

Plant community response to loss of large herbivores: comparing consequences in a South African and a North American grassland

Catherine E. Burns · Scott L. Collins · Melinda D. Smith

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Abstract Loss of biodiversity poses one of the greatest threats to natural ecosystems throughout the world. However, a comprehensive understanding of the impacts of species losses from upper trophic levels is still emerging. Here we compare the impacts of large mammalian herbivore species loss on grassland plant community structure and composition in a South African and North American grassland. Herbaceous plant communities were surveyed at sites without large mammalian herbivores present and at sites with a single species of herbivore present in both locations, and additionally at one site in South Africa with multiple herbivore species. At both the North American and South African locations, plant communities on sites with a single herbivore species were more diverse and species rich than on sites with no herbivores. At the multi-herbivore site in South Africa, plant diversity and richness were comparable to that of the single herbivore site early in the growing season and to the no herbivore site late in the growing season. Analyses of plant community composition, however, indicated strong differences between the multi-herbivore site and the single and no herbivore sites, which were more similar to each other. In moderate to high-productivity ecosystems with one or a few species of large herbivores, loss of herbivores can cause a significant decrease in plant diversity and richness, and can have pronounced impacts on grassland plant community composition. In ecosystems with higher herbivore richness, species loss may also significantly alter plant

C. E. Burns (✉) · M. D. Smith
Department of Ecology & Evolutionary Biology, Yale University, 165 Prospect St, New Haven,
CT 06511, USA
e-mail: catherine.burns@umit.maine.edu

M. D. Smith
e-mail: melinda.smith@yale.edu

Present Address:

C. E. Burns
Department of Wildlife Ecology, University of Maine, 5755 Nutting Hall, Orono,
ME 04469-5755, USA

S. L. Collins
Department of Biology, MSC03-2020, University of New Mexico, Albuquerque, NM 87131, USA
e-mail: scollins@sevilleta.unm.edu

community structure and composition, although standard metrics of community structure may obscure these differences.

Keywords Biodiversity · Community structure · Diversity · Herbivory · Richness · Savanna · Species loss

Introduction

Loss of biodiversity poses one of the greatest threats to natural ecosystems throughout the world, and is increasingly being caused by anthropogenic factors, including land-use change, habitat loss, hunting, and the replacement of diverse suites of species with single species monocultures, such as crops or livestock (Pimm et al. 1995; Frank et al. 1998; WallisDeVries et al. 1998; du Toit and Cumming 1999). Understanding the impacts of biodiversity loss has therefore been a focus of much research, with investigations particularly targeting the implications of decreased diversity in lower trophic-levels. Many such studies indicate that loss of diversity can lead to significant changes in community structure and ecosystem functioning (Tilman et al. 2001; Loreau et al. 2002; Hooper et al. 2005).

Less clearly understood are the impacts of loss at higher trophic levels, such as large herbivores, on composition and structure of lower trophic-level communities (Duffy 2002). These species are also capable of driving ecosystem-wide changes (Hobbs 1996). We investigated the impacts of loss of large mammalian herbivores (those exceeding 5 kg in body mass) on grassland plant community structure (e.g. diversity, richness, dominance) and species composition. Loss of dominant herbivore species from grassland ecosystems in North America has been shown to depress plant species richness and diversity, as well as to drive changes in patterns of spatial heterogeneity in grassland vegetation (Collins et al. 1998; Knapp et al. 1999; Frank 2005; Collins and Smith 2006). In these systems large herbivore species richness was higher historically, but now is typically one to two species (Jacobs et al. 1999). In North America, the effects of losing the remaining dominant herbivore species are relatively well understood (e.g. see Hartnett et al. 1996; Collins et al. 1998; Knapp et al. 1999; Hickman et al. 2004; Frank 2005). In many African grassland conservation areas, such as national parks, a functionally diverse and species-rich large herbivore community still exists. The effects of herbivore species losses from these communities are likely to be more complex, and general rules for predicting the impacts of herbivore loss are still emerging (Milchunas and Lauenroth 1993; Augustine and McNaughton 2004; Bakker et al. 2006; Anderson et al. 2007). Recent advances, however, suggest that while species losses in these multi-herbivore communities generally result in declines in plant diversity, the removal of herbivores can have the reverse effect in low productivity ecosystems (Olf and Ritchie 1998; Bakker et al. 2006).

Our primary goal was to examine two structurally similar grassland ecosystems, one each in North America (NA) and South Africa (SA), to identify similarities and differences in the responses of the herbaceous component of grassland plant communities to loss of large herbivore species. We conducted this research in a tallgrass prairie ecosystem in the Flint Hills of northeastern Kansas, USA, and in the savanna grassland of central Kruger National Park, in northeastern SA. Both ecosystems are characterized by the existence of a continuous grass layer with a discontinuous overstory of shrubs and trees. Tallgrass prairies in NA are highly productive, temperate, mesic grasslands that are located in the central Great Plains and positioned between the drier and less productive shortgrass prairies to the

west and the forested ecosystems of the eastern and northern United States (Knapp et al. 1998). The savanna grasslands of Kruger are part of the lowveld of northeastern SA—low relief plains positioned between the Drakensberg Escarpment to the west and the coastal plain of Mozambique to the east (Venter et al. 2003).

