

Are cattle surrogate wildlife? Savanna plant community composition explained by total herbivory more than herbivore type

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Abstract. The widespread replacement of wild ungulate herbivores by domestic livestock in African savannas is composed of two interrelated phenomena: (1) loss or reduction in numbers of individual wildlife species or guilds and (2) addition of livestock to the system. Each can have important implications for plant community dynamics. Yet very few studies have experimentally addressed the individual, combined, and potentially interactive effects of wild vs. domestic herbivore species on herbaceous plant communities within a single system. Additionally, there is little information about whether, and in which contexts, livestock might functionally replace native herbivore wildlife or, alternatively, have fundamentally different effects on plant species composition. The Kenya Long-term Exclosure Experiment, which has been running since 1995, is composed of six treatment combinations of mega-herbivores, meso-herbivore ungulate wildlife, and cattle. We sampled herbaceous vegetation 25 times between 1999 and 2013. We used partial redundancy analysis and linear mixed models to assess effects of herbivore treatments on overall plant community composition and key plant species. Plant communities in the six different herbivore treatments shifted directionally over time and diverged from each other substantially by 2013. Plant community composition was strongly related ($R^2 = 0.92$) to residual plant biomass, a measure of herbivore utilization. Addition of any single herbivore type (cattle, wildlife, or mega-herbivores) caused a shift in plant community composition that was proportional to its removal of plant biomass. These results suggest that overall herbivory pressure, rather than herbivore type or complex interactions among different herbivore types, was the main driver of changes in plant community composition. Individual plant species, however, did respond most strongly to either wild ungulates or cattle. Although these results suggest considerable functional similarity between a suite of native wild herbivores (which included grazers, browsers, and mixed feeders) and cattle (mostly grazers) with respect to understory plant community composition, responses of individual plant species demonstrate that at the plant-population-level impacts of a single livestock species are not functionally identical to those of a diverse group of native herbivores.

Key words: *Acacia drepanolobium; cattle-wildlife interactions; East Africa; ecological equivalence; elephant; forb; grass; grazing; herbaceous community; human-wildlife conflict; zebra.*

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INTRODUCTION

Wild herbivores continue to be replaced by domestic livestock in African savannas and many other rangelands around the world, with potentially negative consequences for ecosystem structure and function (du Toit and Cumming 1999, Lind et al. 2013). While in some areas livestock have completely replaced native ungulate herbivores, in others livestock have replaced native herbivores only incompletely and at moderate densities, and in some cases this type of mixed use appears to be sustainable (Reid 2012, Veblen et al. 2015). The process of wildlife replacement can be broken into two distinct, but interrelated components: (1) loss or reduction in numbers of individual wildlife species or guilds and (2) addition of livestock. These are often confounded, but

treating them as separate processes raises at least two questions. First, to what extent are livestock able to functionally replace or compensate for the loss of native ungulate wildlife? And, second, where replacement is incomplete, do these two groups of large herbivores have unique, additive, or interactive effects on savanna rangeland dynamics? Answering these questions is important to the management and conservation of rangelands worldwide.

The long-term consequences of herbivory for savanna understory plant communities are diverse because herbivores vary in their diets and their potential effects on plant community composition and structure. Shifts in understory plant community composition are important because they can alter the quality and quantity of forage for livestock and wild herbivores, which can indirectly drive herbivore abundance and diversity (Coe et al. 1976, Olf et al. 2002). In African savannas, wild ungulates include grazers, browsers, and mixed-feeders (Kartzinel et al. 2015) that can affect both the total amount of herbaceous biomass and the relative dominance of grass and forb species (Augustine and McNaughton 1998). Browsing herbivores can also suppress woody species (Moe et al. 2009, 2014, Lagendijk et al. 2011) thereby releasing herbaceous plants from competition and precipitating changes in the herbaceous community (Riginos et al. 2009). Mega-herbivores also can have strong impacts on the plant community: elephants (*Loxodonta africana* Blumenbach) can dramatically alter tree cover (Holdo et al. 2009, Kimuyu et al. 2014), while white rhinos (*Ceratotherium simum* Burchell), can create short-grass grazing lawns that are highly productive and favored by other grazers (Waldram et al. 2008). Given the diverse ecological effects of different wild herbivores, the impacts of wildlife loss are potentially numerous and dependent upon the identity of the species lost (Goheen et al. 2013, Pringle et al. 2014).

