivores in sagebrush steppe ecosystems: livestock and wild ungulates influence structure and function

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Abstract Improving understanding of the connections between vegetation, herbivory, and ecosystem function offers a fundamental challenge in contemporary terrestrial ecology. Using exclosures constructed during the late 1950s, we examined effects of grazing by wild and domestic herbivores on plant community structure, aboveground herbaceous primary production, and nutrient cycling at six sites in semi-arid, sagebrush rangelands during 2001–2002 in Colorado, USA. Enclosures provided three treatments: no grazing, grazing by wild ungulates only, and grazing by wild and domestic ungulates. Excluding all grazing caused an increase in shrub cover ($F = 4.97$, $P = 0.033$) and decrease in bare ground ($F = 4.74$, $P = 0.037$), but also a decrease in plant species richness ($F = 6.19$, $P = 0.018$) and plant diversity ($F = 7.93$, $P = 0.008$). Effects of wild ungulate grazing on plant cover and diversity were intermediate to the effects of combined domestic and wild grazing.

Aboveground net primary production was higher in both grazed treatments than in the ungrazed one ($F_{\text{wild} + \text{domestic}} = 2.98$, $P = 0.0936$ and $F_{\text{wild only}} = 3.55$, $P = 0.0684$). We were unable to detect significant effects of grazing on other ecosystem states and processes including C:N ratios of standing crops, N mineralization potential, or nitrification potential. Best approximating models revealed positive correlation between N availability and herbaceous cover and a negative correlation between herbaceous primary production and the ratio of shrub–herb cover and plant diversity. We conclude that ungulate herbivory, including both wild and domestic ungulates, had significant effects on plant community structure and ecosystem function during this 42-year span. Responses to the wild ungulate treatment were consistently intermediate to responses to the no grazing and wild + domestic grazing treatments. However, we were unable to detect statistical difference between effects of wild ungulates alone and wild ungulates in combination with livestock.

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Introduction

During the last century, arid and semiarid rangelands throughout western North America have been grazed by populations of wild and domestic ungulates—most notably bison (*Bison bison*), pronghorn (*Antilocapra americana*), elk (*Cervus elaphus* Canadensis), mule deer (*Odocoileus hemionus*), domestic sheep (*Ovis ovis*) and cattle (*Bos tarus*). Ungulate herbivory influences the composition of arid and semi-arid land plant communities (see reviews of Milchunas and Lauenroth 1993;

Jones 2000), shapes their disturbance regimes (Madany and West 1983; Zimmerman and Neuenschwander 1984), and modifies the flow of energy and cycling of nutrients between producers and consumers (Coughenour 1991; Frank and McNaughton 1993; Milchunas and Lauenroth 1993; Frank et al. 1994; Hobbs 1996; Hobbs et al. 1996; Frank 1998; Lecain et al. 2000). Ungulates affect plant communities by selectively removing biomass, by physical disturbance, and by excreting nutrients in dung and urine (Hobbs 2006). Better understanding of the relationship between observed patterns in vegetation and biogeochemical processes offers a fundamental challenge in contemporary ecology. These relationships have important implications for ecosystem modeling, herbivore management, and sustaining ecosystem health and services.

Livestock are relatively recent additions to the rangelands of western North America, but their wild ungulate counterparts have an enduring co-evolution with the plant communities of these systems (e.g., Mack and Thompson 1982). The semi-arid, Inter-Mountain Basin Montane Sagebrush Steppe [Southwest Regional Gap Analysis Project (SWREGAP 2005) <http://www.earth.gis.usu.edu/swgap/>; *Artemisia tridentata* ssp. *vaseyana* Shrubland Alliance] of the southern Rocky Mountain Ecoregion (Bailey et al. 1994) that we studied did not support large populations of ungulates before European settlement in the late nineteenth century. Some estimates indicate that current, wild-herbivore densities may also be far greater than historic levels (e.g. Gill et al. 1999); however, even modern estimates in these large areas are problematic (e.g., Rabe et al. 2002). Further, beginning in the late 1800s and early 1900s, domestic cattle and sheep were introduced to these landscapes, grazing many areas to degraded conditions (Mack and Thompson 1982).

It is clear that the influence of large herbivores on plant communities pivots on their evolutionary history (Mack and Thompson 1982; Milchunas and Lauenroth 1993; Augustine and McNaughton 1998), and thus, it is plausible that the effects of wild herbivores on ecosystem states and processes might diverge in fundamentally important ways from the effects of livestock. Several differences in patterns of grazing by wild and domestic herbivores could be responsible for this divergence. Domestic cattle feed predominantly on herbaceous plants while wild ungulates (mule deer, elk, and antelope) include significant quantities of woody tissue in their diets, particularly during winter (Kufeld et al. 1973; Hobbs et al. 1983; Valentine and Bartsch 1990). In addition, most populations of wild ungulates are migratory, using arid rangelands primarily during the winter and early spring when plants are dormant or newly emerged, while grazing by domestic

animals occurs throughout the growing season. Further, low intensity and heterogeneous spatial distribution of grazing pressures before European settlement likely resulted in limited evolutionary pressure of herbivores on plants in the region, and as a result, many plants in the region are susceptible to replacement under intense grazing pressure (Mack and Thompson 1982). Finally, typical stocking rates of livestock potentially create rates of consumption that are much higher than removal by wild herbivores (Hobbs et al. 1996). Thus, it is reasonable to hypothesize that, the differences between wild and domestic herbivores in evolutionary history, dietary preferences, season of use, and grazing intensity should give rise to differences in the effects of these herbivores on semi-arid plant communities.

