Plant community response to loss of large herbivores differs between North American and South African savanna grasslands

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Abstract. Herbivory and fire shape plant community structure in grass-dominated ecosystems, but these disturbance regimes are being altered around the world. To assess the consequences of such alterations, we excluded large herbivores for seven years from mesic savanna grasslands sites burned at different frequencies in North America (Konza Prairie Biological Station, Kansas, USA) and South Africa (Kruger National Park). We hypothesized that the removal of a single grass-feeding herbivore from Konza would decrease plant community richness and shift community composition due to increased dominance by grasses. Similarly, we expected grass dominance to increase at Kruger when removing large herbivores, but because large herbivores are more diverse, targeting both grasses and forbs, at this study site, the changes due to herbivore removal would be muted. After seven years of large-herbivore exclusion, richness strongly decreased and community composition changed at Konza, whereas little change was evident at Kruger. We found that this divergence in response was largely due to differences in the traits and numbers of dominant grasses between the study sites rather than the predicted differences in herbivore assemblages. Thus, the diversity of large herbivores lost may be less important in determining plant community dynamics than the functional traits of the grasses that dominate mesic, disturbance-maintained savanna grasslands.

Key words: disturbance; diversity; fire; forb; grass; grazing; herbaceous community; herbivory; Konza Prairie, Kansas, USA; Kruger National Park, South Africa; large-herbivore exclusion; richness.

Introduction

Multiple disturbances shape herbaceous plant community composition and dynamics of mesic (>500 mm MAP [mean annual precipitation] in the tropics and >600 mm MAP outside the tropics; Bond et al. 2003) grasslands and savannas globally, hereafter referred to as savanna grasslands (sensu Scholes and Walker 1993), with fire and grazing considered key, shared drivers of these systems (Knapp et al. 2004). Moderate grazing by large herbivores generally increases plant community diversity in mesic savanna grasslands, subject to various contingencies, such as climate, productivity, grazing intensity, and herbivore diversity (Milchunas et al. 1988, Olff and Ritchie 1998, Bakker et al. 2006). Furthermore,

the effects of grazing may interact with fire to create higher levels of plant diversity and heterogeneity than under either disturbance alone (Collins and Smith 2006, Koerner and Collins 2013).

Human activities are altering these key disturbances in savanna grasslands worldwide (Reid and Ellis 1995, Fuhlendorf and Engle 2001), with important consequences for ecosystem diversity, structure, and function. Indeed, nearly half of the world's large herbivores are threatened with extinction (IUCN 2013), with local, often diverse, native herbivore fauna eliminated and, in many regions, replaced by a single domesticated grazer. In addition, most savanna grasslands have experienced substantial alterations in natural fire frequency, ranging from complete fire suppression to annual burning and changes in the seasonality of fires, all with corresponding effects on fire intensity (e.g., Smith et al. 2012). Comparative studies focusing on the implications of large-herbivore loss and how these impacts vary with

PLATE 1.   Exclosure located at Konza Praire, Kansas, USA, in annually burned grassland. The vegetation difference inside and outside the exclosure is evident with the tall dominant C_4 grass, *Andropogon gerardii*, flowering inside the exclosure and higher forb cover outside. Photo credit: A. K. Knapp.

alterations in fire regime are lacking, particularly in savanna grasslands that differ in large-herbivore assemblages. Yet, such studies are critical for gaining a more general understanding of the global-scale impacts of modified disturbance regimes (Knapp et al. 2004).

Large herbivores in mesic savanna grasslands often increase herbaceous plant community diversity by decreasing grass dominance and reducing competition for light (Belsky 1992, Bakker et al. 2006). However, the effects of large-herbivore loss are likely to differ between systems with different levels of herbivore diversity (Olff and Ritchie 1998, Young et al. 2013). For example, the loss of a single grazer (i.e., bison *Bos bison* in North America, hereafter NA) is expected to have different impacts on herbaceous plant communities than the loss of multiple types of large herbivores in Southern Africa, hereafter SA (du Toit and Cumming 1999). In NA, bison prefer to eat grasses more than forbs (Plumb and Dodd 1993), reducing grass dominance and increasing plant species diversity, irrespective of fire regime (Collins et al. 1998, Knapp et al. 1999). In contrast, the multispecies large-herbivore communities in SA collectively target both grasses and forbs (Codron et al. 2007). Although species such as blue wildebeest (*Connochaetes taurinus*), plains zebra (*Equus quagga*), and Cape buffalo (*Syncerus caffer*) preferentially eat grass, forbs are utilized to a much greater extent by other species found in the diverse herbivore community. For example, the diet of impala (*Aepyceros melampus*) during the dry season can be as much as 50% forbs (Codron et al. 2007, Van der Merwe and Marshal 2012). In addition, the wet-season diets of steenbok (*Raphicerus campestris*) and greater kudu (*Tragelaphus strepsiceros*) are primarily