In both regions, considerable research effort has consistently shown fire, grazing and precipitation to be the key drivers shaping the structure and function of plant communities (Collins and Wallace 1990; Briggs and Knapp 1995; Snyman 2000, 2002; Bond et al. 2003; du Toit et al. 2003). Further, historic large herbivore species richness in both regions is estimated at 45–50 species (Martin 1984). However, our NA and SA study locations differ with respect to climate (temperate in NA, sub-tropical in SA), the current species richness of large herbivores (low in NA, high in SA), soil nutrient levels (high in NA, low in SA; Scholes et al. 2003a, b), and evolutionary history [short in NA due to recent glaciations, long in SA (Bond et al. 2003)]. We seek to examine whether, in spite of the differences between these ecosystems (i.e. contingent factors, Knapp et al. 2004), there exist common responses of the herbaceous plant communities to a reduction in herbivore biodiversity.

We examined herbaceous plant community structure and composition at sites with and without the native herbivore bison (*Bos bison*) at our NA location in Kansas. At our SA location, we surveyed vegetation at sites with no large herbivore species, with a single species (Cape buffalo, *Syncerus caffer*), and with the full assemblage of large herbivores found in this region of southern Africa. Each of these sites has historically been managed with intermediate fire return intervals of 3–5 years, and has an annual net primary production of 400–500 g m⁻² (Knapp et al. 2004; G. Buis, unpublished data).

We predicted that sites in SA and NA with a single large-bodied herbivore species, Cape buffalo and bison, respectively, would have higher plant species richness and diversity and lower dominance than sites with no herbivores (Olf and Ritchie 1998; Bakker et al. 2006). Because both preferentially consume graminoid species, we proposed that this response would be driven primarily by the consumption and reduction in abundance of the palatable, dominant C₄ grass species at both locations, thereby eliciting a positive response in forb and subdominant grass abundance and richness. This would result in an increase in overall richness and diversity, a decrease in dominance, and an alteration in community composition (Hartnett et al. 1996; Collins et al. 1998). Further, we predicted that the full complement of large herbivores in SA would have a reduced impact on plant community structure (e.g. richness, diversity) compared to a single grazing herbivore species, due to suppression of forb growth and maintenance of the dominant C₄ grass community by smaller-bodied herbivores which preferentially forage on non-graminoid species (du Toit 2003). We predicted strong compositional differences at the multi-herbivore site, however, as grazing tolerant grasses replaced those that were more sensitive to grazing (Martens et al. 1996).

Methods

Study sites

Our research was conducted in Kruger National Park, South Africa (22° 25' to 25° 32' S, 30° 50' to 32° 2' E), and at the Konza Prairie Biological Station in Kansas, USA (39° 05' N, 96° 35' W). At Kruger, we examined herbaceous plant community structure and composition at each of three adjacent study sites in the south-central Satara region of the park, an

extensive area of savanna grassland with level topography and characterized by the coexistence of a suite of C₄ grasses and several dominant woody species. Mean rainfall in the Satara region of Kruger averages 500 mm year⁻¹ (578 mm during the year of our study; SA weather service) with precipitation largely limited to November through March (based on data from 1961 to 1990, Venter et al. 2003). Soils are fine-textured, clayey and largely uniform throughout the Satara region (Venter et al. 2003). The three study sites included one that was open to the full complement of large mammalian herbivores found in the region (approximately 14 herbivore species, e.g. elephant, rhinoceros, wildebeest, zebra, and henceforth referred to as the “multiple herbivore” site), a second that was exposed to a single species of herbivore (“single herbivore” site), the Cape buffalo which is ecologically comparable to bison in North America, and a third in which large herbivores were entirely excluded (“no herbivore” site). To minimize the chances of confounding any herbivore treatment effect with inherent site-specific differences at Kruger, all three study sites were established in areas with comparable productivity, soil type, topographic position, and current and historic fire frequency, and were located less than 1 km apart.

The single herbivore and no herbivore sites were located within a 900 ha Cape buffalo enclosure established at Satara in 2002. Approximately 50–80 Cape buffalo have been stocked and maintained inside the enclosure at a density of approximately 0.08 adult animals/ha since early 2002 (M Kruger, pers comm). All buffalo were free to move throughout the enclosure, with the exception of a 9 ha area that was fenced off to exclude all herbivores. This area was herbivore-free for nearly 4 years prior to our study. Our vegetation sampling was conducted in areas of the Cape buffalo enclosure and adjacent herbivore enclosure that were historically (and currently) burned on average once every 3 years in late winter. The multiple herbivore site was located in an adjacent 16 ha experimental burn plot (EBP), which was open on all sides to movement of animals onto and off of the plot (Enslin et al. 2000; Biggs et al. 2003; Govender et al. 2006). Graded fire guards separate the EBP from the Cape buffalo enclosure. The EBP has been burned approximately every 3 years in the late winter for the past 53 years. None of the sites were burned during the year of our study.

