Oecologia (2014) 175:293–303
DOI 10.1007/s00442-014-2895-9

COMMUNITY ECOLOGY - ORIGINAL RESEARCH

Loss of a large grazer impacts savanna grassland plant communities similarly in North America and South Africa

Stephanie Eby · Deron E. Burkepile · Richard W. S. Fynn · Catherine E. Burns · Navashni Govender · Nicole Hagenah · Sally E. Koerner · Katherine J. Matchett · Dave I. Thompson · Kevin R. Wilcox · Scott L. Collins · Kevin P. Kirkman · Alan K. Knapp · Melinda D. Smith

Received: 26 July 2013 / Accepted: 22 January 2014 / Published online: 20 February 2014

Abstract Large herbivore grazing is a widespread disturbance in mesic savanna grasslands which increases herbaceous plant community richness and diversity. However, humans are modifying the impacts of grazing on these ecosystems by removing grazers. A more general understanding of how grazer loss will impact these ecosystems is hampered by differences in the diversity of large herbivore assemblages among savanna grasslands, which can affect the way that grazing influences plant communities. To avoid this we used two unique enclosures each containing a single, functionally similar large herbivore species. Specifically, we studied a bison (*Bos bison*) enclosure at Konza Prairie Biological Station, USA and an African buffalo (*Syncerus caffer*) enclosure in Kruger National Park, South Africa. Within these enclosures we erected exclosures in annually burned and unburned sites to determine how grazer loss would impact herbaceous plant communities, while controlling for potential fire-grazing interactions. At both sites, removal of the only grazer decreased grass and forb richness, evenness and diversity, over time. However, in Kruger these changes only occurred with burning. At both sites, changes in plant communities were driven by increased dominance with herbivore exclusion. At Konza, this was caused by increased abundance of one grass species, *Andropogon gerardii*, while at Kruger, three grasses, *Themeda triandra*, *Panicum coloratum*, and *Digitaria eriantha* increased in abundance.

Keywords Disturbance · Fire · Grazing · Plant community richness · Species diversity

Introduction

Grazing by large herbivores is recognized as an integral disturbance in mesic (>500 mm) grassland and savanna ecosystems (hereafter referred to as savanna grasslands,

---

Communicated by Truman Young.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-014-2895-9) contains supplementary material, which is available to authorized users.

S. Eby (✉) · S. E. Koerner · K. R. Wilcox · A. K. Knapp · M. D. Smith
Graduate Degree Program in Ecology, Department of Biology, Colorado State University, Fort Collins, CO, USA
e-mail: Sleby@syr.edu

D. E. Burkepile
Marine Sciences Program, Department of Biological Sciences, Florida International University, Miami, FL, USA

R. W. S. Fynn
Okavango Research Institute, Maun, Botswana

C. E. Burns
San Francisco Bay Bird Observatory, Milpitas, CA, USA

N. Govender
Scientific Services, Kruger National Park, Skukuza, South Africa

N. Hagenah · K. J. Matchett · D. I. Thompson · K. P. Kirkman
School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa

D. I. Thompson
South African Environmental Observation Network, Ndlovu Node, Scientific Services, Kruger National Park, Phalaborwa, South Africa

S. L. Collins
Department of Biology, University of New Mexico, Albuquerque, NM, USA

sensu Scholes and Archer 1997). Mesic savanna grasslands are found in both the northern and southern hemispheres, and irrespective of location, large herbivore grazing has been shown to increase plant community diversity and heterogeneity (McNaughton 1976; Collins 1987; Hartnett et al. 1996; Titshall et al. 2000; Frank 2005; Anderson et al. 2007; Collins and Calabrese 2012). Large herbivore grazing in mesic savanna grasslands has been altered in a number of ways by human activities, including the replacement of diverse native herbivore assemblages with a small number of herbivore species (domesticated livestock) or the removal of large herbivores altogether (Sinclair and Fryxell 1985; Archer 1989). Comparative studies are critical in order to gain a more general understanding of the impacts of these herbivore losses on ecosystems worldwide.

However, generalizations about the impact of herbivore loss on plant community structure (diversity, richness, evenness) are hampered by the fact that mesic savanna grasslands differ in evolutionary history, soil fertility, plant community composition and most importantly, large herbivore assemblages. While both North American and Southern African mesic savanna grasslands were historically grazed by multiple large herbivore species, currently grazing by a diversity of species occurs only in Southern African protected savanna grasslands. Studies suggest that different herbivore assemblages affect plant community structure in varying ways (Olff and Ritchie 1998; Bakker and Olff 2003; Olofsson et al. 2004; Smet and Ward 2005; Bakker et al. 2006; Rueda et al. 2013). Thus, when comparing the impacts of large herbivore loss on mesic savanna grasslands, responses are likely to be contingent upon the types and diversity of large herbivores removed.

One approach for generalizing the impacts of large herbivore removal in mesic savanna grasslands is to control for the type and diversity of herbivores (minimizing this contingency) and then assess responses to their exclusion. We employed this approach by utilizing two unique long-term single large herbivore species enclosures located in savanna grasslands on different continents. The first is a 1,000 ha enclosure containing bison located at the Konza Prairie Biological Station (Konza) in northeastern Kansas (USA). The second is a 900 ha enclosure containing African buffalo located in Kruger National Park (Kruger) in northeastern South Africa. Both of these herbivore species are bulk feeders who eat primarily grass (Hofmann and Stewart 1972; Peden et al. 1974). This provided us with a novel opportunity to assess the impacts of removal of two functionally similar native large herbivores on mesic savanna grassland plant communities, and importantly, avoid confounding plant community responses caused by differences in herbivore diversity. Thus, while we were not able to control for differences in evolutionary history, soil fertility, and plant community composition between the sites, we were able to eliminate differences in large herbivore assemblages.

In 2005–2006, we established identical, replicate exclosures within each enclosure in areas that were burned or left unburned. In the absence of grazing, fire has been shown to decrease plant community richness and diversity (Gibson and Hulbert 1987; Collins et al. 1995), but this decrease is prevented by grazing (Collins et al. 1998). By controlling for potential fire-grazing interactions (Pfeiffer and Steuter 1994; Hartnett et al. 1996; van Langevelde et al. 2003; Vermeire et al. 2004; Collins and Smith 2006; Savadogo et al. 2008) and using identical methods to monitor plant community responses over time, we could directly compare trajectories of plant community change at Konza and Kruger. Additionally, we could determine whether these trajectories differed in response to removal of a functionally similar large herbivore. Although the study sites are characterized by a mix of both woody and grass species, we focused on the herbaceous plant community because it is dominated by C_4 grasses at both study sites, and the focal large herbivores primarily impact this aspect of the plant community (McNaughton 1985; Knapp et al. 1999).