forbs, 50% and 80%, respectively (du Toit 2003). Presumably, like bison, grass-eating herbivores reduce grass dominance and increase diversity; however, the presence of forb-eating herbivores simultaneously decreases diversity (Skinner and Chimimba 2005).

To assess the impacts on herbaceous plant communities of losing native large herbivores and to determine if these impacts vary with herbivore diversity and fire regime, we took advantage of long-term (>30-year) fire manipulation experiments in savanna grassland sites in NA (Konza Prairie Biological Station, Kansas, USA) and SA (Kruger National Park, South Africa). We controlled for many of the contingent factors known to modify the effects of grazing by limiting our study to sites in Konza and Kruger with similar climates, levels of plant productivity, and grazing intensities (see Appendix A: Figs. A2 and A3). Using identical exclosures, we experimentally removed large herbivores from each system for seven years. By employing the same methods to monitor the effects of herbivore loss and controlling for fire–grazer interactions, we were able to determine if removal of a single large herbivore at Konza and multiple herbivore species at Kruger resulted in different trajectories of change in the plant community.

We hypothesized that the removal of large herbivores at Konza would result in a rapid decrease in herbaceous community richness and diversity and a change in community composition over time due to increased dominance by grasses, which are selectively grazed by bison (Plumb and Dodd 1993). In contrast, the removal of large herbivores at Kruger would result in a weaker decrease in herbaceous community richness and diversity and change in community composition

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than at Konza, due to the counteractive effects of primarily grass-eating herbivores with that of forb specialists such as impala, kudu, and steenbok (Codron et al. 2007). Further, we predicted that the magnitude of the effect of large-herbivore removal would increase with fire frequency, irrespective of herbivore diversity, because frequently burned areas are generally preferentially grazed over those left unburned in both NA and SA (Fuhlendorf and Engle 2004, Archibald et al. 2005).

METHODS

Study sites

We established large-herbivore manipulations in long-term fire experiments at the Konza site in northeastern Kansas, USA, and the Kruger site in northeastern SA. For details, see Appendix A: Figs. A1–A4; for additional site descriptions, see Buis et al. (2009) and Knapp et al. (2012). Konza, managed for research since 1977, is a native unplowed tallgrass prairie dominated by a small number of perennial, rhizomatous C_4 grasses. To address the role of native grazers and fire–grazing interactions, bison were reintroduced to Konza in 1987 to a 1000-ha fenced area that includes 10 replicate watersheds burned in the spring (mid-April) at 1-, 2-, 4-, and 20-yr intervals. The overall grazing intensity is considered moderate, with ~295 bison present year round (Towne 1999), averaging 129 kg of herbivore/ha.

At Kruger, the Experimental Burn Plots (EBPs) were established in 1954 to determine the effects of fire seasonality and frequency on forage production. Similar to Konza, experimental burns occur in the spring (August) at 1-, 2-, 3-, and 6-yr intervals, along with unburned controls, each applied to ~7-ha plots (Biggs et al. 2003). Our research focused on the Satara, Marheya, and N'wanetsi blocks of the knobthorn-marula EBPs in south-central Kruger, where precipitation, soil type, and the mix of herbaceous and woody plants are similar to those of Konza (Appendix A: Figs. A2–A4). Kruger vegetation is characterized by the coexistence of dominant perennial, caespitose C_4 grasses and woody species. Herbivore abundance and grazing intensity in this area are considered moderate for regional savanna grasslands (du Toit 2003), and 12–14 large herbivore species (e.g., blue wildebeest, plains zebra, impala) commonly graze on the EBPs, averaging 104 kg of herbivore/ha (Burkepile et al. 2013).

