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.

INTRODUCTION
Vertebrate herbivores can be key determinants of grassland plant species composition and diversity (McNaughton et al. 1989; Collins et al. 1998; Olff & 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. 1998; 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;...
unfenced controls on 400- to 900-m
1994 and 1996 we established similar sets of exclosures and
assemblage of mammalian herbivores (Table 1). Between
ground plant productivity and each supported a varied
richness have not yet been addressed in large-scale, cross-
size as determinants of the impact of herbivores on plant
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–
600 g m\(^{-2}\) year\(^{-1}\)) and a variety of vertebrate herbivore
communities. We show that assemblages with large herbiv-
ores increased plant diversity at higher productivity but
decreased diversity at low productivity, while small herbiv-
ores 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 above-
ground plant productivity and each supported a varied
assemblage of mammalian herbivores (Table 1). Between
1994 and 1996 we established similar sets of enclosures and
unfenced controls on 400- to 900-m\(^2\) 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 \(\times\) 0.5 m at the
Short grass steppe, 20 plots of 0.5 \(\times\) 1.0 m at the Tallgrass
prairie, the Montane grassland, Bunch grass steppe and Sage
brush steppe, 10 plots of 0.5 \(\times\) 1.0 m at the Oak savanna
and two plots of 2.0 \(\times\) 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 meas-
ured 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\(^2\). 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

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Table 1  Characteristics of the study sites

<table>
<thead>
<tr>
<th>Site</th>
<th>Habitat type</th>
<th>Geographical position</th>
<th>Fertility (g N kg(^{-1}) soil)</th>
<th>C : N ratio in soils</th>
<th>Precipitation (mm year(^{-1}))</th>
<th>Aboveground annual net primary productivity (g m(^{-2}) 2002)</th>
<th>% Biomass removed</th>
<th>No. replicates</th>
<th>Outside exclosure, all herbivores</th>
<th>Inside large-mesh fence</th>
<th>Inside small-mesh fence</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deseret Sage (UT, USA)</td>
<td>Sage brush steppe</td>
<td>41°11' N 111°5' W</td>
<td>1.51 ± 0.19</td>
<td>14.5 ± 2.0</td>
<td>305 (261)</td>
<td>47 ± 5</td>
<td>36 ± 3</td>
<td>3</td>
<td>Cattle, elk, mule deer, pronghorn rabbits, prairie dogs and rodents</td>
<td>Rabbits, prairie dogs and rodents</td>
<td>Small rodents</td>
</tr>
<tr>
<td>Short Grass Steppe (CO, USA)</td>
<td>Short grass steppe</td>
<td>40°49' N 104°46' W</td>
<td>1.43 ± 0.29</td>
<td>10.7 ± 0.2</td>
<td>322 (160)</td>
<td>97 ± 9*</td>
<td>11 ± 5†</td>
<td>3</td>
<td>Cattle, pronghorn, rabbits and rodents</td>
<td>Rabbits and rodents</td>
<td>Small rodents excluded†</td>
</tr>
<tr>
<td>Deseret Low (UT, USA)</td>
<td>Bunch grass steppe</td>
<td>41°21' N 111°5' W</td>
<td>1.14 ± 0.24</td>
<td>9.8 ± 0.1</td>
<td>305 (261)</td>
<td>125 ± 17</td>
<td>37 ± 5</td>
<td>3</td>
<td>Cattle, elk, mule deer, pronghorn rabbits, prairie dogs and rodents</td>
<td>Rabbits, prairie dogs and rodents</td>
<td>Small rodents</td>
</tr>
<tr>
<td>Deseret High (UT, USA)</td>
<td>Montane grassland</td>
<td>41°25' N 111°25' W</td>
<td>1.51 ± 0.30</td>
<td>12.1 ± 0.4</td>
<td>635 (532)</td>
<td>203 ± 30</td>
<td>30 ± 15</td>
<td>3</td>
<td>Sheep, elk, rabbits and rodents</td>
<td>Rabbits and rodents</td>
<td>Small rodents</td>
</tr>
<tr>
<td>Cedar Creek (MN, USA)</td>
<td>Oak savanna</td>
<td>45°5' N 93°10' W</td>
<td>0.84 ± 0.06</td>
<td>17.9 ± 0.3</td>
<td>825 (840)</td>
<td>222 ± 19</td>
<td>15 ± 7</td>
<td>6</td>
<td>White-tailed deer and rodents</td>
<td>No herbivores &lt; 10 and &gt; 1 kg present</td>
<td>Small rodents</td>
</tr>
<tr>
<td>Konza (KS, USA)</td>
<td>Tallgrass prairie</td>
<td>39°08' N 96°6' E</td>
<td>3.03 ± 0.18</td>
<td>13.5 ± 0.2</td>
<td>835 (676)</td>
<td>302 ± 37</td>
<td>49 ± 5</td>
<td>3</td>
<td>Bison, white-tailed deer and rodents</td>
<td>No herbivores &lt; 10 and &gt; 1 kg present</td>
<td>Small rodents</td>
</tr>
<tr>
<td>Junner Koeland (the Netherlands)</td>
<td>Floodplain grassland</td>
<td>52°32' N 6°29' E</td>
<td>2.76 ± 0.34</td>
<td>11.3 ± 0.2</td>
<td>738 (835)</td>
<td>489 ± 19</td>
<td>20 ± 9</td>
<td>5</td>
<td>Cattle, rabbits and rodents</td>
<td>Rabbits and rodents</td>
<td>Small rodents</td>
</tr>
</tbody>
</table>

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 and the value for September 2001 to September 2002, 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 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 m², 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 × (Sj − Sj)/Sj, where Sj is the species richness in the presence of the herbivore assemblage of interest and Sj is the species richness in the exclusion 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⁻²) and high (300–600 g m⁻²) productivity, and evaluated the effects of different herbivore assemblages on plant diversity and species turnover for each class. The threshold of 300 g m⁻² 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,
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 (0–300 g m$^{-2}$) and high (300–600 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 $> 30$ 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-
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 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⁻²) and high (300–600 g m⁻²) aboveground annual net primary productivity.

<table>
<thead>
<tr>
<th>Aboveground production</th>
<th>0–300 g m⁻²</th>
<th>300–600 g m⁻²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Herbivore assemblage</td>
<td>Large + small</td>
<td>Small</td>
</tr>
<tr>
<td>Change in number of plant species</td>
<td>−3.5 ± 1.2* (n = 19)</td>
<td>−2.6 ± 1.7NS (n = 12)</td>
</tr>
<tr>
<td>Number of species unique to a grazing treatment</td>
<td>6.4 ± 0.9*</td>
<td>4.8 ± 0.8*</td>
</tr>
<tr>
<td>Number of species unique to the ungrazed treatment</td>
<td>10.5 ± 1.2a</td>
<td>8.6 ± 1.5b</td>
</tr>
</tbody>
</table>

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.
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.

The intensity of light competition between established species through biomass removal which may result in reduced local extinction rates (Huisman & Ollf 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 (Ollf 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 & DeVries 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 & Ollf 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; Norddahl 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.

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**REFERENCES**


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**SUPPLEMENTARY MATERIAL**

The following supplementary material is available online at [http://www.Blackwell-Synergy.com](http://www.Blackwell-Synergy.com):

Appendix S1 Site descriptions.