Despite a clear conceptual basis for differences in effects of wild and domestic herbivores on arid land ecosystems, empirical evidence for these differences has not emerged. Here, we examine effects of long-term exclusion of grazing by wild and domestic herbivores on plant community composition, aboveground herbaceous net primary production, and nutrient cycling. Specifically, we address two questions. How does grazing by large mammalian herbivores affect the ecological functions of sagebrush steppe ecosystems? How does the removal of livestock and wild ungulates from formerly grazed communities modify the ecosystem states and processes?

Materials and methods

Research design

We studied effects of grazing-exclusion treatments originally established by the Colorado Department of Fish and Game during the late 1940s and early 1950s (Baker 1948–1956 unpublished data; characteristics of each study site are provided in Electronic Supplement A). Two important and widespread sagebrush community types converge in Colorado. Sagebrush in the northern parks and basins is classified as the sagebrush steppe found in Idaho and eastern Oregon, whereas sagebrush in the southern and far western portions of the state are most similar to the Great Basin sagebrush type (West 1988). Based on the location of several historic grazing treatments (fenced exclosures documented by Baker 1948–1956), we selected a set of six sites of similar age (created between 1954 and 1959) and similar plot dimensions (1-ha fenced plots). These communities were split evenly between three northern sagebrush steppe sites in Middle Park (Grand county), and three Great Basin sagebrush type sites further west and south in Gunnison, Rio Blanco and San Miguel, counties (Colorado). Sites in both community types were dominated by mountain

sagebrush (*Seriphidium vasyanum* Rydberg)¹ with varying amounts of rabbitbrush (*Chrysothamnus viscidiflorus* Nuttall, and *C. depressus* Nuttall) contributing to shrub composition. On the sagebrush steppe sites we routinely found snowberry (*Symphoricarpos longiflorus* Gray, *S. rotundifolius* Gray) and winterfat (*Krascheninnikovia lanata* Pursh), which were rarer on the Great Basin sites. The perennial sub-shrub, *Leptodactylon pungens*, was as ubiquitous across sites as sagebrush. In addition to the shrub canopy, stands of pinon pine (*Pinus edulis* Engelm.) and juniper [*Juniperous osteosperma* (Torr.) Little, *J. monosperma* (Engelm. Sarg.)] occupied portions of the Dry Basin and Bar D landscapes (two of the Great Basin communities) in dense woodland patches and open savanna-like distributions. Nomenclature follows the University of Colorado Museum Herbarium provided by Weber and Wittmann (Weber and Wittmann 2001).

The design included six replications of three treatments: (1) ambient grazing² by wildlife and livestock, (2) grazing by wildlife alone, and (3) an ungrazed reference area. Each replicate contained an area that permitted grazing by wild ungulates, but that excluded domestic ungulates. This enclosure was established with 1-m high, three-strand barbed wire fencing. Each replicate also included an area protected by 3.25-m high, 7.5 × 7.5-cm steel mesh fencing, plus a single strand of barbed wire. This enclosure prevented grazing by all ungulates. The combined grazing treatment (domestic + wild ungulates) was an unfenced, 1-ha area adjacent to the other two enclosures. Hereafter, we will refer to these plots as “no ungulates” (high fence), “wild ungulates” (low fence), and “domestic + wild ungulates” (no fence). This design was unusual in allowing replicated observations of effects of different communities of herbivores accruing over years. Our sampling of the sites extended from the year 2000 (species composition and structure) through 2002 (production and N cycling) resulting in a 40+-year treatment period. One of the replicates we studied (see Woods Gulch in electronic supplement S1) had different dimensions than the others; however, the similarities in the site design and establishment, and distribution across a subset of Colorado semi-arid sagebrush communities encouraged us to utilize the historic design.

Because the spatial distribution of our sites is based on a combination of deterministic (accessibility and target population biases of the Colorado Fish and Game) and a stochastic events (resulting in the preservation of a subset of

the original sites) and not a proper spatial design, extrapolation of our results to other sagebrush communities should be made with caution. Further, the treatments may not reflect the “true” density of wild ungulates in the area because the long-term distribution of animals across these areas was not considered in the design. However, we emphasize that given the spatial and temporal heterogeneity inherent in grazing patterns by herbivores (reviewed by Augustine and McNaughton 1998; but also see Lubchenco 1978; Sommer 1999; Hillebrand 2003), this criticism can be offered for any study of grazing effects using small-scale enclosures. Despite these problems, our work offers value by integrating effects of herbivory over 40 years at replicated sites.

Measurements of plant community composition

We first (2000) sampled vegetation cover and species composition at each site using modified Whittaker plots (Stohlgren et al. 1995) during the peak of the growing season. We estimated cover in each of ten, 1-m² plots nested within a 1,000-m² plot. Each species occurring within a 1-m² plot was recorded along with the sum cover of that species within the plot. Plots were located inside each fenced area (no ungulates and wild ungulates) and outside, adjacent to each fenced area (wild + domestic ungulates).

Measurements of primary production and grazing intensity

We estimated primary production of biomass by herbivores using temporary, movable cages to isolate plots from herbivores (Frank and McNaughton 1992; McNaughton et al. 1996) during two consecutive growing seasons (2001 and 2002). Aboveground net primary production (ANPP) of herbaceous plants was estimated as the positive increments in plant biomass accruing under cages during 30-day intervals during the growing season (April–May, May–June, June–July intervals with sampling visits between each interval). We used a modification of the canopy intercept technique for estimating standing crop biomass inside and outside of cages on each sample date (Frank and McNaughton 1990, 1992). Ten paired open and caged plots (1 m²) were randomly distributed across each treatment. Each point consisted of a caged 1-m² plot and an adjacent, open 1-m² plot.

Models describing the relationship between pin-hits and standing, oven-dry biomass were selected from the choice of a linear or second-order polynomial regression for each of four vegetation classes. We developed individual regressions for each of four life forms: (1) broad-leaved, caulescent grasses; (2) caespitose, bunch grasses; (3) cauline dicots; and (4) rosette or caespitose dicots (equations and statistics provided in Electronic Supplement S2).

