Oecologia (2006) 146: 641–651
DOI 10.1007/s00442-005-0065-9

COMMUNITY ECOLOGY

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Large herbivores influence the composition and diversity of shrub-steppe communities in the Rocky Mountains, USA

Received: 29 May 2004 / Accepted: 18 February 2005 / Published online: 27 October 2005

Abstract It is widely believed that wild and domestic herbivores have modified the structure and composition of arid and semi-arid plant communities of western North America, but these beliefs have rarely been tested in long-term, well-replicated studies. We examined the effects of removing large herbivores from semi-arid shrublands for 40–50 years using 17 fenced exclosures in western Colorado, USA. Shrub cover was greater ($F=5.87$, $P=0.0020$) and cover ($F=3.01$, $P=0.0601$) and frequency ($F=3.89$, $P=0.0211$) of forbs was less inside the exclosures (protected) relative to grazed plots. However, we found no significant effects (minimum $P=0.18$) of protection from grazing on cover or frequency of grasses, biotic crusts, or bare soil. Although mean species richness and diversity were similar between treatments, protected areas had much higher dominance by fewer species, primarily sagebrush. Exclusion of herbivores changed the relationship between species richness and evenness. Consistent with theoretical expectations, species evenness was positively correlated with richness in protected plots ($r^2=0.54$). However, contrary to theory, evenness and richness were inversely related in grazed plots ($r^2_{\text{adjacent}}=0.72$, $r^2_{\text{distant}}=0.84$). We suggest that these differences resulted because grazing acts as a stressor promoting facilitative relationships between plant species that might compete for resources in the absence of grazing. We conclude that exclusion of grazing in the sites we studied caused minor changes in cover and diversity of herbaceous plants, but caused a clear increase in the cover of shrubs. Importantly, the exclusion of ungulates changed the relationship between evenness and richness.

Communicated by Jim Ehleringer

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Keywords Succession · Herbivory · Ungulates · Semi-arid · Sagebrush

Introduction

Selective feeding by large herbivores can influence the composition of plant communities throughout the world (see reviews in Ellison 1960; Milchunas and Lauenroth 1993; Hobbs 1996; Augustine and McNaughton 1998; Jones 2000). The nature of this influence depends on the evolutionary history of herbivores and the plants they consume (Mack and Thompson 1982; Milchunas and Lauenroth 1993). During the last century, populations of wild and domestic ungulates grazed the arid and semi-arid rangelands of the Rocky Mountain region of North America. Because these systems lacked a long evolutionary history with large grazers, they are believed to be particularly susceptible to replacement by less palatable species in response to grazing by domestic herbivores, especially cattle (Mack and Thompson 1982). Ungulate grazing and browsing are believed to contribute to shifts in plant community structure throughout the region (reviewed by Jones 2000), and in particular, to an increase in the dominance of unpalatable, woody plant species (Madany and West 1983; Zimmerman and Neuenschwander 1984; Belsky and Blumenthal 1997; Bork et al. 1998; but also see Detling 1998; Stohlgren et al. 1999; Jones 2000; Van Auken 2000).

However, the theoretical prediction that palatable plant species will be replaced by unpalatable ones depends on the following logic: herbivores select for palatable species, which reduces their fitness and competitive ability relative to unpalatable neighbors. In this way, herbivores force increasing dominance of unpalatable species in plant communities (Augustine and McNaughton 1998). A more recent theory suggests that effects of herbivores on plant communities cannot be predicted based on understanding selective feeding alone, but rather depends on the interplay of selectivity of ungulates with plant tolerance to herbivory (Augustine and McNaughton 1998). The outcome of the interaction of selectivity and tolerance, in turn, depends on ungulate populations, disturbance regimes, nutrient availability, and timing of tissue removal (Augustine and McNaughton 1998).

Many of the empirical conclusions for grazing effects on arid-land plant communities have emerged from exclosure studies that compared a fenced, ungrazed condition with ambient levels of grazing by wild and domestic herbivores (e.g., Norton 1978; Coughenour 1991; Belsky 1992; Kay 1995; Frank and Groffman 1998; Stohlgren et al. 1999; Sarr 2002; Bastin et al. 2003; Tessier et al. 2003). However, lack of replication, unreliable measurement techniques, and inadequate duration of exclusion treatments have made it difficult to draw definitive conclusions from these studies.

Here, we report studies on grazing effects of wild and domestic herbivores on semi-arid shrub-steppe communities in western Colorado, USA. We used contemporary, multi-scale techniques (Stohlgren et al. 1995) to examine changes in plant cover and diversity at 17 sites where livestock and wild ungulate grazing had been excluded for 41–51 years. We hypothesized that long-term protection from large herbivores would result in increased herbaceous plant cover, reductions in woody cover, and enhanced diversity. Our hypothesis was based on the traditional theoretical argument that herbivory conveys a competitive advantage to unpalatable plants (in this case, shrubs) relative to palatable ones (in this case, grasses and forbs). The theoretical alternative is that changes in the balance of shrubs and herbs are likely to be more complex than can be predicted based on palatability alone. Although theory suggests that some intermediate level of disturbance by grazing would likely be associated with maximum species diversity (Milchunas et al. 1988), the previous history of intense grazing on these lands meant it was likely that the protected areas were still recovering from heavy disturbance. Thus, we expected that increased vegetation cover and diversity would characterize that recovery.

Materials and methods

Study sites

We studied 17 exclosures that were constructed in the late 1940s and early 1950s by the Colorado Department of Fish and Game (Baker 1948–1956). Many of the exclosures were constructed using a similar design, a 1-ha (2.5 acre) area surrounded by 2.5-m (8 ft.) fences and topped with barbed wire (Table 1). Others were constructed before the uniform design was established and have varying dimensions, generally less that 1 ha. These experimental treatments were located on public lands with a long history of grazing by wild and domestic herbivores, and on sites that were believed to be particularly attractive to wild ungulates during the winter. They were established for the purpose of studying the effects of ungulates on vegetation.