At Konza, we sampled herbaceous vegetation in a 19 ha watershed with no large herbivores present since 1973, and in an adjacent 100 ha watershed (separated only by a gravel road and fire guard) which has been grazed by bison at a density of approximately 0.2 animals/ha since 1987 (~ 200 animals within roughly 1,000 ha; Knapp et al. 1998, 1999). Both of these watersheds have been burned approximately once every 4 years in early spring since 1977 and 1987, respectively, and were not burned during the year of our study. At Konza, although white-tailed deer (*Odocoileus virginianus*) occasionally occur in low abundances with bison, there is no true “multiple herbivore” treatment comparable to that in South Africa. Mean annual precipitation at Konza is 857 mm year⁻¹ (937 mm during the year of our study; Konza LTER on-line dataset APT011) with most falling during the months of April–September (based on data from 1960 to 2002, SD = 214 mm, from Knapp et al. 2006). Soils across Konza are fine textured silty clay loams (Ransom et al. 1998).

The vegetation structure and composition in Kruger and Konza are representative of their respective ecosystem types—the mesic grasslands of the central US and the more arid grasslands of southern Africa. In Kruger the vegetation is characterized by a mixture of dominant perennial C₄ grasses such as *Bothriochloa radicans*, *Digitaria eriantha*, *Themeda triandra*, and *Urochloa mosambicensis*, and woody species including Knobthorn (*Acacia nigrescens*) and Marula (*Sclerocarya birrea*) trees. At Konza, native C₄ grasses such as

Andropogon gerardii and *Sorghastrum nutans* dominate the landscape, along with a variety of C_3 grass and forb species, and scattered woody species including *Amorpha canescens* and *Ceanothus herbaceus*. At both Konza and Kruger, areas managed with intermediate fire frequencies of 3–4 years support a mixture of these herbaceous and woody species (Eckhardt et al. 2000; Heisler et al. 2003).

Vegetation sampling

At each of the five study sites (three at Kruger, two at Konza), we quantified herbaceous plant community structure and composition near the beginning and end of the growing season. In Kruger, we sampled vegetation plots in December 2005 and March 2006, and at Konza, in June and August 2005. Four transects were established at each site ($N = 12$ plots/site), consisting of three 2×2 m vegetation plots spaced every 15 m along each transect. The four transects at each site were positioned parallel to each other and 25 m apart, spanning an area of 2,250 m² per site. This sampling protocol enabled us to assess patterns of vegetation response to large herbivore species loss at the local scale for our study sites at Konza and Kruger. The generality of the responses we describe—for greater spatial and temporal scales and for other savanna grassland ecosystems—remains to be tested explicitly. As our goal was to assess patterns of response in herbaceous vegetation, when a vegetation plot was to fall within an area dominated by woody plant species, the plot was moved laterally to the nearest point dominated by herbaceous vegetation. As woody plant cover was generally sparse at each site, this occurred infrequently. Each of our study sites was effectively uniform in topography, moisture and vegetation structure (i.e. there were no clear gradients among or within transects). Each 2×2 m plot was subdivided into four 1×1 m subplots. We visually estimated the percent cover of each plant species rooted in each subplot to the nearest 5%. All plots on all transects were sampled both early and late in the growing season, with the exception of the single herbivore site at Kruger, where two out of three plots in each transect were sampled in the early growing season ($N = 8$), due to limited accessibility during the wettest portion of the year, and all plots were sampled late in the growing season ($N = 12$).

Cover data for each species were averaged across the four subplots and then used to compute standard metrics of community structure, including grass, forb, and total species richness (S), Shannon–Weiner diversity (H'), evenness (J), Simpson's dominance (D) and the relative cover of each species (Magurran 1988). These metrics were calculated separately for the early and late growing season data for Kruger, because of difficulty in identifying to species a minority of individuals found during the early season sampling period. A unique identification number was assigned to individuals that we were unable to identify to species. This enabled us to accurately compute metrics of plant community structure based on the full complement of vegetation sampled. We present both early and late season results separately to identify any seasonal variation in patterns or strength of response of the plant community to herbivore treatments. For Konza, the metrics were calculated using the maximum average cover values of each species for the entire growing season (referred to here as cumulative growing season data).

Statistical analyses

We tested for differences among herbivore treatments for each metric of community structure (S , H' , J , and D) using nested analysis of variance (ANOVA) by treatment and transect (treatment), with the latter component included to account for any differences

among transects within a given treatment. Analyses were performed separately for Kruger early season, Kruger late season, and Konza cumulative season datasets. Nested ANOVAs were performed using SPSS version 11.0.4. As no significant transect effects were found at Kruger ($P > 0.05$), and transect effects were not significant or minimal at Konza, we focus on treatment effects when describing our results.

In addition, we used relative abundance data to compute pairwise euclidean distances (ED) between each set of plots at all of the Kruger and Konza sites. Based on this ED matrix, we conducted an analysis of similarity (ANOSIM) to determine if plant community composition at the sites differed significantly. We also used the distance matrices to conduct a non-metric multi-dimensional scaling analysis (NMDS), in which “stress values” are minimized to determine the best possible 2-D and 3-D configuration of the study plots, yielding a visual representation of the similarities between plots and among sites. Finally, we used the relative abundance data to calculate the similarity percentage (SIMPER) and to compute average similarity and dissimilarity among herbivore treatments, and to identify the plant species which most strongly contributed to the similarities within treatments and to the differences among treatments. Specifically, we used ANOSIM analyses to test for differences among groups (herbivore treatments), and SIMPER analyses to identify which plant species contributed most to the differences detected among groups. Primer (version 5) was used to compute each pairwise distance matrix and the ANOSIM, NMDS and SIMPER analyses (Clarke and Gorley 2001). Note that all analyses described here were conducted at the both the 1 m² (subplot) and 4 m² (plot) level, with comparable—and often nearly identical—results. Therefore, for simplicity and to ensure statistical independence, we present only results from the 4 m² plot level.