¹ We likely encountered *Seriphidium arbusculum* on four, or more, of the sites. However, we did not distinguish this species from *S. vasyanum*, because we did not witness the phenology necessary for the distinction (Weber and Wittmann 2001).

² We use the term “graze” to include feeding on grasses, forbs, and shrubs.

Estimation of plant C:N ratios

We retained samples from the clipped plots for analysis, generating replicates within treatments, months, and years. We incinerated ground samples in a combustion thermoanalyzer (Leco CHN-1000; LECO Corporation, St Joseph, Mich.) to determine the organic C and N content in each plant sample. We calculated the standing crop of N as the product of the total standing crop of plant dry matter multiplied by the respective N content of each vegetation group.

Estimation of soil N potentials

Soil N mineralization and nitrification potentials were assessed using laboratory incubations of field-collected soils. We stratified samples within each treatment by associations with shrub canopies, grass patches, or bare ground interspaces creating a 3×3 factorial design using treatments and vegetation associations. We extracted soil surface samples (top 10 cm) from each of the treatments replicating associations with shrub, grass, or absence of cover. We refrigerated samples and returned them to the laboratory where they were stored briefly in an industrial freezer. Moisture content of each sample was estimated by selecting a sub-sample, weighing, oven drying and reweighing each sample. We further divided soil cores, separating one set for immediate extraction using 75 ml of 2 M KCl–PMA, and another for incubation.

Aerobic incubations were conducted in a temperature-controlled room (20°C) for 30 days at laboratory estimated soil water field capacity (Garcia-Montiel and Binkley 1998; Rueth and Baron 2002). After incubation, the second set of samples was extracted using the same technique. NO_3 and NH_4 were measured from each extraction using an autoanalyzer (Alpkem 3500 series; Perstorp Analytical Company, Wilsonville, Ore.). Differences in N concentrations between the pre- and post-incubation soils indicated the mineralization potential (biochemical transformation from ammonium to nitrate) and potential nitrification rate (microbial generation of ammonium), which was indicative of microbial activities in the soils and nutrient availability.

Statistical analyses

The six locations were analyzed as replicates; however, the locations were distributed across a relatively broad region (from a replicate perspective) with many similarities, yet the potential for local environmental differences. Thus, we assumed that environmental differences between these semi-arid sites were minor compared to the similarities manifested as similar community composition and structure. We also considered blocking the data by vegetation

type; however, preliminary analyses indicated that this offered no additional power. From a wider, biogeographic perspective, while these sites bear similarities to identified forms of sagebrush communities, they are all within western Colorado, quite similar to one another, and at the boundaries of classifications, such that they can be considered replicate samples within this transitional region.

ANOVA were conducted on arc-sine square root transformed estimates of percent cover across grazing treatments in each of three vegetation classes: grasses (and grass-likes), forbs, and shrubs. Net differences in the distribution of vegetation cover, species richness and evenness, net annual aboveground production, plant C:N contents, soil N mineralization and nitrification due to treatments were assessed by comparing net treatment effects using ANOVA ($\alpha = 0.10$). We compared effects of the treatment across the growing season by testing repeated, monthly sample intervals of production and plant C:N in a repeated measures ANOVA (RMANOVA; $\alpha = 0.10$). We used unstructured covariance in our analyses because plot locations were moved after each interval (as part of the design) protecting the independence of each sample and homogenizing variance (reduced heteroscedasticity). Analysis of the soil data included statistical comparisons of grazing treatments, vegetation associations, and location (site) across the incubation period (increment) using RMANOVA ($\alpha = 0.10$); unstructured covariance structure was used because there was not an indication of patterned variance in preliminary analyses. We chose $\alpha = 0.10$ to achieve a reasonable compromise between the probability of a type I error and the power of the test in a study where our sample size was fixed by historic precedent and could not be adjusted to increase power.

Differences among treatment means were examined with a priori, single *df* contrasts. We report these contrasts, as well as confidence intervals, on effect sizes. We viewed the contrast between the wild ungulates only (low fence enclosure) and the no grazing treatment (high fence enclosure) as an estimate of the effect of grazing by wild ungulates. We viewed the contrast between the wild + domestic ungulate treatment (no fence) and the no grazing treatment (high fence) as an estimate of the combined effects of grazing by wild and domestic ungulates. We viewed the contrast between the wild ungulates only treatment (low fence) and the wild + domestic ungulates treatment (no fence) as an estimate of the additive effect of domestic ungulates on wildlife herbivory effects.

We examined the effect of plant community structure on ecosystem function by testing all possible models, without interactions, that related measured ecosystem processes (ANPP, N mineralization, nitrification, C:N accumulation) to measured states of the plant community (cover and diversity). We selected best approximating models by

comparing the Akaike weights (w_i) estimated for each model (Burnham and Anderson 1998).

Results

Effects on plant cover and diversity

The combined effects of grazing by wild and domestic ungulates changed the structure and diversity of the sagebrush steppe communities. Cover of shrubs was greater, and there was less bare ground, in the no ungulates plots than in the area grazed by wild and domestic ungulates (shrub cover, $F = 4.97$, $P = 0.0328$; bare ground $F = 4.74$, $P = 0.0366$; Table 1). The ratio of shrub cover to herbaceous cover was almost three-fold greater in the no grazing enclosures relative to the open rangeland ($F = 3.91$, $P = 0.0563$; Table 1). We could not detect effects of wild + domestic grazing on total herbaceous cover or total vegetative cover. However, confidence intervals on the effect size of combined ungulate grazing on total vegetative cover (Table 1) indicated that we could not rule out large reductions in plant cover attributable to grazing, but we could eliminate the possibility of large enhancing effects.