Experimental design

To manipulate the presence of large herbivores, replicate 38.5-m^2 herbivore exclosures (Appendix A: Fig. A4) were established prior to the growing season in 2005/2006 in unburned, intermediate (3- or 4-yr fire return interval), and annually burned grazed areas at both Kruger and Konza, respectively. Three blocks of seven exclosures were established, with co-located paired plots open to grazing in each of the three fire treatments

($n = 21$ exclosures per treatment per site). Because our focus was on herbaceous plant communities, plots were not located beneath trees or where dense shrub patches were present. Previously, we determined that the different assemblages of large herbivores at Konza and Kruger impacted ANPP similarly at both sites (Appendix A: Table A1; for details, see Knapp et al. 2012). Thus, it is unlikely that differences in herbivore impacts on ANPP would confound the plant community response observed.

We surveyed the herbaceous plant community at the beginning and end of each growing season (Konza, June and August; Kruger, January and March) to capture peak abundance of both early- and late-season species. We sampled vegetation in a permanent 2 × 2 m plot located within each of the fenced and paired plots. This 4-m^2 plot was divided into four 1-m^2 subplots, and in each subplot, we estimated percent aerial cover (to the nearest 1%) for each species rooted therein.

Statistical analyses

We calculated species richness (S), evenness (J'), Shannon-Weiner diversity (H'), and the Berger-Parker dominance index (D; Magurran 2004), using maximum cover values of each species over the growing season averaged across the four 1-m^2 subplots per plot. Frequency of occurrence and site richness during the entire study period were calculated for all species encountered. We tested for differences among treatments for total S, grass S, forb S, J', the natural log of H' ($e^{H'}$), and D, using nested, repeated-measures, mixed-model analysis of variance (ANOVA) with fire as the whole-plot treatment, grazing nested within fire, and year as the repeated measure. 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. Significance was set at $\alpha = 0.05$, and analyses were conducted in SAS version 9.3 (SAS Institute, Cary, North Carolina, USA).

