

## LETTER

# Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size

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## Abstract

Mammalian herbivores can have pronounced effects on plant diversity but are currently declining in many productive ecosystems through direct extirpation, habitat loss and fragmentation, while being simultaneously introduced as livestock in other, often unproductive, ecosystems that lacked such species during recent evolutionary times. The biodiversity consequences of these changes are still poorly understood. We experimentally separated the effects of primary productivity and herbivores of different body size on plant species richness across a 10-fold productivity gradient using a 7-year field experiment at seven grassland sites in North America and Europe. We show that assemblages including large herbivores increased plant diversity at higher productivity but decreased diversity at low productivity, while small herbivores did not have consistent effects along the productivity gradient. The recognition of these large-scale, cross-site patterns in herbivore effects is important for the development of appropriate biodiversity conservation strategies.

## Keywords

Cross-site, fertility, grazing, plant–animal, species richness.

*Ecology Letters* (2006) 9: 780–788

## INTRODUCTION

Vertebrate herbivores can be key determinants of grassland plant species composition and diversity (McNaughton *et al.* 1989; Collins *et al.* 1998; Olf & Ritchie 1998; Knapp *et al.* 1999). However, free-ranging large herbivores are disappearing from many ecosystems worldwide through land use changes, decreasing size of nature reserves and increasing habitat fragmentation (WallisDeVries *et al.* 1998; Prins *et al.* 2000). Simultaneously, mammalian herbivores are increasingly introduced into ecosystems either as livestock, for conservation purposes or as alien species in habitats that

lacked grazers during recent evolutionary times (Milchunas *et al.* 1988; WallisDeVries *et al.* 1998; Knapp *et al.* 1999; Wardle *et al.* 2001). The consequences of these changes in herbivore presence for plant diversity are difficult to predict, because available studies on the impact of herbivores yield contrasting results, from positive effects on diversity (Belsky 1992; Collins *et al.* 1998) to neutral (Stohlgren *et al.* 1999; Adler *et al.* 2005) or negative effects (Milchunas *et al.* 1998; Wardle *et al.* 2001; Howe *et al.* 2002).

The contrasting effects of herbivores on plant diversity observed in different habitats may be driven by differences in productivity among sites (Milchunas & Lauenroth 1993;

Proulx & Mazumder 1998; Osem *et al.* 2002). One explanation for the importance of productivity is that herbivores may increase plant diversity in grasslands when their effects alleviate plant competitive exclusion and constraints on species establishment (Grubb 1977; Knapp *et al.* 1999; Eskelinen & Virtanen 2005). This may especially be important under productive conditions, where large herbivores can prevent light competition by tall, dominant plant species (Huisman & Olff 1998; Huisman *et al.* 1999) and increased light availability may lead to enhanced germination and seedling establishment (Jutila & Grace 2002). Alternatively, differences among studies may be caused by differences among sites in herbivore size (Olff & Ritchie 1998; Olofsson *et al.* 2004), where larger, less selectively feeding herbivores increase diversity because they impact dominant plant species (Milchunas & Lauenroth 1993). In contrast, smaller, more selectively feeding herbivores have been suggested to decrease diversity by selectively feeding on nutritious plant species (Brown & Heske 1990; Edwards & Crawley 1999).

The combined effects of site productivity and herbivore size as determinants of the impact of herbivores on plant diversity have not yet been addressed in large-scale, cross-site experimental field studies. We manipulated and measured herbivore impacts on plant diversity at seven sites in North America and Europe that encompass a 10-fold gradient of aboveground plant productivity ( $60\text{--}600\text{ g m}^{-2}\text{ year}^{-1}$ ) and a variety of vertebrate herbivore communities. We show that assemblages with large herbivores increased plant diversity at higher productivity but decreased diversity at low productivity, while small herbivores did not have consistent effects along the productivity gradient. We need this information to predict in which ecosystems different-sized herbivores play a key role in affecting biodiversity, and thus could be protected or excluded.

## METHODS

We selected seven grassland sites in North America and Europe which represented a 10-fold gradient of aboveground plant productivity and each supported a varied assemblage of mammalian herbivores (Table 1). Between 1994 and 1996 we established similar sets of exclosures and unfenced controls on 400- to 900-m<sup>2</sup> plots at a minimum of three locations (blocks) at each of these seven sites. Detailed descriptions of each site can be found in Appendix S1. We experimentally separated the effects of different-sized herbivores by building fences of different mesh size and height in each block (Table 1) to create three treatments per block: (i) unfenced plots that included all herbivores; (ii) plots fenced to exclude larger grazers > 30 kg, such as bison, cattle, elk, deer and pronghorn, but allowing access to

an assemblage of smaller species < 10 kg including large rodents such as prairie dogs and various lagomorphs; and (iii) plots fenced to exclude all mammals > 1 kg, allowing access for only the small herbivorous rodents and insects. Unfortunately, it was practically impossible to physically exclude small herbivores and allow access for the large ones in a field experiment. Therefore, the effects of larger herbivores on the vegetation can only be analysed in a conditional way, i.e. their effect given the presence of smaller species. At two of the sites lagomorphs were present at such low densities that a separate small herbivore treatment could not be justified (see Table 1 for the composition of natural herbivore communities at each site and the site descriptions for estimated biomass densities of herbivores).

