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Herbivore size matters for productivity–richness relationships in African savannas

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Summary

1. Productivity and herbivory often interact to shape plant community composition and species richness with levels of production mediating the impact of herbivory. However, differences in herbivore traits such as size, feeding guild and dietary requirements may result in different impacts of diverse herbivore guilds across productivity gradients.

2. We used size-selective herbivore exclosures to separate the effects of herbivory by larger herbivores, such as elephant, Burchell's zebra and blue wildebeest from those of medium/smaller herbivores, such as impala and warthog, on herbaceous plant communities. These exclosures were established along a 10-fold productivity gradient, ranging from 90 to 950 g m^{-2} of standing plant biomass in the Kruger National Park, South Africa.

3. Exclusion of all herbivores generally increased plant species richness at low productivity, but decreased richness at high productivity. Exclusion of medium/smaller herbivores (e.g. impala, warthog) showed stronger effects on plant richness, particularly loss of forbs, at higher productivity rather than at lower productivity. In contrast, exclusion of larger herbivores had stronger effects on plant richness, typically with increasing forb richness, at low rather than high productivity.

4. The change in species richness appeared linked to changes in light availability following herbivore exclusion. Strong increases in shading led to declines in species richness while more moderate increases in shading led to increases in species richness, possibly due to amelioration of heat and water stress by modest increases in shading.

5. Increasing plant dominance, which likely alters multiple mechanisms of plant interactions, was correlated with declines in plant richness following herbivore exclusion. The impact of increasing dominance on plant richness operated independent of productivity, with the exclusion of impala appearing particularly important in driving this relationship.

6. *Synthesis*. We show that the impact of herbivore losses on plant diversity will be strongly situation dependent and will vary with the herbivores lost (e.g. larger vs. smaller, grazers vs. browsers), plant functional type (e.g. grasses vs. forbs) and environmental context (e.g. productivity). Although larger herbivores are often emphasized for their strong impacts on community dynamics and

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ecosystem processes, we show that smaller, abundant herbivores can exert strong top-down control on plant communities.

Key-words: abiotic gradients, bottom-up effects, foundation species, grazing lawn, mega-herbivore, meso-herbivore, plant dominance, plant–herbivore interactions, top-down effects, wildlife decline

Introduction

Productivity and herbivory often interact to shape plant community composition and species diversity with levels of production mediating the impact of herbivory (Gough & Grace 1998; Olff & Ritchie 1998; Proulx & Mazumder 1998; Burkepile 2013). At high levels of resource availability, large, fast-growing plants are often abundant (Wilson & Keddy 1986; Osem, Perevolotsky & Kigel 2004; Fynn, Morris & Kirkman 2005). However, herbivores often preferentially consume these dominant species, decreasing their competitive advantage and preventing exclusion of subordinate species. In the absence of herbivory, plant biomass and litter accumulate and increase competition for light in productive systems (Knapp & Seasteadt 1986; Collins *et al.* 1998; Wilson & Tilman 2002), resulting in the loss of subordinate species and declines in plant species richness (Gough & Grace 1998; Osem, Perevolotsky & Kigel 2002). While herbivory may increase richness in productive habitats, it may have the opposite effect in low-productivity habitats where nutrients and/or water are often limiting and competition for space and light is likely minimal (Tilman 1988). Here, herbivory may reduce species richness directly via targeting nutritious species or indirectly by increasing resource limitation, stress or the abundance of a few grazing-tolerant species (Milchunas, Sala & Lauenroth 1988; Berendse, Elberse & Geerts 1992). Under these conditions, excluding herbivores may allow recovery and recolonization of plants, resulting in increased species richness (Olff & Ritchie 1998; Osem, Perevolotsky & Kigel 2002).

The complexity of the responses of plants to herbivory is compounded by the multifaceted nature of herbivory. This is especially true in African savannas where diverse herbivore communities include species that differ in guild (grazers, browsers and mixed feeders), dietary requirements and preferences (high vs. low selectivity), feeding morphology and body size (Owen-Smith 1988; du Toit & Cumming 1999; Kartzinel *et al.* 2015). Most studies examining how the interactive effects of herbivory and productivity shape plant communities have focussed on herbivory in general (herbivory vs. no herbivory), while much less is known about how different species or groups of species may differentially affect plant composition and species richness across productivity gradients.

For example, limited evidence suggests that relative body size may influence herbivory impacts on herbaceous plant communities. In an intercontinental experiment, exclusion of relatively large-bodied grazers (e.g. cattle, sheep) decreased plant species richness in productive habitats and increased richness in unproductive habitats (Bakker *et al.* 2006). However, smaller-bodied grazers (e.g. rabbits, rodents) had little effect across the same productivity gradient. Similarly, in South Africa, only the extremely large-bodied, mega-herbivore white rhinoceros (*Ceratotherium simum*) but not smaller herbivores such as impala (*Aepyceros melampus*) and blue wildebeest (*Connochaetes taurinus*) were able to maintain short-grass lawns in high-rainfall areas (Waldram, Bond & Stock 2008). When rhinoceros were removed from less productive areas, however, impala were able to maintain these short-grass lawns. However, a more recent study from the same area suggested that white rhinoceros had less impact on long-term patterns in vegetation structure or functional community composition than did smaller grazers such as Burchell's zebra (*Equus quagga burchelli*) and African buffalo (*Syncerus caffer*) (van der Plas *et al.* 2016). Similarly, in a productive savanna in Kenya, excluding mega-herbivores, mostly African savanna elephant (*Loxodonta africana*), had little effect on herbaceous vegetation, while excluding relatively smaller herbivores such as zebra, wildebeest and impala had the largest effects on herbaceous plant abundance (Goheen *et al.* 2013). Although these studies begin to provide important insights into the effect of herbivore body size on herbaceous plant communities, more studies are needed over ranges of habitat productivities and levels of herbivory to better understand how productivity shapes the impact of herbivory and how this varies with body size and foraging strategy.

Here, we examined whether African herbivores differing in body size and feeding guild had differential impacts on herbaceous plant communities across a gradient of habitat productivity in the Kruger National Park (KNP), South Africa. Specifically, we used size-selective herbivore exclosures to separate the effects of herbivory by larger herbivores, such as blue wildebeest, Burchell's zebra and elephant from those of medium/smaller herbivores, such as impala and warthog (*Phacochoerus aethiopicus*), along a 10-fold productivity gradient. We hypothesized that herbivory, in general, would vary in its impact on plant species richness across the productivity gradient, with herbivore removal increasing richness at low productivity and decreasing richness at high productivity, as predicted by previous work (Milchunas, Sala & Lauenroth 1988; Proulx & Mazumder 1998). Furthermore, we expected that herbivore size would have differing effects across the productivity gradient. In high-productivity areas, we expected the exclusion of larger herbivores (e.g. elephant, buffalo, zebra, wildebeest) to have the largest effects because their larger body size enables them to forage more effectively in taller and lower-quality vegetation and because they have larger

absolute food requirements (Bell 1971; Hopcraft, Olff & Sinclair 2010). Thus, herbivores would prevent competitive exclusion of subordinate plant species and maintain high levels of species richness in areas of higher productivity. In contrast, we expected that effects of excluding medium/smaller herbivores (e.g. impala, warthog) would be strongest in lower-productivity areas. In these resource-limited sites, we expected smaller herbivores would remove a significant amount of plant biomass and that excluding them would increase plant species richness in these often water-stressed sites.

Materials and methods

STUDY AREA AND EXPERIMENTAL DESIGN

Kruger National Park, South Africa (22° 25′ to 25° 32′ S, 30° 50′ to 32° 2′ E), encompasses nearly 2 million hectares of African savanna protected since 1898. This study was conducted in the region near the Satara tourist camp (24° 23′ 52″ S, 31° 46′ 40″ E) in the central region of KNP. The Satara region has a mean annual rainfall of c. 550 mm, with 80–90% falling between November and March. During our study (2006–2013), precipitation averaged 518 mm (range 397–684 mm).

Vegetation in the region is generally open savanna that is comprised of a mixture of C_4 grasses, annual and perennial forbs and woody plants (e.g. *Senegalia* [previously *Acacia*] *nigrescens*, *Dichrostachys cinerea*). Common grasses are *Urochloa mossambicensis*, *Themeda triandra*, *Panicum maximum*, *Bothriochloa radicans* and *Digitaria eriantha*, with areas higher in soil moisture often supporting *Setaria incrassata*, *Chloris mossambicensis*, *Lintonia nutans*, *Echinochloa colona*, *Ischaemum afrum* and *Dinebra retroflexa*. Central KNP supports a diverse assemblage of large mammalian herbivores (≥10 kg; Table S1, Supporting Information) with elephant, white rhinoceros, giraffe (*Giraffa camelopardalis giraffa*), African buffalo, Burchell's zebra, wildebeest, greater kudu (*Tragelaphus strepsiceros*) and impala being most common.

