

## Disproportionate effects of non-colonial small herbivores on structure and diversity of grassland dominated by large herbivores

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The response of semiarid grasslands to small, non-colonial herbivores has received little attention, focusing primarily on the effects of granivore assemblages on annual plant communities. We studied the long-term effects of both small and large herbivores on vegetation structure and species diversity of shortgrass steppe, a perennial semiarid grassland considered marginal habitat for small mammalian herbivores. We hypothesized that 1) large generalist herbivores would affect more abundant species and proportions of litter-bare ground-vegetation cover through non-selective herbivory, 2) small herbivores would affect less common species through selective but limited consumption, and 3) herbivore effects on plant richness would increase with increasing aboveground net primary production (ANPP). Plant community composition was assessed over a 14-year period in pastures grazed at moderate intensities by cattle and in exclosures for large (cattle) and large-plus-small herbivores (additional exclusion of rabbits and rodents). Exclusion of large herbivores affected litter and bare ground and basal cover of abundant, common and uncommon species. Additional exclusion of small herbivores did not affect uncommon components of the plant community, but had indirect effects on abundant species, decreased the cover of the dominant grass *Bouteloua gracilis* and total vegetation, and increased litter and species diversity. There was no relationship between ANPP and the intensity of effects of either herbivore body size on richness. Exclusion of herbivores of both body sizes had complementary and additive effects which promoted changes in vegetation composition and physiognomy that were linked to increased abundance of tall and decreased abundance of short species. Our findings show that small mammalian herbivores had disproportionately large effects on plant communities relative to their small consumption of biomass. Even in small-seeded perennial grasslands with a long history of intensive grazing by large herbivores, non-colonial small mammalian herbivores should be recognized as an important driver of grassland structure and diversity.

Grasslands are grazed by a complex assemblage of herbivores that differ in body size, abundance, diet and foraging strategies. Grazing studies have most often examined effects of large herbivores, probably due to their greater amounts of plant consumption and economic importance. Studies of small herbivores have largely focused on social, central-place foragers that reach high local densities and build conspicuous burrow systems, such as prairie dogs *Cynomys* spp. (Whicker and Detling 1988, Weltzin et al. 1997, Davidson et al. 2010) or European rabbits *Oryctolagus cuniculus* (Bakker et al. 2003, Gálvez et al. 2011). Small granivores in desert annual plant communities (Batzli and Pitelka 1970, Borchert and Jain 1978, Brown and Heske 1990, Valone and Schutzenhofer 2007) and seed/seedling predation in forests (Ostfeld et al. 1997, Manson et al. 2001, Maclean et al. 2011) also have large effects on plant species composition. The role of more evenly dispersed and cryptic small herbivores (hereafter, small herbivores) in structuring

vegetation in perennial grasslands is less studied (Keesing 2000, Howe et al. 2002, Bakker et al. 2006, Bricker et al. 2010). The importance of small herbivores may be greater than initially thought and their effects on plant communities, isolated or in interaction with large herbivores, should be part of an integrated theory of how herbivores influence grassland diversity (Olf and Ritchie 1998, Bakker et al. 2006).

Body size affects metabolic rates of herbivores and their abilities to use diets differing in fiber content, thus determining food quality requirements and herbivore foraging selectivity (Demment and Van Soest 1985, Palo and Robbins 1991). Many large herbivores such as cattle are classified as generalist bulk grazers that impact dominant plants with relatively lower nutrient contents and high standing biomass (Hofmann 1989). Large herbivores can have positive, negative or null effects on plant diversity (Milchunas et al. 1988, Olf and Ritchie 1998) and their

effects on vegetation structure can generally be predicted (Milchunas and Lauenroth 1993). In contrast, small herbivores are more selective grazers that may decrease species richness by feeding on high-nutrient content plant parts (Brown and Heske 1990) and selectively foraging for less abundant subordinate plants. Studies comparing the effects of the two body sizes on vegetation structure and species diversity are rare (but see Bakker et al. 2006, Rueda et al. 2013).

The shortgrass steppe has a long evolutionary history of grazing by large generalist herbivores and is one of the most tolerant ecosystems to grazing by these herbivores (Milchunas et al. 1988, Milchunas and Lauenroth 1993). This grassland is dominated by short statured perennial grasses with a low aboveground-to-belowground biomass ratio (Milchunas et al. 2008). The dominant  $C_4$  short grasses, *Bouteloua gracilis* and *Buchloe dactyloides*, are long-lived and reproduce mostly by tillering or stolons (Bokhari et al. 1975). Grazing by large herbivores at heavy intensities increases basal cover of these short grasses as well as total vegetation cover (Milchunas et al. 1989). This stabilizes the plant community by maintaining the predominance of plant competition for belowground resources, thereby mitigating impacts of common droughts and providing resistance to invasive species (Milchunas et al. 1988, 2008). Exclusion of large herbivores increases abundance of taller grasses (such as *Pascopyrum smithii*) and plant diversity by reducing dominance of sod-forming short grasses such as *B. gracilis* (Milchunas et al. 1989) and by favoring colonization of less abundant opportunistic forbs (Milchunas et al. 1992).

The role of non-colonial small herbivores in the shortgrass steppe is less clear. Lagomorphs and rodents are limited by the absence of a significant litter layer (e.g. for voles *Microtus ochrogaster*) or by the lack of tall grasses, forbs, and shrubs that provide cover (Stapp et al. 2008). Lagomorphs are mainly folivores and selectively consume forbs and shrubs, and consume more plant biomass than rodents (Lauenroth and Milchunas 1991). Ground squirrels may eat flowers and seedheads, but not many leaves, and are true omnivores (Flake 1973). Most specialized granivores are limited in shortgrass steppe by the low seed-to-vegetation production ratios and small seeds of the dominant plant species (Grant and Birney 1979). As a result, unlike in deserts, density and species diversity are relatively low and kangaroo rats *Dipodomys* sp. predominate, especially during the time period of our study (Lauenroth and Milchunas 1991, Stapp et al. 2008). We use the term 'small herbivores' in the context of our study to mean this collective group of folivores and granivores. Based on data collected during the International Biological Program (IBP), their biomass consumption per unit area is relatively low, estimated to be ~3% of aboveground net primary production (ANPP) compared with ~40% by large herbivores at moderate cattle grazing intensity (Lauenroth and Milchunas 1991). Short-term exclusion of large-plus-small herbivores resulted in greater richness of rare species than even long-term exclusion of only large herbivores, indicating that selective consumers of a small proportion of ANPP might promote faster and greater effects on plant diversity than a generalist that consumes a much higher proportion (Bakker et al.