The 17 sties we studied were distributed across a relatively large region in western Colorado with broad environmental similarities but local differences. Climate varies widely across the intermountain parks of the Rocky Mountains in Colorado. However, the relatively narrow elevational range of our sites results in similar estimated, long-term, mean annual precipitation of 25–38 cm on the sagebrush sites and 38–51 cm on the slightly higher, mountain shrub sites (Western Regional Climate Center, data based on PRISM extrapolation of long-term climate records from multiple stations across the state, 1961–1990). Precipitation was highly variable across the second half of the twentith century while the exclosures were in place. During our studies, statewide mean precipitation was 36.25 cm, well below the century-long average of 40.23 cm (NOAA, National

Table 1 Characteristics of the 17 exclosures used to study effects of long-term exclusion of grazing on semi-arid shrub steppe communities

Site code	Location name	Community	Elev. (m)	Aspect	Construction date	Size (ha)	UTM east	UTM north
AP	Antelope Pass	Steppe	2,400	S	August 1955	1.0	385600	4445386
BC	Beaver Creek	Steppe	2,400	SW	Fall 1951	0.1	403641	4433977
BD	Bar D	Great Basin	2,010	W	November 1958	1.0	215620	4433333
BM	Blue Mesa	Great Basin	1,860	S	Fall 1949	0.1	167777	4270072
BR	Broken Road	Steppe	2,320	SW	August 1955	1.0	381843	4447108
DA	Dead Badger	Steppe	2,320	W	August 1956	1.0	381424	4452752
DB	Dry Basin	Great Basin	2,200	NW	May 1959	1.0	189082	4211734
DC	Douglas Creek	Great Basin	1,800	SW	Summer 1953	0.1	187702	4444444
DG	Dillon Gulch	Great Basin	2,300	W	September 1953	0.1	302736	4260819
DM	Dry Mesa	Great Basin	2,200	NW	Fall 1951	0.2	207763	4279455
IC	Irish Canyon	Steppe	1,800	S	November 1957	1.0	184768	4530000
KF	Kelly Flats	Mtn. Shrub	2,100	N	November 1949	1.0	459567	4503626
LR	Laramie River	Steppe	2,500	W	November 1957	1.0	420805	4531237
MC	Mid.Cottonwood Creek	Mtn. Shrub	2,700	S	Summer 1949	0.1	390780	4296163
MI	Minnesota Creek	Mtn. Shrub	2,740	NW	August 1954	0.4	290404	4319444
SP	Saguache Park	Mtn. Shrub	2,770	S	Summer 1956	0.4	350033	4215266
WG	Woods Gulch	Great Basin	2,500	SE	May 1954	0.5	355008	4261777

Slope on most sites was very small. UTM coordinates are located in zone 13

Climate Data Center, Asheville, NC, USA). Despite widespread drought, precipitation across the state and our sites was variable, ranging from 0.5 cm below normal in Meeker, Colorado (northwest), to 1.1 cm below normal in Gunnison and Norwood, Colorado (south-central and southwest), to 3.3 cm below normal in Kremmling, Colorado (north-central; NOAA, National Climate Data Center, Asheville, NC, USA). Statewide summer mean temperature (during the June–August growing season) was 19.9°C; this was 0.9C° above the twentieth century average and part of an increasing trend during that time (NOAA, National Climate Data Center, Asheville, NC, USA).

We divided the 17 sites into three communities based on recognized composition and geographic distinctions (Table 1). Sagebrush steppe was represented by the six northern-most sites, and Great Basin sagebrush was represented by seven southwestern sites. The four mountain shrub sites were distributed across the central portion of the state at slightly higher and wetter elevations (distinctions based on Miller et al. 1994). Sites in both sagebrush community types were dominated by mountain sagebrush (*Seriphidium vasyanum* Rydberg and *S. arbusculum* Nuttall), with varying amounts of rabbitbrush (*Chrysothamnus viscidiflorus* Nuttall, and *C. depressus* Nuttall) contributing to shrub composition. *Leptodactylon pungens* was also ubiquitous across sites. In the mountain shrub communities, we found varying amounts of mountain sagebrush, rabbitbrush, and snowberry, in addition to mountain mahogany (*Cercocarpus montanus* Rafinesque), bitterbrush (*Purshia tridentata* Pursh), serviceberry (*Amelanchier alnifolia* Nuttall, *A.utahensis* Koehne), Rocky Mountain juniper (*Sabina scopulorum* Sarg.), and ponderosa pine (*Pinus ponderosa* Laws. var. scopulorum). The dominant shrubs in these communities are generally considered to be unpalatable to livestock (Jameson 1952), and contribute small fractions of the diets of wild ungulates (Kufled 1972, Kufeld et al. 1973; Hobbs et al. 1981, Hobbs et al 1983, Hobbs and Spowart 1984).

Sampling procedures

We sampled the vegetation at each site using the Modified–Whittaker plot design (Stohlgren et al. 1995) because of its accuracy in estimating both relative cover and species diversity. This sampling design minimized spatial autocorrelation within ten nested sub-plots used in species-level estimation of cover attributes. Absolute cover and height of each species were measured for each 1-m^2 sub-plot based on a single visit during the 2000 growing season. Absolute frequency was estimated simply as the number of plot-level occurrences of each species ($n = 170$ per treatment for all sites combined). Species richness within a treatment was the count of the number of unique species we identified through a thorough search of a 1,000-m^2 plot area. Plots were located inside each fenced area (no ungulate herbivory), outside and adjacent to each area, and at an additional distant location, approximately 100 m away in a random direction. Hereafter, we will refer to these plots as "ungulates excluded," "open adjacent," and "open distant." The distant plots were established to recognize uncontrolled variability in the distribution of species diversity (Stohlgren et al. 1999) resulting in bias that would occur as a result of placement of the exclosures. When a fenced area was smaller than the large 1,000-m^2 plot, we modified the largest plot dimensions and the spacing, not size, of the sub-plots to fit inside the fences.