We selected four study sites with abundant herbivores, similar in concept to nutrient hotspots in other African savannas (Anderson *et al.* 2010), where herbivory was intense with little plant biomass accumulating throughout the year. These sites were separated from each other by 1–14 km, depending on location. A key feature of each site was the presence of well-drained areas with lower productivity and lower-lying, poorly drained areas with higher productivity. The well-drained areas represent portions of the landscape where water transports soils and nutrients downslope into comparatively poorly drained areas. Soil analyses suggested that poorly drained areas had higher clay and lower sand percentages, as well as higher levels of nutrients, than did well-drained areas (Table S2).

Given that soil moisture is an important factor limiting grass productivity (Deshmukh 1984), the extra moisture supplied from downslope runoff, combined with higher soil fertility, results in high productivity in poorly drained areas. Thus, variation in soil moisture across the gradient of well- and poorly drained sites drove a pronounced productivity gradient across sites spanning c. 90–950 g m^{-2} standing plant biomass inside herbivore exclosures. Areas of KNP typically burn every 3–5 years on average (van Wilgen *et al.* 2003), and fire is an important aspect of the ecology of plant communities in KNP (Smith *et al.* 2013). However, our sites did not burn during this study, and they likely rarely burn due to the low fuel loads common on these heavily grazed sites. Thus, fire was not considered an important driver of plant communities during the duration of our study.

We established an experiment across this productivity gradient to test for the effects of different-sized herbivores on the herbaceous vegetation community. We manipulated access to the plant communities using a selective removal experiment that allowed differential access to experimental plots according to herbivore size. The experimental design consisted of three treatments: (i) full exclosures, (ii) exclosures starting at a height of 0·85 m (hereafter 'partial exclosures') and (iii) open access areas. Full exclosures excluded all ungulate herbivores (Table S1). Partial exclosures excluded all animals with a shoulder height 0·85 m or greater (e.g. zebra, wildebeest, buffalo; see Table S1), but allowed access to medium/small herbivores (e.g. impala, warthog). Open access areas allowed access by all herbivores. Thus, we created a gradient in herbivory that ranged from no herbivores to medium/small herbivores only, to medium/small plus large herbivores, similar to other studies assessing impacts of different-sized herbivores (Bakker *et al.* 2006; Hagenah, Prins & Olff 2009; Veblen & Young 2010; Goheen *et al.* 2013; van der Plas *et al.* 2016). Similar to these other studies, our experiment does have the drawback that we cannot examine the impact of only larger herbivores by selectively excluding medium/small herbivores only. Furthermore, our experiment would have also created differential impacts of other mammalian-driven processes such as trampling, granivory and soil disturbance (Cumming & Cumming 2003). Although we did not quantify these processes, they may have contributed somewhat to the changes in plant communities that we observed across the exclosures.

Full exclosures measured 7 m in diameter (enclosing 38·5 m^2 of savanna) and consisted of diamond mesh (5-cm-diameter mesh) to a height of 1·2 m, with a bailing-wire barrier at 2 m (see Koerner *et al.* 2014). Partial exclosures, also 7 m in diameter, consisted of bailing-wire barriers at 0·85, 1·0, 1·2, 1·5 and 2 m above the ground (see Fig. 1 for pictures of the exclosure types). Smaller herbivores and granivores (e.g. rodents), which can also have strong impacts on plant communities (e.g. Keesing 2000), had equal access to all of the treatments. Exclosures and open access areas were located to avoid trees and shrubs as the focus was on herbaceous vegetation. The exclosures and open access areas captured significant heterogeneity in the plant communities as up to eight species of grass and 15 species of forbs (Table S4) were encountered just within the 4 m^2 species composition plots in each treatment (see below for species composition details). Furthermore, many of these grass species have the capacity to become dominants in the plant community, setting the stage for significant changes in the community over time following herbivore exclusion.

Exclosures and open access areas were arranged in a blocked design with one replicate of each treatment in each block. Each treatment within each block had similar initial plant abundance, community composition and productivity based on visual assessment. In November 2006, 14 blocks of exclosures were established at two sites (10 blocks at one site, Mananga and 4 blocks at another, Shibotwana) with 8 additional blocks, split evenly across two additional sites (Satara North and Satara South), added in November 2007. Thus, there were 22 replicates of each exclusion treatment spread across four sites that spanned a broad productivity gradient. The experiment ran until the end of the March 2013 growing season.

RESPONSE VARIABLES

To assess herbivore abundance at our different sites, we used dung surveys to quantify relative herbivore use. Although dung surveys

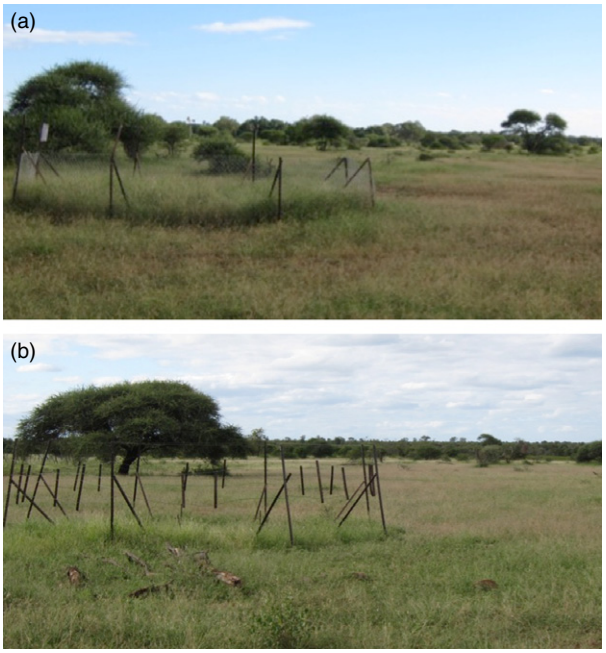


Fig. 1. Photographs of the full exclosure (a) and partial exclosure (b) on a lower-productivity site in the Satara region of Kruger National Park, South Africa. Note the relatively large increase in plant biomass vs. the area outside for the full exclosure, excluding both medium/small (e.g. impala, warthog) and larger (e.g. wildebeest, zebra, buffalo) herbivores, in comparison to the more modest increase in plant abundance in the partial exclosure, excluding only larger herbivores. [Colour figure can be viewed at wileyonlinelibrary.com]

may not be reliable for calculating absolute abundance of herbivores in a given area, they yield reliable estimates of relative abundance across a landscape (Barnes 2001; Cromsigt *et al.* 2009; Burkepile *et al.* 2013; Young *et al.* 2013). Every March (except for 2012), we surveyed 4 m × 100 m dung transects that ran adjacent to the blocks of exclosures at each of our four study sites (n = 3–5 transects per site). We counted herbivore dung piles and identified them to species (Stuart & Stuart 2000) before removing them from the transect to avoid recounting during subsequent surveys.

We used two methods to determine the efficacy of the partial exclosures in excluding larger herbivores ≥0·85 m at the shoulder (Burkepile *et al.* 2016a). First, every c. 4 weeks during the growing seasons of 2007 and 2008, we identified and counted herbivore tracks (Stuart & Stuart 2000) inside 4 m^2 plots in each open access area and paired partial exclosure. Almost all plant biomass was removed from these treatments by the end of the previous dry season, making it feasible to count and identify tracks on the resultant bare ground in the subsequent year. Second, we identified dung piles inside the partial exclosures and in the open access areas across all sites. Although we did not quantitatively assess the efficacy of the full exclosures, we never saw herbivore dung or tracks inside them over the duration of our experiment.

To assess changes in herbaceous plant communities, we surveyed plant community composition during the growing season every January and March during 2007–2013 to capture peak abundance of early- and late-season species, respectively. We sampled one permanent 4 m^2 plot (divided into four 1 m^2 subplots) in each exclosure and open access area. Within each subplot, we estimated the per cent cover (to the nearest 1% when the species was <50% cover or to the nearest 5% when the species was >50% cover) for each plant species (Koerner *et al.* 2014; Burkepile *et al.* 2016a). We also estimated the amount of exposed bare ground (i.e. % area not covered by vegetation), dung and dead leaf litter.

We also measured the effect of herbivore exclusion on light availability, the percentage of photosynthetically active radiation (PAR) reaching the soil surface, in each treatment at the end of the growing season in 2013. Using a ceptometer (Accupar LP-80; Decagon Devices, Pullman, WA, USA), we took three measurements of PAR above the plant canopy in each 1 m^2 subplot and then three measurements of PAR below the plant canopy at the ground surface. We then calculated the percentage reduction in PAR caused by the plant canopy for each exclosure and open access area.