In contrast, livestock assemblages are typically low in species diversity and are mostly grazers (in particular cattle and sheep). Studies of the impacts of livestock addition to savanna systems have generally focused on a few impacts associated with overstocking and degradation (e.g., du Toit and Cumming 1999, Coetsee et al. 2008). Specifically, over-grazing has been shown to cause replacement of palatable grasses with unpalatable grasses and/or woody species (e.g., Coetsee et al. 2008). However, few studies have documented consequences of the addition of moderate numbers of livestock to systems where these animals likely replace (either completely or partially) a diverse wild herbivore assemblage.

There are a number of reasons why livestock may be expected to functionally compensate for losses of native ungulate wildlife. High dietary overlap has been reported between livestock and native grazing herbivores in Europe (La Morgia and Bassano 2009), North America (Van Vuren and Bray 1983), Australia (Dawson and Ellis 1994, Edwards et al. 1995), and Africa (Hoppe et al. 1977,

Voeten and Prins 1999), suggesting some degree of functional redundancy. For example, cattle may partially functionally replace other herbivores both directly, via consumption of excess forage (Young et al. 2005), and indirectly, by accelerating nutrient cycling and increasing production (Frank and Evans 1997). It has even been suggested that livestock grazing may be necessary to maintain critical aspects of ecosystem structure and function when native wild herbivore populations are absent (Perevolotsky and Seligman 1998, Cingolani et al. 2005).

On the other hand, there are reasons to expect that effects of domestic livestock may be very different from those of diverse native herbivores, and the extent to which livestock can functionally compensate for wildlife loss may be limited. Even within a feeding guild (e.g., grazers), herbivore diets vary depending on factors such as gut morphology, body size, and diet selectivity (Demment and Van Soest 1985, Clauss et al. 2003). This partitioning can reduce diet overlap among native herbivores (Kartzinel et al. 2015) so that total herbivory is distributed across many species of the plant community. In contrast, a single or few livestock species might focus their grazing on a narrower set of herbaceous species. Additionally, evidence from North America shows that even animals with very similar diets, such as (domestic) cattle and (wild) bison, show differences in behavior and habitat use (Allred et al. 2013, Kohl et al. 2013) that can influence plant communities. It is even more reasonable to suspect that a native herbivore community that includes not only grazers, but browsers and mixed feeders, would have very different effects on vegetation than grazing livestock.

In shared rangelands (i.e., partial replacement scenarios), livestock and wild ungulates have the potential for additive and interactive effects on plant communities. For example, a shared herbivore preference for highly palatable plant species could result in that species being heavily grazed (Augustine and McNaughton 1998). This could lead to additive effects wherein effects of livestock and wild ungulates combined is equal to the sum of their individual effects. Alternatively, effects may be interactive, for example, if combined livestock and wildlife grazing (1) leads to compensatory plant growth and smaller reductions in cover of palatable plants than expected or (2) pushes plants beyond physiological thresholds (e.g., to death) and reduces cover more than the sum of the individual effects of each herbivore type. Many studies have investigated how individual large herbivore species or assemblages influence herbaceous plant communities (Bagchi and Ritchie 2010, Goheen et al. 2013, Eby et al. 2014, Koerner et al. 2014). Yet few have tested, within a single system, the separate, combined, and potentially interactive effects of livestock vs. wild ungulate herbivory on herbaceous plant community properties, such as diversity, vegetation height, or species cover (but see Veblen and Young 2010, Porensky et al. 2013, Young et al. 2013), and even fewer have investigated responses of overall plant community composition (but see Veblen et al. 2015).

We experimentally investigated the long-term (14-yr) trajectory of herbaceous vegetation change in an exclusion experiment that allowed assessment of the effects of the loss of mega- and meso-herbivore wildlife, addition of cattle, and potentially interactive cattle-wildlife effects. We investigated (1) to what extent cattle are able to functionally replace or compensate for the loss of wildlife and (2) when replacement is incomplete, whether wild herbivores and moderate densities of cattle have additive or interactive effects on savanna plant community composition.