Statistical analyses

Data were collected by species, but were aggregated into categories for analysis: graminoids, forbs, and shrubs. Graminoids included grasses (*Poaceae*) and sedges (*Cyperaceae*). Forbs included all herbaceous, dicotyledonous species and non-graminoid monocots, e.g. *Lilaceae*. We examined the effects of excluding grazing using a one-way analysis of variance for a completely random design. Frequency and cover data were transformed (arcsine square-root) before analyses to normalize the variance. Differences between treatment means (ungulates excluded, open adjacent, open distant) were established using the results of a priori contrasts. Historic vegetation cover (circa 1950) and community blocks were considered as covariates in these comparisons; however, they did not change the interpretation of the data. Therefore, we present the simple analysis here. We used an alpha level of .10 to reject null hypotheses to achieve a compromise between reducing the probability of a type 1 error and increasing the power of the test.

We evaluated treatment effects on species diversity by comparing several indices, which are good indicators of diversity when used as a group (Magurran 1988). We used frequency and cover as abundance data for the calculation of diversity and evenness indices (Hartnett and Wilson 1999), because the proportional abundance of species is different relative to these measures. The use of frequency is standard (Magurran 1988); however, the robustness of cover as an indicator of abundance has been established in low-cover communities, e.g. arid and semi-arid regions (Chiarucci et al. 1999). We chose the common, Shannon–Weiner Diversity Index (H) and Evenness ratio (E) to indicate plant diversity by closely reflecting species richness, but including relative abundance. We included the Simpson Index (D) and Berger Parker Index (d) measures, because they indicate deviation from evenness by estimating relative dominance (the inverse of evenness) based on ratios of abundance of one species to the abundance of all species. We calculated the inverse of the Simpson Index (1-D) so that large values indicated increased diversity and decreased dominance by one or a few species. The Berger–Parker Index reflects the dominance of the single, most dominant species (generally sagebrush in this case) based on the proportional abundance of this species (Magurran

1988). Finally, we used Jaccard's coefficient (Krebs 1989) to compare overlap of species between protected and grazed treatments, because it directly compares species composition between plots (Stohlgren et al. 1999).

Results

Plant cover and frequency

Averaged across all replicates, shrub cover was two times greater inside exclosures relative to adjacent areas outside of exclosures ($F = 5.87$, $P = 0.0020$, Fig. 1a). Similar frequencies of shrubs inside and outside of exclosures indicated that increased cover of shrubs inside the fences resulted primarily from canopy expansion rather than increased recruitment of new individuals (Fig. 1b). Grazing exclusion caused a significant reduction in the cover ($F = 3.01$, $P = 0.0601$) and frequency ($F = 3.89$, $P = 0.0211$) of forbs. We found no significant effects (minimum P among all responses $= 0.18$) of grazing exclusion on cover or frequency of grasses, biotic crusts, or bare ground.

Analysis of data by community type (Figures 2 and 3) identified responses that were obscured when data were pooled across sites but provided mixed statistical

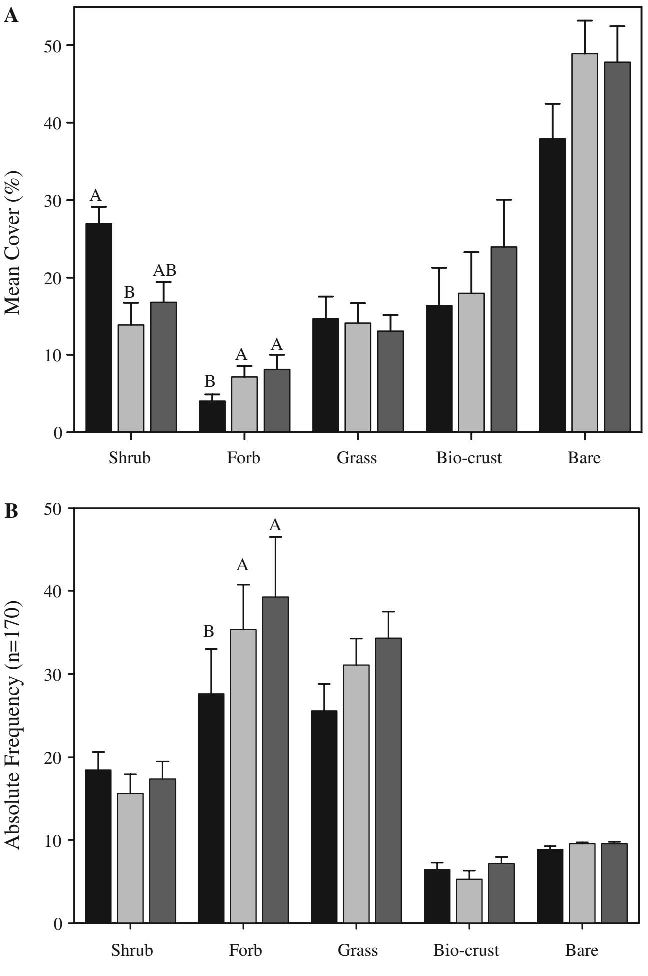

Fig. 1 The distribution of vegetation cover (**a**) and frequency (**b**) inside and outside of grazing exclosures averaged across all 17 sites. Within vegetation types, *bars with different letters* reflect significant differences in specified one-way contrasts between treatments ($\alpha = 0.10$). *Dark bars* (*left*) indicate ungulates excluded; *light gray bars* (*middle*) indicate open adjacent plots; *medium gray bars* (*right*) indicate open distant plots. *Error bars* indicate one-standard error about the mean estimate