Beginning in 2008, we measured accumulated biomass at the end of each growing season (March) using a disc pasture metre. Within each 1 m^2 subplot of our permanent monitoring plots, we took four disc pasture metre readings. We then averaged the 16 readings for each plot and converted these averages into biomass using a calibration curve established for KNP (Trollope & Potgieter 1986). These biomass values are not a strict measure of annual primary production as they cannot discriminate between current year's growth and residual previous growth (when present). Rather, the calculations give reliable estimates of plant biomass accumulation in each treatment. Thus, the biomass accumulated in the full exclosures where herbivores had no access serves as a proxy for habitat productivity.

STATISTICAL ANALYSES

To assess potential differences in herbivore abundance across sites, we used mixed models to test for site, year and site × year interactions. When we detected either site or year effects (there were no site × year interactions), we used Tukey's HSD to determine post hoc differences within those effects. To assess the effectiveness of the partial exclosures, we used one-way ANOVA (impala) or Wilcoxon signed-rank tests (wildebeest, zebra, warthog) to compare data on tracks or dung piles between the two treatments. Although elephant dung was never found in the partial exclosures, it was found so infrequently in open access areas that meaningful statistics were not possible.

We calculated several metrics of plant community composition for each exclosure/open access area. We used maximum cover values of each species over the growing season averaged across the four 1 m^2 subplots per plot to calculate plant cover (total, grass and forb), species richness [total (S), grass (S_G) and forb (S_F)], Shannon–Wiener diversity index (H') and Berger–Parker Index (D), which is the relative abundance of the most abundant species in each plot. As a proxy for habitat productivity in each exclosure block, we used standing plant biomass from the full herbivore exclosure averaged across all years of the experiment. We present analyses of plant community composition only for 2013, the last year of data collection, as this allowed us to analyse the cumulative impact of herbivore exclusion on plant communities.

For each response metric (e.g. richness, diversity, light reduction), we calculated the strength of the herbivore effect as the log response ratio of different pairings within each exclosure block. Thus, for each block we calculated three effect sizes: (i) the effect of excluding all herbivores calculated as ln(full exclosure/open access area), (ii) the effect of excluding only larger herbivores (e.g. elephant, buffalo, zebra, wildebeest) calculated as ln(partial exclosure/open access area) and (iii) the effect of excluding only medium/smaller herbivores (e.g. impala, warthog) calculated as ln(full exclosure/partial exclosure). Positive effects indicated that excluding herbivores increased the response, while negative effects indicated that excluding herbivores reduced the response.

Previous studies have shown that herbivore exclusion impacts the similarity in plant community structure differentially across productivity gradients (Milchunas & Lauenroth 1993; Bakker *et al.* 2006). Thus, we also calculated community similarity between herbivore treatments using Euclidean distance (ED) (Collins, Micheli & Hartt 2000). Similarity, as measured by ED, increases as the degree of difference in composition among sample units decreases. We used ED rather than per cent similarity because ED is less affected by species richness and therefore more accurately measures community heterogeneity than per cent similarity (Collins, Micheli & Hartt 2000). In each exclosure block, we calculated how community similarity was affected by removing: (i) all herbivores (by comparing the full exclosure to the open access area), (ii) only larger herbivores (partial exclosure vs. open access area) and (iii) only medium/smaller herbivores (full vs. partial exclosure).

We used Bayesian linear regressions to determine how the effect size of herbivore removals varied across the productivity gradient, where each effect size was the response variable and plant biomass in the full exclosure was the predictor. Because we used effect sizes as a response, both the intercept and slope were of interest. For example, a significant intercept but non-significant slope would suggest that herbivore removals do impact plant communities (i.e. the effect $\neq 0$), but that the effect does not vary with habitat productivity. A significant slope would suggest that the effect of herbivore removal changes across the productivity gradient.

Prior to regressions addressing productivity relationships, we standardized the biomass data so that it had a mean of zero. Thus, the intercept of the regressions represented the effect of herbivore removal at average levels of plant biomass and not at zero plant biomass, which would make little sense ecologically. As a consequence, a regression of the effect of herbivore removal on species richness vs. plant biomass that had a significantly negative intercept would indicate that at average plant biomass herbivore removal had a negative effect on plant species richness. In addition, given that changes in light availability (Borer *et al.* 2014) and plant dominance (Eby *et al.* 2014; Koerner *et al.* 2014) may impact changes in plant species richness, we regressed the response ratio of species richness vs. these other metrics.

All regressions were Bayesian linear regressions, run using STAN v2.8 (Stan Development Team, 2015) accessed via PYSTAN. All coefficient and variance parameters were given uninformative prior distributions. MCMC models were run using 25 000 burn-in iterations to achieve convergence and another 25 000 sampling iterations. We ran four chains, resulting in 100 000 samples for each posterior distribution. Chain convergence and autocorrelation were assessed using trace plots of posterior samples. $\bar{R} = 1$ for all parameters in all models, indicating convergence. We generated 95% Bayesian credible intervals for each parameter, as well as calculating the exact probability that the coefficient was < or >0.

Results

HERBIVORE ABUNDANCE AND EXCLUSION EFFICACY

At all sites, we periodically observed herds of impala (200+ individuals), zebra (50+ individuals) and wildebeest (30+ individuals), which were the most common herbivores (Fig. 2). Buffalo and elephant also appeared relatively frequent with other herbivores such as warthog, giraffe, kudu and steenbok being less abundant but frequently present in dung surveys. White rhinoceros dung was rarely encountered on transects, but rhinoceros middens were evident near all sites, suggesting rhinoceros grazing across all sites.

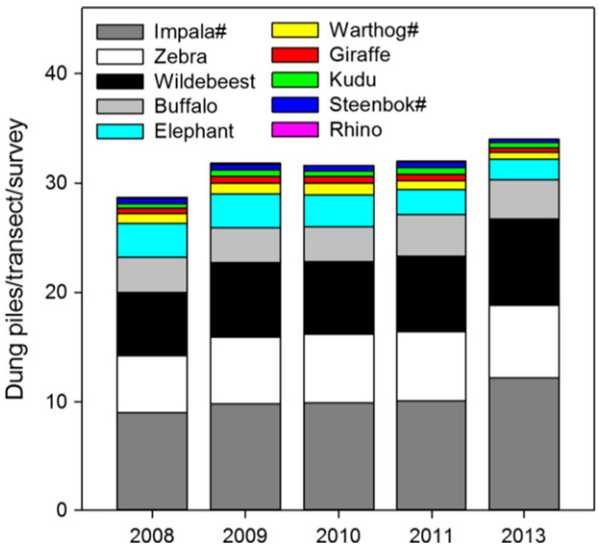


Fig. 2. Density of herbivore dung per transect per survey for 2008–2013, excluding 2012 when data were not collected. Bars are mean values for each herbivore species indicated. Error bars have been omitted for clarity. # marks medium/small species that can access the partial exclosures. [Colour figure can be viewed at wileyonlinelibrary.com]

Herbivore abundance was similar among sites but variable across years for most species (Fig. S1). There were no differences in abundance across sites for impala, wildebeest, zebra, buffalo or warthog (Table S3), although impala and wildebeest differed across years. The Mananga site had the highest elephant dung densities and Satara North the lowest. Dung of giraffe, kudu and rhinoceros was not encountered frequently enough for meaningful statistical analysis. Overall, the analyses showed no obvious consistent differences in herbivore use of our four study sites for the duration of our research, suggesting similar levels of herbivory across our different sites.

Surveys of tracks and dung in the exclosures showed that adults of numerically dominant, large herbivores such as zebra and wildebeest, which were abundant in the adjacent open access areas, were successfully excluded by the partial exclosures (Fig. S2). In contrast, both track counts and dung surveys suggested that impala and warthog used open access areas and partial exclosures similarly (Fig. S2). We recorded tracks of immature zebra or wildebeest inside the partial exclosures only very rarely (less than 1% of the time). Dung and tracks of adult zebra and wildebeest, as well as elephant, were never observed within the partial exclosures.