We hypothesized that removal of a single, but functionally similar, large herbivore from the Konza and Kruger study sites would result in similar trajectories of herbaceous plant community change. Previous studies at Konza have shown that long-term ungrazed sites have lower plant species richness regardless of fire regime (Collins and Calabrese 2012), as a consequence of increased dominance by a few C_4 grass species, which is further increased with frequent burning (Collins et al. 1995; Collins et al. 1998). The increased dominance results in a larger decrease in plant species richness with frequent burning when compared to infrequently burned sites (Hartnett et al. 1996). Thus, we expected that the decline in plant richness and diversity would be greatest with large herbivore exclusion when combined with frequent burning at Konza. We expected these plant community responses to be mirrored at Kruger as a result of African buffalo having a similar impact as bison on dominance by C_4 grasses.

Methods

Study sites

Our study utilizes two long-term large herbivore enclosures: one located at Konza and the other located in the south-central Satara region of Kruger. Konza is a 3,487 ha ecological research site located in the Flint Hills region of northeastern Kansas (USA), consisting primarily of native, unplowed, tallgrass prairie. The topography is typical of the Flint Hills region, with relatively steep slopes and distinct upland (silt loam soils) and lowland (silty clay loam soils) sites. Most of the plant species are perennial (Freeman 1998), and herbaceous communities are dominated by a small number of C_4 grasses, including *Andropogon gerardii*, *Panicum virgatum*, *Schizachyrium scoparium* and *Sorghastrum nutans*. Intermixed in this matrix of grasses is a diverse array of less abundant C_3 grass and forb species (Freeman 1998). The climate is temperate (July mean temperature = 27 °C), and precipitation averages 835 mm year,$^{-1}$ with approximately 70 % (585 mm) falling as rain during the April to September growing season (Knapp et al. 1998).

In 1992, a 1,000 ha area was fenced with the purpose of reintroducing bison to the study site (Knapp et al. 1999). This enclosure includes ten watershed units burned in early spring (mid-April) at a range of fire frequencies (1-, 2-, 4-, and 20-years). In April of 2006, we selected an annually burned watershed (hereafter referred to as burned) and a 20-year burned watershed (last burned in 1991, hereafter referred to as unburned) for our experiment. In each watershed, we established three 90 × 45 m blocks (each separated by at least 200 m) in relatively homogeneous upland sites. Within each block, we erected seven 38.5 m^2 (7 m diameter) exclosures, and paired with each exclosure was an unexclosed, equal sized plot (located >5 m from each exclosure, hereafter referred to as paired plots). The exclosure-paired plot combinations were located at least 10 m from each other. The exclosures were constructed of cattle fencing (1.2 m height) fixed to t-posts (1.5 m tall). During the study period bison averaged 330 ± 26 individuals per year (0.33 ha^{-1}, data from the CBW011 data set, http://www.konza.ksu.edu/knz/pages/data/knzdata.aspx and G. Towne personal communication). White-tailed deer (*Odocoileus virginianus*) were also present in the enclosure at low densities (<0.06 ha^{-1}), but were excluded from the exclosures. Differences in biomass between exclosures and paired plots were determined in 2012, at the end of the growing season, using a disc pasture meter. Within each 1 × 1 m subplot of our 2 × 2 m permanent monitoring plots, (see *Vegetation Sampling* for further details) we took four disc pasture meter readings (Trollope and Potgieter 1986). We then averaged the 16 readings for each plot and converted these to biomass using a calibration curve established for Konza. Differences in biomass between exclosures and paired plots averaged 192 ± 15 g m^{-2} in the burned blocks and 192 ± 24 g m^{-2} in the unburned blocks.

Kruger National Park is a 2 million ha reserve situated in the Limpopo and Mpumalanga provinces of northeast South Africa. Herbaceous vegetation of the south-central Satara region of the park, where the study was conducted, is primarily perennial and dominated by a few C_4 grasses, such as *Bothriochloa radicans*, *Digitaria eriantha*, *Panicum coloratum* and *Themeda triandra*. A number of forb species make up the bulk of the diversity. The soils in the area are clayey (Venter et al. 2003). The climate of the Satara region is subtropical, with a mild, dry, and frost-free dormant season and warm summers (January mean temperature = 29 °C). Rainfall is 502 mm year^{-1}, with 78 % (393 mm) of it falling during the growing season (November to April, (Venter et al. 2003).

In 2001, a 900 ha enclosure was erected for the purpose of breeding tuberculosis-free African buffalo. The enclosure was divided into six large burning blocks, with one of the blocks burned annually, two left unburned, and three burned once since 2002. In November 2005, we selected one annually burned block and one unburned block (unburned since 2002) for the experiment. Within each block, we established three 90 × 45 m blocks, each containing seven exclosures and paired plots (n = 21 exclosures per burned area). The exclosure-paired plot combinations were located at least 10 m from each other within the block. The design of the exclosures was identical to Konza (see above), except for the use of chain-link fence instead of cattle panels and the addition of two strings of wire located at the top of the t-posts. During the study period, the enclosure contained on average 80 ± 11 buffalo (0.09 ha^{-1}, N. Govender, unpublished data). Although care was taken to keep the enclosure free of other large herbivores, warthog (*Phacochoerus aethiopicus*), giraffe (*Giraffa camelopardalis*), and plains zebra (*Equus quagga*) also were present at low densities (<0.03 ha^{-1} each) in the enclosure during the study period. Differences in biomass, sampled using a disc pasture meter at the end of the growing season in 2012 (Trollope and Potgieter 1986), between exclosures and paired plots averaged 100 ± 25 g m^{-2} in the burned blocks and 185 ± 22 g m^{-2} in the unburned blocks.