Species richness and evenness were lower in the no ungulates treatment relative to wild + domestic treatment (richness $F = 6.19$, $P = 0.0181$; evenness $F = 7.93$, $P = 0.0081$; Table 1). Differences in richness and Shannon–Weiner diversity between treatments were apparent in the spatial separation demonstrated in Fig. 1; these results showed consistently greater diversity with grazing disturbance.

Wild + domestic grazing had greater effects on shrub cover than grazing by wild ungulates alone ($F = 3.89$, $P = 0.0571$; Table 1). We failed to observe other significant contrasts between wild and wild + domestic grazing. However, strongly skewed confidence intervals on effect sizes suggested that increased replication could show that bare ground and evenness were greater in the combined ungulate treatment than in the wildlife only treatment. Moreover, means for the wild ungulate treatment were intermediate to the other treatments for all plant cover and diversity responses except herbaceous cover.

Effects on herbaceous production

ANPP averaged approximately 7 g/m^2 higher in the wild + domestic ungulate and the wild ungulate treatments relative to the no grazing treatment ($F_{\text{wild + domestic}} = 2.98$, $P = 0.0936$ and $F_{\text{wild only}} = 3.55$, $P = 0.0684$; Table 1; Fig. 2). The enhancing effect of grazing on ANPP was greatest at low levels of ANPP (Fig. 2). We did not detect

Table 1 Mean values by treatment and results of contrast comparisons reflecting the difference between the treatment means indicated in each column. Means for each response variable with the same letter are not significantly different. ANPP Aboveground net primary production

Response	Wild and domestic ungulates		Wild ungulates		No ungulates		Confidence intervals on effect sizes ^a			
	Mean	SEM	Mean	SEM	Mean	SEM	Wild and domestic vs. wild ungulates	Wild and domestic vs. no ungulates	Wild vs. no ungulates	
Sum vegetation cover	34.54	2.15	43.71	5.89	44.37	5.44	(−20.64, 2.31)	(−21.31, 1.64)	(−12.14, 10.81)	
Shrub cover	17.41 b	2.43	25.14 a	3.35	26.15 a	2.44	(−14.37, −1.09)	(−15.38, −2.10)	(−7.65, 5.63)	
Herbaceous cover	17.13	1.05	18.57	2.86	18.22	3.20	(−7.54, 4.67)	(−7.19, 5.02)	(−5.76, 6.45)	
Shrub:herbaceous	1.11 a	0.18	1.50 a,b	0.20	3.07 b	1.19	(−2.08, 1.28)	(−3.65, −0.28)	(−3.25, 0.11)	
Bare ground	48.41 a	5.95	39.61 a,b	3.91	32.62 b	5.30	(−3.47, 21.06)	(3.52, 28.06)	(−5.27, 19.26)	
Richness	20.83 a	0.75	19.67 a,b	0.64	17.50 b	1.31	(−1.10, 3.43)	(1.07, 5.60)	(−0.10, 4.43)	
Shannon–Weiner (H')	2.42 a	0.07	2.21 a,b	0.08	2.00 b	0.15	(−0.04, 0.45)	(0.16, 0.66)	(−0.04, 0.45)	
ANPP	36.74 a	1.97	37.33 a	2.38	30.24 b	3.41	(−6.96, 5.78)	(0.13, 12.86)	(0.72, 13.45)	
Plant C:N May	21.30	0.69	20.62	0.69	21.92	0.96	(−1.19, 2.55)	(−2.49, 1.25)	(−3.21, 0.61)	
Plant C:N July	33.69	1.28	31.71	1.23	34.30	1.70	(−1.42, 5.38)	(−4.02, 2.78)	(−6.00, 0.80)	
Potential N mineralization ($\mu\text{g N/g soil}$)	983.04	152.90	1,213.46	124.94	1,031.29	104.99	(−539.40, 78.60)	(−357.30, 260.80)	(−126.80, 491.20)	
Potential nitrification ($\mu\text{g N/g soil}$)	1,109.56	168.03	1,353.29	126.34	1,192.22	88.99	(−559.20, 71.70)	(−398.10, 232.80)	(−154.40, 476.50)	

^a Calculated based on the difference between the treatment means indicated, i.e. wild and domestic vs. wild ungulates vs. wild and domestic mean – wild ungulates mean

Fig. 1 Differences in richness (a, b) and evenness (Shannon–Wiener diversity; c, d) between grazing treatments. The diagonal lines represent unity