Using time lag analysis (Collins 2000, Collins and Smith 2006), we determined the effects of grazing, fire, and their interaction on the rate of community change over time. To do so, we created a species × time Euclidian Distance (ED) resemblance matrix for each plot within a treatment. For each time series, the slope of the linear regression of the square root of the time lag vs. ED was used as our measure of rate of community change at the plot level. Differences in slopes between treatments were tested using mixed-model ANOVAs, with grazing treatment (random effect) nested within fire treatment. In addition, we plotted the mean ED values at each time lag for each treatment, and calculated an overall linear regression model. If the slope of the regression was significant, positive, and linear, this would imply that the assemblage in question was undergoing directional change (Collins 2000).
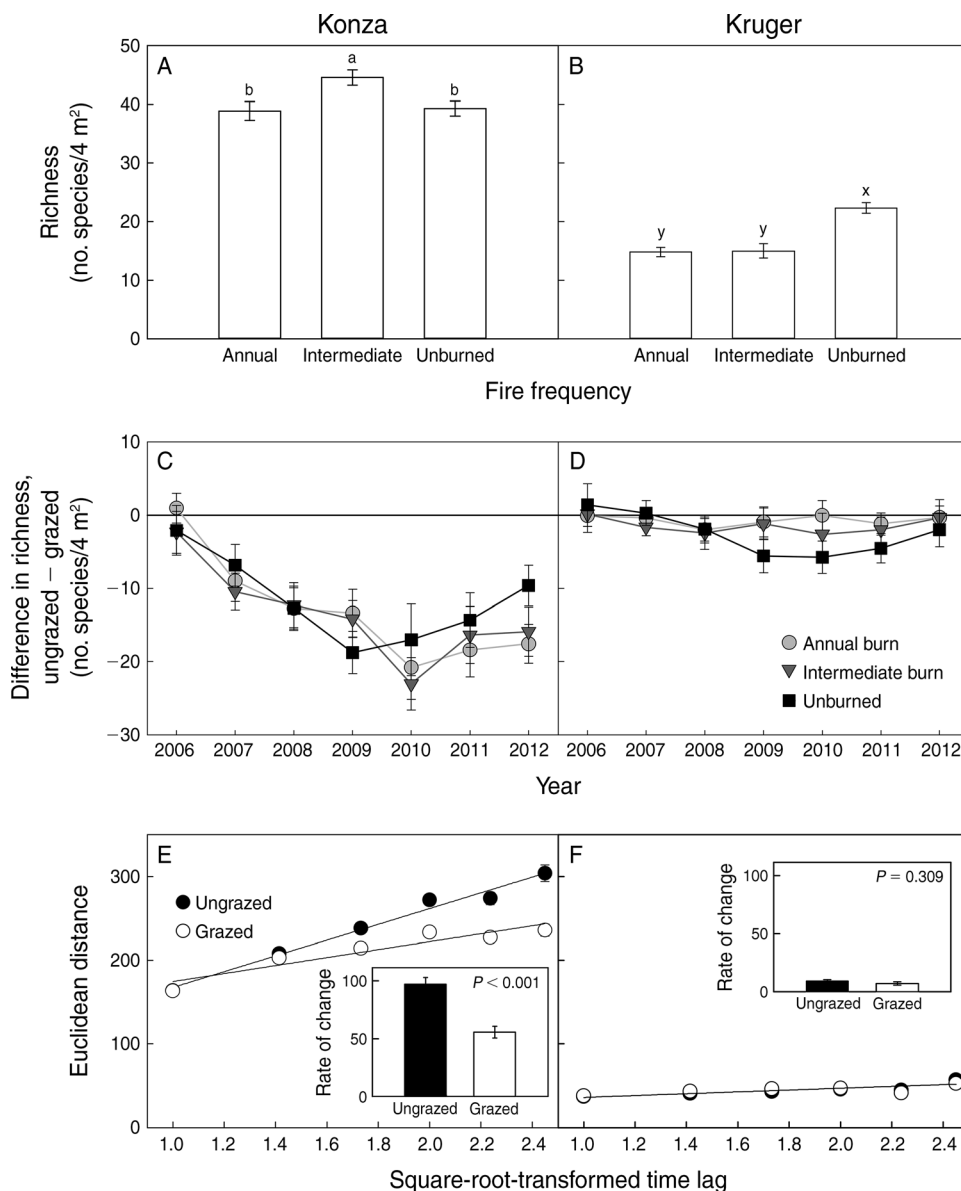
Fig. 1. Comparison of Konza Prairie, Kansas, USA (left-hand panels) and Kruger National Park, South Africa (right-hand panels). (A, B) Effects of fire frequency (annual, intermediate 3- to 4-yr return interval, or unburned) in the presence of grazing on total plant species richness (S) in herbaceous plant communities of mesic savanna grasslands in Konza and Kruger. Richness (mean $\pm$ SE) is measured at the 4-m^2 plot level. Significant differences ($\alpha < 0.05$) between fire treatments within a site are represented by different lowercase letters. (C, D) Difference (ungrazed minus grazed, mean with 95% CI) in total species richness due to large herbivore removal through time for the annual, intermediate (3–4 yr), and unburned fire treatments for Konza and Kruger. When CIs overlap with zero (black horizontal line), there is no significant effect of herbivore removal on richness (see Appendix: Fig. C1). (E, F) The Euclidean distance between a single plot through time (square-root-transformed years). The slopes represent the rate of herbaceous plant community change over time with removal of large herbivores (irrespective of fire frequency treatment) for (E) Konza and (F) Kruger, based on time-lag analysis (see *Methods: Statistical analysis* for details). (E, F insets) The effects of herbivore removal on the rate of community change (slope, mean $\pm$ SE) at the plot level.

RESULTS

Plant species richness was consistently higher (at the site and plot level) at Konza than at Kruger. From 2006 to 2012, we encountered a total of 183 species (42 grass, 141 forb/woody) at Konza and 156 (26 grass, 130 forb/woody) at Kruger across all plots. At the beginning of the experiment in 2006, with all sites previously grazed, total richness was highest with the intermediate fire frequency at Konza ($F_{2,60} = 5.13$; $P = 0.009$; Fig. 1A), whereas at Kruger richness was highest in unburned sites ($F_{2,60} = 18.48$; $P < 0.001$; Fig. 1B).