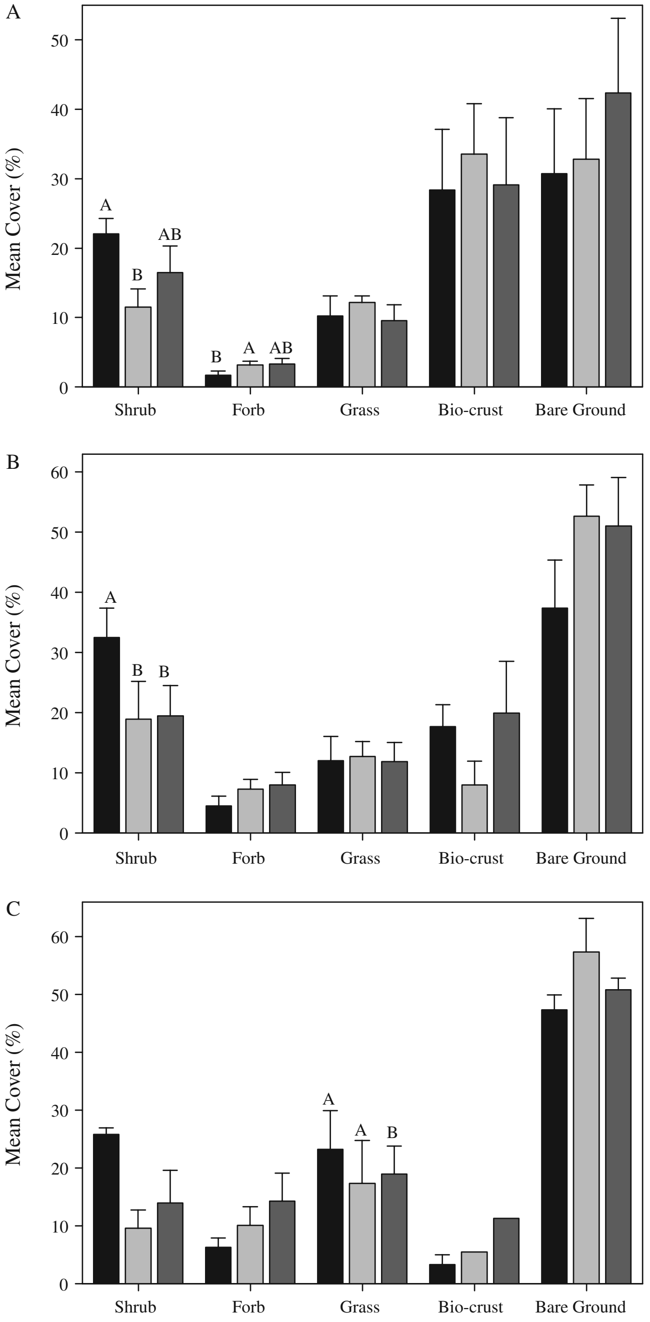

Fig. 2 Distribution of cover in Great Basin (**a**) and Steppe (**b**) sagebrush-dominated communities, and Mountain Shrub (**c**) communities. *Bars with different letters* reflect significant differences in specified one-way contrasts between treatments ($\alpha = 0.10$), within vegetation types. *Bar colors* and *error bars* provide the same indications as Fig. 1

results because of reduced power. Trends in frequency were generally different from trends in cover. Relatively high frequencies of forbs and grasses indicated that these species were more prominent in these communities than indicated by cover alone. We observed a significantly lower frequency of forbs in protected Great Basin sites ($F = 4.09$, $P = 0.019$). Mean contrasts revealed significantly more shrub cover ($t = 1.95$, $P = 0.077$, all excluded vs. open adjacent) in protected Great Basin communities and in protected sagebrush steppe sites ($t = 2.18$, $P = 0.048$, all excluded vs. open adjacent; and $t = 2.03$, $P = 0.063$, all excluded vs. open distant; Figure 2). In Great Basin sites, shrubs ($t = -1.87$, $P = 0.068$) and forbs ($t = -2.57$, $P = 0.011$) were less frequent with protection (Fig. 3), which was coincident with less forb cover ($t = -1.83$, $P = 0.095$, all excluded vs. open adjacent). Similarly, on the sagebrush steppe, forbs were less frequent with protection from grazing ($t = -2.11$, $P = 0.037$; Fig. 3). Exclosures in mountain shrub communities had greater shrub cover and less grass cover than open areas had ($F = 2.96$, $P = 0.090$) ($F = 7.00$, $P = 0.0081$), but there were no differences in forbs (Figs. 2c and 3c).