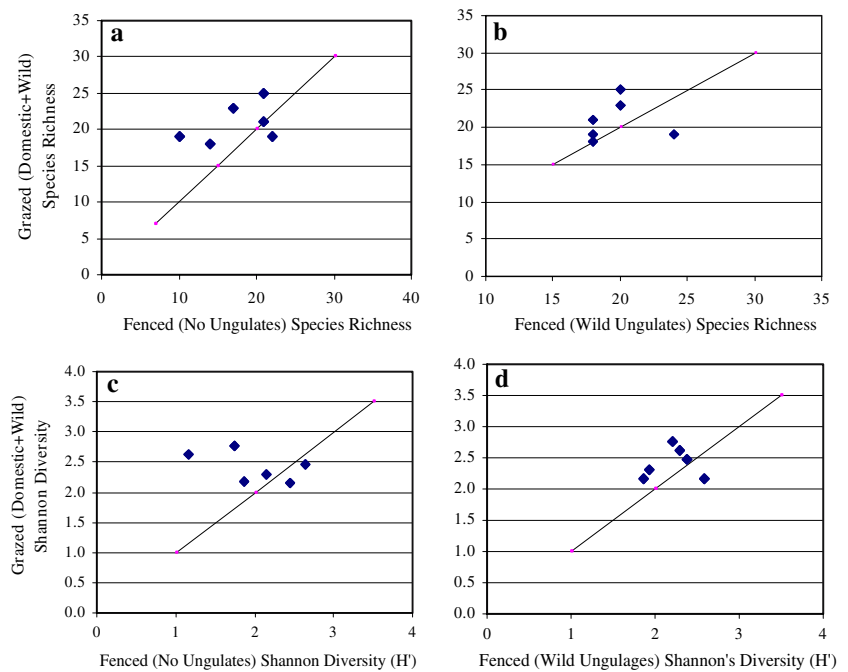
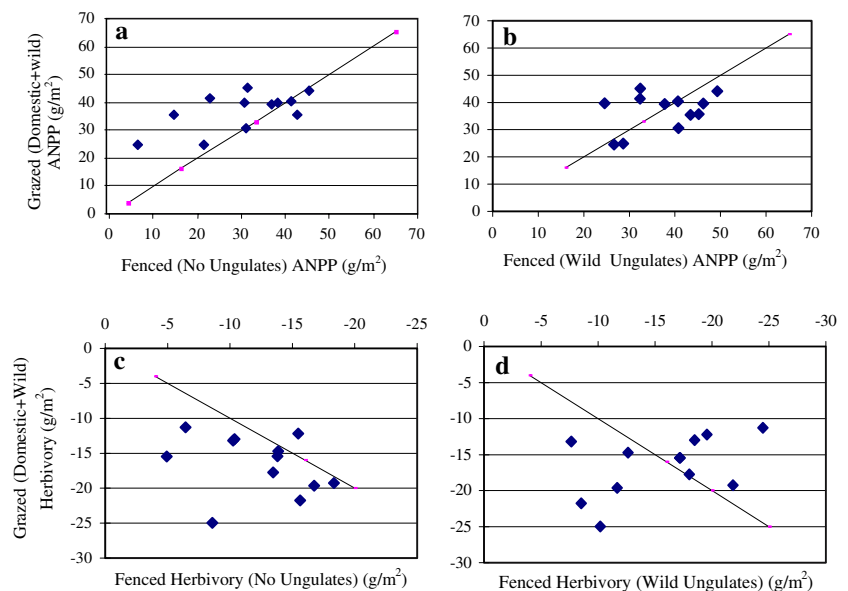


Fig. 2 The treatment effect on aboveground net primary production (ANPP) (a, b), and measured herbivory (removal) (c, d) for 2 years and six replicates. a, c The x-axis represents plots with no ungulate herbivory. b, d Plots with wild herbivores, but no cattle, along the x-axis. Solid diagonal lines represent unity



significant differences in ANPP between the wild ungulate only treatment relative to the combined grazing treatment (Table 1; Fig. 2).

Trends in soil N potential

We were unable to detect effects of grazing on potential N mineralization or nitrification (Table 1). However, we found differences in N cycling between different sites and local vegetation associations; differences that appeared to be related to local variation in plant cover. Mineralization and nitrification rates were lower in bare patches compared to vegetated patches (Fig. 3). Moreover, we

found that the association of surface soils with vegetation was a significant predictor of the differential distribution of nitrification potential ($F = 17.97$, $P < 0.0001$) and N mineralization potential ($F = 18.05$, $P < 0.0001$; Table 2). These models also revealed significant differences in N cycling among study sites ($F_{\text{nitrification}} = 11.59$, $P < 0.0001$; $F_{\text{mineralization}} = 9.86$, $P < 0.0001$; Table 2).

Trends in plant C:N

We found no effect of treatment on C:N ratios of herbaceous plant tissue (Table 1). Means were similar and confidence intervals on effect sizes were relatively tight,

Fig. 3 Distribution of changes in NO_3 and NH_4 concentrations determined from 30-day incubation. Differences between vegetation associations are compared using the two axes. Soils from six sites are combined with separation in symbols based on grazing treatments (*solid diamonds* no ungulates, *open squares* wild ungulates only, *crosses* domestic + wild ungulates)

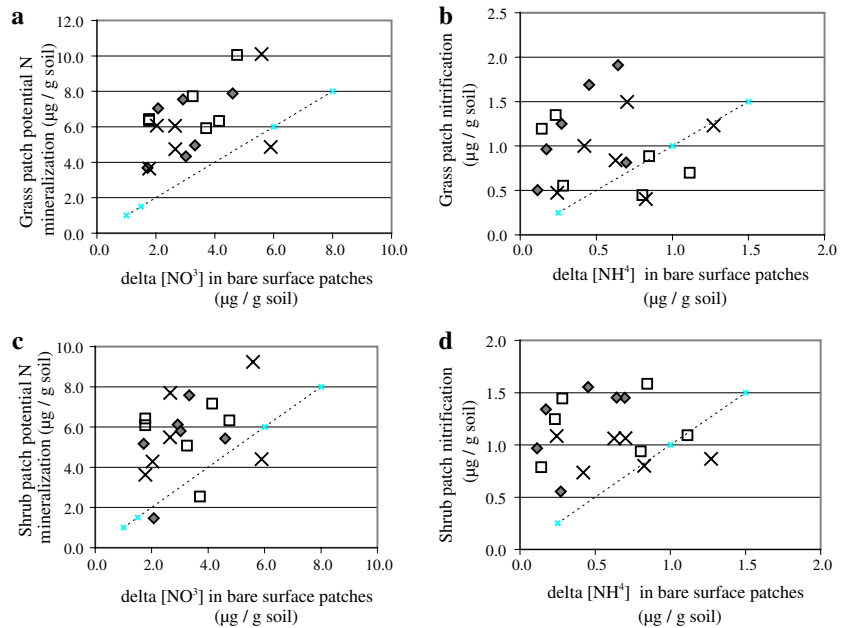


Table 2 Net potential nitrification and daily N mineralization from 30-day in vitro incubation at field capacity. Result of repeated measures ANOVA for within-subject effects of the hypothesis that there was no change during the incubation (*Increment*) and no difference between treatment, replicate, and vegetation association. *TRT* Grazing treatment effect, *SITE* Between-replicate effect, *VEG* effect due to association with shrub canopy, grass patch, or bare ground