TABLE 1. Effects of fire (F), the removal of grazing (G), and their interaction (F × G) over the seven-year study period (Yr = year) on species richness (S), evenness (J′), Shannon's diversity ($e^{H′}$), and Berger-Parker dominance (D) of the herbaceous plant community in mesic savanna grasslands in North America (Konza) and South Africa (Kruger).

Site and treatment	df	Total S		Grass S		Forb S	
		F	P	F	P	F	P
A) Konza							
F	2	3.16 (5.73)	0.119	2.35 (5.96)	0.177	2.67 (5.67)	0.153
G	1, 114	242.91	<**0.001**	93.77	<**0.001**	243.12	<**0.001**
F × G	2, 114	0.48	0.621	0.87	0.421	0.18	0.838
Yr	6	30.10 (12.2)	<**0.001**	31.66 (12.1)	<**0.001**	24.41 (12.5)	<**0.001**
Yr × F	12	2.22 (23.9)	**0.047**	2.77 (708)	**0.001**	1.83 (23.8)	0.101
Yr × G	6	79.73 (684)	<**0.001**	55.40 (708)	<**0.001**	55.26 (684)	<**0.001**
Yr × F × G	12	4.58 (684)	<**0.001**	2.44 (708)	**0.004**	4.75 (684)	<**0.001**
B) Kruger							
F	2, 120	29.06	<**0.001**	3.10	**0.049**	38.00	<**0.001**
G	1, 120	10.74	**0.001**	15.77	<**0.001**	3.98	**0.048**
F × G	2, 120	1.22	0.300	0.55	0.578	0.99	0.374
Yr	6, 711	181.94	<**0.001**	57.88	<**0.001**	175.21	<**0.001**
Yr × F	12, 711	9.29	<**0.001**	3.73	<**0.001**	10.92	<**0.001**
Yr × G	6, 711	4.63	<**0.001**	3.38	**0.003**	3.37	**0.003**
Yr × F × G	12, 711	2.22	**0.010**	0.78	0.667	2.94	<**0.001**

Notes: Statistical results are from mixed-model repeated-measures ANOVAs conducted for each site and community metric separately. Where numerator and denominator values apply to all measures within a row, both df values are given in column 2; where denominator df values differ within a row, they are shown in parentheses after each respective F statistic. Significant results (P < 0.05) are in boldface.

At both sites, the effects of large-herbivore removal on plant community structure varied significantly with fire frequency and over time (Table 1). The effects of herbivore removal were more rapid at Konza, with total S, grass S, and forb S, $e^{H′}$, and J′ per 4-m^2 plot being significantly reduced after only two years of herbivore exclusion for all fire treatments (Fig. 1C; Appendix B: Figs. B1 and B2). In contrast, effects of herbivore exclusion on these measures were lagged (by 3–5 years) and transient at Kruger, and only occurred for the intermediate and unburned fire treatments (Fig. 1D; Appendix B: Figs. B1 and B2). After seven years of large-herbivore removal, the ungrazed plots at Konza had lost ~14 species/4-m^2 plot, and thus had ~40% fewer species than grazed plots. This decline in total S was stronger under annual and intermediate fire frequencies (49% and 44%, respectively) compared to the unburned treatment (32%; Fig. 1C). In contrast, herbivore removal for the same period at Kruger had no cumulative effect on measures of community structure for any fire frequency (Fig. 1D; Appendix B: Figs. B1 and B2).

At Konza, large-herbivore removal significantly increased the plot-level rate of community change (Fig. 1E, inset; $F_{1, 120} = 31.90$; P < 0.001). Both ungrazed and grazed treatments at Konza had significant rates of change (Fig. 1E), with ungrazed plots ($y = 94.13x + 73.41$; $r^2 = 0.98$, P < 0.001) having a stronger directional rate of change (steeper slope) than grazed plots ($y = 47.55x + 127.06$; $r^2 = 0.85$, P = 0.006). In contrast, the rate of community change was much lower for Kruger (Fig. 1F; ungrazed, $y = 10.97x + 24.92$; $r^2 = 0.70$, P = 0.023) than for Konza, and large-herbivore removal did

not affect the plot-level rate of community change at Kruger (Fig. 1F, inset; $F_{1, 120} = 1.09$; P = 0.309).