At peak standing crop at each site (in June to August 2001) we counted the number of plant species and recorded species composition in all grazing treatments. Plant species richness was determined at different spatial scales by measuring in circles, which increased from 0.25- to 0.5-, 1.0-, 2.0- and 3.0-m radius. Depending on the size of the grazing treatments at each site, one or two replicate circles were counted.

Species cover was estimated at each site as the percentage of surface area covered by each plant species (with a maximum of 100% total cover). The amount of plots sampled per block and size of the plots varied per site according to the local monitoring programme: 45 plots of 0.2 × 0.5 m at the Short grass steppe, 20 plots of 0.5 × 1.0 m at the Tallgrass prairie, the Montane grassland, Bunch grass steppe and Sage brush steppe, 10 plots of 0.5 × 1.0 m at the Oak savanna and two plots of 2.0 × 2.0 m at the Floodplain grassland. No data on plant species cover were available for one block at the Bunch grass steppe. Data of all subplots were pooled per block per grazing treatment before further calculation.

Aboveground annual net primary production was measured during the growing season in 2002 within temporary cages that were placed in the treatment grazed by the large and small herbivores combined. The cages excluded both large and small herbivores. Biomass was collected at peak standing crop in July or August by clipping an area of 0.25 m<sup>2</sup>. For shrubs only current year growth was collected. Standing crop was sampled simultaneously next to the cages in the treatment where large and small herbivores had access to estimate the amount of biomass removed through grazing. Additionally, standing crop was sampled in the grazing treatment where large and small herbivores had been excluded during the entire experiment to estimate shoot-root ratios. The number of replicates within each grazing treatment and block varied from two to 10 between sites.

To determine root biomass we took soil samples in the strips where above ground biomass was clipped. In each grazing treatment several samples (one to three) from 0- to

**Table 1** Characteristics of the study sites

Site	Habitat type	Geographical position	Fertility (g N kg <sup>-1</sup> soil)	C : N ratio in soils	Precipitation (mm year <sup>-1</sup> )	Aboveground net primary productivity (g m <sup>-2</sup> 2002)	% Biomass removed	No. replicates	Outside enclosure, all herbivores	Inside large-mesh fence	Inside small-mesh fence
Deseret Sage (UT, USA)	Sage brush steppe	41°11' N 111°5' W	1.51 ± 0.19	14.5 ± 2.0	305 (261)	47 ± 5	36 ± 3	3	Cattle, elk, mule deer, pronghorn rabbits, prairie dogs and rodents	Rabbits, prairie dogs and rodents	Small rodents
Short Grass Steppe (CO, USA)	Short grass steppe	40°49' N 104°46' W	1.43 ± 0.29	10.7 ± 0.2	322 (160)	97 ± 9*	11 ± 5†	3	Cattle, pronghorn, rabbits and rodents	Rabbits and rodents	Small rodents excluded‡
Deseret Low (UT, USA)	Bunch grass steppe	41°21' N 111°5' W	1.14 ± 0.24	9.8 ± 0.1	305 (261)	125 ± 17	37 ± 5	3	Cattle, elk, mule deer, pronghorn, rabbits, prairie dogs and rodents	Rabbits, prairie dogs and rodents	Small rodents
Deseret High (UT, USA)	Montane grassland	41°25' N 111°25' W	1.51 ± 0.30	12.1 ± 0.4	635 (532)	203 ± 30	30 ± 15	3	Sheep, elk, rabbits and rodents	Rabbits and rodents	Small rodents
Cedar Creek (MN, USA)	Oak savanna	45°5' N 93°10' W	0.84 ± 0.06	17.9 ± 0.3	825 (840)	222 ± 19	15 ± 7	6	White-tailed deer and rodents	No herbivores < 10 and > 1 kg present	Small rodents
Konza (KS, USA)	Tallgrass prairie	39°08' N 96°62' E	3.03 ± 0.18	13.5 ± 0.2	835 (676)	302 ± 37	49 ± 5	3	Bison, white-tailed deer and rodents	No herbivores < 10 and > 1 kg present	Small rodents
Junner Koeland (the Netherlands)	Floodplain grassland	52°32' N 6°29' E	2.76 ± 0.34	11.3 ± 0.2	758 (835)	489 ± 19	20 ± 9	5	Cattle, rabbits and rodents	Rabbits and rodents	Small rodents

All values represent mean values (± 1 SE). Precipitation is given as long-term average, ranging from 18 to 97 years of measurements (see site descriptions). The precipitation from September 2001 to September 2002, the full year previous to biomass sampling in 2002, is displayed between brackets. Full site descriptions, including sources for climatic data, can be found in Appendix S1.

\*Measured in 2001, due to extreme drought at this site in 2002.

†Grazing intensity is c. 40% of primary production, but cages underestimate consumption due to compensatory regrowth in shrub-grassland shortgrass communities.

‡The mesh width of the fence that excluded small herbivores was so narrow that small rodents were also excluded at this site.