Source	df	Type III SS	Mean square	F-value	Pr > F
Nitrification					
Increment ^a	1	0.7783	0.7783	264.23	<0.0001
Increment \times TRT	2	0.0068	0.0034	1.16	0.3149
Increment \times SITE	5	0.1707	0.0341	11.59	<0.0001
Increment \times VEG	3	0.2680	0.0893	30.33	<0.0001
Error (Increment)	258	0.7600	0.0029		
N mineralization					
Increment	1	879.6341	879.6341	309.45	<0.0001
Increment \times TRT	2	4.5892	2.2946	0.81	0.4472
Increment \times SITE	5	140.2025	28.0405	9.86	<0.0001
Increment \times VEG	3	247.4540	82.4847	29.02	<0.0001
Error (Increment)	258	733.3924	2.8426		

^a Increment reflects changes over time, i.e. due to incubation

indicating that our failure to detect differences did not result from low statistical power.

Relationships between community structure and ecosystem processes

Regression modeling revealed that herbaceous primary production, N mineralization potential, and nitrification potential, were best predicted using a combination of plant

cover and diversity indices as independent variables (Table 3). The most parsimonious model of primary production indicated a negative effect of the ratio of shrub:herbaceous cover, a positive effect of plant richness and a negative effect of Shannon–Weiner diversity ($W_r = 0.467$, $r^2 = 0.52$; Table 3). The best models for N mineralization and nitrification also included a combination of shrub and herbaceous cover and the two diversity measures, richness and the Shannon–Weiner index diversity ($W_r = 0.553$, $r^2 = 0.49$, and $W_r = 0.580$, $r^2 = 0.51$, respectively; Table 3). The best fitting models for both nitrification potential and N mineralization potential indicated negative effects of shrub cover, positive effects of herbaceous cover, and negative correlation with the Shannon–Weiner index. Other descriptive models indicated positive effects of plant richness on N cycling in addition to cover and diversity index correlations (Table 3).

Best approximating models of standing N in May and July (the amount of biomass, adjusted to reflect its N content) included a positive herbaceous cover effect and a negative richness effect ($r^2 = 0.87$ and $r^2 = 0.91$, respectively; Table 3). Our best multivariate models of plant C:N explained only a small portion of the variability in plant C:N, but we previously connected these processes and pools to vegetation associations so this lack of correlation was not surprising.

Discussion

This paper focuses on two questions. How does grazing by large mammalian herbivores affect the structure and function

Table 3 Selected models relating ecosystem processes to vegetation cover and diversity. *RMSE* Root mean squared error, *AIC* Akaike's information criterion, *w_r* weighted Akaike index, *herb.* herbaceous, *potent.* potential, *Nmin.* N mineralization

Dependent Variable	Equation	RMSE	df	r ²	AIC	w _r
ANPP _{herb.} =	40.16 – 2.42 Shrub:herb. + 0.98 richness – 8.91 Shannon	6.90	32	0.52	142.84	0.467
ANPP _{herb.} =	21.47 – 1.63 Shrub:herb. + 0.85 Shannon	7.29	33	0.45	145.87	0.102
ANPP _{herb.} =	5.16 + 0.41 Herb. cover + 1.15 richness	7.31	33	0.44	146.10	0.091
Nitrification potent. =	2,148.79 – 25.12 + 44.87 Herb. cover – 525.52 Shannon	338.87	32	0.49	423.21	0.553
Nitrification potent. =	2,144.85 – 27.15 Shrub cover + 43.63 herb. cover + 13.79 richness – 613.26 Shannon	342.56	31	0.50	424.84	0.244
Nitrification potent. =	1,653.79 – 28.44 Shrub cover + 49.89 herb. cover + 34.54 shrub:herb. + 16.41 richness – 481.12 Shannon	345.50	30	0.51	426.28	0.119
Nmin. potent. =	1,991.08 – 24.80 Shrub cover + 44.55 herb. cover – 519.17 Shannon	327.70	32	0.51	420.79	0.580
Nmin. potent. =	1,990.55 – 25.08 Shrub cover + 44.38 herb. cover + 1.85 richness – 530.93 Shannon	332.91	31	0.51	422.78	0.214
Nmin. potent. =	1,504.50 – 26.36 Shrub cover + 50.58 herb. cover + 34.19 shrub:herb. + 4.44 richness – 400.14 Shannon	335.68	30	0.51	424.20	0.106
Standing N _{May} =	6.96 + 2.70 Herb. cover – 0.82 richness	9.03	31	0.87	152.51	0.295
Standing N _{May} =	–6.08 + 2.55 Herb. cover	9.28	32	0.85	153.43	0.186
Standing N _{May} =	7.94 – 0.09 Shrub cover + 2.77 herb. cover – 0.83 richness	9.15	30	0.87	154.27	0.122
Standing N _{July} =	4.70 + 1.46 Herb. cover – 0.36 richness	3.96	33	0.91	101.91	0.271
Standing N _{July} =	–1.13 + 1.40 Herb. cover	4.06	34	0.90	102.90	0.165
Standing N _{July} =	4.04 + 0.06 Shrub cover + 1.42 herb. cover – 0.35 richness	3.99	32	0.91	103.35	0.132
Plant C:N _{May} =	20.65 – 0.16 Herb. cover + 0.18 richness	2.39	31	0.22	62.05	0.192
Plant C:N _{May} =	23.56 – 0.12 Herb. cover	2.42	32	0.17	62.16	0.181
Plant C:N _{May} =	22.06 – 0.18 Herb. cover + 0.27 richness – 1.25 Shannon	2.39	30	0.24	63.01	0.118
Plant C:N _{July} =	27.37 + 2.65 Shannon	4.87	34	0.04	115.89	0.128
Plant C:N _{July} =	28.46 + 0.25 Richness	4.90	34	0.03	116.37	0.100
Plant C:N _{July} =	34.77 – 0.07 Shrub cover	4.93	34	0.02	116.79	0.081

of sagebrush steppe ecosystems? How does the addition of livestock to communities of wild ungulates modify the effects of wild species on ecosystem states and processes? We obtained a clear answer to the first question and an answer that was less clear for the second one.