Results

South Africa—Kruger National Park

Total plant species richness was lowest in the no herbivore site in both the early and late growing season at Kruger. Richness was higher with both single and multiple herbivore species than in the absence of herbivores early in the growing season, and was significantly higher in the single herbivore site late in the growing season (Table 1). Grass and forb richness followed similar trends, with the single herbivore site always showing the highest richness, and the no herbivore site typically the lowest (Table 1). Likewise, plant diversity was highest in the single herbivore site both early and late in the growing season (Fig. 1a; Table 1). No significant differences among sites in evenness were found during either sampling period (Table 1). Dominance was highest in the herbivore-free site early in the growing season, but did not differ among sites late in the growing season (Table 1). The relative cover of all grasses combined was highest in the herbivore-free site in the early growing season, but was not significantly different late in the growing season (Table 1).

ANOSIM results indicated that the strongest differences in plant community composition lay between the sites with no and multiple herbivores, and secondarily between the single and multi-herbivore sites (Table 2). There was no statistically significant difference in plant community composition between the no and single herbivore sites (Table 2). Plots with multiple herbivores grouped more closely with each other in the NMDS ordination than with the no and single herbivore plots (Fig. 2a, b). In contrast, the no and single herbivore plots largely overlap in two-dimensional space (Fig. 2a, b). For the final,

Table 1 Herbivore treatment comparison of plant community structure measured at the 4 m² plot level for Kruger National Park early and late in the growing season, and for the cumulative growing season at Konza Prairie

| Dependent variable | Treatment effect | | | Est. marginal means | | |
|--|------------------|-----------|----------|---------------------|-------------------|--------------------|
| | <i>F</i> | <i>df</i> | <i>P</i> | None | Single | Multiple |
| <i>Kruger early growing season</i> | | | | | | |
| Total richness | 4.6 | 2.9 | 0.042 | 13.3 _a | 21.0 _b | 18.3 _b |
| Grass richness | 2.0 | 2.9 | 0.195 | 4.4 _a | 5.8 _a | 4.8 _a |
| Forb richness | 5.3 | 2.9 | 0.029 | 8.9 _a | 15.3 _b | 13.5 _b |
| Diversity (H') | 15.4 | 2.9 | 0.001 | 1.2 _a | 1.8 _b | 1.6 _{ab} |
| Evenness | 11.6 | 2.9 | 0.002 | 0.47 _a | 0.59 _a | 0.56 _a |
| Dominance | 9.3 | 2.9 | 0.006 | 0.46 _a | 0.28 _b | 0.33 _{ab} |
| Grass relative cover | 10.4 | 2.9 | 0.004 | 89.9 _a | 80.2 _b | 77.2 _b |
| <i>Kruger late growing season</i> | | | | | | |
| Total richness | 12.2 | 2.9 | 0.003 | 12.3 _a | 18.8 _b | 13.9 _a |
| Grass richness | 6.2 | 2.9 | 0.020 | 4.8 _a | 6.5 _b | 4.2 _a |
| Forb richness | 10.5 | 2.9 | 0.004 | 7.5 _a | 12.3 _b | 9.8 _{ab} |
| Diversity (H') | 3.0 | 2.9 | 0.098 | 1.4 _a | 1.7 _b | 1.4 _a |
| Evenness | 0.5 | 2.9 | 0.651 | 0.56 _a | 0.59 _a | 0.55 _a |
| Dominance | 1.6 | 2.9 | 0.256 | 0.37 _a | 0.29 _a | 0.36 _a |
| Grass relative cover | 1.9 | 2.9 | 0.205 | 85.3 _a | 81.3 _a | 77.9 _a |
| <i>Konza cumulative growing season</i> | | | | | | |
| Total richness | 38.0 | 1.6 | 0.001 | 21.6 | 40.0 | |
| Grass richness | 34.7 | 1.6 | 0.001 | 7.7 | 12.1 | |
| Forb richness | 35.2 | 1.6 | 0.001 | 13.9 | 27.9 | |
| Diversity (H') | 23.3 | 1.6 | 0.003 | 1.88 | 2.69 | |
| Evenness | 9.5 | 1.6 | 0.022 | 0.61 | 0.73 | |
| Dominance | 14.8 | 1.6 | 0.009 | 0.27 | 0.13 | |
| Grass relative cover | 1.8 | 1.6 | 0.226 | 66.4 | 62.6 | |

The entries followed by alphabets are statistically significant at 0.05

two-dimensional ordination, stress was 0.17 ($R^2 = 0.86$) in the early growing season and 0.16 ($R^2 = 0.87$) in the late growing season.

cDifferences in the relative abundance of dominant grasses were the primary driver of the observed differences between herbivore treatments at Kruger (Table 3). In both the early and late growing season, the top five species contributing to the differences between treatments—always grass species—accounted for 65–75% of the overall differences between sites (Table 3). These dominant grasses responded in different ways to herbivory. Palatable species such as *Digitaria eriantha* and *Themeda triandra* tended to decline with increasing herbivore species richness (Table 4). Other species such as *Urochloa mosambicensis* exhibited an opposite pattern, increasing in abundance with increasing herbivore richness (Table 4).