Vegetation sampling

Within each exclosure and paired plot, a 2 × 2 m permanent monitoring plot was established in order to sample plant species composition (n = 84 plots per enclosure). Each plot was subdivided into four 1 × 1 m subplots. The percent aerial cover of each plant species rooted in each subplot was visually estimated to the nearest 1 %, each year from 2006 to 2012. Sampling occurred during both the early and late growing season at Konza (June and August) and Kruger (January and March) to ensure that both early and late season species were recorded. The maximum cover (early or late season) for each species was determined for each subplot and then averaged across the four subplots. Average maximum cover values for each species were used to compute standard metrics of community structure, including grass, forb and total species richness, Shannon–Weiner diversity, evenness, Berger–Parker dominance and

Table 1 Results of repeated measures, mixed-model analysis of variance for the effects of large herbivore removal (grazing) and fire frequency (fire) over time (year) on grass and forb richness, evenness, diversity, and dominance at the Konza Prairie Biological Station (Konza) in Kansas, USA and the Kruger National Park (Kruger) in South Africa

Source	Grass Richness			Forb Richness		Evenness		Diversity		Dominance	
	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Konza											
Grazing	1	51.11	<0.0001	138.06	<0.0001	46.47	<0.0001	88.55	<0.0001	54.85	<0.0001
Fire	1	0.44	0.5	1.21	0.3	1.11	0.3519	0.1	0.8	0.44	0.5
Year	6	31.67	<0.0001	40.0	<0.0001	7.46	0.0001	14.19	<0.0001	2.8	0.1
Fire × grazing	1	1.24	0.3	0.01	0.9	4.18	0.04	2.05	0.2	16.95	<0.0001
Year × fire	6	4.62	0.0001	4.33	0.02	1.78	0.14	4.13	0.02	1.29	0.3
Year × grazing	6	35.53	<0.0001	41.6	<0.0001	9.69	<0.0001	26.29	<0.0001	17.39	<0.0001
Year × fire × grazing	6	3.97	0.001	7.61	<0.0001	11.09	<0.0001	12.04	<0.0001	14.03	<0.0001
Kruger											
Grazing	1	21.25	<0.0001	11.89	0.001	2.19	0.14	13.79	0.0004	9.33	0.003
Fire	1	1.16	0.3	2.06	0.23	3.83	0.054	0.61	0.5	1.57	0.21
Year	6	15.93	<0.0001	30.31	<0.0001	0.79	0.6	7.05	0.002	0.1	0.8
Fire × grazing	1	15.87	0.0002	5.01	0.03	0.46	0.5	8.78	0.004	3.03	0.04
Year × fire	6	26.4	<0.0001	11.38	0.0002	2.38	0.09	9.31	0.001	5.59	0.005
Year × grazing	6	5.3	<0.0001	5.9	<0.0001	1.63	0.14	7.10	<0.0001	1.17	0.3
Year × fire × grazing	6	5.02	<0.0001	0.48	0.8	2.59	0.02	6.16	<0.0001	1.97	0.07

the average relative cover of a subset of common grass species.

Statistical analysis

We tested for differences among treatments for grass and forb richness, evenness, the inverse natural log of diversity, and dominance using nested, repeated measures, mixed-model analysis of variance with fire as the whole plot treatment, the large herbivore removal treatment nested within fire, and year as the repeated measure. The exclosures and paired plots were nested within a single burned or unburned area at each site. Although our split-plot design did not allow us to formally test for the interactions between fire and herbivory, we were able to assess the effects of herbivory under both burned and unburned conditions. Konza and Kruger were always evaluated with separate models. When main effects or interactions were significant, mean separations to test for differences among treatments were performed using least square means post hoc comparisons. We used Pearson's correlations to test for correlations between grass and forb richness and dominance. We calculated the absolute value of the proportional change in grass and forb richness between ungrazed and grazed plots (difference between the richness in ungrazed plots versus the richness in grazed plots divided by the richness in grazed plots) in the burned and unburned areas. We also calculated the change in relative cover between ungrazed and grazed plots in burned and unburned areas for the four most abundant grass species found in grazed plots, and used *t* tests to determine if changes in relative cover were different from zero. All analyses were conducted in SAS (SAS Institute V.9.3; Cary, NC).

Results

At Konza, the removal of grazing and fire regime interacted over time to significantly affect grass and forb species richness, diversity, evenness, and dominance (Table 1). Although grass and forb richness decreased rapidly (after 1–2 years) with removal of bison in both the burned and unburned sites (Fig. 1), the proportional change in grass and forb richness, after 7 years of removal, was greater with burning (Fig. 2). Rapid declines were also observed for evenness (Fig. 3) and diversity (Fig. 4) with burning, with less rapid declines observed in unburned areas. Dominance rapidly increased in burned areas, with a less rapid increase seen in unburned areas (Fig. 5).

Similar to Konza, the removal of grazing and fire regime also interacted over time to significantly affect grass richness, diversity, and evenness at Kruger (Table 1). Grass richness started to decline 2 years after the removal of African buffalo, but only in burned areas (Fig. 1). Similar to grass richness, the decline in forb richness occurred after 2 years of buffalo exclusion in the burned treatment only, but then remained constant thereafter (Fig. 1). Overall, the proportional decrease in grass and forb richness with removal of African buffalo was similar with burning at