Effects on community structure

Forty-two years of exclusion of grazing by wild and domestic ungulates caused fundamental shifts in the composition and diversity of sagebrush steppe plant communities. The most notable change was a threefold increase in the ratio of shrub cover to herbaceous cover in areas where grazing was excluded; based on local observations, the shrub cover within the protected areas was aberrant from the size and density of shrubs in the immediately surrounding landscape. Total vegetative cover increased inside wild ungulate + livestock exclosures relative to the open grazing treatment, but we failed to detect changes in herbaceous

cover there, despite increases in the cover of shrubs. Excluding grazing by all large herbivores caused clear reductions in biological diversity as indicated by richness and evenness.

We cannot assert statistically that the effects of wild ungulate grazing were modified by the addition of livestock because confidence intervals on the effect-size of wild ungulates versus wild and domestic ungulates overlapped zero for all responses observed. However, some confidence intervals on the additive effect of livestock were strongly skewed, indicating that we cannot rule out effects that could be quite large. This was particularly true for total vegetative cover, shrub cover, Shannon–Weiner values, and potential N mineralization and nitrification. Although we could not detect differences between the wild ungulates only treatment and the other treatments, means of the wild ungulate only treatment were intermediate to the other two treatments for all metrics of community composition and diversity. This suggests that adding livestock to the native

ungulate community increased the impact of native ungulates on plant community structure.

Previous studies of grazing-exclusion effects on community structure of semi-arid rangelands in western North America have produced mixed conclusions. In contrast to our findings, Stohlgren et al. (1999) found no statistically significant differences in plant cover or species diversity due to herbivore exclusion in several Rocky Mountain grasslands. Willms et al. (2002) also found no significant differences in species diversity as a result of excluding grazing in mixed-grass prairie. These results contrast with other evidence indicating that species diversity may decline in the presence of grazing (Reynolds and Trost 1980; Chew 1982; Hillerbrand 2003). Other studies have shown similar effects of grazing on shrub cover, specifically, increased woody cover in response to grazing exclusion (Schultz and Leininger 1990; Coughenour 1991; Singer 1996). However, Singer (1995) found responses of shrubs to grazing only on low elevation sites, predominantly big sagebrush (*Seriphidium tridentatum*), but no effects on *Seriphidium vaseyanum*, typical of slightly higher elevations and deeper soils, which predominate our sites.

Our results may differ from studies that failed to find effects on plant cover and diversity because many of these studies suffered from a short duration of grazing treatments or low power when making comparisons within a vegetation type. For example, analyses of effects reported by Stohlgren et al. (1999) made comparisons across nine grassland sites, lumping plant communities across western North America. It is not surprising that, in the face of such variation, significant effects of grazing on plant communities were not detected. Ours is the first, replicated and long-term, controlled study of grazing effects within a targeted vegetation type. Additional, similar, research in other regions and vegetation types would be beneficial for comparison of long-term effects.

Effects on ecosystem states and processes

Long-term exclusion of large herbivores from sagebrush steppes appeared to cause substantial reductions in herbaceous ANPP relative to the grazed condition. Further, expansion of woody species has been shown to reduce herbaceous ANPP in mesic grasslands (Lett and Knapp 2006), and arid grasslands (Aguiar et al. 1996; Huenneke et al. 2002), resulting in a loss of ecosystem function when shrub production does not compensate for the loss in herbaceous production. The combined wild domestic and the wild ungulates only treatments showed significantly greater ANPP than the ungrazed treatment. Milchunas and Lauenroth (1993) analyzed data from arid and semi-arid rangelands around the world and found a significant influence of protection from grazing in shrub communities, and a potential for

increased primary production in grazed systems compared to ungrazed systems. Positive correlation between grazing intensity and production has been observed on sagebrush steppe rangelands in Yellowstone National Park (Frank and McNaughton 1992, 1993). However, these correlations likely reflected relatively short-term effects of grazing. We are the first to show enhancing, long-term effects of grazing on herbaceous ANPP in sagebrush steppe. We surmise that at least part of these effects may have come from negative feedback of increased dominance of shrubs in the grazing-excluded treatment. Our wild ungulates only treatment had (high) shrub cover similar to ungrazed areas, but wild ungulate activities were sufficient to stimulate primary production such that ANPP was not significantly different from the open grazing treatments (Table 1). This is an additional indication of the interaction, because if primary production were only connected to competition, we would expect to find grass production inversely correlated with shrub cover (e.g., Heisler et al. 2003; Beeskow et al. 1995).

In contrast to our findings on ANPP, we failed to find any effects of grazing exclusion on other ecosystem states and processes. This failure can be attributed to replication that was inadequate to overcome variability in N cycling and availability among sites; however, we were restricted in this aspect of the design because we were using historic structures. Confidence intervals on effect sizes for N mineralization and nitrification were particularly broad.

Relationships between community structure and ecosystem processes

Our regression analysis revealed relationships between cover and diversity of sagebrush communities and ecosystem processes. Best approximating models predicting herbaceous ANPP, N mineralization and nitrification potentials, and N standing crop consistently contained independent variables indexing community composition, shrub cover, herbaceous cover, or their ratio. Increasing shrub cover and declining herbaceous cover were consistently correlated with declines in these dependent variables.