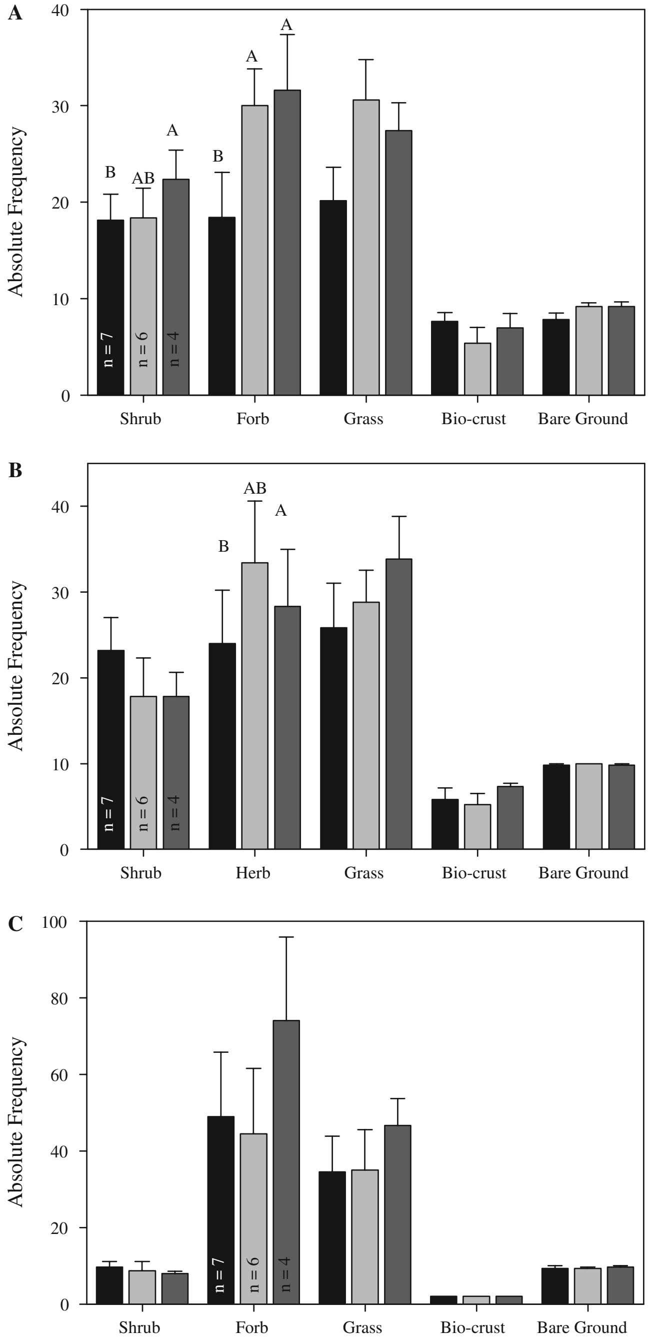

Fig. 3 Frequency distributions for Great Basin (**a**) and steppe (**b**) sagebrush-dominated communities, and Mountain Shrub (**c**) communities. *Bars with different letters reflect* significant differences in specified one-way contrasts between treatments ($\alpha = 0.10$), within vegetation types. *Bar colors* and *error bars* provide the same indications as Fig. 1

Grazing effects on species diversity

We compared species diversity between protected treatments and the surrounding grazed communities using species richness and diversity indices designed to reflect the relative dominance of species. Differences in species richness and evenness [Shannon–Weiner diversity (H) and Evenness (E)] were small and non-significant (Table 2). However, comparisons of the cover-based dominance indices between plots indicated greater dominance in ungrazed areas than in grazed ones, and stronger dominance by sagebrush in protected plots than in grazed plots (Simpson's index $F = 3.62$, $P = 0.036$; Berger–Parker index $F = 1.50$, $P = 0.235$; Table 2). The inverse Simpson index (1-D) indicated a stronger skewed distribution of species dominance on protected plots than on grazed plots, and the Berger–Parker index (d) specified a significant increase in the dominance of the single, most-dominant species (sagebrush) within protected plots.

Comparison of the species composition between grazed and ungrazed areas using Jaccard's coefficient revealed that although many species are common among plots, there were species at each site that were unique to both grazed and ungrazed environments (Table 2). Jaccard's coefficients indicate the similarity in species composition between sites (therefore, the inverse is indicative of unique species). Differences between the open adjacent and open distant plots indicated that new species continued to accumulate as we placed additional plots on the landscape (Table 2), interacting with the effects of the treatment. That is, some species were found only on grazed plots, and other species were found only on protected plots. However, increasing diversity across the landscape interacted with the treatment. The presence of unique species on the open distant plots indicated that at least part of the effect of exclosures on plant community composition was actually a result of the grain of spatial heterogeneity on the landscape relative to the sites where exclosures were established, rather than an effect attributable to herbivory. Species-

Table 2 Comparison of diversity indices between treatments

Treatment	Frequency abundance			Cover abundance		
	Ungulates excluded	Open adjacent	Open distant	Ungulates excluded	Open adjacent	Open distant
Mean richness	40	41	46	40	41	46
Shannon (H')	2.89	2.91	3.06	2.22	2.34	2.14
Evenness (E)	0.91	0.92	0.92	0.73	0.76	0.68
Inverse Simpson's (1-D)	0.94	0.94	0.95	0.77^{b}	0.89^{a}	0.89^{a}
Berger–Parker (d)	0.12^{a}	$0.1^{a,b}$	0.09^{b}	0.34^{a}	0.26^{b}	$0.31^{a,b}$
Jaccard's coefficients (ungulates excluded vs. others)	–	0.632	0.583			
Jaccard's coefficients (open adjacent vs. others)	0.632	–	0.622			

Values indicate mean values for each index and treatment. Means with different letters are significantly different ($\alpha = 0.10$)

Table 3 Cover estimates of selected species of each treatment

Species	Ungulates excluded			Open adjacent			Open distant		
	n	Mean cover (%)	SE	*n*	Mean cover (%)	SE	*n*	Mean cover (%)	SE
Shrubs									
Chrysothamnus depressus	3	0.35	0.23	3	2.87	1.21	4	1.70	1.13
Chrysothamnus viscidiflorus	8	3.20	1.08	7	4.38	0.76	11	2.60	0.73
Leptodactylon pungens	8	1.24	0.35	6	1.02	0.30	7	1.62	0.57
Seriphidium spp.[a]	14	21.31	2.22	12	11.40	3.58	11	13.50	3.01
Sub-shrubs and perennial herbs									
Antennaria spp.	9	0.74	0.38	6	2.78	1.14	5	3.20	2.53
Artemisia frigida	5	0.72	0.35	5	0.76	0.35	7	0.82	0.40
Astragalus spp.	3	0.13	0.06	4	0.20	0.10	1	0.30	
Chrysopsis villosa	3	0.50	0.28	1	0.55		4	3.19	1.24
Erigeron spp.	5	0.14	0.05	4	0.90	0.54	9	0.26	0.05
Eriogonum spp.	6	0.84	0.41	5	0.93	0.41	8	0.84	0.37
Gutierrezia sarothae	3	0.20	0.13	1	3.20		2	1.40	1.10
Melilotus officinal	9	0.22	0.04	5	0.27	0.09	4	0.24	0.06
Oxytropis spp.	2	0.28	0.23	1	1.35		1	0.05	
Packera multilobatus	5	0.23	0.08	1	0.05		2	0.08	0.03
Penstemon caespitosus	6	1.46	0.56	2	4.18	0.18	4	2.44	1.31
Penstemon spp.	3	0.08	0.03	4	0.13	0.06	3	0.63	0.56
Phlox spp.	2	0.23	0.18	2	0.05	0.00	2	1.08	1.03
Sphaeralcea coccinea	4	0.06	0.01	6	1.52	0.70	6	0.53	0.32
Gramminoids									
Achnatherum speciosa	5	0.89	0.27	4	1.18	0.33	6	1.38	0.32
Agropyron cristatum	3	12.92	6.15	4	9.80	3.53	4	11.81	3.92
Anisantha tectorum	2	0.45	0.05	5	0.34	0.15	4	0.24	0.09
Carex spp.	7	0.65	0.35	8	1.71	0.97	7	0.38	0.06
Chondrosium gracile	4	1.28	0.56	6	3.11	0.85	5	2.28	0.81
Elymus elymoides	10	0.31	0.08	10	0.16	0.03	9	0.40	0.19
Festuca idahoensis	4	4.20	2.10	4	1.49	0.88	2	0.45	0.25
Festuca spp.[b]	2	15.35	15.25	1	2.80		1	7.85	
Hesperostipa comata	7	1.88	0.97	7	1.74	0.81	10	1.61	0.95
Koleria macrantha	10	0.66	0.21	7	0.54	0.23	8	1.06	0.36
Muhlenbergia spp.[c]	3	14.15	6.79	3	13.62	10.89	4	6.51	3.40
Achnatherum hymenoides	2	1.50	1.30	5	0.23	0.07	4	0.71	0.49
Pascopyrum smithii	8	0.88	0.27	9	0.60	0.17	7	0.73	0.15
Poa spp.	3	0.50	0.06	3	0.43	0.13	4	0.34	0.13
Poa fendleriana	9	5.77	2.06	7	2.64	0.98	9	1.90	0.56
Pseudoroegnaria spicatum	3	0.93	0.35	4	3.94	1.79	3	2.35	1.24
Cactae									
Opuntia spp.	8	0.16	0.06	5	0.15	0.06	6	0.27	0.09
Pediocactus simpsonii	7	0.09	0.03	7	0.11	0.03	6	0.13	0.05