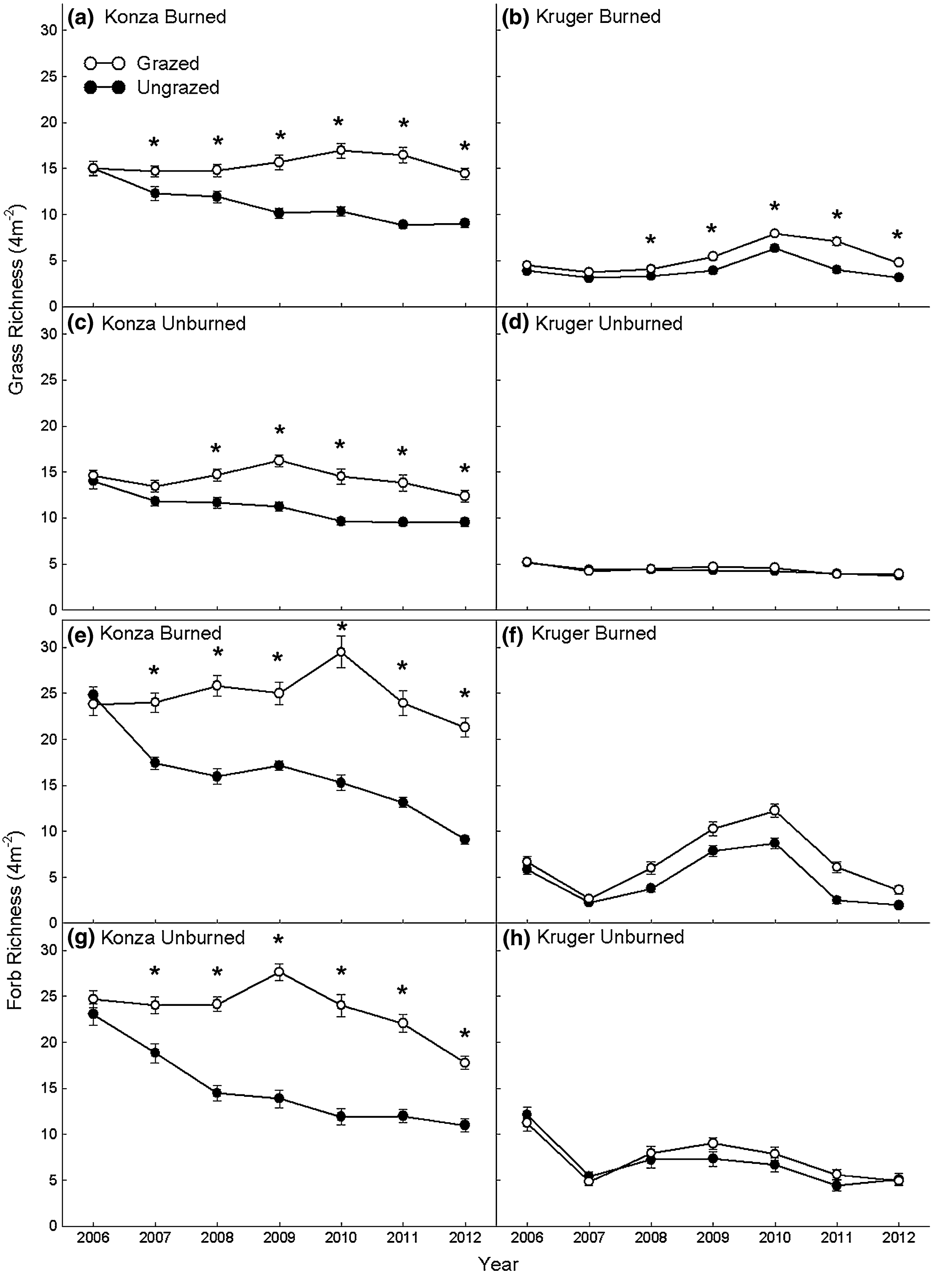

Fig. 1 Dynamics of **a**–**d** grass and **e**–**h** forb richness over time in grazed and ungrazed, burned and unburned herbaceous communities at the Konza Prairie Biological Station (Konza) in Kansas, USA and the Kruger National Park (Kruger) in South Africa. *Asterisks* denote significant differences between mean plot richness (±1 SE) in grazed and ungrazed treatments within a year at a site ($P \leq 0.05$)

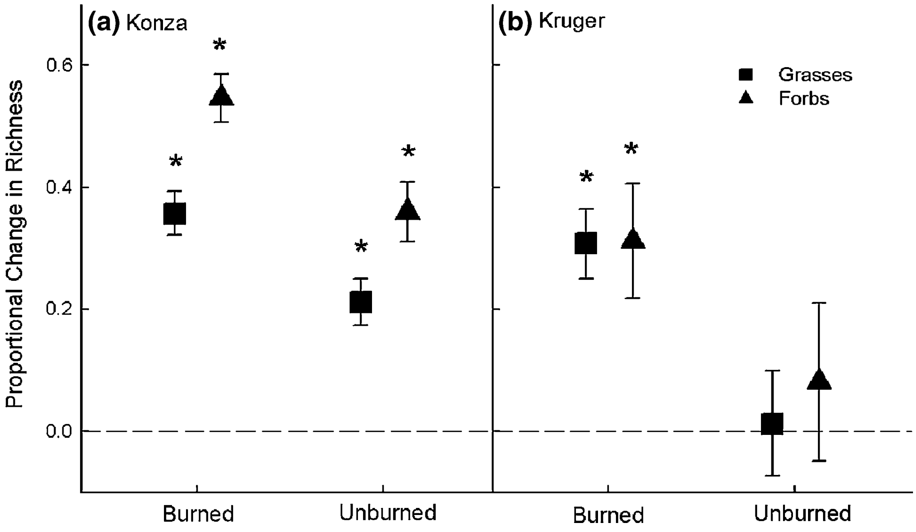

Fig. 2 Proportional change (ungrazed–grazed/grazed) in grass and forb richness with removal of grazing in burned and unburned herbaceous communities at **a** Konza and **b** Kruger for the last year of the study (2012). *Asterisks* denote a significant difference in mean (±1 SE) proportional richness between ungrazed and grazed plots ($P \leq 0.05$)

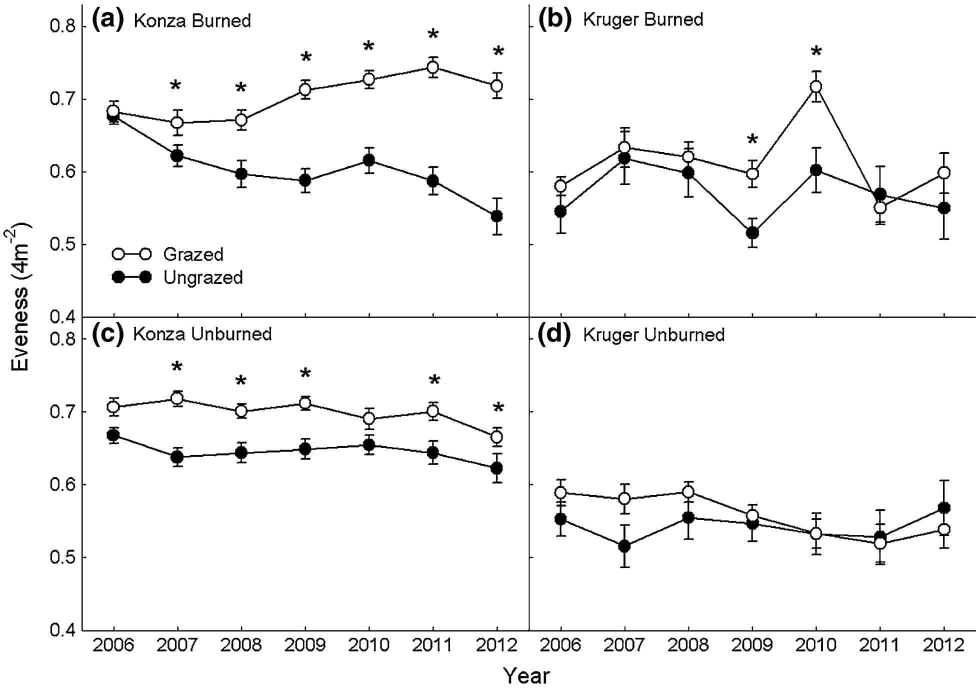

Fig. 3 Dynamics of evenness over time in grazed and ungrazed, burned and unburned herbaceous communities at **a**, **c** Konza and **b**, **d** Kruger. *Asterisks* denote significant differences between mean plot evenness (±1 SE) in grazed and ungrazed treatments within a year at a site ($P \leq 0.05$)

Kruger, whereas the proportional change in forb richness was greater than grass richness at Konza, irrespective of fire frequency (Fig. 2).