North America—Konza Prairie

Patterns of responses in plant community structure at Konza to no herbivores or a single herbivore species were comparable to that at Kruger. Total richness, grass and forb

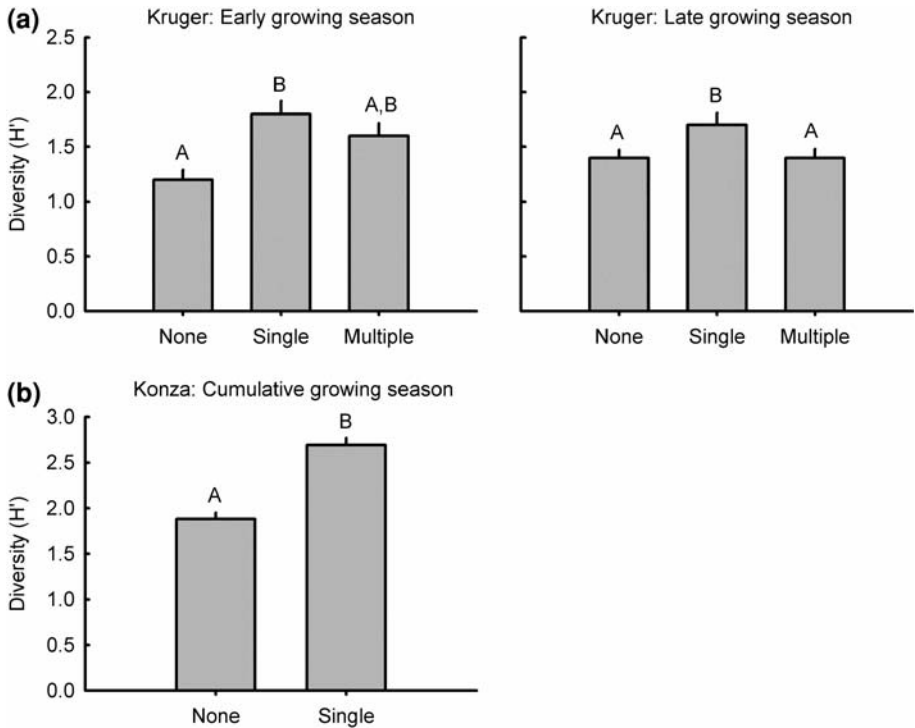


Fig. 1 Total plant diversity, including all forbs and grasses, across sites with different herbivore species richness for the early and late growing season at Kruger (a), and for the cumulative growing season at Konza (b). Bars show means \pm 1 SE. Letters above each bar indicate significantly different treatments

Table 2 Analysis of similarity (ANOSIM) results for plant community composition between sites with no, a single, or multiple herbivore species in Kruger National Park and in Konza Prairie

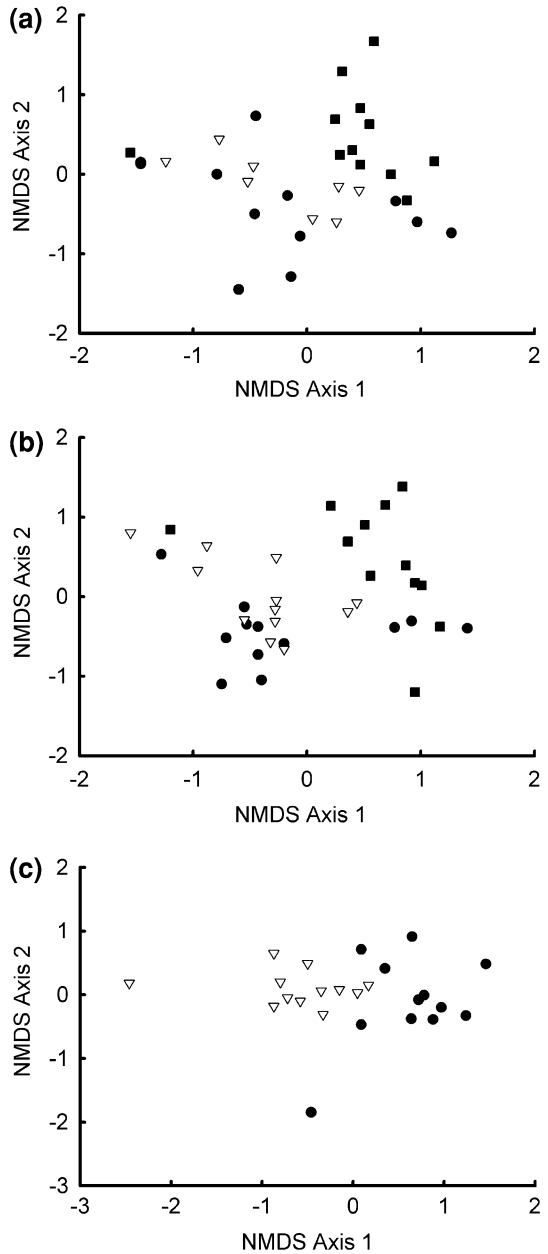
| | Kruger early growing season | | Kruger late growing season | | Konza prairie cumulative growing season | |
|--------------------|-----------------------------|----------|----------------------------|----------|---|----------|
| | <i>R</i> statistic | <i>P</i> | <i>R</i> statistic | <i>P</i> | <i>R</i> statistic | <i>P</i> |
| Global model | 0.162 | 0.004 | 0.295 | 0.001 | 0.502 | 0.001 |
| None to single | -0.079 | 0.829 | 0.040 | 0.184 | 0.502 | 0.001 |
| None to multiple | 0.278 | 0.001 | 0.434 | 0.001 | – | – |
| Single to multiple | 0.237 | 0.017 | 0.414 | 0.001 | – | – |