40-cm depth were collected. For the Sagebrush steppe, Bunchgrass steppe, Montane prairie and Tallgrass prairie no samples deeper than 20 cm could be obtained because of a hard subsurface caused by a petrocalcic layer in several sites and the presence of rocks in the Tallgrass prairie. We assumed that no roots would be found below 20 cm in these sites. Root samples were washed and dried at 70 °C and root weight was ash corrected. We calculated characteristic site and block shoot–root ratios by dividing aboveground standing biomass by root biomass in the treatment where large and small herbivores were excluded. Samples were pooled within each block before data analysis.

We used the amount of soil nitrogen and the C : N ratio of soils in the treatment where large and small herbivores were excluded to characterize soil fertility at each site. Separate soil samples were taken simultaneously with the root samples from the upper 10-cm soil. The samples for soil nutrient analysis were analysed for C and N content through dry combustion on a C/N analyser (ECS 4010; Costech Analytical Technologies Inc., Valencia, CA, USA). We collected precipitation data from existing sources for each site, which can be found in the detailed descriptions of each site in Appendix S1. Both the long-term average precipitation is given and the value for September 2001 to September 2002, the full year previous to biomass sampling in 2002.

### Data analysis

To analyse the impact of herbivores on plant species richness, we used a type III ANCOVA model with herbivore assemblage and scale of measurement as fixed factors, above ground plant production as a covariate and species richness (log-transformed to achieve homogeneity of variance) as the dependent variable and we included all interactions in our model. We chose to analyse our study as a single design, thus using each replicate block, as the locations of blocks could vary considerably in their aboveground production

**Table 2** Results of the analysis of covariance of the factors affecting absolute plant species richness

	<i>F</i>	d.f.	<i>P</i> -value
Herbivore assemblage	6.25	2,315	0.002
Scale of measurement	47.00	4,315	< 0.001
Production	11.71	1,315	0.001
Herbivore assemblage × scale	0.14	8,315	0.99
Herbivore assemblage × production	5.07	2,315	0.007
Scale × production	3.46	4,315	0.009
Herbivore assemblage × scale × production	0.11	8,315	0.99

The impact of the herbivore assemblage depended on plant production of the grasslands, as shown by the significant herbivore assemblage × production interaction.

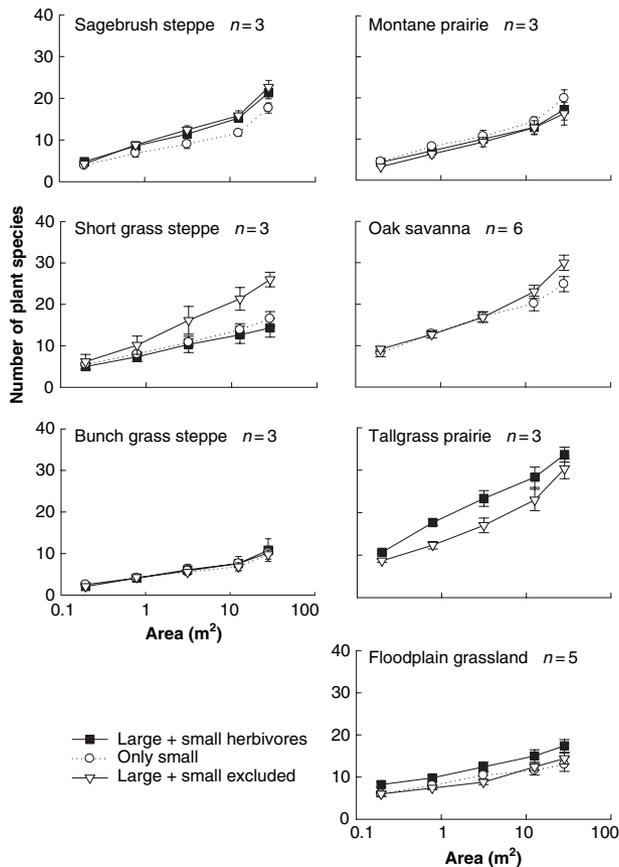
within sites (Fig. 2). This analysis of covariance showed that the impact of herbivores on species richness was independent of the scale of measurement (ranging from 0.2 to 28 m<sup>2</sup>, see Results and Table 2). Therefore, we only included the largest scale of measurement in our subsequent analyses. We analysed the relationship between production and herbivore impact on species richness further by calculating the relative differences in mean species richness between grazing treatments within each block of each site, expressed as a percentage,  $100 \times (S_i - S_j)/S_j$ , where  $S_i$  is the species richness in the presence of the herbivore assemblage of interest and  $S_j$  is the species richness in the enclosure of all herbivores > 1 kg. Relative effects of different-sized herbivores on plant species richness were analysed with an analysis of covariance with plant production and (log)shoot–root ratio as covariates respectively. The effects of large and small herbivores and only small herbivores were plotted separately and analysed with regression analysis.

To test whether herbivores significantly altered plant species richness and composition, we divided our experimental blocks into two classes of low (0–300 g m<sup>-2</sup>) and high (300–600 g m<sup>-2</sup>) productivity, and evaluated the effects of different herbivore assemblages on plant diversity and species turnover for each class. The threshold of 300 g m<sup>-2</sup> corresponds roughly to the biomass above which light penetration to the soil surface is < 5% and thus limiting to the establishment of many plant species (Huisman & Olff 1998; Huisman *et al.* 1999). For each herbivore assemblage and production class we tested whether the change in plant species number was significantly different from 0 with a one-sample *t*-test. The effect of herbivores on shifts in species presence is expressed as the number of species that are unique to a grazed treatment or to the treatment where large and small herbivores were excluded. The effects of herbivore assemblage and production class on shifts in species presence are tested with an ANOVA, with herbivore assemblage and production class as fixed factors, followed by *post hoc* Tukey tests. All statistical tests were performed in SPSS 12.0 (SPSS Inc. 2003).