At Kruger, more lagged responses (starting 3 years after removal) were observed for diversity only in the burned areas (Fig. 4), while evenness only showed decreases after 4–5 years of grazer removal (Fig. 3). Dominance showed minor increases after 3–4 years of African buffalo removal in both burned and unburned areas (Fig. 5).

Dominance was negatively correlated with grass richness (Pearson correlation coefficients: Konza: burned = −0.72, unburned = −0.57; Kruger: burned = −0.46, unburned = −0.30; all *P* values <0.001) and forb richness (Pearson correlation coefficients: Konza: burned = −0.68, unburned = −0.60; Kruger: burned = −0.48, unburned = −0.26; all *P* values < 0.001) at both sites for both burn treatments. After 7 years of large herbivore exclusion, dominance had increased in both the burned and unburned treatments at Konza (Fig. 6), but the increase in dominance was greater with burning (57 vs. 44 %, respectively). At Kruger, dominance also increased after 7 years of exclusion of African buffalo, but only with burning (Fig. 6). The increase in dominance at Konza was driven primarily by increased relative cover of *A. gerardii* (Fig. 7). This increase was greater with burning, whereas it was still evident, but not significant in the unburned treatment (Fig. 7).

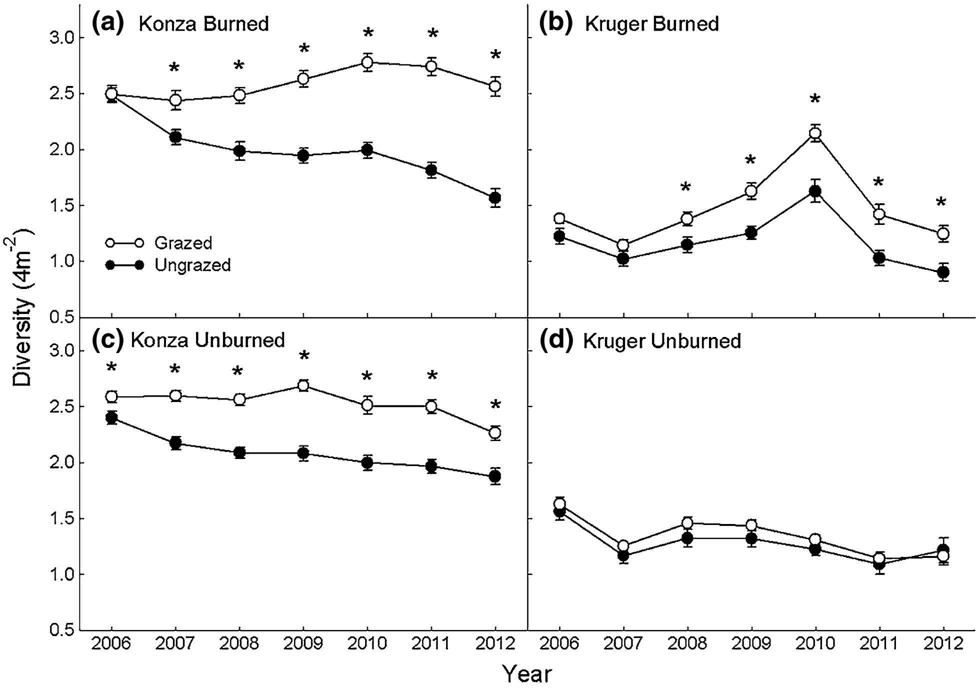

Fig. 4 Dynamics of diversity over time in grazed and ungrazed, burned and unburned herbaceous communities at **a**, **c** Konza and **b**, **d** Kruger. *Asterisks* denote significant differences between mean plot diversity (±1 SE) in grazed and ungrazed treatments within a year at a site ($P \leq 0.05$)

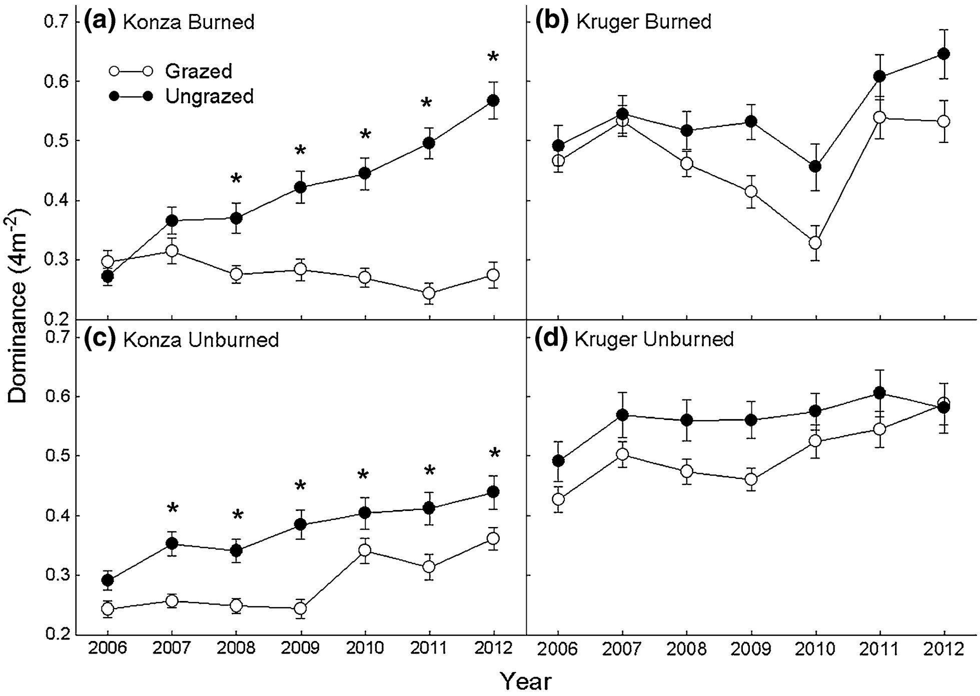

Fig. 5 Temporal dynamics of dominance in grazed and ungrazed, burned and unburned herbaceous communities at **a**, **c** Konza and **b**, **d** Kruger. *Asterisks* denote significant differences between mean plot dominance (±1 SE) in grazed and ungrazed treatments within a year at a site ($P \leq 0.05$)

The increase in dominance at Kruger with burning could not be attributed to a single species; instead, three common grasses (*T. triandra*, *P. coloratum*, and *D. eriantha*) tended to increase in abundance in the burned treatment (Fig. 7), but these increases were variable and plot-specific. Conversely, it is likely that there was no increase observed in dominance with removal of African buffalo in the unburned treatment at Kruger, because of the opposing responses of two grasses, with *D. eriantha* increasing by 15 % and *T. triandra* decreasing by 21 % (Fig. 7).