2006, Milchunas 2011). Based on only two early years of data, effects of small herbivores on species richness observed in a very wet year were generally not evident in the following drought year with low ANPP, when drought- and grazing-tolerant species predominated in all treatments (Milchunas 2011). The potential relationship between annual fluctuations in ANPP and grazing effects remains to be studied in a longer term perspective.

Here, we examine the long-term (14 year) effects of exclusion of large (cattle) and large-plus-small herbivores (cattle, rabbits and rodents) on plant community structure and diversity of shortgrass steppe in pastures moderately grazed (average 40% forage utilization) by cattle. Previous studies of grazing in shortgrass steppe have mainly been in heavily grazed pastures (average 60 % forage utilization), and have not included the separate effects of small mammals. The study period spanned record productive and unproductive years, and drought equal in magnitude to the extreme 1930s Dust Bowl. We addressed three main questions. First, how does moderate grazing by large herbivores affect plant community structure and diversity? We hypothesized that large generalist herbivores affect species diversity through effects on dominant and abundant species and affect litter cover through non-selective intense levels of grazing relative to that by small mammals. Large generalist consumption is also expected to influence community structure in terms of the proportions of litter-bare ground-vegetative cover. Second, what is the long-term importance of small herbivores in plant communities dominated by large herbivores? We hypothesized that small herbivores would affect the richness and abundance of less common species through selective but limited consumption and would not have effects on the components of community structure mentioned above for large herbivores. Third, is there a relationship between annual fluctuations in site productivity and the effects of the different-sized herbivores on richness of abundant, common, and uncommon plant species? A positive relationship has been observed between precipitation or ANPP and the effects of grazing by large herbivores on structure and diversity across plant communities at a global scale (Milchunas et al. 1988, Milchunas and Lauenroth 1993, Bakker et al. 2006) and within local regions at topographic scales (Milchunas et al. 1989, Osem et al. 2004). In contrast, Bakker et al. (2006) in a cross-site study and Rueda et al. (2013) at a topographic scale did not find a relationship between ANPP and the effects of small herbivores on plant species richness. Do structural and diversity responses vary with annual fluctuations in precipitation and ANPP on a temporal scale? We hypothesized that the effects of both large and small herbivores on plant species richness increase with ANPP because uncommon species will be relatively more abundant in wet years when not suppressed by herbivores. The effects of herbivores in dry years will decline as the community has lower species richness and is dominated by the abundant drought- and grazing-tolerant species. We expect that long-term effects of herbivores (mainly by the larger herbivores) on general structural characteristics and on species richness and diversity are associated with changes in the relative abundance of tall versus short plant species. Therefore, we examined herbivore body size effects on grassland structure by

testing specific hypotheses related to the proportions of litter-bare ground-vegetative cover, total species richness and diversity, and plant groups based on abundance (abundant, common and uncommon species) and plant size (tall vs short species).

## Methods

### Study site

The study site is the Central Plains Experimental Range (CPER) in shortgrass steppe of northeastern Colorado, USA (40°49'N, 104°46'W). Mean annual precipitation over the past 73 years was 342 mm (SD = 96.5 mm); 70% occurred during the growing season (May–September). Mean monthly air temperatures range from  $-5^{\circ}\text{C}$  (January) to  $22^{\circ}\text{C}$  (July). There are two abundant plant communities at the CPER: 1) with and 2) without *Atriplex canescens*, tall, true-shrub component (species nomenclature: <<http://plants.usda.gov/java/>> Natural Resource Conservation Service, Plants Database). The abundance of rabbits and rodents is generally greater in communities with *A. canescens* (Stapp et al. 2008). This study was in an *Atriplex* plant community, with moderate densities of the shrub. Basal plant cover (cross-sectional area of tillers and stems at ground level) is low and dominated by the drought- and grazing-tolerant  $C_4$  short grass *B. gracilis* (Milchunas et al. 1989). Other important species include  $C_4$  short grass *B. dactyloides*,  $C_3$  tall grass *P. smithii*, cactus *Opuntia polyacantha*, forb *Sphaeralcea coccinea* and several half-shrub species. Mean long-term ANPP is  $70\text{ g m}^{-2}\text{ year}^{-1}$ , (range of  $35\text{--}145\text{ g m}^{-2}\text{ year}^{-1}$  from 1940–1990; Milchunas et al. 1994). These plant communities were heavily grazed by bison for 10 000 years (Milchunas et al. 2008), with occasional but decreasing bison herds grazing through the 1870s coincidental with increasing numbers of cattle (Hart 2008).

### Experimental design

At the start of the CPER in 1939, long-term cattle grazing intensity treatments (each 65–130 ha) and exclosures (each 0.36 ha) were established in areas that were not previously overgrazed by livestock (Klippel and Costello 1960). From 1939 to 1960, stocking rates for moderately grazed pastures averaged 2.6 ha yearling heifer $^{-1}$  month $^{-1}$  over a six-month period (early May through early November) spanning the growing season (Klippel and Costello 1960). Stocking rates for a particular year depended on numbers of animals necessary to graze approximately 40% of ANPP. Since 1961, pastures were managed so that  $\sim 36\text{ g m}^{-2}$  of herbage was left at the end of the grazing season. Thus, average percent consumption remained constant since 1939, but management changed from percent removal to set residual in 1961. Cattle are the most abundant large herbivore, consuming an average of 40% of ANPP, while rabbits and rodents are estimated to remove  $\sim 3\%$  in upland grassland communities (Lauenroth and Milchunas 1991).

In 1992, new large herbivore exclosures (1 ha) were constructed within moderately grazed pastures. This resulted in two treatments: 1) sites previously grazed and still

continuing to be grazed by both large (L) and small (S) herbivores, '+L+S' (considered the control in this study), and 2) sites previously grazed and now ungrazed by large herbivores, but still grazed by small herbivores '-L+S'. In 1996, large-plus-small mammal exclosures (previously grazed, now ungrazed by both large and small herbivores, '-L-S') were constructed at three replicates adjacent to the '-L+S' exclosures to allow comparisons of treatments with similar within-site soil and topographic units. These paired exclosures were in areas not affected by colonial black-tailed prairie dogs *Cynomys ludovicianus*, which are present on some parts of the CPER. Exclosures prevented grazing by small herbivores that include lagomorphs (rabbits and hares, three species, biomass averages  $254\text{ g ha}^{-1}$  wet weight) and rodents (largely six species, biomass averages  $368\text{ g ha}^{-1}$ ). Actual cattle stocking rates in our experimental pastures averaged  $0.65\text{ AUM ha}^{-1}$ , which translates into  $54\text{ }167\text{ g}$  of cattle biomass  $\text{ha}^{-1}$ ; for comparison, peak biomass of rodents and lagomorphs was estimated to be  $1025\text{ g ha}^{-1}$  and  $1060\text{ g ha}^{-1}$ , respectively; Stapp unpubl.). The '-L-S' exclosures were 0.1 ha, constructed of 0.5 cm mesh hardware cloth, buried to 1.5 m and flared out 0.5 m underground to deter digging mammals, and 1 m high with a solid steel strip along the top to deter climbing rodents, plus two strands of barbed wire above the hardware cloth to prevent cattle scratching.