IMPACT OF HERBIVORE EXCLUSION ON PLANT SPECIES RICHNESS

Herbaceous plant biomass ranged from 89 to 951 g m^{-2} in full herbivore exclosures. The effect of total herbivore exclusion on plant species richness showed a significant negative relationship with plant biomass (Table 1, Fig. 3a). Excluding herbivores led to a gain of two to four species at lower productivity, but a loss of three to seven species at higher

Table 1. Results of Bayesian regression analyses of the effect of herbivore exclusion on plant community metrics vs. standing plant biomass. Values are median intercept and slope. We standardized biomass data to a mean of zero. Thus, the intercept is the effect size of herbivore removal at average plant biomass, not at zero biomass. Pr = probability of an effect either greater (for positive numbers) or less (for negative numbers) than 0. For example, an intercept with median of −0·121 and Pr = 0·980 means that there is a 98% probability that the intercept is <0. Conversely, an intercept with a median of 0·131 and a Pr = 0·962 means that there is a 96·2% probability that the intercept is >0. Regressions are from plant community data from 2013 vs. standing plant biomass from full herbivore exclosures (averaged over 2008–2013)

Herbivore exclusion effect	Intercept	Pr	Slope	Pr	Intercept	Pr	Slope	Pr
	Species richness vs. Biomass				Species diversity vs. Biomass			
All	−0·100	0·959	−0·267	0·999	−0·144	0·982	−0·168	0·990
Large	0·042	0·857	−0·129	0·998	−0·023	0·670	−0·092	0·954
Medium/small	−0·143	0·971	−0·098	0·904	−0·122	0·946	−0·076	0·843
	Grass richness vs. Biomass				Forb richness vs. Biomass			
All	−0·323	0·994	−0·129	0·856	0·001	0·505	−0·276	0·996
Large	−0·099	0·905	−0·099	0·896	0·145	0·980	−0·125	0·960
Medium/small	−0·225	0·955	−0·030	0·590	−0·143	0·950	−0·151	0·955

productivity. Exclusion of only larger herbivores showed a similar pattern to excluding all herbivores (Fig. 3b), although with a smaller range of effect sizes. In contrast, excluding smaller herbivores led to declines in species richness, on average, across almost the whole productivity range (Fig. 3c). The negative model intercept suggests that at mean levels of biomass there was a negative effect of medium/small herbivore exclusion on species richness (corresponding to an average loss of two species) and that this effect varied little across the biomass gradient (slope = −0·098, Pr = 0·904). On the whole, patterns for species diversity were very similar to richness (Table 1, Fig. S2).

Patterns in overall plant species richness were often a combination of contrasting patterns in grass and forb species richness. Grass richness declined regardless of the type of herbivore exclusion (Table 1, Fig. 3d–f), with exclosures losing up to five species. This pattern was similar across the range of productivity as was evident by negative model intercepts without obvious slopes. Exclusion of medium/small herbivores appeared to more strongly influence the overall pattern of declines in grass richness (intercept = −0·225, Pr = 0·955) given that the effect of excluding larger herbivores (intercept = −0·099, Pr = 0·905) was only half as strong, with marginal evidence for this effect.

For forb richness, exclusion of all herbivores led to increases of up to five or six forb species at low productivity but declines of five to seven species at high productivity (Table 1, Fig. 3g). However, exclusion of larger vs. medium/smaller herbivores appeared to have different effects. Excluding larger herbivores increased forb richness (average of one species; maximum of seven species) across much of the productivity range, although the effect weakened with increasing plant biomass (Fig. 3h). In contrast, excluding medium/small herbivores resulted in a decline in forb richness at average productivity (average loss of one species), with losses of five to eight species at high productivity (Fig. 3i). Thus, exclusion of large herbivores tended to increase forb richness while exclusion of medium/smaller herbivores appeared to suppress forb species across much of the range of productivity.

IMPACT OF HERBIVORE EXCLUSION ON BARE GROUND, SHADING AND PLANT DOMINANCE

Excluding herbivores decreased the amount of bare ground regardless of productivity (Table S5), with full exclosures having <2% bare ground while open access areas had 14% bare ground on average (Table S4). When all herbivores were excluded, there was some evidence of a negative relationship between the effect of herbivore removal on bare ground and the effect on plant species richness (Table S5). Thus, as the effect of herbivore removal on bare ground became more strongly negative, the effect removing herbivores on plant richness tended to be more positive.

Excluding herbivores increased shading by the plant canopy regardless of the exclosure type (Table 2, Table S4) with the plant canopy in full exclosures intercepting c. 65% of PAR on average. Although herbivore exclosures decreased light by up to 70–90% in the most productive areas, the effect size of light reduction decreased as productivity increased. Thus, the greatest relative increase in shading occurred at lower productivity where plant biomass outside of the exclosures was relatively low (Table 2). In contrast, at higher productivity, there was often a significant amount of plant biomass in open access areas, already intercepting c. 50–60% of PAR. Thus, when herbivores were excluded, the increase in plant biomass, and subsequent increase in shading, was proportionately less than in the lower-productivity areas.

There were positive correlations between the effect of herbivore exclusion on shading vs. the effect on species richness regardless of exclosure type (Fig. 4a–c). Thus, exclosures that had relatively higher increases in shading also experienced increased species richness. In contrast, we saw reduced species richness at comparatively lower relative increases in shading following herbivore exclusion. However, the absolute level of shading in the herbivore exclosures did influence how herbivore exclusion impacted plant species richness. There were strong negative relationships between the absolute levels of PAR reduction in the herbivore exclosures and the effect of herbivore removal on species richness (Table 2, Fig. 4d–f).

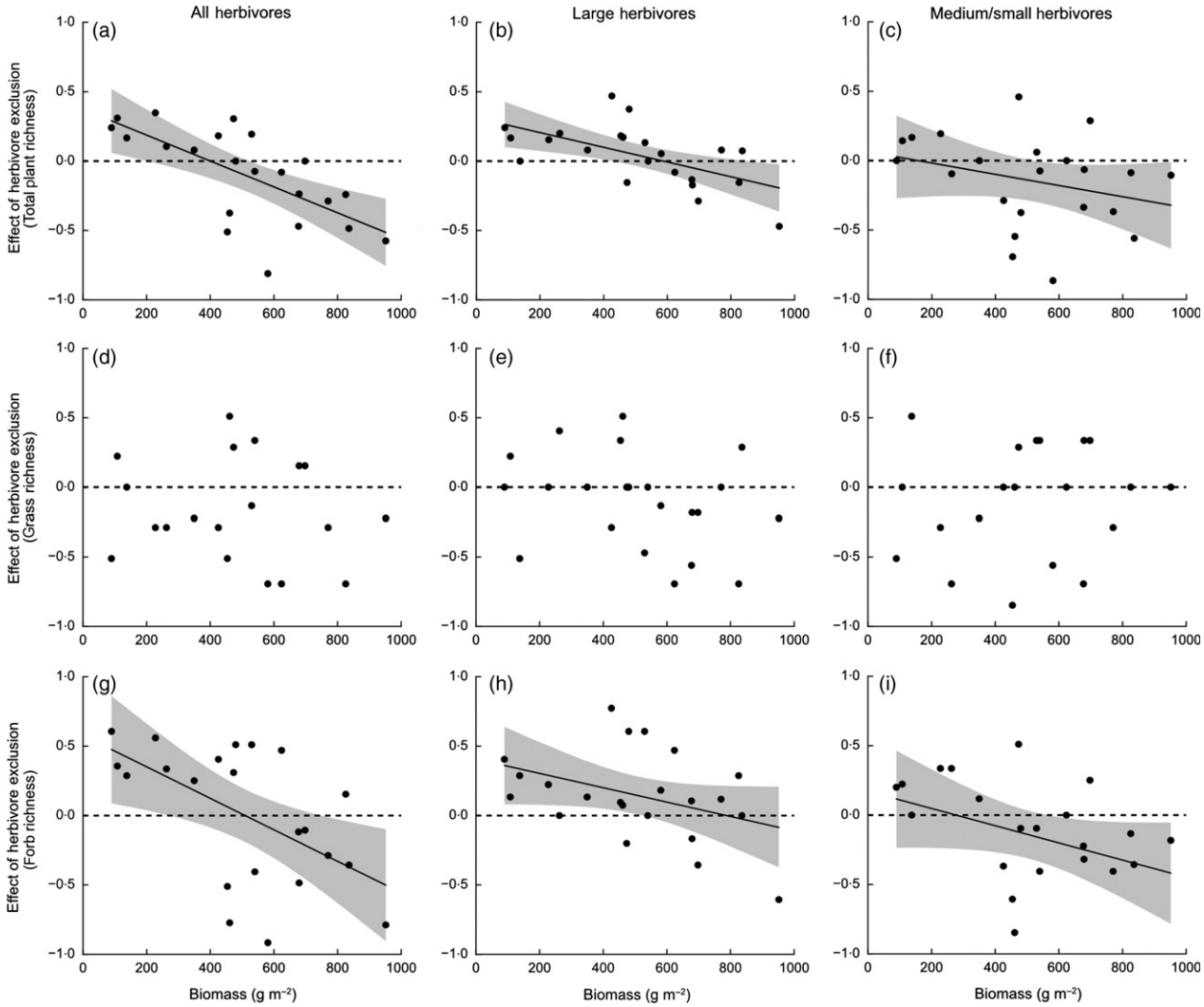


Fig. 3. Effect sizes for exclusion of all herbivores [ln(full exclosure/open access area)], large herbivores only [ln(partial exclosure/open access area)] or medium/small herbivores only [ln(full exclosure/partial exclosure)] on overall species richness (a–c), grass species richness (d–f) or forb species richness (g–i) across a gradient of plant biomass. Biomass is the g m^{-2} for the full exclosure within each block of treatments averaged over 2008–2013. The lines on the figure show the median posterior prediction from Bayesian regression analyses. The shaded area shows the 95% Bayesian credible interval of the predicted relationship. This interval was determined by calculating fitted values (i.e. regression lines) for all 4000 posterior draws and then taking the 2·5% and 97·5% quantiles of the fitted values.