Shifts in plant community composition under grazing are expressed as proportion dissimilarity using Whittaker's index of dissimilarity (Whittaker 1952). When species composition is exactly the same and every species is present in the same proportion the index is 0, at maximum difference the index is 1.

### RESULTS

Species–area curves showed that the number of plant species generally increased with plot size, but herbivore effects seemed to differ between our study sites (Fig. 1). We found evidence that the effects of herbivores on mean plant species richness, 7 years after the start of the experiment,



**Figure 1** Species–area curves of the different grazing treatments in the seven study sites. Data represent means  $\pm$  ISE. For each site the number of replicate blocks is indicated (*n*).

depended on an interaction between grassland aboveground productivity and the presence of herbivores ( $F_{2,315} = 5.07$ ,  $P = 0.007$ , Table 2) and was independent of the scale of measurement ( $F_{8,315} = 0.14$ ,  $P = 0.99$ ). Because the impact of herbivores did not depend on the scale of measurement we chose to use the largest plot size ( $28 \text{ m}^2$ ) in further analyses. At this scale plant species richness was not significantly related to plant production ( $R^2 = 0.05$ ,  $P = 0.28$ ), measured in the treatment where large and small herbivores were excluded. The change in plant species richness in the different grazing treatments compared with the treatment where large and small herbivores were excluded was significantly affected by production ( $F_{1,39} = 7.70$ ,  $P = 0.008$ , Fig. 2), but did not differ between grazing by large and small or only small herbivores ( $F_{1,39} = 0.91$ ,  $P = 0.35$ ) and there was no interaction between herbivore assemblage and production ( $F_{1,39} = 2.36$ ,  $P = 0.13$ ). The assemblage including large and small herbivores had an increasingly positive effect on species richness towards higher productivity (Fig. 2a), while the assemblage including only smaller herbivores  $< 10 \text{ kg}$  did not have consistent

effects on plant diversity along the productivity gradient (Fig. 2b). There was a positive relationship between plant production and shoot–root ratio of the whole vegetation where large plus small herbivores were excluded ( $R^2 = 0.45$ ,  $P < 0.001$ ). The change in species richness between grazed and ungrazed treatments depended on the shoot–root ratio ( $F_{1,39} = 16.40$ ,  $P < 0.001$ ), but not on the type of herbivore assemblage ( $F_{1,39} = 1.39$ ,  $P = 0.25$ ) and there were no interactions ( $F_{1,39} = 0.76$ ,  $P = 0.39$ ). The joint effect of large and small herbivores on plant diversity changed from negative to positive with increasing shoot–root ratio of the vegetation (Fig. 2c), while this effect was almost significant when only small herbivores were present (Fig. 2d).

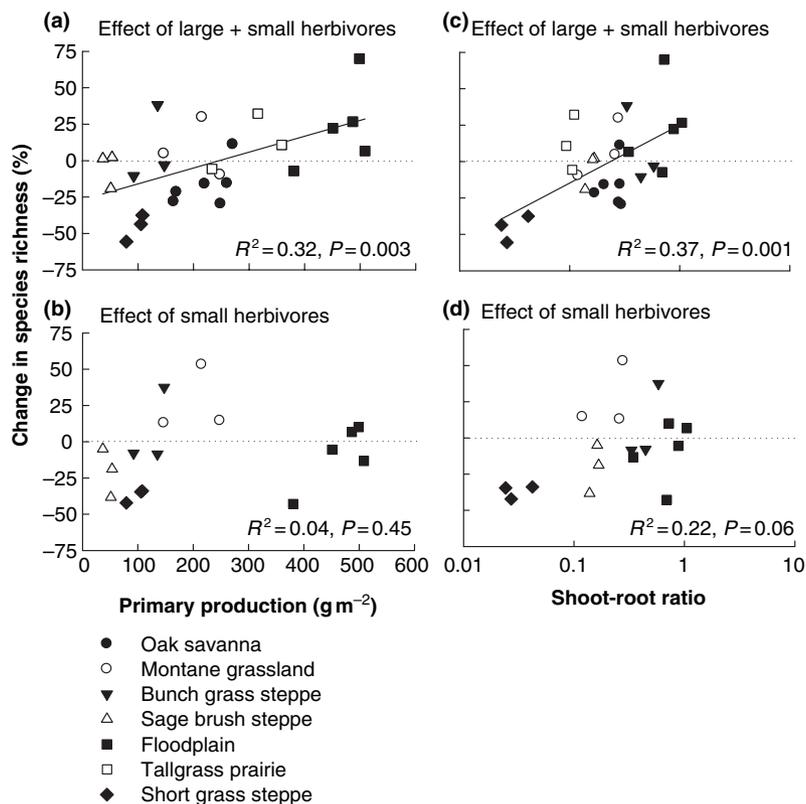
When we simplified the productivity gradient by dividing our experimental blocks into two classes of low ( $0\text{--}300 \text{ g m}^{-2}$ ) and high ( $300\text{--}600 \text{ g m}^{-2}$ ) productivity, the interaction between productivity and herbivore size was significantly present (Table 3). We found, as expected from Fig. 2 that in the presence of all herbivores, including those  $> 30 \text{ kg}$ , plant species richness was significantly lower compared with the exclusion of all herbivores at low productivity while it was significantly higher at high productivity (Table 3). In contrast, in the presence of only small herbivores diversity was generally lower than where these species were excluded ( $t = -1.84$ ,  $P = 0.085$ ) but these effects were not significant at either low or high productivity blocks (Table 3).