### Field sampling

We sampled changes in basal cover of plant species. Measures such as canopy cover or biomass, unless they are from temporarily caged plots, confound current-year removal by grazing with potential long-term effects on population dynamics (Milchunas et al. 2008). Basal cover of individual plant species, litter, and bare ground were estimated using Daubenmire quadrats ( $20 \times 50\text{ cm}$ ) and cover classes of: 1 = present to  $< 5\%$ ; 2 = 5 to  $< 15\%$ ; 3 = 15 to  $< 25\%$ ; 4 = 25 to  $< 40\%$ , 5 = 40 to  $< 60\%$ , 6 = 60–100%. Thirty-five randomly placed Daubenmire quadrats were sampled in each treatment-replicate-year (total:  $315\text{ quadrats year}^{-1}$ ) during the peak standing live period in July annually for 14 years (1998–2011, total: 4410 quadrats sampled). Quadrat values for basal cover of all species, litter, and bare ground were adjusted proportionally to 100% after converting to the midpoint of the cover classes. We measured ANPP at each site in long-term large herbivore exclosures by harvesting peak-standing-crop of live-plus-recent-dead forage in six to ten  $0.25\text{ m}^2$  quadrats (oven-dried at  $55^{\circ}\text{C}$ ). These long-term large herbivore exclosures were used to represent potential site productivity because cattle grazing reduces ANPP (Milchunas et al. 1994) and the other exclosures sampled were in a transitional stage during early years of the study. Biomass of cacti (common) and full-shrubs (uncommon) were not included because of their patchy distribution.

To estimate abundance of nocturnal rodents (Heteromyidae, Cricetidae), rodents were live-trapped (marked and released) for four consecutive nights twice per year (May, September) on three trapping webs in the same general area as the exclosures. Each web was 3.14 ha, with 124 Sherman live traps spaced at 10-m intervals

along spokes of the web. To estimate abundance of diurnal thirteen-lined ground squirrels *Ictidomys tridecemlineatus* (Sciuridae), the same webs were trapped for four consecutive days in June and July, with 62 shaded traps at 20-m intervals. For both nocturnal and diurnal rodents, we averaged the number of unique captures from the two sessions on each site to calculate an annual mean. Abundance of lagomorphs was estimated by spotlighting on one night in April and July along a 32-km route.

## Statistical analyses

Quadrat cover values were averaged within each combination of year, grazing treatment (+L+S, -L+S, -L-S) and site (replicate pastures) resulting in 126 observations (14 years  $\times$  3 grazing treatments  $\times$  3 replicate sites). On the basis of abundance in the control (+L+S), species were grouped into abundant ( $> 1\%$  basal cover), common ( $\leq 1\%$  and  $\geq 0.1\%$ ) and uncommon ( $< 0.1\%$ ) classes (Supplementary material Appendix A1). Plant species were classified into short, medium, and tall according to relative plant height at this specific site, but the medium group with only four uncommon species was dropped from analyses. *Bouteloua gracilis* was analyzed independently because of its dominance in the community. Community-level parameters included species richness (number of species per treatment–replicate–year), species dominance (% cover of the first most abundant species with respect to total vegetation basal cover) and species diversity (exp.  $H'$ , Shannon and Weaver 1949).

The effects of grazing, year and year-by-grazing interaction on the response variables were analyzed in SAS Proc Mixed (SAS Inst.) using a repeated measures ANOVA (autoregressive, lag one correlation structure on the random errors) in which site was a random effect, grazing, year and year-by-grazing interaction were fixed factors. Effects of grazing within years were examined using the 'sliceby' option. Tukey tests were used to separate significant ( $p < 0.05$ ) or marginally significant ( $0.05 < p < 0.1$ ) differences among treatments. Marginally significant differences were considered because three replicates limited statistical power. By comparing the effects of grazing treatments, we inferred effects of exclusion of small herbivores (comparison between -L-S and -L+S). The effects of small herbivores based on a comparison between the simultaneous exclusion of large-plus-small herbivores and the control grazed by both herbivores is mainly useful if the exclusion of large-only herbivores did not have significant effects. However, since it was not possible to exclude small herbivores while allowing large ones in, inferences concerning effects of small herbivores must be viewed with caution because the simultaneous exclusion of both could have synergistic or antagonistic effects. In some cases data were square-root or log-transformed to satisfy equal variance requirements based on examination of plots of residuals. The influence of ANPP on the response of species richness to grazing treatments was analyzed with a mixed model that included species richness as the response variable, ANPP as the explanatory variable, and year and site as random factors. We tested if slopes differed among grazing treatments and from zero.

## Results

Annual precipitation (from October until September) varied from 231 to 612 mm and ANPP varied from 29 to 208 g m<sup>-2</sup> over the 14-year study period (Fig. 1a). The period of study thus represented both years of severe drought and high precipitation, and a wide range of ANPP. Small herbivore abundance was relatively low during the extended dry period from 2000 to 2004, and then remained high throughout the latter half of the study (Fig. 1b). Rabbit numbers began to increase in 2000 and peaked in 2006. Heteromyid granivores, especially kangaroo rats *Dipodomys ordii* increased in 2004 and remained very abundant for the remainder of our study. Cricetid omnivores responded to abundance of vegetative cover produced in previous relatively wet years (1999, 2005 and 2009). Numbers of omnivorous ground squirrels *Ictidomys tridecemlineatus* peaked in 2002 and have continued to decline since then.

Main effects of grazing on total vegetation cover were small and marginally significant (Fig. 2a, Table 1). Cover decreased in the large-plus-small exclusions compared to the all-herbivore controls. Total vegetation basal cover was not as sensitive as ANPP to annual wet–dry cycles, but declined to under 30% during 2002 and 2008 droughts (Fig. 1a, Supplementary Material Appendix A2a). In contrast, litter cover increased with increasing level of herbivore exclusion (Fig. 2b, Table 1). Bare ground displayed patterns with grazing generally inverse to litter (Fig. 2c, Table 1). For the three general categories of ground cover, the exclusion of large herbivores increased litter and decreased bare ground cover; and the additional exclusion of small herbivores had those effects and also decreased total vegetation cover.