Note: The *R* statistic is a relative measure of separation, with a value of zero indicating that there are no differences among treatments and a value of 1 indicating that all samples within a treatment are more similar to one another than they are to any sample in another treatment

richness, plant diversity, and evenness were all higher when bison were present than when they were absent (Table 1; Fig. 1b). Species richness was nearly two-fold higher with bison than without (Table 1). Correspondingly, dominance was higher when herbivores were absent (Table 1).

ANOSIM analysis revealed strong differences in the composition of the communities found at these two sites (Table 2). Similarly, NMDS ordination indicated tight clustering

Fig. 2 Non-metric multi-dimensional scaling (NMDS) ordination of vegetation in plots with different herbivore species richness at Kruger National Park and Konza Prairie. The multi-herbivore plots (*square symbols*) at Kruger form a distinct cluster in both the early (a) and late growing season (b), whereas the single (*triangles*) and no herbivore plots (*circles*) largely overlap. The single (*triangles*) and no herbivore plots (*circles*) at Konza form two distinct clusters (c)



of plots from the no herbivore and single herbivore sites (Fig. 2c). For the final, two-dimensional ordination, stress was 0.16 ($R^2 = 0.91$).

At Konza, a combination of 15 grass and forb species accounted for 75% of the observed differences between sites (Table 3). Of the top five contributors (by percentage) to the differentiation between sites, three species were forbs, and two were dominant grasses (Table 3). The dominant grasses typically responded in similar ways, exhibiting a reduction in abundance in the presence of grazing, while the multitude of forb species showed a range of

Table 3 The percent contribution of the five species most strongly contributing to the observed differences among herbivore treatment groups, based on SIMPER analysis

| None to single herbivore | | Single to multiple herbivores | | None to multiple herbivores | |
|-------------------------------|-------------|-------------------------------|-------------|-------------------------------|-------------|
| Species | Contrib (%) | Species | Contrib (%) | Species | Contrib (%) |
| Kruger early growing season | | | | | |
| <i>Themeda triandra</i> | 23.98 | <i>Themeda triandra</i> | 18.98 | <i>Urochloa mosambicensis</i> | 18.65 |
| <i>Bothriochloa radicans</i> | 19.99 | <i>Urochloa mosambicensis</i> | 18.46 | <i>Themeda triandra</i> | 17.66 |
| <i>Digitaria eriantha</i> | 19.00 | <i>Bothriochloa radicans</i> | 14.68 | <i>Bothriochloa radicans</i> | 16.94 |
| <i>Panicum coloratum</i> | 7.44 | <i>Digitaria eriantha</i> | 7.90 | <i>Digitaria eriantha</i> | 14.65 |
| <i>Brachiaria deflexa</i> | 5.26 | <i>Panicum coloratum</i> | 5.72 | <i>Panicum coloratum</i> | 8.43 |
| Kruger late growing season | | | | | |
| <i>Digitaria eriantha</i> | 21.43 | <i>Urochloa mosambicensis</i> | 17.23 | <i>Digitaria eriantha</i> | 20.79 |
| <i>Themeda triandra</i> | 20.26 | <i>Themeda triandra</i> | 16.90 | <i>Urochloa mosambicensis</i> | 19.54 |
| <i>Bothriochloa radicans</i> | 16.44 | <i>Digitaria eriantha</i> | 15.92 | <i>Bothriochloa radicans</i> | 15.36 |
| <i>Panicum coloratum</i> | 7.30 | <i>Bothriochloa radicans</i> | 13.95 | <i>Themeda triandra</i> | 11.85 |
| <i>Urochloa mosambicensis</i> | 6.38 | <i>Panicum coloratum</i> | 4.95 | <i>Panicum coloratum</i> | 8.01 |
| Konza | | | | | |
| <i>Andropogon gerardii</i> | 16.28 | | | | |
| <i>Aster ericoides</i> | 10.54 | | | | |
| <i>Ambrosia psilostachya</i> | 7.00 | | | | |
| <i>Aster oblongifolius</i> | 6.96 | | | | |
| <i>Andropogon scoparius</i> | 6.51 | | | | |

Values listed indicate the percentage of the total differences among herbivore treatments that are explained by variation in the abundance of each listed plant species

Note that for the Kruger National Park sites, all of the top five contributors are grass species, and for the Konza Prairie sites, three of the top five contributors are forb species (*Aster ericoides*, *Ambrosia psilostachya*, and *Aster oblongifolius*). Nomenclature follows from Barkley (1986) and Van Oudtshoorn (1999)

responses with some, such as *Ambrosia psilostachya*, increasing markedly in abundance while other species declined when herbivores were present (Table 4).