Thus, the strongest declines in richness occurred where absolute light levels were the lowest. However, more modest reductions in PAR often led to increased species richness.

Only exclusion of all herbivores consistently increased plant dominance (i.e. the abundance of the most abundant species) given the positive intercept (intercept = 0·127, Pr = 0·946). This relationship did not vary with productivity (Table 2). On average, the most dominant species represented 70% of the plant community in herbivore exclosures as compared to 50% in open access areas (Table S4). Increased dominance was linked to declines in species richness with the effect of excluding herbivores on species richness becoming more negative as the effect on dominance increased (Table 2, Fig. 4g). This was especially apparent when assessing the effect of excluding medium/small herbivores; decreased dominance following herbivore removal led to increases in species richness while increased dominance led to declines in species richness (Fig. 4i).

IMPACT OF HERBIVORE EXCLUSION ON COMMUNITY SIMILARITY

When we used ED to assess how herbivore exclusion impacted plant community similarity, we found some evidence of a negative relationship (slope = −4·99, Pr = 0·900) between productivity and ED when all herbivores were excluded (Table 1, Fig. 5a). Thus, when herbivores were excluded, the plant communities in the exclosures tended to be more different from the open access areas at lower productivity, but more similar to open access areas at higher productivity. There was no linear relationship between productivity and similarity when excluding only larger herbivores.

Table 2. Results of Bayesian regression analyses of the effect of herbivore exclusion on light/plant community metrics vs. standing plant biomass or effect on plant richness vs. effect on light/plant community metrics. Values are median intercept and slope. We standardized biomass data to a mean of zero. Thus, the intercept is the effect size of herbivore removal at average plant biomass, not at zero biomass. Pr = probability of an effect either greater (for positive numbers) or less (for negative numbers) than 0. For example, an intercept with median of −0·121 and Pr = 0·980 means that there is a 98% probability that the intercept is <0. Conversely, an intercept with a median of 0·131 and a Pr = 0·962 means that there is a 96·2% probability that the intercept is >0. Regressions are from plant community data from 2013 vs. standing plant biomass from full herbivore exclosures (averaged over 2008–2013)

Herbivore exclusion effect	Intercept	Pr	Slope	Pr	Intercept	Pr	Slope	Pr
	Relative shading (PAR effect size) vs. Biomass				Relative shading (PAR effect size) vs. Richness			
All	1·333	0·999	−0·680	0·999	−0·380	0·999	0·214	0·998
Large	0·780	0·999	−0·230	0·940	−0·090	0·910	0·173	0·990
Medium/small	0·551	0·999	−0·460	0·999	−0·230	0·990	0·156	0·910
	Absolute shading (% PAR reduction) vs. Richness							
All	0·540	0·989	−0·012	0·999				
Large	0·203	0·992	−0·003	0·980				
Medium/small	0·277	0·866	−0·006	0·964				
	Dominance vs. Biomass				Dominance vs. Richness			
All	0·127	0·946	0·087	0·869	−0·059	0·782	−0·330	0·934
Large	0·067	0·825	0·051	0·746	0·039	0·780	0·043	0·611
Medium/small	0·059	0·784	0·036	0·680	−0·108	0·955	−0·580	0·997
	Community similarity (Euclidian distance) vs. Biomass							
All	59·08	0·999	−4·99	0·900				
Large	48·19	0·999	4·82	0·829				
Medium/small	54·54	0·999	−9·88	0·960				

However, areas where the larger herbivores were present vs. absent appeared to be more similar at both low- and high-productivity areas and most dissimilar at moderate productivity (Fig. 5b). In contrast, excluding medium/small herbivores showed a negative relationship (slope = −9·88, Pr = 0·960) between productivity and ED (Fig. 5c), with exclusion resulting in more dissimilar communities at lower productivity.

Discussion

The interactive effects of herbivory and productivity on plant community structure and species richness have been well studied in savanna and grassland ecosystems (e.g. Milchunas & Lauenroth 1993; Borer *et al.* 2014). We expanded on the topic by focusing on how different groups of African ungulates, based on body size, impact plant communities across a productivity gradient. As we hypothesized, exclusion of all herbivores generally increased plant species richness at low productivity but decreased richness at high productivity. These results are similar to those from exclusion experiments at local, topographically determined productivity gradients (Osem, Perevolotsky & Kigel 2002, 2004) as well as for productivity gradients at regional (Frank 2005; Young *et al.* 2013), continental (Lezama *et al.* 2014) and intercontinental scales (Milchunas & Lauenroth 1993; Bakker *et al.* 2006).

However, we show several key patterns that expand on previous works. Contrary to our hypotheses, exclusion of medium/small herbivores (e.g. impala, warthog) showed stronger effects on plant richness at higher productivity rather than at lower productivity. In particular, the loss of forb species at higher productivity was linked to exclusion of medium/small herbivores. In contrast, larger herbivores had stronger effects on plant richness at low rather than high productivity, with a strong increase in forb richness following large herbivore exclusion across almost the whole productivity gradient. Increases in shading following herbivore exclusion appeared to drive species losses at higher productivity. However, at lower productivity, similar increases in shading resulted in increases in plant richness, possibly due to amelioration of heat and water stress. In addition, increases in plant dominance were correlated with declines in plant richness following herbivore exclusion. Although increases in plant dominance are often emphasized as driving species loss following herbivore exclusion at higher productivity (e.g. Olff & Ritchie 1998), we showed that the negative effects of increasing dominance on plant richness operated independent of productivity, with the exclusion of impala appearing particularly important for driving this relationship.

THE ROLE OF LARGER VS. MEDIUM/SMALL HERBIVORES

Rather than larger or smaller herbivores dominating effects on plant communities (e.g. Olofsson *et al.* 2004; Bakker *et al.* 2006; van der Plas *et al.* 2016), exclusion of both groups appeared to have unique, sometimes contrasting, impacts on plant community dynamics. For example, exclusion of larger herbivores appeared to increase species richness at lower