Ecosystem properties respond to the effects of herbivory by ungulates through variation in species composition of plant communities, differences in plant growth and reproductive phenologies, and variability in the affects of other disturbances, particularly fire (Hobbs 1996; Augustine and McNaughton 1998). We found that herbaceous production and N cycling in this semi-arid shrubland were negatively affected by woody cover and positively affected by herbaceous cover. Additionally, trends in cover were affected by herbivore treatments. Belsky and Blumenthal (1997) reviewed research on the effects of livestock grazing and concluded that ungulates produced a range of effects, such as reduced herbaceous cover and litter, compacted soils,

reduced water infiltration rates, and increased erosion potential. In contrast, Milchunas and Lauenroth (1993) found a significant potential for increased primary production in grazed systems compared to ungrazed systems. However, they concluded that the effects of herbivores on above- and belowground production were minimized by environmental stresses applied by regional abiotic patterns in soil and climate (Milchunas and Lauenroth 1993). Our findings provide some support for each of these views. We clearly identified differences in vegetation structure and extent of bare ground due to the grazing treatments, but we also detected enhanced ANPP in grazed areas.

The correlations between N mineralization and nitrification potentials, and the N content of the vegetation (standing N) and shrub and herbaceous cover indicate the association of herbaceous vegetation (and litter) with more rapid N cycling, and the relatively negative effect of shrub cover and litter on N cycling in this system. The fact that herbaceous cover and productivity of grazed areas remained high relative to the ungrazed one suggests that belowground processes, such as N cycling, are maintained; however, increased bare ground in grazed treatments may counteract the net benefit when budgets are calculated across a wide area.

We did not find significant differences in plant C:N between treatments. We did find changes in mean C:N over the growing season as N contents declined while grasses and herbs matured and completed reproductive cycles. Regression results indicated that vegetation cover affected spring C:N, possibly revealing an effect of greater soil N availability in the spring, or greater N concentrations in young plants. Studies which have simulated differences in herbivory frequency (clipping of vegetation) have documented significant increases in N concentrations and net N yield (standing N) with greater removal (Green and Detling 2000; Leriche et al. 2003). However, this effect is dependent on N availability. Our results did not indicate differences in plant C:N between treatments; considering that we also did not find significant differences in N cycling rates, these findings support the conclusions of Leriche et al. (2003) suggesting that N limits may supersede herbivory effects.

Interactions between vegetation and the activities of ungulates are manifested in indirect effects of the herbivores on nutrient cycling. Herbivores react to the distribution of resources (vegetation as food and protective cover) and have a direct impact on vegetation and nutrient distributions (Augustine and McNaughton 1998). Soil N cycling changes as litter quantity and quality are altered by herbivory and by the addition of readily available N to upper levels of the soil in urine and feces (Hobbs 1996, 2006). As a result, existing heterogeneity in the spatial distribution of N within landscapes is amplified by ungulate

selection of habitats and patches (Hobbs 1996, 2006; Augustine et al. 2003). Therefore, as herbivores directly affect the composition and structure of the vegetation, they also affect plant–soil relationships by altering biomass and nutrient inputs. We observed differences in N cycling relative to vegetation cover, which indicated that ungulate driven shifts in cover might drive changes in ecosystem processes through shifts in the composition of vegetation. However, we did not find significant differences in herbaceous cover, potential N mineralization, or nitrification between grazing treatments. Our investigations did not preclude the alternate possibility, i.e., a previous decline or scarcity in N availability may be driving patterns in both cover and animal distributions as previously described by Hobbs (1996) and Augustine et al. (2003). Because N availability is a critical component of primary production, this remains a logical possibility. Similarities in plant C:N across treatments (Fig. 4; Table 3) indicated that the plants did not realize differences in N availability during this study. Similarly, Stark et al. (2002) found ungulate herbivory increased N in lichen, but no response in tree leaves in Finland. They concluded that grazing did not affect nutrient acquisition by plants (or the subsequent N content of litter produced). Alternatively, Bolton et al. (1990) documented a clear relationship between vegetation cover and incoming solar radiation and soil moisture, which affected the soil microbial environment and rates of N cycling.

Observed differences in N cycling between vegetated and bare patches of ground suggest effects of microclimate. Ungulates disrupted this relationship by affecting relative amounts and distributions of shrub and herbaceous cover, N distribution, or both, thereby potentially altering ecosystem function by altering soil inputs and environments. Although we did not detect differences in N cycling rates between treatments, the differences in N cycling with respect to vegetation associations and the differences in cover between grazing treatments indicate that the effects of changes in soil microbial activities may be forthcoming. These results contrast significant differences between grazed and ungrazed plots in Yellowstone National Park (Frank and Groffman 1998). However, differences in microbial productivity and N cycling rates in that study were correlated with patterns of soil C and N, and specifically, the labile portion of these elements in the soil profile (Frank and Groffman 1998). The distribution of nutrients and favorable soil microclimates has spatial patterns associated with shrub (Bolton et al. 1990; Bolton et al. 1993; Smith et al. 1994) or grass (Schlesinger et al. 1996; Burke et al. 1998) distributions in these semi-arid systems. Therefore, limiting environmental conditions (climate and soils) and the pre-existing spatial distribution of soil quality may further account for differences between our results and other studies.

Conclusions

We observed that four decades of exclusion of grazing from sagebrush steppe plants changed plant community structure, biological diversity, and ecosystem functions; most notably, a reduction in herbaceous ANPP associated with increased dominance of shrubs. The magnitude of changes in plant community structure appeared to be influenced by the intensity of grazing and the composition of the herbivore community. Alternate states characterized by marked differences in community structure of grazed ecosystems are likely controlled by the combination of differences in abiotic environmental conditions, history of disturbance, and the recent intensity and distribution of herbivores (Laycock 1991; Tausch et al. 1993; Augustine and McNaughton 1998). Our results indicate that changes in structure attributed to differences in ungulate use, especially ratios between shrub and herbaceous cover, are important for predicting ecosystem properties and function.

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