The response of species dominance to grazing treatments (Fig. 2d, Table 1) followed, in general, the results for *B. gracilis* (Fig. 2e, Table 1). This species was the most abundant in this community, representing an average of 68, 67 and 54% of total vegetation basal cover in the grazed controls, large herbivore exclusions, and large-plus-small herbivore exclusions, respectively. Cover of *B. gracilis* in the large herbivore exclusions was similar to controls, but decreased with the additional exclusion of small herbivores (Fig. 2e). *Bouteloua gracilis* declined from the wet period in the late 1990s through the last drought year 2008 and then regained initial cover during the 2009 to 2011 wet period, except in the large-plus-small herbivore exclusions (Supplementary material Appendix A2e).

For total species richness, grazing was not significant as a main effect (Table 1, Fig. 3a), with large herbivore exclusion positively affecting richness in only two years (Supplementary material Appendix A4a). Total species richness tended to be low during less productive years, but there was a general increasing trend after the severe drought of 2002 until the drought of 2008 (Supplementary material Appendix A4a) when the dominant short grass *B. gracilis* was at relatively low cover (Supplementary material Appendix A2e). Species diversity ( $H'$ ) followed a temporal pattern of increases and decreases coupled to fluctuations in total species richness (Supplementary material Appendix A4a–b). However, the response of species diversity to grazing



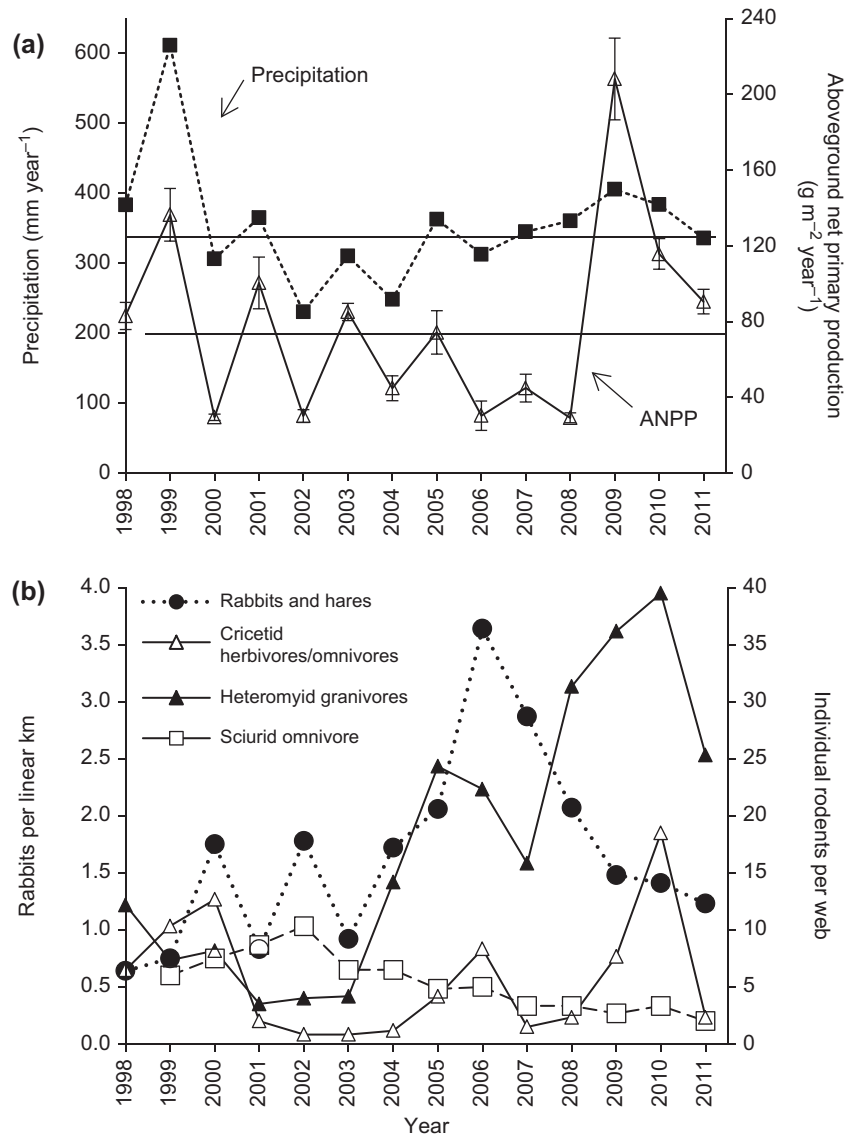


Figure 1. (a) Annual precipitation (mm year<sup>-1</sup>, October–September) and aboveground net primary production (ANPP) (g m<sup>-2</sup> year<sup>-1</sup>) for the 14-year period of study. ANPP was estimated at the long-term large herbivore ungrazed (since 1939) treatments adjacent to treatments reported in this study. Long term means of ANPP and annual precipitation (1939–1990) are horizontal lines. (b) Changes in the relative abundance of small mammalian herbivores during the study period. Rabbits include summed counts of three species (*Lepus californicus*, *L. townsendii* and *Sylvilagus audubonii*) seen on the spotlight route. Heteromyid granivores included, in order of abundance, *Dipodomys ordii*, *Chaetodipus hispidus* and *Perognathus flavus*. Cricetid omnivores included *Peromyscus maniculatus*, *Reithrodontomys megalotis* and *R. montanus*; *Microtus ochrogaster* was the only cricetid folivore, which was only caught in 1998–2000. Sampling for diurnal *Ictidomys tridecemlineatus* (Scuriidae) began in 1999. Values are means across trapping webs (3.14 ha each web) or seasons (Methods); standard errors are omitted for clarity.

(Fig. 3b, Table 1) was more related to grazing effects on species dominance (Fig. 2d). Thus, diversity increased in the large-plus-small exclosures compared to the controls.