DISCUSSION

Using comparable methods, we quantified herbaceous plant community responses to the loss of large herbivores in two savanna grasslands in NA (Konza) and SA (Kruger) exposed to similar long-term fire manipulations. As predicted, removal of a single grazer (bison) at Konza caused significant change in community structure (S, $e^{H′}$, J′), with reductions in richness and diversity occurring only one year after herbivore exclusion. These effects increased over time and were moderated by fire frequency, with the greatest reductions in richness and diversity in annually burned sites compared to a weaker, yet still significant, reduction without burning. In contrast, plant community structure at Kruger was relatively resistant to the removal of multiple types of large herbivores, regardless of fire frequency.

In NA tallgrass prairie, frequent fire in the absence of large grazers negatively affects plant species richness and diversity and leads to large changes in community composition over time compared to sites without fire (Collins et al. 1995). However, in the presence of large herbivores, the effects of fire are much reduced, with only a slight increase in richness at intermediate fire frequency compared to annual and unburned sites (Collins et al. 1998, Collins 2000, Collins and Smith 2006). Our results are consistent with these findings. Although previous research found no combined effect of fire and grazing on grass species richness or diversity for the same study site at Kruger (Smith et al. 2012), we

TABLE 1. Extended.

J'		$e^{H'}$		D	
F	P	F	P	F	P
1.08 (6)	0.398	1.84 (6)	0.238	0.41 (6.01)	0.683
73.02	<0.001	141.13	<0.001	80.40	<0.001
2.12	0.125	1.31	0.275	1.45	0.240
6.97 (36)	<0.001	14.90 (36)	<0.001	19.79 (36)	<0.001
1.19 (36)	0.325	1.80 (36)	0.085	1.25 (36)	0.292
13.89 (684)	<0.001	38.69 (684)	<0.001	24.98 (684)	<0.001
7.11 (684)	<0.001	7.15 (684)	<0.001	8.17 (684)	<0.001
8.02	<0.001	13.21	<0.001	12.04	<0.001
0.53	0.469	3.73	0.056	1.21	0.274
0.03	0.970	0.57	0.566	0.07	0.936
10.50	<0.001	56.06	<0.001	22.79	<0.001
3.07	<0.001	3.74	<0.001	2.80	0.001
2.34	0.030	4.02	<0.001	3.02	0.006
1.42	0.151	1.55	0.101	0.95	0.497

found that grazing and fire at annual and intermediate frequencies reduced total herbaceous species richness and diversity, whereas unburned, grazed sites had the highest plant species richness and diversity. After seven years of large-herbivore removal at Konza, initial site differences produced by the combined effects of fire and grazing were no longer present, with richness and diversity of ungrazed plots similar in all fire treatments. However, the annually burned, ungrazed plots tended to have the lowest richness. Because herbivore removal had only minor and transient effects on the plant community in Kruger, the effects of fire frequency on richness observed at the beginning of the study persisted through time, with the unburned plots remaining the most species-rich and diverse.

Many studies in savanna grasslands have found that large-herbivore grazing increases plant species richness and diversity (e.g., Belsky 1992, Hartnett et al. 1996, Bakker et al. 2006, Jacobs and Naiman 2008). This response is driven by reduced abundance of, and dominance by, the tall C_4 grasses that are targeted by grazers (Knapp 1985, Milchunas et al. 1988, Knapp et al. 1999). At both the Konza and Kruger sites, dominance was negatively correlated with richness, with the strongest correlation in annually burned sites, followed by intermediate and then unburned sites (Pearson's R: at Konza, $R = -0.751$ for annually burned, $R = -0.687$ for intermediate, $R = -0.649$ for unburned sites; at Kruger, $R = -0.641$, $R = -0.574$, and $R = -0.479$ for annually burned, intermediate, and unburned sites, respectively; $P < 0.001$ for all). However, large-herbivore removal increased dominance at Konza but not Kruger, with the magnitude of this increase at Konza being positively related to increasing fire frequency (Fig. 2A, B; Appendix C: Fig. C1). Reduction in richness and diversity mirrored this fire

frequency relationship. Thus, we found strong support, as others have (Gruner and Taylor 2006, Hillebrand et al. 2007), for increased dominance as the mechanism driving the decline in diversity with herbivore removal.