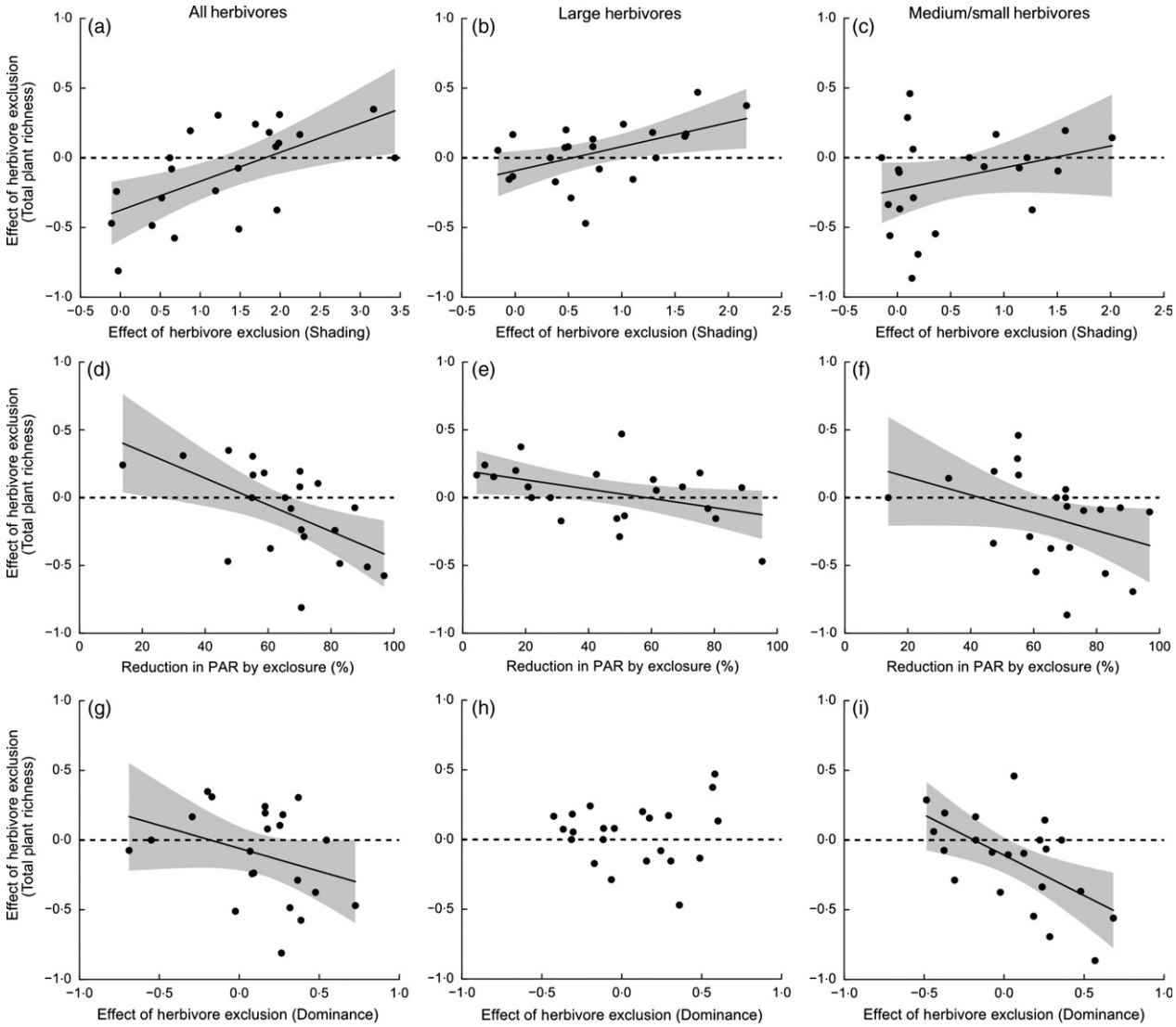


Fig. 4. Effect sizes for exclusion of all herbivores, large herbivores only or medium/small herbivores only (see Fig. 3 for details) on the relationship between effects on species richness vs. relative shading (a–c), on the relationship between effects on species richness vs. absolute shading (d–f), and on the relationship between effects on species richness vs. dominance (g–i). Regression line and credible intervals as in Fig. 3.

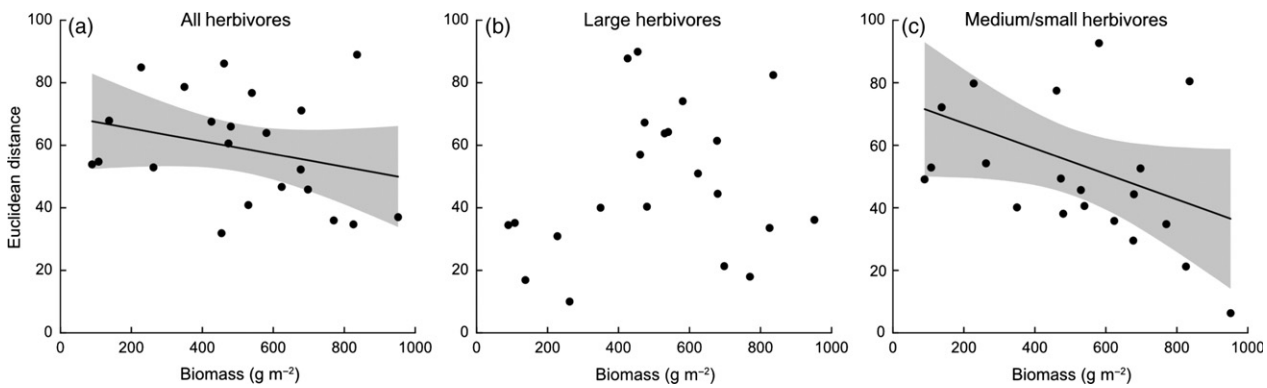


Fig. 5. Similarity of plant communities (Euclidean distance) following exclusion of (a) all herbivores (i.e. similarity of full exclosures vs. open access areas), (b) larger herbivores (i.e. similarity of partial exclosures vs. open access areas) or (c) medium/small herbivores (i.e. full exclosures vs. partial exclosures) across a gradient of plant biomass (g m^{-2}). Higher numbers for Euclidean distance indicate increasing dissimilarity of the plant communities between the two treatments. Regression line and credible intervals as in Fig. 3.

productivity while exclusion of medium/small herbivores appeared to suppress species richness at higher productivity (Fig. 3). These patterns are different from other recent studies, which often show that removal of larger herbivores generally has the strongest impacts on plant diversity and community structure, especially in areas of higher productivity (e.g. Bakker *et al.* 2006; Waldram, Bond & Stock 2008). These results were also contrary to our hypotheses as we expected excluding medium/small herbivores would have more of an impact on diversity in lower-productivity habitats while excluding larger herbivores would have stronger impacts in higher-productivity habitats.

One reason for the strong impact of excluding both large and medium/small herbivores in our study, as compared to previous studies, may have been due to differences in the relative abundance of the different groups. In an intercontinental comparison, Bakker *et al.* (2006) showed that only removing larger herbivores had strong impacts on plant communities. However, in their study, larger herbivores were abundant grazers (e.g. cattle, sheep, bison) while smaller herbivores were typically rabbits and other small rodents, which were likely orders of magnitude less abundant in terms of biomass making their lack of effect on plant communities unsurprising. However, in our study, medium/small herbivores, particularly impala, are the numerically abundant herbivore in KNP (Owen Smith & Ogutu 2003), consistent with their strong impacts on plant communities.

Furthermore, we may have seen strong effects of smaller herbivore exclusion on richness and diversity because our experiment likely created a gradient in grazing pressure across the three treatments, and the impact of herbivores on plant communities often intensifies as grazing pressure increases (e.g. Milchunas & Lauenroth 1993). During the wet season, impala are primarily grazers in KNP with grasses often representing over 90% of their diet (du Toit 2003). Thus, the partial exclosures likely resulted in an intermediate level of grazing with larger-bodied buffalo, zebra and wildebeest absent, but impala, the most numerically abundant herbivore, present. The large impacts on plant richness, diversity and dominance often only manifested when the impala were also excluded with the full exclosures (i.e. compare the effects of excluding Large Herbivores vs. All Herbivores). Thus, the impact of removing the medium/small herbivores may have had less to do with them being smaller and more to do with impala being important, numerically abundant grazers in the wet season.

MECHANISMS DRIVING CHANGES IN PLANT RICHNESS

Most studies examining the effects of removing herbivores on plant diversity typically focus on cattle, sheep or other grazers (e.g. Collins *et al.* 1998; Osem, Perevolotsky & Kigel 2002; Bakker *et al.* 2006; Lezama *et al.* 2014). Thus, when these single grazer species are removed, the competitively superior grasses dominate and out-compete forb species, lowering plant diversity. However, the diverse guild of African herbivores often has over a dozen species of grazers, browsers and mixed feeders whose impacts on plant communities could be more complex than having one or a few dominant grazers.

In our study, the differential effects of grazers and browsers likely interacted with differences in plant competitive strategies to drive the often contrasting responses of grass and forb richness. For example, excluding larger herbivores, which comprised both abundant grazers (e.g. buffalo, zebra, wildebeest) and browsers (e.g. kudu), had no consistent effect on grass richness but increased forb richness across most of the productivity range. Grasses likely have a suppression-based strategy, which requires rapid growth rates and over topping neighbours, while forbs use a more tolerance-based strategy, which requires shade tolerance to withstand competition (MacDougall & Turkington 2004). Forbs often contribute the greatest amount to the diversity of grasslands but are rarely dominant (Uys, Bond & Everson 2004). In our study, communities often had up to two times more forb species than grass species. However, forbs were the dominant species in only 12% of the exclosures or open areas. Thus, many forb species may exist through tolerance of competition by the dominant grasses, at least until light or some other resource becomes too limiting. Thus, after excluding larger herbivores, forbs likely increased in richness by escaping consumption from browsers (e.g. kudu) while being able to tolerate moderate increases in competition with grasses following removal of grazers (e.g. wildebeest, zebra, buffalo).