Grazing significantly affected basal cover of tall and short plant height categories (Table 1). Short species basal cover decreased with increasing level of herbivore exclusion (Fig. 2f). The capacity to recover after the 2002 and 2008 droughts decreased with increasing level of herbivore exclusion (Supplementary material Appendix A3a). When *B. gracilis* was excluded from this plant group, the negative effect of exclusion of large-plus-small herbivores was not observed (Table 1). Main effects of grazing on richness

of short species were marginal, with a small decrease in richness of short species in the large-plus-small exclosures compared to the controls (Fig. 3c). Tall species basal cover increased with increasing level of herbivore exclusion (Fig. 2g) and the effects started earlier than for short species (Supplementary material Appendix A3 a–b). The capacity of tall species to recover after the droughts of 2002 and 2008 followed a pattern opposite to that of short species and increased with increasing level of herbivore exclusion (Supplementary material Appendix A3b). Richness of tall species increased in the exclosures compared to the controls and both types of exclosures showed similar values

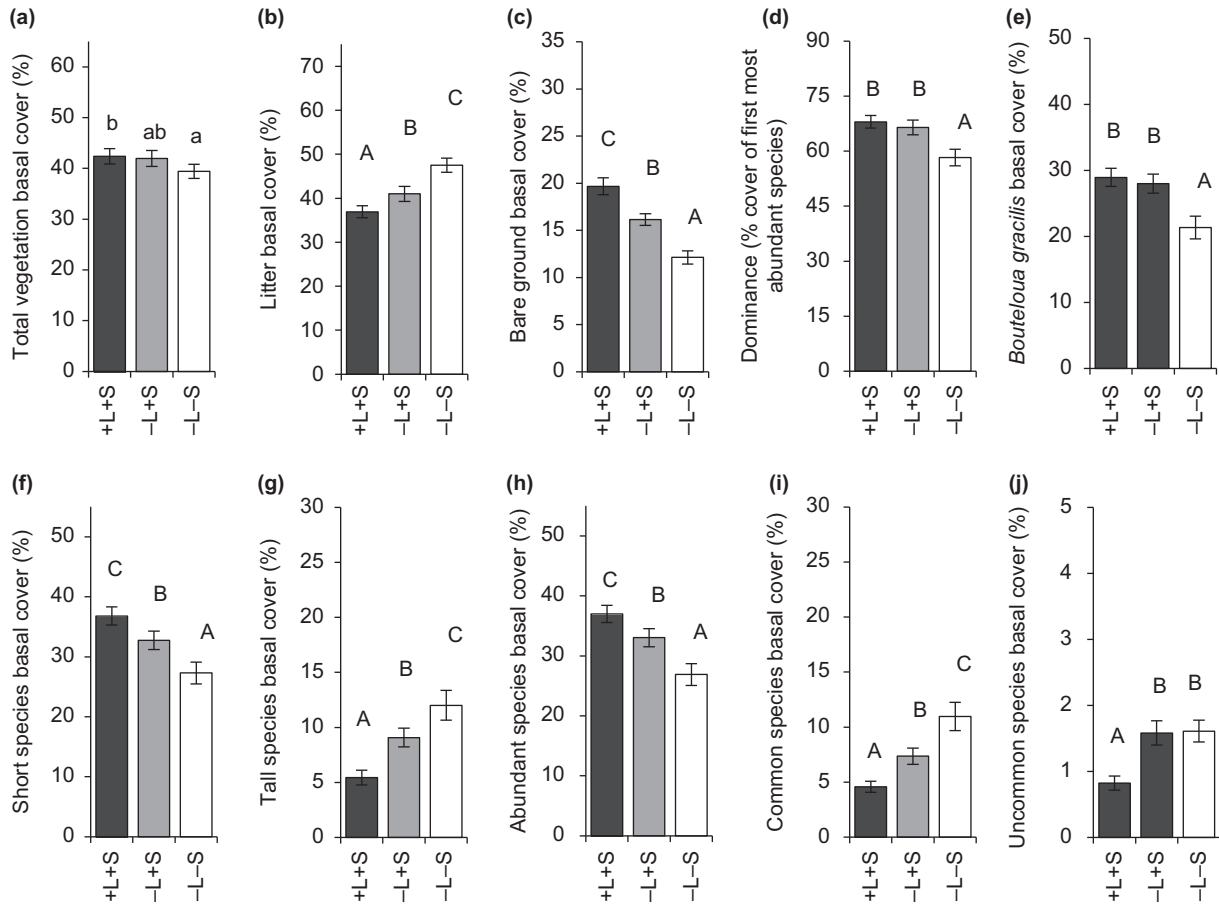


Figure 2. (a) Total vegetation, (b) litter, (c) bare ground, (d) dominance, (e) *Bouteloua gracilis*, and (f) short (g) tall, (h) abundant, (i) common, and (j) uncommon species basal cover (% of total), except dominance basal cover (% of total vegetative cover of the first most abundant species) for the main effect of grazing: '+L+S' grazed by large and small herbivores (control), '-L+S' ungrazed by large and grazed by small herbivores, and '-L-S' ungrazed by both large and small herbivores. Error bars are  $\pm 1$  SE. Bars not sharing a common letter are significantly different, with capital letters indicating ( $p < 0.05$ ) and lower case indicating marginally significant ( $0.05 < p < 0.1$ ) based on a Tukey test.

(Fig. 3d). In sum, basal cover of short species decreased and tall species increased in both types of exclosures. Large herbivore exclusion also increased richness of tall species, and the additional exclusion of small herbivores decreased (although marginally) the richness of short species.

Grazing treatment significantly affected basal cover of plant species categorized as abundant, common, or uncommon (Table 1). Abundant species comprised the majority of vegetation cover in the control (87%) and the effects of grazing treatments (Fig. 2h) were similar to the short species group (Fig. 2f) due to the high dominance of short species. Exclusion of large herbivores did not affect the abundant species richness, but the additional exclusion of small herbivores decreased the abundant species richness (Fig. 3e). Common species basal cover increased with increasing level of herbivore exclosure (Fig. 2i). On the contrary, the richness of common species was similar in the three grazing treatments (Fig. 3f). Basal cover and richness of uncommon species increased similarly in both types of exclosures compared to the control (Fig. 2j, 3g). Abundant species in this plant community were, in terms of species richness, 80% short and 20% tall species, common species

were 31% short and 69% tall species, and uncommon species were 17% short, 56% tall and 27% unclassified (Supplementary material Appendix A1). In sum, large herbivore exclosure decreased basal cover of abundant species and increased basal cover of common and uncommon species, and richness of uncommon species. The additional exclusion of small herbivores decreased richness of abundant species.

Year was a significant factor in most analyses but there is no significant interaction between year and grazing treatment for any variable (Table 1). However, the within-year analyses showed that most significant effects of grazing on basal cover of total vegetation, litter, bare ground, *B. gracilis*, and plant groups (except uncommon species) occurred in the later years of the experiment (Supplementary material Appendix A2, A 3).