At Konza, the removal of bison increased dominance by a single, long-lived, rhizomatous C_4 grass species, *Andropogon gerardii* (see Plate 1), present in 98% of all plots (Fig. 2C). This was the most abundant species in both grazed and ungrazed areas (Appendix C: Fig. C2). Bison preferentially graze *A. gerardii* (Plumb and Dodd 1993), and this grass is also favored by frequent burning (Knapp 1985). Thus, when bison were removed, abundance of *A. gerardii* increased rapidly (Appendix C: Fig. C1), with the magnitude of this increase being greatest with annual burning (Appendix C: Fig. C2). In contrast to Konza, no single species occurred in all plots at Kruger (Fig. 2D), with higher turnover of species occurring across plots (Bray-Curtis dissimilarity is 56.35 ± 0.02 [mean ± SE] at Konza and 69.08 ± 0.04 at Kruger). At Kruger, the species of grass that dominated any particular site was strongly dependent on fire frequency and not grazing (Fig. 2B). With fire, an unpalatable, caespitose C_4 grass (*Bothriochloa radicans*) dominated, whereas a more palatable C_4 grass (*Panicum coloratum*) dominated in the unburned treatment (Appendix C: Fig. C3; van Oudtshoorn 2002). This plot-level turnover of species was also evident in the less common grass and forb species. Although both sites have an equal number of rare species (<25% frequency of occurrence, Fig. 2C, D), richness per plot was much lower at Kruger, and thus the spatial turnover of common and rare species was higher than at Konza.

The lack of a strong increase in dominance due to large-herbivore removal at Kruger may have occurred for several reasons. First, the dominant caespitose grasses appear to be less responsive to changes in
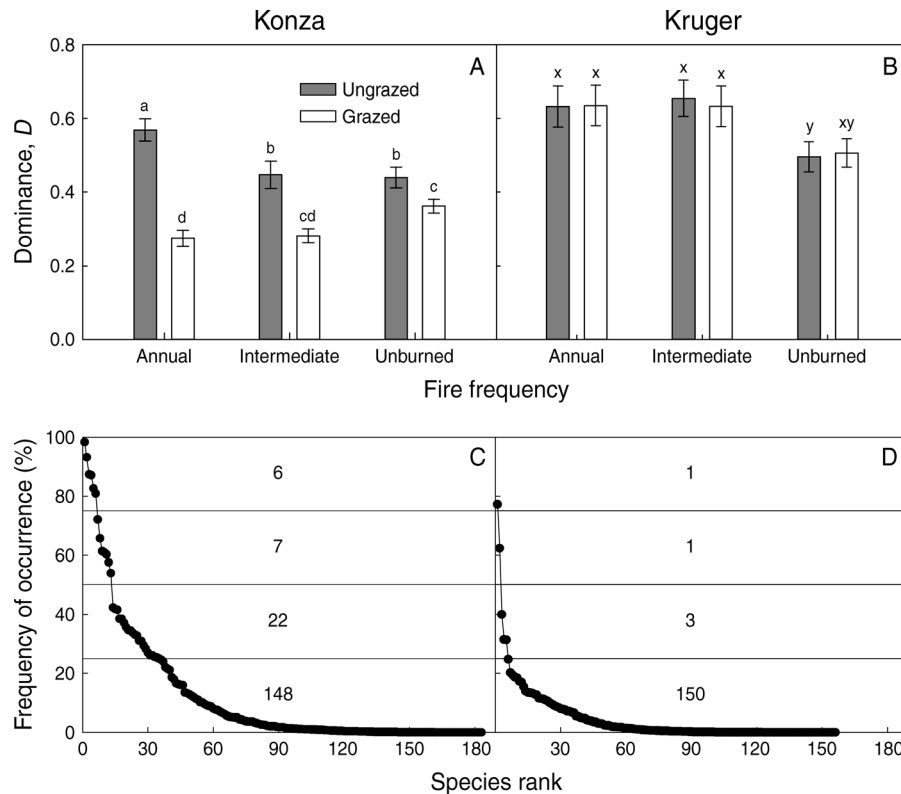
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FIG. 2. (A, B) Mechanisms of plant community response to removal of large herbivores: dominance (Berger-Parker index, D, mean $\pm$ SE) per 4-m^2 plot with (open bars) and without (gray bars) large herbivores for each fire treatment in Konza (North America) and Kruger (South Africa) for 2012 only. Significant differences ($\alpha < 0.05$) between fire frequency and large herbivore removal treatments within a site are represented by different lowercase letters. (C, D) Frequency of occurrence of all plant species encountered during the study period for Konza and Kruger, by species rank. For both sites, the first-ranked species are C_4 grasses (Konza, *Andropogon gerardii*; Kruger, *Bothriochloa radicans*). Reference lines at 25%, 50%, and 75% relative frequency are shown. The number of species in each division is indicated within the reference lines.