Discussion

A more general understanding of the impacts of large herbivore loss on mesic savanna grassland plant communities

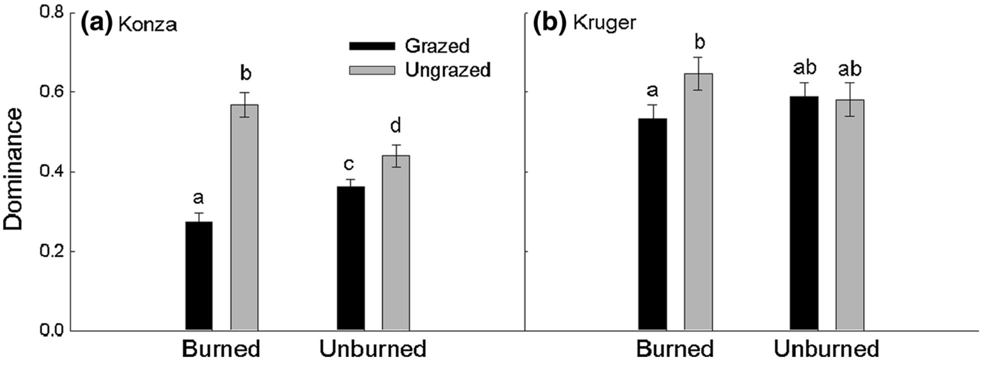

Fig. 6 Plant species dominance (mean ±1 SE) after 7 years of large herbivore removal (ungrazed) in burned and unburned herbaceous communities at **a** Konza and **b** Kruger. Significant differences between treatments are represented by *different letters* ($P \leq 0.05$)

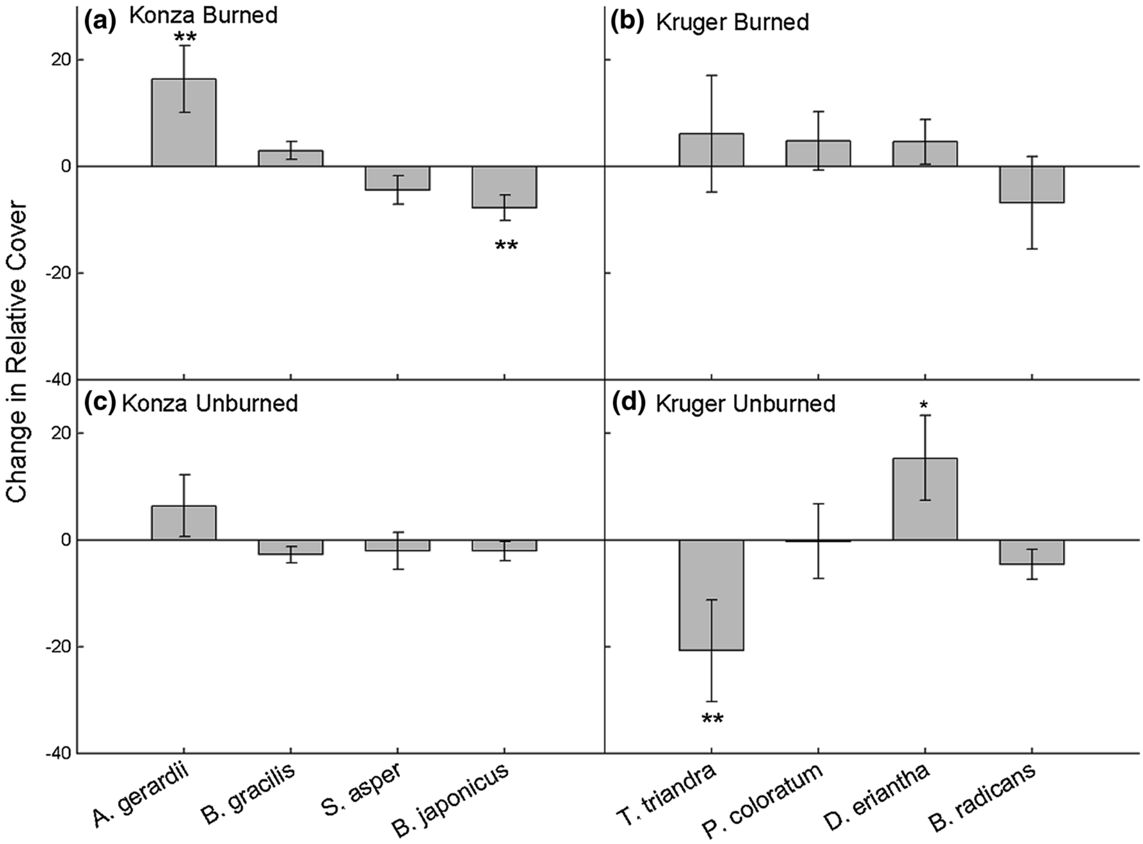

Fig. 7 Difference in relative cover between ungrazed and grazed plots (mean ±1 SE) for the four most abundant grass species, found in grazed plots, after 7 years of large herbivore removal in burned and unburned herbaceous communities at **a**, **c** Konza and **b**, **d** Kruger. *Asterisks* indicate that the change is significantly different from zero (**$P \leq 0.05$; *$P = 0.066$)

has been hindered by the fact that large herbivore assemblages can differ quite dramatically on different continents and these different assemblages appear to affect plant community structure in different ways (Olff and Ritchie 1998; Bakker and Olff 2003; Olofsson et al. 2004; Smet and Ward 2005; Bakker et al. 2006; Rueda et al. 2013). Thus, when comparing the impacts of large herbivore loss, herbaceous community responses will likely be contingent upon the types and diversity of large herbivores removed, as well as other factors, such as evolutionary history, soil fertility, and plant composition and diversity, that can differ between savanna grasslands on different continents. The goal of this study was to control for one of these contingencies, herbivore diversity, by removing a single, functionally similar large herbivore species from a North American (Konza) and South African (Kruger) mesic savanna grassland. This allowed us to test the hypothesis that loss of a single, grass-feeding large herbivore would affect herbaceous plant community richness and diversity similarly at both sites, despite differences in evolutionary history, soil fertility, and plant diversity.

We found that the removal of bison at Konza and African buffalo at Kruger resulted in a decrease in plant species richness and diversity over time at both study sites (Figs. 1, 4). Furthermore, there was an interaction of grazing removal with fire at both sites, although it is important to note that there are limitations as to how much can be inferred from these results, given that fire was not replicated at larger spatial scales at either study site. For Konza, frequent burning resulted in a much larger decrease in plant richness with the exclusion of a single large herbivore than when fire was absent (Figs. 1, 2). For Kruger a reduction in plant richness was observed only with frequent burning (Fig. 1). Previous studies have found that burning decreases plant community richness and diversity (Gibson and Hulbert 1987; Collins et al. 1995). Thus, although there were similar responses to large herbivore removal, the nature of the grazing removal-fire interaction appears to be different between Konza and Kruger.