MATERIALS AND METHODS

Study site

The Kenya Long-term Exclusion Experiment (KLEE) is located on the Mpala Ranch and Conservancy (0°17' N, 36°52' E; 1800 m asl) in Laikipia, Kenya. During our data collection period, January 1999–September 2013, rainfall at the site averaged 596 ± 51 (SE) mm/yr (range 364–1003 mm/yr) and exhibited a weakly trimodal pattern, with major peaks in April–May (82 ± 12 mm/month) and October–November (71 ± 10 mm/month) and a minor peak in August (57 ± 7 mm/month). The study area is underlain with black cotton soils, poorly drained vertisols with high (>50%) clay content (Ahn and Geiger 1987). These black cotton soils are widespread over large areas of eastern Africa and together with other similar vertisols cover millions of hectares of semi-arid Africa (Ahmad 1996, Deckers et al. 2001). *Acacia drepanolobium* Sjost. comprises 97% percent of tree canopy cover in KLEE (Young et al. 1998), and 85% of herbaceous cover is composed of five grass species: *Pennisetum mezianum* Leeke,

P. stramineum Peter, *Themeda triandra* Forssk., *Lintonia nutans* Stapf., and *Brachiaria lachnantha* (Hochst.) Stapf. (Porensky et al. 2013).

The Mpala Ranch and Conservancy are managed for both wildlife conservation and livestock production. Cattle are stocked at low to moderate densities (0.10–0.15 cattle/ha; Table 1), but prior to 1992 the area encompassed by KLEE was more heavily stocked (T.P. Young, *personal observation*). Wild ungulates, in descending order of density (Table 1), include zebra (*Equus burchelli* Gray), Grant's gazelle (*Gazella granti* Brooke), eland (*Taurotragus oryx* Pallas), hartebeest (*Alcelaphus buselaphus* Pallas), elephant (*L. africana* Blumenbach), giraffe (*Giraffa camelopardalis* L.), Cape Buffalo (*Syncerus caffer* Sparrman), oryx (*Oryx gazella beisa* L.), and Grevy's zebra (*Equus grevyi* Oustalet). Wildlife in this region are present year-round and do not undergo large seasonal migrations.

Experimental design

The KLEE experiment was established in 1995 and uses semi-permeable barriers to differentially exclude and allow access to 200 × 200 m (4-ha) treatment plots by different combinations of cattle, wildlife (40–1000 kg, including zebras and several gazelle species), and mega-herbivores (elephants and giraffes; however, we do not consider giraffe effects on herbaceous vegetation because they feed strictly on trees). The experiment consists of three replicate blocks arranged from north to south and separated by 100–200 m. Within each of the three blocks are six 4-ha plots (total plots = 18) assigned to the following treatments: (1) MWC, mega-herbivore, wildlife and cattle accessible; (2) MW, mega-herbivore and wildlife accessible; (3) WC, Wildlife and cattle accessible;

TABLE 1. Densities, average body mass, and mass per unit area for major ungulate species at our study site.

Treatment, feeding guild	Common name	Scientific name	Number/km ²	Body mass (kg)	kg/km ²
C, grazer	cattle	<i>Bos taurus</i>	14.72 (13.16)	322	4740 (4238)
W, grazer	zebra (plains)	<i>Equus burchelli</i> (<i>quagga</i>)	1.46	242	353
W, mixed	Grant's gazelle	<i>Gazella (Nanger) granti</i>	0.76	62	47
W, browser	eland	<i>Taurotragus oryx</i>	0.36	560	202
W, grazer	hartebeest	<i>Alcelaphus buselaphus</i>	0.18	161	29
M, mixed	elephant	<i>Loxodonta africana</i>	0.17	4000	680
M, browser	giraffe	<i>Giraffa camelopardalis</i>	0.15	1340	201
W, grazer	buffalo	<i>Syncerus caffer</i>	0.12	550	66
W, grazer	oryx	<i>Oryx gazella beisa</i>	0.10	170	17
W, grazer	zebra (Grevy's)	<i>Equus grevyi</i>	0.04	395	16
M	all mega-herbivores				881
W	all meso-herbivores				730
Total wildlife					1611