The number of plant species unique to a grazed treatment depended on the herbivore assemblage and the production class as well as their interaction (herbivore assemblage:  $F_{1,39} = 15.84$ ,  $P < 0.001$ , production:  $F_{1,39} = 4.38$ ,  $P = 0.04$ , herbivore assemblage  $\times$  production:  $F_{1,39} = 6.94$ ,  $P = 0.01$ ). A *post hoc* Tukey test revealed that significantly more species were unique to the treatment including large plus small herbivores at high production relative to all other treatments (Table 3). The number of plant species unique to the ungrazed treatment was not significantly different between herbivore assemblages or production classes (herbivore assemblage:  $F_{1,39} = 1.82$ ,  $P = 0.19$ , production:  $F_{1,39} = 2.62$ ,  $P = 0.11$ , herbivore assemblage  $\times$  production:  $F_{1,39} = 0.04$ ,  $P = 0.85$ ).

The change in plant community composition under grazing was affected by productivity ( $F_{1,37} = 18.54$ ,  $P < 0.001$ ), but not by the type of herbivore assemblage ( $F_{1,37} = 0.003$ ,  $P = 0.96$ , productivity  $\times$  herbivore assemblage  $F_{1,37} = 0.47$ ,  $P = 0.50$ ). Herbivores had an increasingly stronger impact on plant community composition towards higher plant production (Fig. 3).

## DISCUSSION

We found that the impact of herbivores on plant species richness depended on habitat aboveground plant produc-



**Figure 2** How various herbivores affected plant species richness along the primary productivity gradient. The figure shows the effect of herbivore assemblage on plant species richness in relation to aboveground primary productivity (a,b) and to the shoot–root ratio of the vegetation (c,d). The joint effect of large and small herbivores on plant diversity changed from negative to positive with increasing production and increasing shoot–root ratio of the vegetation, while these effects were not significant when only small herbivores were present. Relative effects of different-sized herbivores on plant species richness were analysed across the productivity gradient using regression across blocks as blocks varied in aboveground productivity within sites.

**Table 3** The change in plant species richness and species shifts when comparing grazed treatments with the treatment where large and small herbivores were excluded (the ungrazed treatment) at low (0–300 g m<sup>-2</sup>) and high (300–600 g m<sup>-2</sup>) aboveground annual net primary productivity

Aboveground production	0–300 g m <sup>-2</sup>		300–600 g m <sup>-2</sup>	
Herbivore assemblage	Large + small	Small	Large + small	Small
Change in number of plant species	-3.5 ± 1.2* (n = 19)	-2.6 ± 1.7 <sup>NS</sup> (n = 12)	3.9 ± 1.3* (n = 7)	-1.4 ± 1.3 <sup>NS</sup> (n = 5)
Number of species unique to a grazing treatment	6.4 ± 0.9 <sup>a</sup>	4.8 ± 0.8 <sup>a</sup>	12.0 ± 1.6 <sup>b</sup>	4.2 ± 0.7 <sup>a</sup>
Number of species unique to the ungrazed treatment	10.5 ± 1.2 <sup>a</sup>	8.6 ± 1.5 <sup>a</sup>	8.1 ± 1.1 <sup>a</sup>	5.6 ± 0.9 <sup>a</sup>

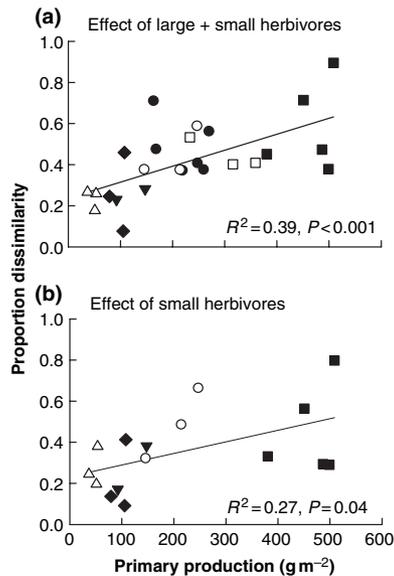
Data are mean values ± 1 SE. For each herbivore assemblage and production class we tested whether the change in plant species number is significantly different from 0 with a one-sample *t*-test. NS, *P* > 0.05; \**P* < 0.05. Different letters indicate statistically different numbers of species unique to grazing treatments and production classes.

tion in a predictable manner: herbivores had a negative impact on plant diversity at low plant production and a positive impact at high plant production, but only when larger herbivore species were included in the assemblage. This relationship emerged from a single-field experiment over a 10-fold production gradient consisting of different grassland plant communities and different local herbivore communities, indicating that this pattern does not depend on the properties of specific plant or herbivore species. With these results we can generalize similar patterns that were found in a Mediterranean annual plant community

(Osem *et al.* 2002) and Yellowstone National Park (Frank 2005).