Decreased plant species richness and diversity in the absence of grazing has been observed previously (Collins 1987; Hartnett et al. 1996; Titshall et al. 2000; Frank 2005; Anderson et al. 2007; Collins and Calabrese 2012). The mechanism for this decrease is an increase in the dominance of a few key grasses. When grazers are present, they preferentially consume grasses, which allows for an increase in forb abundance (Hofmann and Stewart 1972; Vinton and Hartnett 1992; Collins et al. 1998). We found that increased dominance was important for influencing plant richness at both sites. At Konza, dominance was negatively correlated with both grass and forb richness, and this correlation was greater with burning, where grass dominance was greater. We found that when bison were removed, dominance increased in both the burned and unburned treatments, but that this increase was greatest with burning (Figs. 5, 6). The increased dominance was driven primarily by a single grass species, *A. gerardii* (Pearson correlation coefficient: burned = 0.89 unburned = 0.96, *P* values <0.0001; Fig. 7). However, because the increase in abundance of *A. gerardii* was not as great in the unburned treatment (Fig. 7), the decline in richness and diversity was not as large as with burning. The lower increase in abundance in unburned treatments is likely due to the fact that *A. gerardii* abundance is enhanced by frequent fire (Collins 1987), thus the increase in dominance in the absence of fire was not as pronounced because of this lower abundance.

The nature of the grazing removal-fire interaction was different at Kruger, because although dominance was negatively correlated with grass and forb richness, dominance was not influenced by a single grass species, but rather a few common, palatable grass species (*Themeda triandra*, *Panicum coloratum*, and *Digitaria eriantha*) known to decrease in abundance with grazing (van Oudtshoorn 2012; Fig. 7). With frequent burning and grazer removal, each of these species tended to increase in abundance (Fig. 7). However, no species was present within every plot, and therefore no single species contributed exclusively to the observed increase in dominance (Pearson correlations of species cover versus dominance: *D. eriantha* $= -0.1$, $P = 0.32$; *P. coloratum* $= 0.34$, $P < 0.0001$; *T. triandra* $= 0.4$, $P = 0.0004$). In the absence of fire, the lack of increase in dominance at Kruger, following grazer removal, was due to increased cover of *D. eriantha* offsetting decreased cover of *T. triandra* (Fig. 7). It may be that *D. eriantha* can cope with the increased litter accumulation that occurs in the absence of fire, when combined with the removal of grazing, better than *T. triandra*, which is intolerant of the shading created by litter in the absence of fire and grazing (Fynn et al. 2011). Thus, *D. eriantha* may outcompete *T. triandra* when African buffalo grazing is excluded. Therefore, the difference seen in the grazer removal-fire interaction between the two sites is likely due to the fact that at Konza dominance is only influenced by one grass species, while at Kruger, several grass species affect dominance and the effects of fire on their abundance varies.

Another important difference between Konza and Kruger in plant community response to removal of a single grazer was that the decline in richness and diversity was greater at Konza than at Kruger (Figs. 1, 3 and Online Resource Fig. 1). This appears to be driven more by decreases in forb richness than grass richness with the removal of grazers (Figs. 1, 2 and Online Resource Fig. 1), although both decreased in number. This difference in the relative impact on forb species may be due to the fact that the Konza plots contain three times as many forb species as the Kruger plots (Fig. 1). This higher forb richness may indicate the presence of more rare species at Konza than at Kruger and these rare species may be lost more quickly with grazer removal. Grazing has been shown to increase the presence of rare species (Porensky et al. 2013). The greater decline in richness and diversity at Konza could also be because the higher number of bison within the enclosure at Konza created higher grazing intensity at Konza than at Kruger. Grazing intensity has been shown to have an impact on plant species richness and diversity with high levels of grazing intensity decreasing richness and diversity (Milchunas et al. 1988; Savadogo et al. 2007). However, differences in aboveground standing biomass between ungrazed and grazed sites were similar in both places (Konza: burned = 192 ± 15 g m^{-2}, unburned = 192 ± 24 g m^{-2}, Kruger: burned = 100 ± 25 g m^{-2}, unburned = 185 ± 22 g m^{-2}), suggesting that off take was also similar. Lastly, the reason that grazer removal caused a smaller decline in richness and diversity at Kruger could be because prior to the buffalo enclosure being erected, the area was grazed by a higher density and diversity of herbivores who consumed both grasses and forbs. Grazing by a higher density and diversity of herbivores, at nearby sites, has been shown to have a lower impact on plant community richness (Koerner et al. 2014). A limited number of these herbivores were able to get into the enclosure during the experiment, and this may also have decreased differences between grazed and ungrazed plots. However, deer were also present inside the enclosure at Konza, which should have had a similar effect as the mixed feeder herbivores present in the Kruger enclosure.

Since this study involved the removal of a single, primarily grass-feeding large herbivore from a site in North America (Konza) and a site in South Africa (Kruger), we were able to compare the impacts of grazing on the herbaceous plant communities between these two ecosystems. Our results show that at both sites, the removal of a single large herbivore causes decreases in the richness and diversity of the herbaceous plant community. Furthermore, the mechanism for these decreases was the same at both sites, with increased dominance of palatable grass species, in the absence of grazing, driving the decreases in richness and diversity. Thus, when a single large herbivore is lost from mesic savanna grasslands in North America and South Africa, it appears that not only will there be declines in plant species richness and diversity, but the mechanism for these declines, increased dominance, will also be the same. This is despite the fact that the two systems differ in evolutionary history, soil fertility, and plant species community composition. There is a need for further comparative studies to test if increased dominance is a generalizable mechanism that causes decreased plant species richness and diversity when functionally similar, large herbivores are removed from a broad range of grassland and savanna ecosystems.

Acknowledgments Thanks to H. Archibald, E. Amendola, M. Avolio, L. Calabrese, A. Chamberlain, C. Chang, K. Duffy, L. Ladwig, K. La Pierre, A. Lease, K. Murphy, T. Nelson, T. Schreck, A. Walters, J. Taylor, L. Zeglin, and A. Zinn for assisting in the field. Thanks to J. M. Blair, Konza Prairie LTER, Kruger National Park, L. Woolley, and SAEON for logistical support. Earlier drafts of this manuscript benefitted from comments by T. Young and two anonymous reviewers. The experiments comply with the current laws of South Africa where the research was performed. This research was supported by grants to M. Smith from the NSF Ecosystem Studies and Geography and Regional Science Program (DEB-0841917) and the Andrew W. Mellon Foundation.