Notes: Density estimates are for *Acacia drepanolobium* savanna encompassing Mpala Ranch and Conservancy and neighboring Jessel and Segera properties. Wildlife estimates are from aerial surveys conducted in 1999, 2001, and 2003–2005 (N. Georgiadis, *personal communication*; Georgiadis et al. 2007). Cattle estimates (first row) exclude 2004 and 2005 data during which no cattle were observed during the sampling period; values in parentheses reflect manager-reported stocking densities (2500 cattle/190 km²) for the Mpala Ranch and Conservancy. Wildlife body mass estimates are from Kingdon (1997), and cattle body mass estimate is from Augustine (2010).

(4) W, wildlife accessible; (5) C, cattle accessible; (6) O, no large herbivore access. One small antelope, steinbuck (*Raphicerus campestris* Thunberg), occurs in the area and is able to access all experimental treatment plots (Young et al. 2005). For full details of the experimental design, see Young et al. (1998).

Dung pellet data collected in treatment and control plots indicate that treatments are >90% effective at creating the desired treatments (see Young et al. 1998, 2005; D. M. Kimuyu et al., *unpublished manuscript*). Dung data indicate that wildlife use of KLEE MWC plots is strongly related to numbers of animals on the landscape (regression of wildlife densities from Table 1 vs. average 2006–2013 dung pellet counts for the six most common KLEE grazers: $R^2 = 0.76$).

Groups of 100–120 head of cattle are herded into C, WC, and MWC plots for 2 h on each of two to three consecutive days, typically three to four times per year. The exact timing and number of grazing days largely depends on forage availability, but plots rarely experience more than 16 weeks without cattle grazing. This grazing regime reflects typical cattle management strategies for the region wherein livestock graze in one general area for several days at a time until forage is depleted and then move to a different area to allow forage to recover in the previous area. The landscape is not fenced into paddocks, and herders actively manage livestock so that the entire range undergoes similar episodic grazing throughout the year. The stocking rate of the KLEE plots is similar to the moderate overall ranch stocking rate. Fire has not been an active part of this ecosystem since the 1960s (R. L. Sensenig, *personal communication*).

Data collection

Herbaceous vegetation in all 18 KLEE plots has been sampled biannually (in February and June) or annually (in June) since 1995. Sampling periods follow rainy periods that are similar in terms of average rainfall (April/May vs. October/November rainfall 1999–2012, paired $t = -0.63$, $P = 0.50$). We analyzed data from 25 surveys between January 1999 and June 2013. (Due to improvements in species identification, pre-1999 surveys were not fully comparable to later data.) Each of the eighteen 4-ha KLEE treatment plots contains a central hectare that is divided into a 10×10 m grid of 100 sampling stations. Aerial plant cover and composition are assessed at these stations by counting the number of pins hit by each species over a 10-point pin frame (with vertical pins separated by 5 cm; maximum one hit per pin per species). All 100 grid points were sampled 1999–2005, and every fifth grid point (20 per plot) was sampled from 2006 to 2013.

We analyzed aerial cover data for each of the eighteen herbivore treatment plots in each time period. For grass, forb, and total cover, we assessed absolute percent cover which is the sum of all pins hit (e.g., all forb hits) divided by the total number of pins (1000 per plot per sample

period before 2006, or 200 after 2006). For ordination and individual species analyses, we analyzed relative cover, which is the total number of pins hit by a species divided by the total number of pins hit across all species within a given herbivore plot in a given time period. Relative cover provides an index of the contribution of each species to the herbaceous community while controlling for differences in total biomass due to herbivore treatments and interannual variations in rainfall.

Plant biomass

We also took measurements of plant biomass to (1) quantify herbivore utilization (i.e., residual plant biomass) across plots and (2) examine how well residual biomass related to plant community composition and pin hits (plant cover). In the 18 plots, we clipped herbaceous material from three randomly located 1×1 m quadrats in February and June of 2010, 2011, and 2012 (six sampling dates). Clippings were dried to constant weight. We calculated average biomass (g/m^2) for each time interval within each plot (mean of three quadrats per plot and sampling date).