Herbivores can affect plant species diversity by modifying local extinction or colonization rates, or both (Glenn & Collins 1992; Olff & Ritchie 1998). The question whether herbivores increase or decrease plant diversity over a productivity gradient thus translates into the question how herbivore impact on extinction and colonization rates changes with productivity.

Herbivores may have positive effects on plant species richness at high plant production when they can limit the



**Figure 3** Herbivore effects on plant community composition along the primary productivity gradient. The graph shows the dissimilarity in species composition due to exclusion of large plus small (a) or small (b) herbivores. The study sites are indicated with different symbols; see Fig. 2 for description of the symbols.

intensity of light competition between established species through biomass removal which may result in reduced local extinction rates (Huisman & Olf 1998; Huisman *et al.* 1999). Although we did not measure which factor limited plant growth at each site, the shoot–root ratio, our proxy for the traits required to compete for belowground resources vs. light (Olf 1992; Poorter & Nagel 2000), does match the proposed increasing importance of light limitation over our productivity gradient. Different plant traits are required to cope with light vs. nutrient or water limitation (Tilman 1985; Tilman & Wedin 1991). The response of plant species to grazing may interact with the adaptation of plant traits to belowground or aboveground limiting factors for growth (Pakeman 2004). Milchunas & Lauenroth (1993) and Osem *et al.* (2002) hypothesized that in unproductive habitats, where most of the plant biomass is located belowground, mammalian herbivores have little impact on species composition, whereas with increasing productivity more biomass is allocated aboveground, increasing the potential for herbivores to affect species composition. Our data support this hypothesis: the impact of herbivores on the plant community composition (expressed as dissimilarity) increased with increasing plant production. Although our results were consistent with the hypothesis that herbivores reduce the intensity of light competition between plants, the positive effect of large plus small herbivores on diversity under productive conditions was explained by enhanced colonization of new species, rather than lower loss of

species from plots. This result suggests that grazers enhanced diversity through alleviating (light) limitations on recruitment, rather than diminishing the intensity of competition between established species.

Herbivores can contribute to increased colonization rates by increasing light availability which enhances germination rates and seedling survival (Bakker & De Vries 1992; Jutila & Grace 2002). Additionally, herbivores can disturb the vegetation canopy and create bare soil patches, which can serve as regeneration sites for plant species (Bakker & Olf 2003). Seeds of numerous species can survive herbivore consumption or attach to fur, making herbivores vectors for plant dispersal (Malo & Suarez 1995; Cosyns *et al.* 2005). However, herbivore consumption of seeds and seedlings can also be a major source of reduced recruitment of plant species (Brown & Heske 1990; Edwards & Crawley 1999; Howe *et al.* 2002). So far, the interaction between positive and negative effects of herbivores on plant colonization rates is unclear. In grasslands without large mammalian herbivores, plant species richness changes from being propagule to recruitment site limited with increasing productivity (Foster *et al.* 2004; Stevens *et al.* 2004). Following these findings, we can hypothesize that the positive effects of herbivores on colonization rates that we found at high plant production may result from an increase in recruitment sites through herbivore disturbance, whereas negative effects at low productivity may result from propagule predation. However, Eskelinen & Virtanen (2005) found that plant species richness was limited both by seed and microsite availability under grazing in a low productive tundra system, therefore, the interaction between grazing and productivity on species colonization rates remains to be tested.

In our study, we did find an interaction between grazing by large and small herbivores and plant production on species richness. However, when large herbivores were excluded and only small herbivores were present, we did not find a consistent effect of grazing on plant species richness. Small herbivores can have strong effects on grassland plant diversity and community composition (Brown & Heske 1990; Edwards & Crawley 1999; Van der Wal *et al.* 2000; Howe *et al.* 2002; Olofsson *et al.* 2004), but other studies showed little response of the vegetation to small mammal herbivory (Gibson *et al.* 1990; Norrdahl *et al.* 2002). Our results show that small herbivores had considerable impacts in some blocks, but not in others. We cannot discriminate whether variation in small herbivore densities between or within sites may partially account for the lack of pattern that we found or that small herbivores simply had little impact in some sites.

In our study the division between large and small herbivores was mainly determined by practical limitations of fence types used in the field. Within and between the

categories of large and small herbivores, different feeding modes were represented, for example, cattle and bison are mostly grazers, whereas most deer species are browsers and rodents and lagomorphs could be granivorous. Accounting for these differences in herbivore feeding selectivity might help to further unravel the mechanisms underlying the patterns that we found.