Competition for light is often emphasized as the primary mechanism driving changes in species richness when herbivores are removed from grasslands (Milchunas & Lauenroth 1993; Borer *et al.* 2014). When we excluded herbivores at the lower range of productivity, we saw increases in species richness, particularly in annual forbs (e.g. *Indigastrum parviflorum*, *Indigofera rhytidocarpa*, *Gisekia africana*). These increases in species richness were strongly positively associated with moderate increases in shading and moderately positively associated with decreases in bare ground in herbivore exclosures, both of which may have reduced stress on plant seedlings. However, the herbivore exclosures with the highest absolute levels of shading (PAR reduction), often in the highest productivity areas, had the highest losses of species. This increased competition for light is often linked to increased dominance of large grasses in more productive areas (e.g. Olff & Ritchie 1998). However, we also showed that increases in plant dominance following herbivore exclusion led to declines in species richness, regardless of productivity. This effect was especially pronounced when considering the effect of medium/smaller herbivores (i.e. impala). Only a few studies have linked changes in dominance to changes in species richness (Eby *et al.* 2014; Koerner *et al.* 2014; Burkepile *et al.* 2016a). However, plant communities can have strong dominance in both high- (Smith & Knapp 2003) and low- (Collins & Xia 2015) productivity systems. Thus, changes in dominance may be a generalizable mechanism driving the varied responses of richness to herbivore exclusion across productivity gradients due to the concomitant changes in the availability of many resources, such as light, water, nutrients and space.

LOSS OF DIVERSE HERBIVORE GUILDS AND PLANT COMMUNITY SIMILARITY

Both theory (Milchunas, Sala & Lauenroth 1988) and previous research (Milchunas & Lauenroth 1993; Bakker *et al.* 2006; Anderson, Ritchie & McNaughton 2007) has suggested that exclusion of herbivores leads to increasingly dissimilar plant communities as primary productivity increases. When we assessed how exclusion of all herbivores impacted plant community similarity across productivity, we showed that there was only a marginal relationship between community similarity (inside vs. outside exclosures) and productivity. The difference in results between our study and previous work could be because most other studies have focused almost completely on the effects of removing large grazers. However, feeding by grazers and browsers in African savannas may compensate for each other to minimize changes in the plant community (Burkepile *et al.* 2016a). Thus, the exclusion of both types of herbivores in our study could result in much less dramatic and more similar changes in community composition regardless of productivity. For example, previous empirical work comparing North American vs. Southern African savanna grasslands has shown similar plant community responses between continents when only grazers are excluded (Burns, Collins & Smith 2009; Eby *et al.* 2014), but dissimilar responses when comparing grazers vs. grazers plus browsers (Koerner *et al.* 2014). Work from other African savannas with much larger herds of dominant grazers (e.g. Serengeti) as compared to KNP shows more dissimilar plant communities following herbivore exclusion at higher productivity (Anderson, Ritchie & McNaughton 2007). Here, when we isolated the effect of excluding the medium/small herbivores, mostly impala – the wet season grazer –, there was a negative relationship between productivity and their effect on community similarity, with communities becoming more similar with increasing productivity. Thus, having one dominant grazer may have driven these more linear changes in community similarity as found in other studies (e.g. Milchunas & Lauenroth 1993; Bakker *et al.* 2006).

However, the pattern in community similarity is opposite to that shown by other studies, which suggest that community similarity decreases following herbivore exclusion as productivity increases. The increase in similarity with increasing productivity that we showed may have been due to how herbivore exclusion altered the abundance of dominant species. At lower productivity, herbivore exclusion facilitated the colonization of new species, such as the grass *U. mossambicensis*, which often became dominant in the community. However, forbs and unpalatable grasses often dominated open access areas. In more productive communities, however, large grasses such as *S. incrassata* and *P. maximum* and large forbs such as *Indigophera schimperi* were often the most abundant species in open access areas and then increased in dominance in herbivore exclosures. These dominant grasses then outcompeted relatively uncommon forbs and smaller grasses. Thus, at low productivities the dominant species often changed between herbivore exclosures and open access areas, resulting in very dissimilar communities. However, at higher productivities the same species were dominant in both herbivore exclosures and open access areas but simply increased in abundance with herbivore exclusion, resulting in fairly similar communities despite the loss of some subordinate species.

Conclusions

Ecosystems continue to lose important herbivore species world-wide with larger herbivores often being lost first (Ripple *et al.* 2015), a pattern mimicked by our exclosures in a South African savanna. We show that the impact of losses of these herbivores on plant communities will be strongly context dependent and will vary with the herbivores lost (e.g. larger vs. smaller, grazers vs. browsers), plant functional type (e.g. grasses vs. forbs) and environmental context, as other recent studies have suggested (Waldram, Bond & Stock 2008; Goheen *et al.* 2013; van der Plas *et al.* 2016). Loss of impala appear especially important for impacting species richness, likely by regulating plant dominance and preventing competitive exclusion, especially in high-productivity areas. This pattern was surprising given the strong emphasis on the role of mega-herbivores in African savannas (Owen-Smith 1988; Waldram, Bond & Stock 2008; Cromsigt & te Beest 2014). However, our work and several other recent studies (e.g. Goheen *et al.* 2013; Pringle *et al.* 2014; Burkepile *et al.* 2016a; van der Plas *et al.* 2016) have shown strong roles of abundant, medium/small herbivores in controlling plant community dynamics even in the presence of larger herbivores.

Despite the differential impacts of herbivores differing in body size and foraging mode, we show that excluding herbivores increases plant richness at low productivity and increases plant richness at high productivity, similar to other recent studies. Local soil moisture determined productivity in our experiment, in contrast with region-wide or continental-scale studies where precipitation gradients often drive productivity (e.g. Milchunas & Lauenroth 1993; Bakker *et al.* 2006; Young *et al.* 2013; Lezama *et al.* 2014). Thus, in our study, areas across the range of productivity were often separated by metres or a few kilometres, instead of hundreds of kilometres, and had similar levels of herbivory, herbivory diversity and plant species pools. The same cannot be said for the larger-scale studies that often included sites with different baseline plant species richness, different herbivores and varying grazing intensities. However, studies ranging from local to intercontinental scales show very similar patterns in the responses of the plant communities across productivity gradients. These common patterns strongly suggest that the mechanisms shaping the herbivory–productivity–richness relationship may operate independent of scale and may be a robust, general concept in ecology.

Authors' contributions

D.E.B. and R.W.S.F. designed the experiment; all authors contributed to data collection; D.E.B. and N.P.L. analysed the data; D.E.B. and R.W.S.F. led the writing of the manuscript; all authors contributed critically to manuscript development.

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Data accessibility

Data are deposited in the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.j6p0b (Burkepile *et al.* 2016b).

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Supporting Information

Details of electronic Supporting Information are provided below.

Table S1. Mammalian herbivores (>10 kg) observed on the Experimental Burn Plots in the central region of Kruger National Park. Biomass estimates for an average individual from each species from Estes (1991).

Table S2. Soil properties of well-drained and poorly drained areas. Soil profiles are averages of $n = 11$ samples taken across all four study sites ($n = 2$–4 per site).

Table S3. Results of fixed effects tests from mixed models testing for differences in herbivore dung density across sites and years for the common herbivore species.

Table S4. Summary statistics for plant community metrics.

Table S5. Results of Bayesian regression analyses of the effect of herbivore exclusion on per cent bare ground vs. standing plant biomass and effect of exclusion on per cent bare ground vs. effect of exclusion on plant species richness.

Fig. S1. Density of dung piles per transect (means ± SE) of the most common herbivores across sites and across years of our study. Note that there is often year-to-year variation in density. However, few species have consistent differences among sites. See Table S3 for statistics testing differences across sites, years and their interaction.

Fig. S2. Tracks per species composition plot (a & b) and dung piles (c & d) per partial exclosure or open access area for either 2007 or 2008.

Fig. S3. Effect sizes for exclusion all herbivores [ln(full exclosure/open access area)] (a), large herbivores only [ln(partial exclosure/open access area)] (b), or small herbivores only [ln(full exclosure/partial exclosure)] (c) on plant species diversity across a gradient of plant biomass.

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COMMENTARY

Herbivore size matters for productivity-richness relationships in African savannas: Commentary on Burkepile *et al.* (2017)

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Since the Late Pleistocene, human impact has increasingly resulted in defaunation, or human-caused animal loss, leading to largely impoverished vertebrate communities (Dirzo *et al.* 2014; McCauley *et al.* 2015). These extinctions are not random, but are strongly size-selective with large animals going first. This trend is continuing, with native large herbivores being currently increasingly threatened around the globe (Ripple *et al.* 2015). As a consequence, native herbivore communities both lose their largest members, hence, decreasing in average size, but simultaneously decrease in diversity. This may have strong consequences for the herbivore's impact on biodiversity, ecosystem functioning and landscape structure (Dirzo *et al.* 2014; Bakker *et al.* 2016a). However, field tests of the effect of size-selective loss of vertebrate herbivores remain rare.