Discussion

Loss of large herbivores

Despite their inherent differences (e.g. in climate, soil nutrient levels, and evolutionary history), the response of grassland plant diversity and species richness to loss of a single

Table 4 Mean relative abundance (% of total biomass cover \pm SE) of the top five species causing the observed overall dissimilarities among plant communities in sites with no, a single, or multiple herbivore species, for Kruger early and late growing season and for Konza cumulative growing season

| Plant species | No herbivore species | Single herbivore species | Multiple herbivore species |
|---------------------------------|----------------------|--------------------------|----------------------------|
| Kruger early growing season | | | |
| <i>Digitaria eriantha</i> | 22.2 \pm 7.7 | 11.1 \pm 5.0 | 0.04 \pm 0.04 |
| <i>Themeda triandra</i> | 25.0 \pm 8.1 | 25.0 \pm 9.0 | 6.5 \pm 6.0 |
| <i>Urochloa mosambicensis</i> | 0.2 \pm 0.1 | 3.3 \pm 0.7 | 28.5 \pm 6.5 |
| <i>Bothriochloa radicans</i> | 33.3 \pm 7.6 | 28.9 \pm 5.9 | 26.5 \pm 5.9 |
| <i>Panicum coloratum</i> | 8.7 \pm 4.4 | 1.7 \pm 1.2 | 7.0 \pm 4.7 |
| Kruger late growing season | | | |
| <i>Digitaria eriantha</i> | 33.1 \pm 7.2 | 24.6 \pm 5.4 | 0.03 \pm 0.03 |
| <i>Themeda triandra</i> | 17.0 \pm 5.6 | 25.4 \pm 7.3 | 5.5 \pm 4.9 |
| <i>Urochloa mosambicensis</i> | 0.3 \pm 0.2 | 7.6 \pm 2.4 | 31.4 \pm 6.4 |
| <i>Bothriochloa radicans</i> | 25.4 \pm 6.5 | 14.8 \pm 3.5 | 25.7 \pm 6.6 |
| <i>Panicum coloratum</i> | 8.8 \pm 3.2 | 1.0 \pm 0.5 | 7.1 \pm 5.2 |
| Konza cumulative growing season | | | |
| <i>Andropogon gerardii</i> | 42.2 \pm 3.3 | 25.3 \pm 2.5 | |
| <i>Andropogon scoparius</i> | 9.0 \pm 3.3 | 3.3 \pm 0.7 | |
| <i>Ambrosia psilostachya</i> * | 1.7 \pm 0.5 | 9.6 \pm 1.4 | |
| <i>Aster ericoides</i> * | 13.6 \pm 2.9 | 2.1 \pm 0.3 | |
| <i>Aster oblongifolius</i> * | 8.2 \pm 2.7 | 0.3 \pm 0.1 | |

Nomenclature follows from Barkley (1986) and Van Oudtshoorn (1999)

*Forb species—all other species are grasses

herbivore species was similar at our study sites at Konza Prairie and Kruger National Park. Consistent with expectations for moderate to high-productivity grasslands (Olf and Ritchie 1998; Bakker et al. 2006), a reduction in herbivore richness from a single large herbivore species to no species resulted in a decline in plant species richness and diversity and an increase in dominance at both sites. Other studies have likewise found plant richness and diversity to be lower when the single dominant large herbivore is absent or at extremely low densities (in tallgrass prairie: Collins 1987; Collins et al. 1998; Trager et al. 2004; Hickman et al. 2004, in Mediterranean grasslands: Noy-Meir 1995; Harrison et al. 2003, and across ecosystems: Proulx and Mazumder 1998). The increase in diversity and species richness and decrease in dominance that we observed with herbivory, particularly early in the growing season, was largely caused by a reduction in the abundance of dominant grasses when herbivores were present (presumably due to foraging activity), and to a subsequent increase in forb richness, and in some cases increases in the richness of sub-dominant grasses (in accord with Hartnett et al. 1996; Collins et al. 1998).

Although there were strong parallels in the responses of plant communities to the presence or absence of a single herbivore at Kruger and Konza, there were two key differences. First, though ANOSIM and NMDS analyses for Konza showed strong divergence between single and no herbivore treatments, these same analyses did not detect differences between these two treatments at Kruger. Therefore, although common metrics of community structure revealed differences between the single and no herbivore sites, plant community composition was quite similar among these two sites at Kruger. This

difference between responses at Kruger and Konza is likely due to either more intense grazing pressure (Hickman et al. 2004) at Konza where stocking density in the single herbivore treatments was approximately twice that at Kruger or to the greater time elapsed since the no herbivore site had been grazed at Konza. Although shorter than at Konza, the amount of divergence time at Kruger was sufficient for the development of significant differences in plant community composition between the multi-herbivore treatment and the no and single herbivore treatments, suggesting that the latter effect may be relatively weak (Milchunas and Lauenroth 1993). Second, the primary contributors to the differences in plant community composition among sites were quite different, with a few dominant grasses driving dissimilarity at Kruger vs. a large suite of forbs and grasses at Konza.