Our results highlight the importance of habitat productivity in predicting the impact of mammalian herbivores on grassland diversity. Large grazers, such as bison, have specific importance in maintaining plant diversity in productive systems such as tallgrass prairie in North America (Collins *et al.* 1998) or grasslands in Europe (Bakker 1989; Ritchie & Olff 1999). Large herbivores and people (agriculture) often compete for the same high productivity areas (Olff *et al.* 2002). The conservation or re-introduction of large grazers in the few remaining highly productive natural grasslands worldwide is likely crucial for the plant diversity in these areas. However, large grazers should not be introduced everywhere as they can have negative effects on diversity, especially in unproductive areas (such as arid ecosystems) or areas that have no recent evolutionary history of abundant large herbivore grazing (Milchunas *et al.* 1988). In light of continuing global loss of native large herbivores from natural areas and continued introduction of livestock into new areas, the recognition of the trends shown by our results is critical for developing strategies of appropriate biodiversity conservation management.

## ACKNOWLEDGEMENTS

We thank Heidi Hillhouse for data collection on Konza and Cedar Creek; Mark Lindquist, Nicole Kaplan, Judy Hendryx, and the LTER field crew for their assistance at the short grass steppe; Heather and Nathan Jackson, Leah Perfetti and Molly Schmelzle for assistance at Deseret Ranch; Julia Stahl and Marieke Harteveld for field assistance at Junner Koeland; Cathleen McFadden for performing the chemical analyses; the USDA-ARS that maintains the long-term grazing treatment pastures on the short grass steppe; Deseret Land and Livestock (Woodruff Utah) and the Netherlands National Forest Service for access to their lands. We thank Scott Collins and two anonymous referees for their comments on an earlier version of this paper. This study was supported with grants from the US National Science Foundation (NSF) and the Netherlands Organisation for Scientific Research (NWO). This is publication 3796 of the NIOO-KNAW Netherlands Institute of Ecology.

## REFERENCES

Adler, P.B., Milchunas, D.G., Sala, O.E., Burke, I.C. & Lauenroth, W.K. (2005). Plant traits and ecosystem grazing effects: com-

- parison of US sagebrush steppe and Patagonian steppe. *Ecol. Appl.*, 15, 774–792.
- Bakker, J.P. (1989). *Nature Management by Grazing and Cutting*. Kluwer Academic Publishers, Dordrecht.
- Bakker, J.P. & De Vries, Y. (1992). Germination and early establishment of lower salt-marsh species in grazed and mown salt marsh. *J. Veg. Sci.*, 3, 247–252.
- Bakker, E.S. & Olff, H. (2003). The impact of different-sized herbivores on recruitment for subordinate herbs in grasslands. *J. Veg. Sci.*, 14, 465–474.
- Belsky, A.J. (1992). Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. *J. Veg. Sci.*, 3, 187–200.
- Brown, J.H. & Heske, E.J. (1990). Control of a desert-grassland transition by a keystone rodent guild. *Science*, 250, 1705–1707.
- Collins, S.L., Knapp, A.K., Briggs, J.M., Blair, J.M. & Steinauer, E.M. (1998). Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science*, 280, 745–747.
- Cosyns, E., Delporte, A., Lens, L. & Hoffmann, M. (2005). Germination success of temperate grassland species after passage through ungulate and rabbit guts. *J. Ecol.*, 93, 353–361.
- Edwards, G.R. & Crawley, M.J. (1999). Herbivores, seed banks and seedling recruitment in mesic grassland. *J. Ecol.*, 87, 423–435.
- Eskelinen, A. & Virtanen, R. (2005). Local and regional processes in low-productive mountain plant communities: the role of seed and microsite limitation in relation to grazing. *Oikos*, 110, 360–368.
- Foster, B.L., Dickson, T.L., Murphy, C.A., Karel, I.S. & Smith, V.H. (2004). Propagule pools mediate community assembly and diversity–ecosystem regulation along a grassland productivity gradient. *J. Ecol.*, 92, 435–449.
- Frank, D.A. (2005). The interactive effects of grazing ungulates and aboveground production on grassland diversity. *Oecologia*, 143, 629–634.
- Gibson, D.J., Freeman, C.C. & Hulbert, L.C. (1990). Effects of small mammal and invertebrate herbivory on plant species richness and abundance in tallgrass prairie. *Oecologia*, 84, 169–175.
- Glenn, S.M. & Collins, S.L. (1992). Effects of scale and disturbance on rates of immigration and extinction of species in prairies. *Oikos*, 63, 273–280.
- Grubb, P.J. (1977). Maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev.*, 52, 107–145.
- Howe, H.F., Brown, J.S. & Zorn-Arnold, B. (2002). A rodent plague on prairie diversity. *Ecol. Lett.*, 5, 30–36.
- Huisman, J. & Olff, H. (1998). Competition and facilitation in multispecies plant-herbivore systems of productive environments. *Ecol. Lett.*, 1, 25–29.
- Huisman, J., Grover, J.P., Van der Wal, R. & Van Andel, J. (1999). Competition for light, plant-species replacement and herbivore abundance along productivity gradients. In: *Herbivores: Between Plants and Predators* (eds Olff, H., Brown, V.K. & Drent, R.H.). Blackwell Science, Oxford, pp. 239–269.
- Jutila, H.M. & Grace, J.B. (2002). Effects of disturbance on germination and seedling establishment in a coastal prairie grassland: a test of the competitive release hypothesis. *J. Ecol.*, 90, 291–302.
- Knapp, A.K., Blair, J.M., Briggs, J.M., Collins, S.L., Hartnett, D.C., Johnson, L.C. *et al.* (1999). The keystone role of bison in North American Tallgrass Prairie. *Bioscience*, 49, 39–50.