Burkepile *et al.* (2017) performed such a test and address the question how the loss of vertebrate herbivores affects plant species richness in African savanna. They incorporated the size-selectivity of herbivore extinctions in their design by using size-selective exclosures to separate the effect of losing only the larger herbivores as elephant, zebra and wildebeest from that of losing all vertebrate herbivores >1 kg together. They subsequently replicated this design across a 10-fold gradient in plant production within Kruger National Park, South Africa.

Herbivore impact on plant species richness along a productivity gradient

The study design incorporates the notion that herbivores affect plant species richness systematically across a productivity gradient: herbivores reduce plant species richness at low production and increase it at high productivity (Bakker *et al.* 2006; Borer *et al.* 2014). So far, nothing new, as Burkepile *et al.* (2017) confirm this pattern. However, these previous tests worked mostly with presence or absence of herbivores only, whereas the size-selective exclosures give more information on the role of the different herbivores. Although this has been done previously, this was in already severely impoverished herbivore communities as nowadays present in most of Europe and North-America. Hence, the relationship between plant production and herbivore impact on plant species richness that we know comes from the impact of one or two herbivore species. In contrast, African herbivore communities are species-rich and thus the question is whether this may result in different dynamics and impacts then studying only one or two species. And it does. Although the general patterns hold, the surprising result is that the large herbivores negatively affect plant species richness at low production, whereas the small to medium-sized herbivores affect species richness positively at high production. Although the herbivore community is species rich, the results are predominantly explained by the role of a single species: impala.

Interestingly, the important role of impala affecting savanna vegetation has been found before in suppression woody plant colonization as well as selectively feeding on fruits from woody species, thus contributing strongly to seed dispersal (Sankaran, Augustine & Ratnam 2013; Pringle *et al.* 2014). Burkepile *et al.* (2017) now demonstrate that they can also strongly affect grassland plant diversity.

Impala were the most abundant herbivores in the study sites, which explains part of their strong impact. However, that is only part of the answer as it is the feeding strategy of the impala causing the impact on plant species richness: their diet consists mostly of grasses, hence forbs profit from impala grazing on grasses and subsequent suppression of grass competition. Thus, feeding on the dominant competitor warrants their impact on plant species richness. Although this effect is usually attributed to large bulk grazers, this study shows that medium-sized herbivores may have similar effects.

The finding that density as well as the diet selection of the herbivores are the parameters determining their impact on the vegetation has important implications for the interpretation of other studies on herbivore impact. Many studies investigating the impact of herbivores are set in sites with managed herbivore populations. Native herbivore densities can be kept very low due to hunting (for instance deer), leaving herbivores seemingly functionally unimportant (e.g. Bakker *et al.* 2016a). However, this may just be because the herbivores are managed to avoid them causing impact on vegetation, which is perceived as damage (Morellet *et al.* 2007; Tanentzap *et al.* 2011). Thus, when generalizing herbivore impact on vegetation and ecosystems one should be aware of the role of

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herbivore density and the role of humans managing the herbivore densities.

Furthermore, the study of Burkepile *et al.* (2017) points to the importance of feeding selectivity of the herbivores. Indeed, Burkepile *et al.* (2017) find a strong relation between the dominance of the plant species and the impact of the herbivores on plant species richness: when reducing the dominant, the impacts on species richness are increasingly positive. This sheds new light on the current theory: it is not just a matter of large herbivores being bulk grazers, removing dominant plants at high production, thereby preventing light limitation among the plants and thus promoting species richness (Borer *et al.* 2014). Instead, the role of limiting plant dominance is not just for large herbivores, but also for smaller ones, if present at sufficient densities, and not just at high production, but across the whole productivity gradient, as Burkepile *et al.* (2017) demonstrate. That herbivores regulate plant diversity through their impact on plant dominance is a principle already outlined by Olff & Ritchie (1998), but is not often taken into consideration.

Towards new approaches to predict herbivore impact

As a consequence, new approaches are needed to predict under what conditions herbivores will preferentially or mainly consume the dominant plant species and when the subordinates. Although light limitation coincides with productivity, herbivore selectively may not, as plant quality is determined by the resource limitation of the plant, including light, and also water and nutrients. Therefore, plants at high productivity may be very poor or very high in quality, depending on whether nutrients, water or light is limiting their growth (Olff & Ritchie 1998) and similarly for plants at low productivity. Selective herbivore feeding on dominant or subordinate species may depend on which have the best quality, which varies with the type of resource limiting plant growth, and not systematically with production per se.

Furthermore, it may be the traits of the herbivores themselves that allow prediction of their feeding selectivity. The study of Burkepile *et al.* (2017) stresses to take into account herbivore traits to allow prediction of their effects on ecosystems. In that sense, the title is a bit misleading as the authors themselves state: the impact of removing small to medium herbivores had less to do with them being smaller as with impala being a numerically abundant grazer in the wet season with a preference for dominant plants. This illustrates that the classical division of large vs. small to medium herbivores and the classification of them as bulk grazers vs. selective grazers is primitive and in need of revision.

Altogether, revising our current relatively straightforward theory of the impact of large vs. small herbivores on plant species richness along a productivity gradient may seem a big task, which may lead to some discouragement. At least, Burkepile *et al.* (2017) conclude in their synthesis that the impact of herbivore loss on plant diversity will be strongly situation dependent, which may seem to render the results very local and context specific. However, this is not doing justice to the findings that there are emerging general patterns with respect to the role of herbivore selectivity and plant dominance to predict herbivore impact, but these just need more future elaboration. Several recent developments are very helpful in this respect, which are addressed in the following section.

Functional grouping of herbivores

Expanding the classical division of herbivores in large vs. small to medium into grouping of herbivores based on their traits would greatly facilitate a better understanding of herbivore impacts in multi-species assemblages. Recently, Hempson, Archibald & Bond (2015) made a functional grouping of savanna herbivores based on their body weight, sociality, diet selection and dependence on water sources. Bakker *et al.* (2016b) grouped large aquatic herbivores based on their aquatic plant dependency and territoriality. This functional approach to vertebrate herbivore communities allows fine-tuning of the predictions of their impact on vegetation and ecosystems. Better knowledge of herbivore diets becomes more and more available due to stable isotope techniques (Codron *et al.* 2007) as well as DNA analyses of plants and herbivores and their faeces (Kartzinel *et al.* 2015), which strongly facilitates the functional grouping of vertebrate herbivores.

However, functional grouping of herbivores is one thing, testing their impact another, and in this respect using size-selective or factorial exclosures is a very important tool to study the effect of herbivore diversity (Sankaran, Augustine & Ratnam 2013; Young *et al.* 2013; Keesing & Young 2014). Size-selective or factorial exclosures are designed to not exclude all herbivores in once, but to allow access to different subgroups of the local herbivore community depending on the type of fencing, resulting in different grazing treatments. For instance, the largest herbivores can be excluded with a fence where small herbivores can still pass underneath and both small and large herbivores with a small-mesh fence such as done by Burkepile *et al.* (2017). Furthermore, statistical patterns in large datasets based on monitoring data, may reveal the connection between herbivore diversity and plant diversity (Greve *et al.* 2012). The development of techniques such as LiDAR – a surveying method that measures distance to a target by illuminating that target with a laser light – allows large-scale 3D vegetation mapping either airborne or ground-based, which can be linked to animal behaviour and impact (Davies & Asner 2014). This increasingly allows collection of large amounts of detailed data of on herbivore impacts, which may be species specific. In Kruger, using LiDAR, it was possible to measure the decreasing height of adult trees over time, which set apart the effect of elephants relative to the rest of the herbivore community (Asner *et al.* 2009).

Outlook

Although these are very exciting developments, more work is needed on the underlying mechanisms of the effect of herbivore diversity. In particular, the question whether there are compensatory or additive effects of different herbivore species

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in diverse communities (e.g. Ritchie & Olff 1999) should be investigated. Also very important in this respect are the interactions among the herbivores: does the loss of herbivore species result in lower total herbivore densities or do other species compensate by increasing their abundance? This elaborates on the notion that the effect of herbivore diversity may be modulated strongly by their realized densities (e.g. Bakker *et al.* 2016a).

The findings presented by Burkepile *et al.* (2017) are not just relevant for terrestrial grasslands but apply to a wide range of ecosystems, including aquatic ones (e.g. Burkepile & Hay 2008). Furthermore, the study is very relevant to predict effects of herbivore loss, but also has application in conservation, where herbivore species are added, such as in trophic rewilding, where more complete native large herbivore assemblages are being restored (Seddon *et al.* 2014). Prediction of the impact of rewilding on biodiversity is a topic of ongoing debate. Knowledge of the impact of natural diverse herbivore assemblages as presented in Burkepile *et al.* (2017) can strongly contribute to predict the impacts of diverse vs. impoverished herbivore assemblages (Svenning *et al.* 2016).

Data accessibility

This paper does not use data.

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