Data analysis

To assess the long-term effects of herbivore treatments on plant community composition, we used a partial redundancy analysis (RDA) ordination in which time was included as a co-variable (McCune and Grace 2002, Lepš and Šmilauer 2003). Including time as a co-variable allowed us to identify treatment effects and treatment \times time interactions while controlling for overall temporal trajectories of community change. Results include sample and species scores along a set of constrained RDA axes that relate plant community composition to treatments and time \times treatment interactions. We then analyzed extracted sample scores for the first and second RDA axes with linear mixed models (LMMs); this approach allowed us to determine the effects of herbivore type and number of guilds on plant community composition while accounting for effects of block, temporal auto-correlation, previous years' rainfall, and interactions among predictor variables.

To prepare data for RDA analysis, we excluded plant species that occurred in <5% of all samples (all plots over all sample periods; sensu Harrison et al. 2010, Alday et al. 2013). This reduced the dataset from 89 taxa (78 species and 11 multispecies groups) to 55 taxa (46 species and nine multispecies groups; Appendix S1). Of these 55, the 44 rarer taxa combined accounted for <0.2% of total plant cover. We then used the vegan library (version 2.0-8) for R (version 3.0.1 R Core Team 2013) to analyze relative percentage of cover data. We identified the two dominant constrained RDA axes (hereafter simply called RDA axes) that, when summed, explained 81.9% of treatment-related sample variance (see Table 2), then extracted species and sample scores

TABLE 2. Percent of variance in herbaceous community composition (2001–2013) explained by time, herbivore treatment, and RDA axes 1 and 2.

Variance component	Percentage of variation explained
Time	48
Treatment and treatment \times time	23
RDA axis 1	13.2 (57.5)
RDA axis 2	5.6 (24.4)

Notes: For RDA axes, the first number represents the percentage of total variance explained by the RDA axis, while the number in parentheses represents the percentage of the (23%) variance in treatment and treatment \times time explained by the RDA axis.

for these axes. Data transformations (e.g., Wisconsin square-root transform and log transform) did not qualitatively affect our results but reduced the percent variance explained by RDA axes. To maximize the amount of variance addressed with these and subsequent analyses, we present results from ordinations on untransformed data.

We used LMMs to examine the effect of herbivore type (wild vs. domestic) and total number of herbivore guilds on the following response variables: (1) extracted sample scores for each of the first and second RDA axes, (2) absolute percent cover for each of grass, forb, and total pin hits, and (3) relative percent cover for each of the eight plant species that scored $\geq |0.50|$ along at least one of the first two RDA axes. For these analyses, block and plot nested within block were included as random factors, and we used a compound symmetry covariance structure to address the non-independence of repeated surveys in the same plots. Fixed effects included cattle (presence vs. absence), wildlife (2, 1, 0 as categorical variables to describe, respectively, loss of neither mega- nor meso-herbivores, loss of mega-herbivores only, and loss of both mega- and meso-herbivores), time (continuous variable between 0 and 173 months), and all possible interactions thereof.

Previous work has shown that rainfall in the preceding rainy seasons are important predictors of plant composition in this system (Porensky et al. 2013). Although this paper does not specifically address the effects of rainfall (which will be addressed in a subsequent paper), we included rainfall co-variables to account for rainfall-related variability. These included rain_t (total rainfall during the rainy season just before the vegetation survey, summed over four months), rain_{t-1} (total rainfall during the previous rainy season), and rain_{t-2} (total rainfall during the rainy season before that), as well as interactions of all these rainfall variables with cattle, wildlife, and cattle \times wildlife factors. The three rainfall variables were not highly correlated (Pearson correlation coefficients < 0.35 ; VIFs < 2 ; see Appendix S2). All LMMs were performed in R (version 3.0.1 R Core Team 2013) using the nlme package (Pinheiro et al. 2013).

Because these analyses focused primarily on plant community trajectory, we performed additional analyses to investigate herbivore effects on the final plant community (i.e., in year 18 of the long-term experiment). First, for the eight individual plant-species analyses, we repeated the same LMM procedures described previously for only the final (month 173) time step, removing month and rainfall variables. Second, to examine differences in plant community composition among herbivore treatments, we performed permutational multivariate analysis of variance (PERMANOVA) tests on each of the first two sample periods (January 1999 and 2000) and each of the last two sample periods (June 2012 and 2013). We used the Adonis function in vegan (R version 2.0-8) to test the simultaneous response of all plant species to block (three levels) and herbivore treatment (six levels) during each of the first two and last two sampling periods (four separate analyses; permutations = 999). The Adonis function uses sequential evaluation of block prior to treatment, which is similar to treating block as a random factor. We used Bray–Curtis (Sørensen) dissimilarity matrices for all plant community analyses.