- Malo, J.E. & Suarez, F. (1995). Herbivorous mammals as seed dispersers in a Mediterranean dehesa. *Oecologia*, 104, 246–255.
- McNaughton, S.J., Oesterheld, M., Frank, D.A. & Williams, K.J. (1989). Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature*, 341, 142–144.
- Milchunas, D.G. & Lauenroth, W.K. (1993). Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecol. Monogr.*, 63, 327–366.
- Milchunas, D.G., Sala, O.E. & Lauenroth, W.K. (1988). A generalized model of the effects of grazing by large herbivores on grassland community structure. *Am. Nat.*, 132, 87–106.
- Milchunas, D.G., Lauenroth, W.K. & Burke, I.C. (1998). Livestock grazing: animal and plant biodiversity of shortgrass steppe and the relationship to ecosystem function. *Oikos*, 83, 65–74.
- Norrdahl, K., Klemola, T., Korpimäki, E. & Koivula, M. (2002). Strong seasonality may attenuate trophic cascades: vertebrate predator exclusion in boreal grassland. *Oikos*, 99, 419–430.
- Olf, H. (1992). Effects of light and nutrient availability on dry-matter and N-allocation in 6 successional grassland species: testing for resource ratio effects. *Oecologia*, 89, 412–421.
- Olf, H. & Ritchie, M.E. (1998). Effects of herbivores on grassland plant diversity. *Trends Ecol. Evol.*, 13, 261–265.
- Olf, H., Ritchie, M.E. & Prins, H.H.T. (2002). Global environmental controls of diversity in large herbivores. *Nature*, 415, 901–904.
- Olofsson, J., Hulme, P.E., Oksanen, L. & Suominen, O. (2004). Importance of large and small mammalian herbivores for the plant community structure in the forest tundra ecotone. *Oikos*, 106, 324–334.
- Osem, Y., Perevolotsky, A. & Kigel, J. (2002). Grazing effect on diversity of annual plant communities in a semi-arid rangeland: interactions with small-scale spatial and temporal variation in primary productivity. *J. Ecol.*, 90, 936–946.
- Pakeman, R.J. (2004). Consistency of plant species and trait responses to grazing along a productivity gradient: a multi-site analysis. *J. Ecol.*, 92, 893–905.
- Poorter, H. & Nagel, O. (2000). The role of biomass allocation in the growth response of plants to different levels of light, CO<sub>2</sub>, nutrients and water: a quantitative review. *Aust. J. Plant Physiol.*, 27, 595–607.
- Prins, H.H.T., Grootenhuis, J.G. & Dolan, T.T. (eds) (2000). *Wildlife Conservation and Sustainable Use*. Kluwer Academic Publishers, Dordrecht.
- Proulx, M. & Mazumder, A. (1998). Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology*, 79, 2581–2592.
- Ritchie, M.E. & Olf, H. (1999). Herbivore diversity and plant dynamics: compensatory and additive effects. In: *Herbivores: Between Plants and Predators* (eds Olf, H., Brown, V.K. & Drent, R.H.). Blackwell Science, Oxford, pp. 175–204.
- SPSS Inc. (2003). *SPSS 12.0*. SPSS Inc., Chicago, IL.
- Stevens, M.H.H., Bunker, D.E., Schnitzer, S.A. & Carson, W.P. (2004). Establishment limitation reduces species recruitment and species richness as soil resources rise. *J. Ecol.*, 92, 339–347.
- Stohlgren, T.J., Schell, L.D. & Vanden Heuvel, B. (1999). How grazing and soil quality affect native and exotic plant diversity in rocky mountain grasslands. *Ecol. Appl.*, 9, 45–64.
- Tilman, D. (1985). The resource-ratio hypothesis of plant succession. *Am. Nat.*, 125, 827–852.
- Tilman, D. & Wedin, D. (1991). Plant traits and resource reduction for five grasses growing on a nitrogen gradient. *Ecology*, 72, 685–700.
- Van der Wal, R., Van Wijnen, H., Van Wieren, S., Beucher, O. & Bos, D. (2000). On facilitation between herbivores: how Brent Geese profit from brown hares. *Ecology*, 81, 969–980.
- WallisDeVries, M.F., Bakker, J.P. & Van Wieren, S.E. (1998). *Grazing and Conservation Management*. Kluwer Academic Publishers, Dordrecht.
- Wardle, D.A., Barker, G.M., Yeates, G.W., Bonner, K.I. & Ghani, A. (2001). Introduced browsing mammals in New Zealand natural forests: aboveground and belowground consequences. *Ecol. Monogr.*, 71, 587–614.
- Whittaker, R.H. (1952). A study of summer foliage insect communities in the Great Smoky Mountains. *Ecol. Monogr.*, 22, 1–44.

## SUPPLEMENTARY MATERIAL

The following supplementary material is available online at <http://www.Blackwell-Synergy.com>:

### Appendix S1 Site descriptions.

Editor, Don Waller

Manuscript received 6 October 2005

First decision made 15 November 2005

Second decision made 28 January 2006

Manuscript accepted 20 February 2006