We did not find these effects to be amplified when herbivore richness was further enhanced at Kruger. Rather, as we predicted, when multiple herbivore species were present, metrics of plant community structure were either intermediate relative to sites with a single herbivore and no herbivores, or were not significantly different from the no herbivore site. Dominance was enhanced and forb richness was suppressed relative to the single herbivore treatment, which we propose was due to the presence of a suite of forb browsers that occurred in this treatment and were absent in the single herbivore treatment (du Toit 2003). In contrast, plant community composition in the multiple herbivore site was significantly different from that found in either the single or the no herbivore site. Grazing-tolerant grasses such as *Urochloa mosambicensis* dominated the multi-herbivore study site, whereas species known to be intolerant of sustained grazing pressure (Trollope et al. 1989; Martens et al. 1996; Van Oudtshoorn 1999) such as *Digitaria eriantha* and *Themeda triandra* were more common at the single and no herbivore sites. In contrast to our findings based on plant richness and diversity, these compositional patterns suggest that losses of large herbivores from systems with a diverse herbivore assemblage may also result in significant alteration to plant communities.

It is possible that these compositional differences between sites were present prior to establishment of the Cape buffalo enclosure. However, Jacobs and Naiman (2008) found that plant community structure changed rapidly within an enclosure south of our study site in Kruger. Also, we have evidence that these differences are indeed the consequence of a reduction in herbivore richness or complete removal of large herbivores. As part of an ongoing study (J. Bowers, unpublished data), vegetation surveys were conducted in twelve sections (covering an area of 200 m² each) located within the single herbivore and no herbivore sites just prior to the completion of the Cape buffalo enclosure in 2002. Although differences in sampling methods preclude direct comparison with our data, patterns in the abundance of grasses known to be sensitive to sustained grazing pressure suggest that plant communities in the area to be enclosed and the adjacent multiple herbivore site were quite similar prior to fencing and herbivore removal (J. Bowers, unpublished data; 0.04 and 6.8% cover on the multiple species site and 0.69 and 3.7% in the pre-enclosure area for *D. eriantha* and *T. triandra*, respectively). The low cover of grazing-intolerant grasses observed in 2002 contrasts with our study, which found that the relative abundance of both of these grass species had increased on the single and no herbivore sites—consistent with expected plant responses to a decrease in herbivory—but that the relative abundance of these species had remained low on the multiple herbivore site (Table 4).

Variation in the intensity of herbivory across herbivore richness levels is also a likely contributor to the patterns we have described (Milchunas et al. 1988; Hickman et al. 2004; del Pozo et al. 2006). Across most natural gradients of herbivore species richness there also exists a simultaneous gradient in the intensity of herbivory. The more herbivore species there are in an area, the higher the total herbivore abundance and the greater the diversity

of herbivore foraging strategies, and consequently the greater the intensity of herbivory. Herbivore richness and abundance are nearly always confounded in nature and are therefore difficult to tease apart, particularly in field studies of large herbivores (such as ours). Thus, changes in plant communities that accompany loss of large herbivores probably result from the interaction between loss of herbivore functional types (grazers, browsers, forb specialists) and decreases in grazing intensity.

We have reported findings from one growing season and for survey plots representative of local scale processes. Consequently, we cannot rule out the possibility that the treatment effects we have reported here are due in part to the scale at which we sampled and/or to the duration of this investigation. Indeed, though grazing has been shown to enhance plant richness and diversity here and elsewhere, this effect may weaken or even reverse at larger spatial scales (Brown and Allen 1989; Olff and Ritchie 1998; Stohlgren et al. 1999; Dorrough et al. 2007, but see Pykala 2003; Frank 2005; Collins and Smith 2006). Comparisons of plant community responses to herbivore species loss at larger spatial and temporal scales, using analogous sampling methods across study locations (e.g. across continents), are currently lacking and are needed to confirm the generality of the results presented here.

Implications for grassland conservation

Though we documented several differences in the responses of plant communities to a loss of herbivore biodiversity at Kruger and Konza, we observed important similarities that should enhance ongoing efforts to understand and mediate the consequences of herbivore species loss in grassland ecosystems generally, despite differences in herbivore diversity and other contingent factors in grasslands found around the world. First, our results support previous findings that, at small spatial scales, in moderate to high-productivity systems with one or a few species of herbivores present, loss of herbivores should cause a significant decrease in plant diversity and richness. Second, we show that the consequences of herbivore loss can be manifest quite rapidly—in this study within 4–5 years following herbivore removal in SA. Similarly, a recent study conducted within a riparian region of Kruger National Park (Jacobs and Naiman 2008) documented significant declines in species richness and changes in dominance patterns of herbaceous species after only 2–3 years of herbivore exclusion. Finally, our study indicates that reductions in herbivore species richness from many to one species can have pronounced impacts on the structure and composition of grassland vegetation. Although standard metrics of community structure may suggest that plant diversity at sites with a single herbivore are comparable to (or greater than) that at sites with a full suite of herbivores, the composition of these plant communities may actually be quite different. We propose that these changes in composition—which result in shifts in the dominant plant species in the community—may have subsequent ripple effects through other components of the ecosystem, such as insects, birds and small mammalian herbivores (Joern 2005; Fuhlendorf et al. 2006; Palmer et al. 2008), which can be closely associated with plant species composition or vegetation structure. This suggests that efforts to conserve these complex grassland ecosystems would benefit from maintaining or restoring intact herbivore communities consisting of a suite of species that utilize different foraging strategies.

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