Differences in distributions relative to the grazing treatment indicated differential responses of species to herbivory and protection. '*n*' is the number of sites on which each species occurred. SE describes one-standard error about the mean cover estimate

[a] *Seriphidium vaseyanum*, *S. arbusculum*, and *S. tridentatum*

[b] *Festuca thurberi* and *F.arizonica*

[c] *Muhlenbergia filiculmus* and *M.montana*

specific reactions to the treatments demonstrated the mechanism of change in plant communities induced by ungulates through different reactions of different species (Table 3). Many species had greater cover with grazing pressures, e.g. *Chrysothamnus depressus*, *Antennaria* spp., *Gutierreaiz sarothae*, *Achnatherum speciosa*, *Chondrosium gracile*, and *Pseudoroegnaria spicatum*; however, several grass species, e.g. *Achnatherum hymenoides*, *Festuca* spp., and *Poa fendleriana*, apparently benefited from the protected environment (Table 3).

Grazing reversed the relationship between species richness and evenness. Enclosed areas showed a positive, linear correlation between species richness and evenness, ($F = 16.11$, $P = 0.0013$, $r^2 = 0.54$; Fig. 4a), but grazed areas showed an inverse correlation ($F = 30.11$, $P < 0.0001$, $r^2 = 0.72$ for open adjacent plots, and $F = 57.37$, $P < 0.0001$, $r^2 = 0.84$ for open distant plots; Fig. 4b). This reversal was not present when we calculated evenness using frequency-based abundance; rather, treatments displayed similar, natural log relationships between richness and evenness (Fig. 4c). These patterns indicated that without grazing, greater richness was associated with increased evenness. However, when ungulate herbivores were present, greater richness occurred with less evenness, i.e. a more skewed abundance distribution.

Discussion

Grazing effects on plant cover

We found that the exclusion of large herbivores had a pronounced effect on the cover of forbs and shrubs on