Finally, we used simple linear regressions to examine relationships among herbivore treatments, plant biomass, and plant community responses. We tested total plant biomass as a predictor of total pin hits to verify that pin hits reflect actual biomass across all herbivore treatments. We also regressed RDA axis 1 score on total plant biomass and total pin hits (cover). For each variable, we averaged values over all available sampling periods and then averaged across blocks to create a single value (± 1 SE) for each of the six treatments.

RESULTS

Overall patterns

Our results summarize data from 25 surveys, 450 sample units, and 262,800 pin drops across 14 yr. We found a strong, positive relationship between total plant biomass and total pin hits (Fig. 1a; $R^2 = 0.93$, $P = 0.002$), the measure of plant cover we used throughout our analyses; this verifies that pin hits are representative of actual herbaceous biomass across different herbivore treatments.

Total grass cover (i.e., pin hits of all grass species combined; 88% of all pin hits) in all plots increased through time (LMM time effect, $F_{1,407} = 70.4$, $P < 0.0001$), coincident with release from the more intense grazing of previous (pre-1992) management. Relative cover of two of the dominant grass species, *B. lachnantha* and *Botriochloa insculpta*, increased dramatically over time, while the other four dominant grasses, *L. nutans*, *P. mezianum*, *P. stramineum*, and *T. triandra*, showed strong to weak declines in relative cover (Fig. 2; Appendix S3). Total forb cover (12% of all pin hits) also increased over time, but only in plots without cattle (and instead declined in plots with cattle; LMM cattle \times time effect, $F_{1,407} = 16.07$,