grazing compared to the dominant rhizomatous grass at Konza. *Andropogon gerardii* is able to rapidly take advantage of available space via asexual reproduction when grazing is removed (Milchunas et al. 1988), whereas caespitose grasses are more limited in their ability to expand spatially, due to a greater reliance on sexual reproduction (Mack and Thompson 1982). Second, due to the longer evolutionary history of grasses with large herbivores in Kruger vs. Konza (Axelrod 1985, Bond et al. 2003), unpalatable dominant grasses in Kruger are likely to slow the temporal turnover of species. For example, the unpalatable *B. radicans* increases in response to selective grazing of preferred palatable grasses (e.g., *Digitaria eriantha*, *P. coloratum*) by large herbivores (van Oudtshoorn 2002). Thus, removal of large herbivores from sites dominated by this species is likely to result in little change (Fig. 1F). This inertia arises not only because dominance by *B. radicans* is unaffected by the removal of large herbivores (Fig. 2D; Appendix C: Figs. C1 and C3), but also because this species may prevent other palatable species, such as *P. coloratum* and *D. eriantha*, from increasing in abundance (Anderson and Briske 1995).

The lack of plant community response at Kruger to removal of multiple herbivores is consistent with the expectation that the suite of herbivores in SA has no net effect on plant community richness because they consume both grasses and forbs (du Toit 2003). Although this might result from differences in grazing intensities at Kruger vs. Konza, similar herbivore densities and impacts on ANPP (Knapp et al. 2012) suggest that this is probably not the case. Instead, constraints on community change are stronger at Kruger than at Konza, and these constraints arise primarily from the greater spatial turnover of dominant species between plots and between sites burned at different frequencies and the dominance by an unpalatable grass when grazing is present.

Conventional wisdom is that Northern Hemisphere and Southern Hemisphere savanna grasslands are fundamentally different (Bond et al. 2003, Scholes et al. 2003, Lusk and Bellingham 2004). With this seven-year comparative experiment, we show that although plant community responses to the removal of a key disturbance were indeed different, an important mechanism driving community structure—the degree of

dominance and its effects on plant richness and diversity—were similar in both ecosystems. In both systems, increasing dominance results in a decrease in richness and diversity. Thus, we propose that similar processes (i.e., competitive hierarchies) are acting in each savanna grassland, but the longer evolutionary history with fire and grazing, dominance by unpalatable, caespitose grasses, and higher beta diversity at Kruger relative to Konza results in highly divergent rates of herbaceous plant community change with the loss of herbivores. Overall, our research demonstrates that characteristics of dominant species can govern system responses to altered disturbance regimes in mesic, disturbance-maintained savanna grasslands, and it highlights the need for more methodologically controlled, comparative studies to determine the mechanisms underlying how alterations in key drivers will impact savanna grasslands worldwide.

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Supplemental Material

Appendix A

Site and herbivore exclosure design information (*Ecological Archives* E095-068-A1).

Appendix B

Plant community response metrics through time (*Ecological Archives* E095-068-A2).

Appendix C

Mechanisms underlying community change (*Ecological Archives* E095-068-A3).

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