References

Anderson TM, Ritchie ME, McNaughton SJ (2007) Rainfall and soils modify plant community response to grazing in serengeti national park. Ecology 88:1191–1201

Archer S (1989) Have southern texas savannas been converted to woodlands in recent history? Am Nat 134:545–561

Bakker ES, Olff H (2003) Impact of different-sized herbivores on recruitment opportunities for subordinate herbs in grasslands. J Veg Sci 14:465–474

Bakker ES, Ritchie ME, Olff H, Milchunas DG, Knops JMH (2006) Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. Ecol Lett 9:780–788

Collins SL (1987) Interaction of disturbances in tallgrass prairie: a field experiment. Ecology 68:1243–1250

Collins SL, Calabrese LB (2012) Effects of fire, grazing and topographic variation on vegetation structure in tallgrass prairie. J Veg Sci 23:563–575

Collins SL, Smith MD (2006) Scale-dependent interaction of fire and grazing on community heterogeneity in tallgrass prairie. Ecology 87:2058–2067

Collins SL, Glenn SM, Gibson DJ (1995) Experimental analysis of intermediate disturbance and initial floristic composition: decoupling cause and effect. Ecology 76:486–492

Collins SL, Knapp AK, Briggs JM, Blair JM, Steinauer EM (1998) Modulation of diversity by grazing and mowing in native tallgrass prairie. Science 280:745–747

Frank DA (2005) The interactive effects of grazing ungulates and aboveground production on grassland diversity. Oecologia 143:629–634

Freeman CC (1998) The flora of Konza prairie: a historical review and contemporary patterns. In: Knapp AK, Briggs JM, Hartnett DC, Collins CL (eds) Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, New York, pp 69–80

Fynn R, Morris C, Ward D, Kirkman K (2011) Trait–environment relations for dominant grasses in South African mesic grassland support a general leaf economic model. J Veg Sci 22:528–540. doi:10.1111/j.1654-1103.2011.01268.x:

Gibson DJ, Hulbert LC (1987) Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie. Vegetatio 72:175–185

Hartnett DC, Hickman KR, Walter LEF (1996) Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. J Range Manag 49:413–420

Hofmann RR, Stewart DRM (1972) Grazer or browser: a classification based on the stomach-structure and feeding habits of east African ruminants. Mammalia 36:226–240

Knapp AK, Briggs JM, Blair JM, Turner CL (1998) Patterns and controls of aboveground net primary production in tallgrass prairie. In: Knapp AK, Briggs JM, Hartnett DC, Collins CL (eds) Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, New York, pp 193–221

Knapp A, Blair J, Briggs J, Collins S, Hartnett D, Johnson L, Towne E (1999) The keystone role of bison in North American tallgrass prairie. Bioscience 49:39–50

Koerner SE, Burkepile DE, Fynn RWS, Burns CE, Eby S, Govender N, Hagenah N, Matchett KJ, Thompson DI, Wilcox KR, Collins SL, Kirkman KP, Knapp AK, Smith MD (2014) Plant community response to loss of large herbivores differs between North American and South African savanna grasslands. Ecology (in press)

McNaughton SJ (1976) Serengeti migratory wildebeest: facilitation of energy flow by grazing. Science 191:92–94

McNaughton SJ (1985) Ecology of a grazing ecosystem: the serengeti. Ecol Monogr 55:259–294

Milchunas DG, Sala OE, Lauenroth WK (1988) A generalized model of the effects of grazing by large herbivores on grassland community structure. Am Nat 132:87–106

Olff H, Ritchie ME (1998) Effects of herbivores on grassland plant diversity. TREE 13:261–265

Olofsson J, Hulme PE, 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

Peden DG, Dyne GMV, Rice RW, Hansen RM (1974) The trophic ecology of *Bison bison* L. On shortgrass plains. J Appl Ecol 11:489–497

Pfeiffer KE, Steuter AA (1994) Preliminary response of sandhills prairie to fire and bison grazing. J Range Manag 47:395–397

Porensky L, Wittman S, Riginos C, Young T (2013) Herbivory and drought interact to enhance spatial patterning and diversity in a savanna understory. Oecologia 173:591–602

Rueda M, Rebollo S, GarcÃa-Salgado G (2013) Contrasting impacts of different-sized herbivores on species richness of mediterranean annual pastures differing in primary productivity. Oecologia 172:449–459

Savadogo P, Sawadogo L, Tiveau D (2007) Effects of grazing intensity and prescribed fire on soil physical and hydrological properties and pasture yield in the savanna woodlands of Burkina Faso. Agric Ecosyst Environ 118:80–92

Savadogo P, Tiveau D, Sawadogo L, Tigabu M (2008) Herbaceous species responses to long-term effects of prescribed fire, grazing and selective tree cutting in the savanna-woodlands of West Africa. Perspect Plant Ecol Evol Syst 10:179–195

Scholes RJ, Archer SR (1997) Tree-grass interactions in savannas. Annu Rev Ecol Syst 28:517–544

Sinclair ARE, Fryxell JM (1985) The Sahel of Africa: ecology of a disaster. Can J Zool 63:987–994

Smet M, Ward D (2005) A comparison of the effects of different rangeland management systems on plant species composition, diversity and vegetation structure in a semi-arid savanna. Afr J Range Forage Sci 22:59–71

Titshall LW, O'Connor TG, Morris CD (2000) Effect of long-term exclusion of fire and herbivory on the soils and vegetation of sour grassland. Afr J Range Forage Sci 17:70–80

Trollope WSW, Potgieter ALF (1986) Estimating grass fuel loads with a disc pasture meter in the Kruger national park. J Grassl Soc South Afr 3:148–152

van Langevelde F, van de Vijver C, Kumar L, van de Koppel J, de Ridder N, van Andel J, Skidmore A, Hearne J, Stroosnijder L, Bond W (2003) Effects of fire and herbivory on the stability of savanna ecosystems. Ecology 84:337–350

van Oudtshoorn F (2012) Guide to grasses of southern Africa, 3rd edn. Brizia Publications, Pretoria, South Africa

Venter FJ, Scholes RJ, Eckhardt HC (2003) The abiotic template and its associated vegetation pattern. In: Du Toit JT, Rogers KH, Biggs HC (eds) The Kruger experience: ecology and management of savanna heterogeneity. Island Press, Washington, pp 83–129

Vermeire LT, Mitchell RB, Fuhlendorf SD, Gillen RL (2004) Patch burning effects on grazing distribution. J Range Manag 57:248–252

Vinton MA, Hartnett DC (1992) Effects of bison grazing on *Andropogon gerardii* and *Panicum virgatum* in burned and unburned tallgrass prairie. Oecologia 90:374–382