We assessed if the effects of large and small herbivores on total species richness and richness of abundant, common and uncommon species varied with ANPP. Total and uncommon species richness had a significant positive relationship with increasing ANPP (Table 2). In the four cases the differences in the slopes of the regressions among grazing treatments were not significant.

Table 1. ANOVA results (repeated, mixed model) for the effects of grazing, year, and grazing × year interaction on categories of ground cover and vegetative basal cover for three grazing treatments and 14 years in the shortgrass steppe. Significant ( $p < 0.05$ ) or marginally significant ( $p < 0.10$ ) differences are in regular and italic bold, respectively.

	Grazing DF = 2 F (p-value)	Year DF = 13 F (p-value)	Grazing × Year DF = 26 F (p-value)
Total vegetation basal cover	2.90 ( <b>0.0735</b> )	19.41 (< <b>0.0001</b> )	0.81 (0.7238)
Litter cover	29.4 (< <b>0.0001</b> )	20.9 (< <b>0.0001</b> )	1.47 (0.1058)
Bare ground cover	28.74 (< <b>0.0001</b> )	3.69 ( <b>0.0002</b> )	0.86 (0.6599)
Total richness of species	2.58 (0.1155)	23.42 (< <b>0.0001</b> )	1.06 (0.4092)
<i>Bouteloua gracilis</i>	9.15 ( <b>0.0026</b> )	9.04 (< <b>0.0001</b> )	0.85 (0.6410)
Dominance	4.27 ( <b>0.0471</b> )	3.99 (< <b>0.0001</b> )	0.70 (0.8407)
Species diversity ( <i>H'</i> )	5.20 ( <b>0.0271</b> )	12.17 (< <b>0.0001</b> )	0.75 (0.7853)
Short			
Basal cover	15.60 ( <b>0.0001</b> )	11.28 (< <b>0.0001</b> )	0.93 (0.5720)
Basal cover ( <i>B. gracilis</i> not included)	8.75 ( <b>0.0041</b> )	13.37 (< <b>0.0001</b> )	0.60 (0.9225)
Species richness	2.55 ( <b>0.0962</b> )	9.43 (< <b>0.0001</b> )	0.77 (0.7627)
Tall			
Basal cover	18.73 ( <b>0.0002</b> )	8.68 (< <b>0.0001</b> )	1.19 (0.2839)
Species richness	5.49 ( <b>0.0147</b> )	8.56 (< <b>0.0001</b> )	0.89 (0.6251)
Abundant species			
Basal cover	15.29 ( <b>0.0002</b> )	11.86 (< <b>0.0001</b> )	0.91 (0.5952)
Basal cover ( <i>B. gracilis</i> not included)	3.09 ( <b>0.0946</b> )	5.58 (< <b>0.0001</b> )	0.73 (0.8109)
Species richness	6.34 ( <b>0.0076</b> )	3.24 ( <b>0.0008</b> )	0.95 (0.5436)
Common species			
Basal cover	15.00 ( <b>0.0005</b> )	10.84 (< <b>0.0001</b> )	0.85 (0.6751)
Species richness	0.75 (0.4855)	9.91 (< <b>0.0001</b> )	0.72 (0.8183)
Rare species			
Basal cover	10.70 ( <b>0.0006</b> )	5.70 (< <b>0.0001</b> )	1.01 (0.4638)
Species richness	3.72 ( <b>0.0469</b> )	11.25 (< <b>0.0001</b> )	<b>1.50 (0.0953)</b>

## Discussion

### Effect of large herbivore exclusion

The exclusion of large domestic herbivores (which remove approximately 40% of ANPP) increased basal cover of taller species and decreased shorter ones, but did not affect basal cover of the dominant *Bouteloua gracilis*. The decrease of tall species with grazing is a well-known effect that occurs in many grasslands, although usually is more marked in mesic systems with a long evolutionary history of grazing (Milchunas et al. 1988, Díaz et al. 2007). Tall growth forms, with relatively greater investment in above-ground rather than below-ground production, are more intolerant of grazing by large herbivores. Large herbivore exclusion also decreased cover of abundant species and increased cover of common and uncommon ones, which was directly linked to the increase in tall growth forms. This was because, in terms of species richness, tall species predominate in the common and uncommon groups in this plant community. Changes in litter cover associated with large herbivore exclusion can only be partly explained by direct removal of vegetation consumption. The majority of aboveground tissue turns over in three years in this system, based on  $^{14}\text{C}$  labeling (Milchunas and Lauenroth 2001). Increased litter during latter years of this study suggests indirect effects since direct effects of consumption on litter accumulation would have equilibrated early in the study.

Exclusion of large herbivores alone did not significantly alter the general indicators of plant community structure: total vegetation basal cover, species dominance, total species

richness, and species diversity. These results contrast with a decrease in dominance of *B. gracilis* and increase in species richness and diversity found after 45 years of exclusion of heavy grazing (which remove approximately 60% of ANPP; Milchunas et al. 1989). Our results suggest that long-term moderate grazing, compared to heavy grazing, does not reduce total species richness or fully stimulate/activate tillering capacities of *B. gracilis* as seen under more heavily grazed conditions (Milchunas et al. 1988, 1989, Milchunas and Lauenroth 1989).

### Effect of the additional exclusion of small herbivores

Shortgrass steppe has a relatively low biomass, density, and diversity of small, non-colonial rodents compared with desert grasslands and tallgrass prairie (Stapp et al. 2008). We could not separate the effects of folivores and granivores, but based on historical estimates from upland grasslands, collectively they were expected to consume relatively little plant biomass (~3% of ANPP; Lauenroth and Milchunas 1991). As a consequence, we hypothesized that small herbivores would affect cover and richness of less abundant species, through selective but limited consumption, but they would not affect cover of dominant and abundant species or general plant community characteristics.