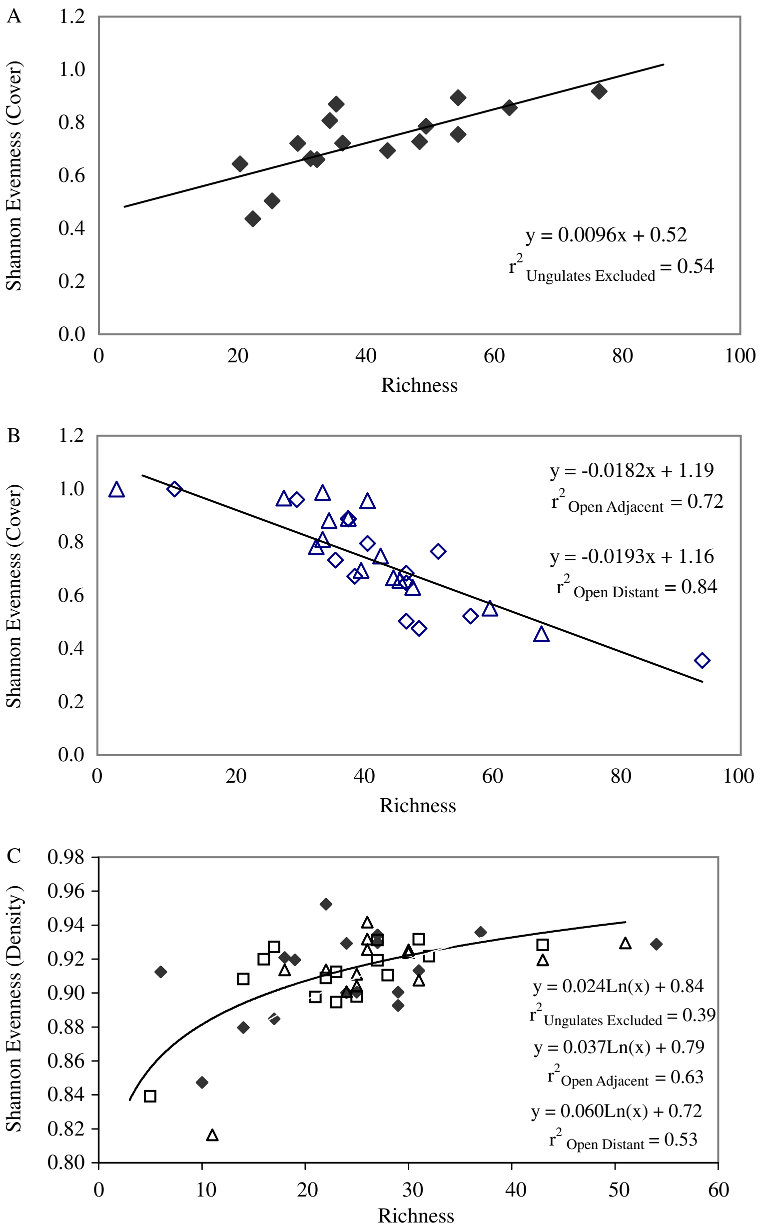

Fig. 4 Grazing pressure affects the relationship between species richness and evenness within communities of similar mean diversity. **A** shows the positive relationship between richness and cover-based evenness in the protected plots, and **B** demonstrates the negative relationship between richness and cover-based evenness where ungulates grazed. This relationship demonstrates that the dominance of large species (i.e., shrubs) did not inhibit, and possibly enhanced, niche availability for herbaceous species. **C** demonstrated that frequency-based evenness is predicted by a lognormal distribution of richness; we found no significant difference between these distributions based on the treatment. The *solid diamonds* represent the ungulates excluded plots; *open boxes* represent open adjacent plots; *open pyramids* represent open distant plots

semi-arid rangelands. However, contrary to our hypothesis, we found that the cover of shrubs increased dramatically in response to protection from ungulate herbivory while forbs declined. Excluding ungulates produced no detectable effect on the cover of grass, biotic crusts, or bare ground. Stohlgren et al. (1999) reported similar findings from studies of semi-arid grasslands and shrub steppe in the Rocky Mountains—shrub cover increased within exclosures while bare ground and herbaceous cover were largely unaffected by elimination of grazing. Other studies in similar habitats have also shown that cessation of grazing can increase the cover of shrubs (e.g., Schultz and Leininger 1990; Coughenour 1991; Singer 1996; Anderson and Inouye 2001) and forbs (Reardon 1996) while exerting nominal or no effects on net herbaceous cover (Coughenour 1991, Courtois et al. 2004). Our observations were made in a dry year, which might account for the absence of detectable effects on grass cover, because herbaceous species cover is highly responsive to precipitation patterns (Fahnestock and Detling 1999; Ludwig et al. 2000; Anderson and Inouye 2001). Trends in the frequency of grasses suggested that grazing may have increased the presence (occurrence rather than stature) of grasses, but our results were not significant.

Biotic soil crusts were a dominant cover type in the Great Basin sagebrush community, and the vigor of crust organisms in this community type may have partially compensated for newly exposed bare ground. Physically developed crusts were also found on the steppe and mountain shrub sites, but they were a lesser part of these communities. Contrary to previous research that indicated major impacts on biotic soil crust communities by cattle (Beymer and Klopatek 1992; Jones 2000; Floyd et al. 2003), we did not detect significant differences in the extent of biotic crust cover relative to the presence of ungulates. Belnap (2002) confirmed that surface disturbances significantly reduce nitrogen cycling by crust organisms. Thus, it is likely that trampling by animals outside of the protected areas did have an effect on the functional capabilities of these soil communities. However, our lack of significant findings indicated that either the damage incurred by footsteps was minimal (but see Belnap and Gillette 1998; Belnap 2002; Belnap and Warren 2002), the crust organisms quickly recovered from damage (but see Floyd et al. 2003), or our methods were insufficient to recognize differences in soil community development.

Many earlier studies on the effects of large herbivores on community composition can be criticized on the basis of poor replication (but see Courtois et al. 2004); our inferences are based on more replicated exclosures within shrublands than in any previous work. It is also possible that earlier work failed to allow enough time for the effects of herbivore exclusion to emerge. Our work spanned over 40 years.

Predictions of theory: the role of selectivity and plant tolerance

These results offer evidence supporting the theoretical prediction (Augustine and McNaughton 1998) that herbivore-induced changes in community composition are controlled by a suite of factors influencing ungulate selectivity and plant tolerance to herbivory. Traditional reasoning based on selectivity alone predicts that shrubs would expand in grazed rather than in protected areas because the dominant shrubs, particularly sagebrush, tend to be unpalatable by virtue of high concentration levels of secondary compounds in leaves. Hence, based on considerations of selectivity alone, woody plants should benefit from the presence of large herbivores while the more palatable grasses and forbs should suffer, producing patterns in community composition diametrically opposed to the patterns we observed. Our work suggests that tolerance of herbaceous plants for grazing may outweigh any advantage conveyed to unpalatable shrubs by herbivory. Grazing tolerance may also be implicated in the lower cover of unprotected shrubs—if shrubs are intolerant of herbivory, as would be expected for slow growing plants with high investment in plant defense (reviewed by McNaughton and Augustine 1998), then even occasional browsing my cause them to perform more poorly than rapidly growing, grazing-tolerant herbs.

Grazing effects on plant diversity

Studies of grazing effects on plant species diversity in semi-arid rangelands have offered mixed conclusions. Bai et al. (2001) described a curvilinear relationship between diversity and range condition in a semi-arid rangeland characterized by parallel increases in diversity and herbaceous structural parameters with rest from grazing. Belsky (1992) documented reduced diversity with protection on African savanna cover from grazing, physical disturbance, and differences in species growth strategies (especially vegetative vs. sexual reproduction). McNaughton (1983) found and documented similar patterns of reduced diversity inside grazing exclosures and attributed the difference to the dominance of tall individuals in the absence of herbivore reductions of these species. In contrast, Reynolds and Trost (1980) found decreased richness due to sheep grazing in sagebrush, and Chew (1982) found increased richness with rest from grazing in Arizona grasslands. Others found little to no significant shifts in the composition of semi-arid grasslands due to ungulates (Coughenour 1991; Singer 1995; Augustine and McNaughton 1998; Stohlgren et al. 1999; Willms et al. 2002).