Contrary to our hypothesis, exclusion of small herbivores increased basal cover of the common plant species, but had no additional effect on uncommon species. Small mammals could directly affect plant species abundance through many mechanisms, including consumption of seeds, seedlings, and plant parts and soil disturbances (Maron and Crone 2006,

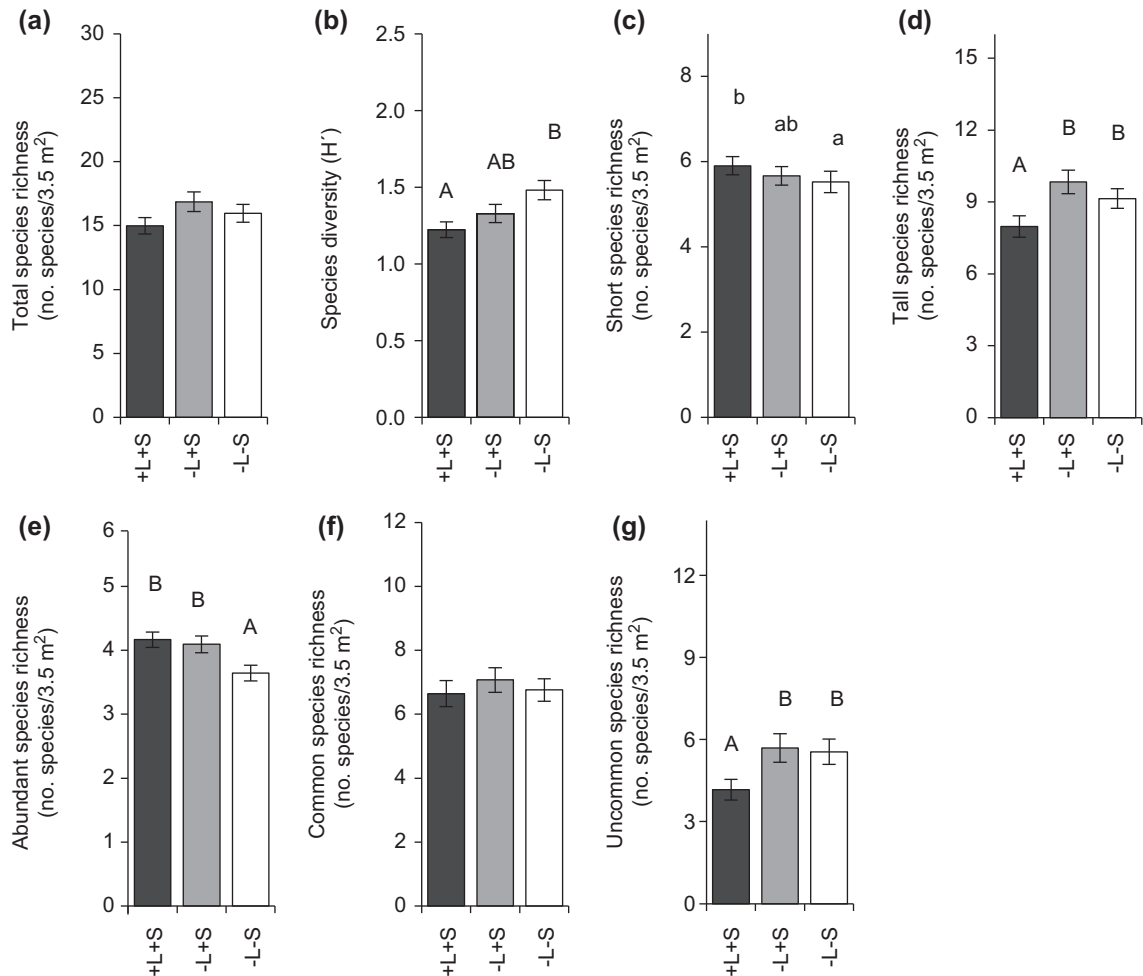


Figure 3. (a) Total species richness, (b) species diversity, and (c) short (d) tall, (e) abundant, (f) common, and (g) uncommon species richness (no. species  $3.5\text{ m}^{-2}$ , except species diversity (exp.  $H'$  Shannon and Weaver 1949)) for the main effect of grazing: '+L+S' grazed by large and small herbivores (control), '-L+S' ungrazed by large and grazed by small herbivores, and '-L-S' ungrazed by both large and small herbivores. Error bars are  $\pm 1$  SE. Bars not sharing a common letter are significantly different, with capital letters indicating ( $p < 0.05$ ) and lower case indicating marginally significant ( $0.05 < p < 0.1$ ) based on a Tukey test.

Bricker and Maron 2012). Uncommon species as a group were not affected by the additional exclusion of small herbivores, but the tall annual *Tragopodium dubium*, was an example of one uncommon species that did increase with small herbivore exclusion (43% frequency vs 0–2.4% in grazed or large herbivore exclusion; see Supplementary material Appendix 1 for basal cover in the three grazing treatments). Due possibly to the conspicuous, tall, large seed heads, a small herbivore effect on this species was evident in the

early years of this experiment, suggesting a direct suppression through selective consumption. Low but selective consumption by small herbivores was also sufficient to limit population growth of common species, which could be an indirect or a cumulative direct effect because effects in this case increased during latter years of study.

In contrast to our hypotheses, additional exclusion of small herbivores affected all general categories of ground cover (litter, total vegetation basal cover, and bare ground).

Table 2. Significance levels (p-values) for linear regression analyses used to test relationships between species richness and aboveground net primary production (ANPP). (A) Significance of ANPP within grazing treatments (difference from slope of zero) and (B) significance among grazing treatments (difference in slopes among grazing treatments). A positive or negative relationship between the dependent variable and ANPP is indicated as (+) or (–), respectively. Significant ( $p < 0.05$ ) or marginally significant ( $p < 0.1$ ) differences are in bold.

Dependent variable	(A) ANPP (p-values)			(B) Grazing treatment (p-values)
	Grazed control	Large herbivore exclusion	Large-plus-small herbivore exclusion	ANPP $\times$ Grazing interaction
Total richness of species	(+) <b>0.0351</b>	(+) <b>0.0490</b>	(+) <b>0.0233</b>	0.9323
Species richness of abundant species	(–) 0.2288	(–) 0.1572	(–) 0.1332	0.9569
Species richness of common species	(+) <b>0.0805</b>	(+) 0.4367	(+) 0.2118	0.5289
Species richness of uncommon species	(+) <b>0.0322</b>	(+) <b>0.0072</b>	(+) <b>0.0057</b>	0.7630



Litter increased by 4% with exclusion of large herbivores and 7% with additional exclusion of small herbivores. Greater litter accumulation with small herbivores exclusion may be related to long-term, indirect effects resulting from increased basal cover of taller plant species and decreases in short species compared to large herbivore exclusions. Greater aboveground biomass allocation of tall versus short species (Milchunas et al. 2008, Li et al. 2008) as well as increased C/N ratio, lignin/N ratio and percent lignin of tall versus short species (Murphy et al. 2002) could explain the litter accumulation through both increased aboveground production and decreased decomposition. Low but selective consumption by small herbivores that had large indirect effects suggests small mammals influence competitive interactions among plants (Brown and Heske 1990). Increase in cover of taller plant species and decrease of shorter ones shifts competition from soil resources (mainly, water and minerals) to canopy resources (mainly light), favoring colonization by less abundant tall species (Tilman 1988, Milchunas et al. 1988). These indirect effects would explain the decrease in the basal cover of the dominant short grass, *B. gracilis*, with the additional exclusion of small herbivores. Low amounts of consumption of *B. gracilis* by small herbivores would not directly affect a species that is so heavily dominant and not dependent on seed production. A prostrate growth form, large crown biomass, and extensive rooting system (Milchunas and Lauenroth 1989) makes this species less vulnerable to heavy grazing by large herbivores and drought, but reduces its competitiveness for light in presence of taller species. Our results suggest that indirect effects of limited but selective consumption by small herbivores are manifest in terms of altered resource availability, general community characteristics, shifts in abundance of dominant species, and decreased total vegetation basal cover.

Effects of small mammals on litter, bare ground, and total vegetation basal cover developed in later years of this experiment. This emphasizes the importance of long-term studies and suggests that effects of excluding small mammals on plant community structure may be even greater in future years. We note that, collectively, abundance of small herbivores increased markedly at our study site during the course of our study (especially after 2004; Fig. 1b), and, in the case of granivores, has remained unusually high. Both direct (consumption) and indirect effects of these small herbivores may therefore be greater than predicted based on past estimates of their consumption and diets. Our experimental design does not allow us to separate the effects of folivores and granivores. However, folivores may also decrease flower-head production and seed rain, and impact seeds (Edwards and Crawley 1999). Separating the effects of different small herbivores is a priority for future research.

Even though some effects were large, we did not find the long-term additional exclusion of small herbivores to have a consistent or large effect on total species richness in this study. Exclusion of small mammals favored mainly the cover of common tall-statured species, which were present in all grazing treatments. Our results are not similar to Bakker et al. (2006) and Milchunas (2011) that observed greater

richness with exclusion of small mammals using large contiguous species–area plots during two early years at the same study site, but the large number of small non-contiguous quadrats we used generally resulted in greater richness even for the same years of sampling (see Supplementary material Appendix A5 for comparison and details).

Our results indicate an important effect of small mammal herbivores on general attributes of plant community structure. These findings agree with other studies addressing plant community structure following exclusion of small mammals in deserts (Brown and Heske 1990, Guo et al. 1995, Valone and Schutzenhofer 2007), grasslands (Keesing 2000, Howe et al. 2002, Bricker et al. 2010), savannas (Maclean et al. 2011) and forest ecosystems (Olofsson et al. 2004, Ostfeld et al. 1997, Manson et al. 2001). Gibson et al. (1990) suggests small mammal herbivores are of lesser importance in the latter compared with earlier successional stages of some grasslands, and Baez et al. (2006) found small effects when low primary productivity constrains the abundance of herbivores. Most studies finding significant effects were in ecosystems with relatively high densities of small mammals or they showed a notable increase in density in the absence of large herbivores. Small mammal populations in shortgrass steppe increase with decreased grazing pressure by cattle (Grant et al. 1982, Stapp et al. 2008), but the relatively small changes in physiognomy and species composition of the plant community in absence of large herbivores limit the response of the small mammal populations compared with other more productive grasslands. Many of the above-mentioned studies were in ecosystems dominated by annual plants and where granivorous rodents controlled large-seeded plants. Our study expands this prior work to a perennial grassland, and emphasizes that a relatively low density and diversity of non-colonial small herbivores can play an important role in plant communities dominated by large herbivores and small-seeded perennial plants.

### **Influence of plant productivity on the effects of exclusion of large and small herbivores**

Mean ANPP over the 14 years of study was similar to that observed from 1939–1990 (Milchunas et al. 1994). The 14-year study period also included extreme dry years equivalent to those seen during the 1930s Dust Bowl drought as well as unusually wet, high productivity years. We hypothesized that the effects of large and small herbivores on species richness would increase in more productive years because uncommon species would be more abundant, and hence herbivore effects could manifest. We found significant positive relationships between total species richness and ANPP, and between richness of uncommon species and ANPP, within all herbivore treatments. However, the difference in slopes of the regressions among grazing treatments were not significant, indicating that grazing by both large and small herbivores does not alter species richness–ANPP relationships. Therefore, we rejected our hypothesis that grazing effects on species richness would be greater in more productive years. For small herbivores, our finding is consistent with Bakker et al. (2006) and Rueda et al. (2013). Productivity is considered

a major factor influencing the extent of changes in structure and species diversity of plant community due to large herbivore grazing (Milchunas et al. 1988, Proulx and Mazumder 1998). The overall weak effects of herbivores on species richness found in this study are likely closely related to the lack of grazing effects on species richness–ANPP relationships. Small herbivores did not affect total species richness or richness of uncommon species. Large herbivores only affected richness of uncommon species in these moderately grazed pastures in contrast to total species richness effects under heavy grazing (Milchunas et al. 1989).

Total vegetation basal cover was lowest in 2002 and 2008, corresponding to drought years. The capacity of short species to recover after both droughts decreased with increasing level of herbivore exclusion while the opposite was observed for tall species. Additionally, vegetation basal cover was greatest in the presence of both large and small herbivores. Thus, our results support the concept that the increase in basal cover of short grasses and total vegetative cover under grazing by large and small herbivores has a stabilizing effect on this plant community by maintaining the predominance of plant competition for belowground resources, thereby mitigating impacts of drought (Milchunas et al. 1988). The present study suggests that, under moderate grazing by large herbivores, small herbivores are important in this stabilizing role of grazing, contributing to resilience of the plant community after extreme events.

### Concluding remarks

Our results suggest an important effect of small herbivores on abundant rather than on uncommon components of the plant community. When the exclusion of large herbivores and the exclusion of large plus small herbivores both significantly altered the same vegetation variable, the direction of the effects was complementary and additive. No evidence was found for counteracting effects between large versus small herbivores. Plant species height (tall vs short species) was a robust indicator of the effects of both herbivore types, and this promoted indirect effects in the small-plus-large mammal exclosures that included basic alterations of vegetation and ground-cover characteristics. Grazing by the combination of large and small herbivores favored recovery of short grasses after intense droughts, providing resilience to the shortgrass steppe and contributing to the long-term maintenance of vegetation basal cover.

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Supplementary material (available online as Appendix oik-00403 at <[www.oikosoffice.lu.se/appendix](http://www.oikosoffice.lu.se/appendix)>). Appendix A1–A6.