We failed to detect the effects of ungulate herbivory on plant diversity at the local scale we studied (Table 2). These results complement the results of Stohlgren et al. (1999), who also found no significant differences in species diversity due to exclusion from herbivores in several Rocky Mountain grasslands. They cited the naturally rich distribution of species across the landscape, limited current and historic herbivory pressures, and the lack of competitive advantages for individual species as factors potentially responsible for the lack of effects. We did find differences in dominance as indicated by the Simpson and Berger–Parker indices. This difference resulted primarily from the prevalence of sagebrush within exclosures.

Milchunas et al. (1988) hypothesized that the effects of herbivory on plant diversity depend on the regional environmental context, specifically the moisture regime and evolutionary history of grazing. Given the limits and adaptations induced by the historic environment, the model of Milchunas et al. (1988) suggests that plant diversity in semi-arid communities with a long history of grazing should be greatest at low to intermediate intensities of herbivory. Alternately, communities lacking that history, should show a gradual, linear decline in diversity as grazing pressure increased. Anderson and Briske (1995) suggested that interspecific competition and effects of herbivores can be overridden by abiotic limitations, suggesting that shifts in composition are lessened in resource-limited environments. A combination of the subtle change in plant community diversity portrayed by the model of Milchunas et al. (1988) and the environmental limits suggested by Anderson and Briske (1995) is consistent with our finding of few significant differences in plant diversity attributable to 40 years of exclusion of ungulate herbivores.

Comparison of species composition between plots using Jaccard's coefficients indicated decreasing species overlap with distance, meaning that composition varied naturally across the local landscape. This pattern, similar to the one identified by Stohlgren et al. (1999), helps explain the lack of significance in treatment effects on species richness, because trends in composition varied at the same scale as the experiment design. Several species benefited (i.e., had higher cover) from the presence of large herbivores (e.g., *Antennaria* spp., *Gutierrezia sarothae*, *Penstemon caespitosus*, *Achnatherum speciosa, Chondrosium gracile*, and *Pseudoroegnaria spicatum*). Whereas other species, for example fescues (*Festuca* spp.) and mutton grass (*Poa fendleriana*), were most prolific in the protected environment.

Relationships between richness and evenness

Comparison of treatment effects on diversity among all sites identified an important interaction between herbivory, richness, and evenness. Changes in cover-based evenness occurred primarily in response to shifts in dominance, primarily sagebrush, which was significantly affected by the treatment. In areas where grazing was present, evenness decreased as richness values increased; in ungrazed areas, evenness increased with richness. Strong positive correlations between evenness and richness are the theoretical expectation based on the outcome of a stochastic process where the expected value of the birth rate equals the death rate for a set of species in a community (reviewed by Stirling and Wilsey 2001). Thus, positive correlations form the null model, and departures from the prediction of the null model indicate effects of the environment or biotic interactions.

We can unequivocally assert that herbivory caused significant departures from this null model that we studied in the system. To explain this departure, we suggest that grazing acts as an environmental stress. Accumulating evidence suggests that increasing physical and biotic stresses on plants promotes facilitative interactions between plant species and reduces the strength of competitive interactions (e.g., Greenlee and Callaway 1996; Tielborger and Kadmon 2000; Tewksbury and Lloyd 2001). Thus, increasing dominance of shrubs (i.e., reduced evenness) may enhance conditions for the coexistence of herbs in grazed areas, thereby promoting richness in grazed systems but fails to do so in the absence of herbivory. We suggest that shrubs may create habitats where grazing-intolerant plants can exist alongside grazing-tolerant ones. Aguiar and Sala (1994) and Aguiar et al. (1992) demonstrated significant associations of herbaceous seedling establishment patterns with shrub canopies on the Patagonian steppe. Shrubs can provide refuges where plants sensitive to grazing receive protection from herbivores, increasing species richness (Callaway et al. 2000; Milchunas and Noy-Meir 2002, Rebollo et al. 2002). Whereas, in the absence of large herbivores, changes in light availability and resource availability may be responsible for selection towards a different set of herbaceous species (Breshears et al. 1997; Bakker et al. 2003).

Conclusions

Thus, it appears from our work, and the work of others, that exclusion of large herbivores from semiarid shrublands in the Rocky Mountains promotes increased woody plant cover, but fails to cause marked shifts in herbaceous cover. Disturbance may be a necessary precursor of the exclusion of large herbivores to cause substantial increases in herbaceous cover (Brown and Archer 1999). Our findings of limited effects of protection from grazing on plant community composition cannot be taken as evidence that large effects of grazing on species diversity did not occur before exclosures were established. It is possible that historic grazing early in the 1900s created a shrub-dominated condition that remains stable even in the absence of herbivory (for a similar example, see Dublin et al. 1990). Herbivory can strongly influence community assembly and these influences may persist even when herbivores are removed from the community (Howe et al. 2002). Accumulating evidence indicates that once woody species become dominant due to prior shifts instigated by grazing or disturbance, the resulting plant community may persist for decades (Anderson and Inouye 2001).

We conclude that almost five decades of release from grazing caused relatively subtle changes in the herbaceous composition of these semi-arid shrub communities but caused marked changes in woody plant cover and in the relationship between components of plant diversity, evenness, and richness. The observed increase in woody plant cover occurring with protection from herbivory is not consistent with traditional explanations based on ungulate diet selectivity but instead may reflect the relative intolerance of shrubs to even low levels of browsing by ungulates.

Acknowledgements We are grateful to the staff at the Natural Resource Ecology Laboratory, Colorado State University, for their help in this research. We are particularly indebted to the diligent field crews who assisted in the data collection: M. Astele, B. Chemel, S. Farrell, J.P. Jensen, J. Levick, I. Roblee-Hertzmark, D. Rosie, S. Street, and A.Young. We appreciate the cooperation and assistance of the U.S. Forest Service staff for the Gunnison, Grand Mesa, and Uncompahgre National Forests and field office staff of the Bureau of Land Management in Craig, Grand Junction, Gunnison, Kremmling, and Montrose. This research was funded by the Colorado Division of Wildlife.

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