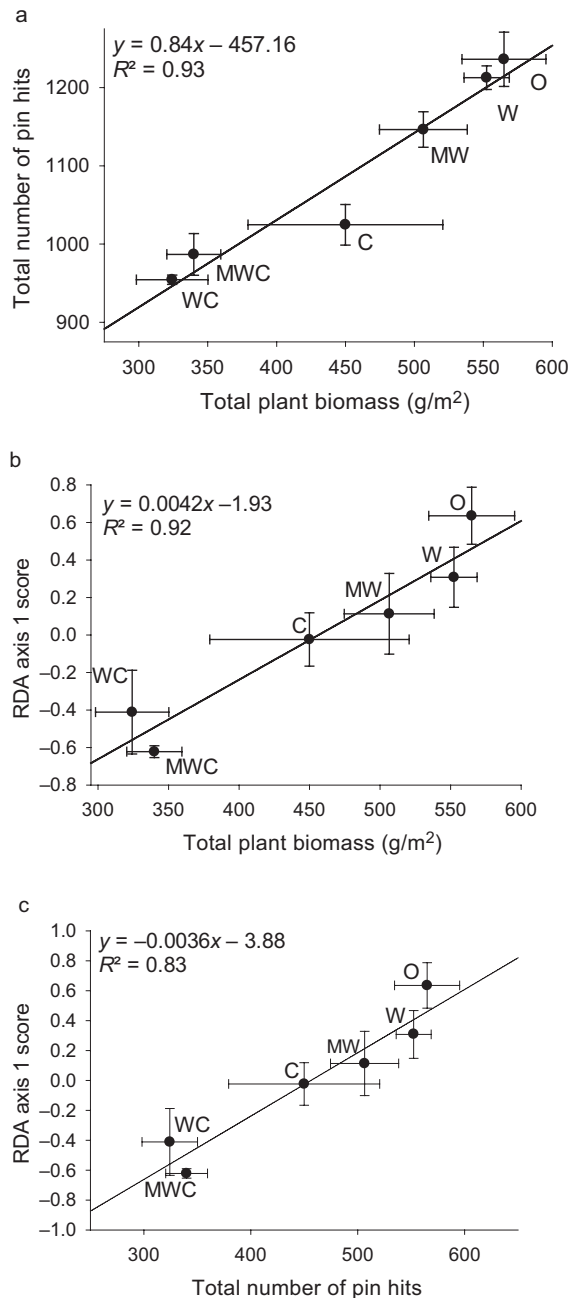


FIG. 1. (a) Plant biomass vs. pin hits, (b) plant biomass vs. RDA 1 score, and (c) pin hits vs. RDA 1 score. All values are means and 1 SE of three reps per treatment (with each treatment value averaged over all available time steps). Abbreviations are C, cattle allowed; W, meso-herbivore wildlife allowed; M, mega-herbivores allowed; and O, all large herbivores excluded.

$P = 0.0001$), suggesting that cattle continued to suppress forbs. Relative cover of the two dominant forbs, *Pseudognaphalium* spp. and *Rhyncosia holstii*, increased over time in plots without cattle (Fig. 2; Appendix S3).

Total plant cover and biomass were reduced in plots accessible to large herbivores (i.e., significant main

effects of cattle and wildlife treatments; Appendix S3). Cattle reduced total cover by 17% (LMM cattle effect, $F_{1,10} = 124.63$, $P < 0.0001$), driven by both a 15% reduction in grass cover (LMM cattle effect for grass cover, $F_{1,10} = 60.22$, $P < 0.0001$), and a 19% reduction in forb cover (LMM cattle effect for forb cover, $F_{1,10} = 31.23$, $P = 0.0002$) in cattle-accessible plots. Meso-herbivore wildlife reduced total cover by 4% (LMM wildlife effect, $F_{2,10} = 4.26$, $P = 0.046$; Tukey test comparing 0 vs. 1 wildlife guild, $P = 0.08$), driven mostly by a 6% reduction in forb cover (LMM wildlife effect for forb cover, $F_{2,10} = 13.96$, $P = 0.001$; Tukey test comparing 0 vs. 1 wildlife guild, $P = 0.27$). Relative to plots with no wildlife, the combination of both mega-herbivores and meso-herbivore wildlife reduced total cover by 6% (Tukey test comparing 0 vs. 2 wildlife guilds, $P = 0.01$; Appendix S3), including a 21% reduction in forb cover (Tukey test comparing 0 vs. 2 wildlife guilds, $P < 0.00001$). There were no significant wildlife or mega-herbivore effects on grass cover (LMM wildlife effect, $F_{2,10} = 0.94$, $P = 0.42$), nor were there any significant cattle \times wildlife interactions for total, forb, or grass cover (Appendix S3).

Plant community divergence over time

Together, RDA axes 1 and 2 explained 81.9% of the variation in plant community composition associated with treatment and treatment \times time, and 18.8% of total variation (Table 2). Six grass and two forb species scored highly ($\geq |0.5|$) on RDA axes 1 or 2 (Fig. 3). Each of these species satisfied one or both of the following criteria: (1) was one of the five most dominant plant species in the community (each representing $>5\%$ relative plant cover across all plots and years), (2) showed >0.25 correlation between relative cover and at least one of RDA axes 1 and 2. RDA species score results indicate that changes in plant community composition were associated with increases or decreases in cover of these eight species (Fig. 3).

Linear mixed models of extracted RDA axis 1 sample scores indicate that plant communities in the six different herbivore treatments were similar at the beginning of the sampling period (not long after the establishment of the experiment), but shifted directionally over time and had diverged from each other substantially by 2012 (Figs. 4 and 5; LMM cattle \times time interaction, $F_{1,408} = 354.1$, $P < 0.0001$; wildlife \times time interaction, $F_{2,408} = 20.04$, $P < 0.0001$; Appendix S3). In this partial RDA analysis, time, herbivore treatment, and herbivore treatment \times time interactions explained 71% of the total variance in herbaceous community composition (Table 2). These results are consistent with NMDS analyses (see Appendix S4) and PERMANOVA results that indicated no significant differences among treatments in the earliest sample periods (year 1999, $P = 0.13$; year 2000, $P = 0.30$), but significant treatment effects in the last two sampling years (year 2012, $P = 0.001$; year 2013, $P = 0.001$; Fig. 5).

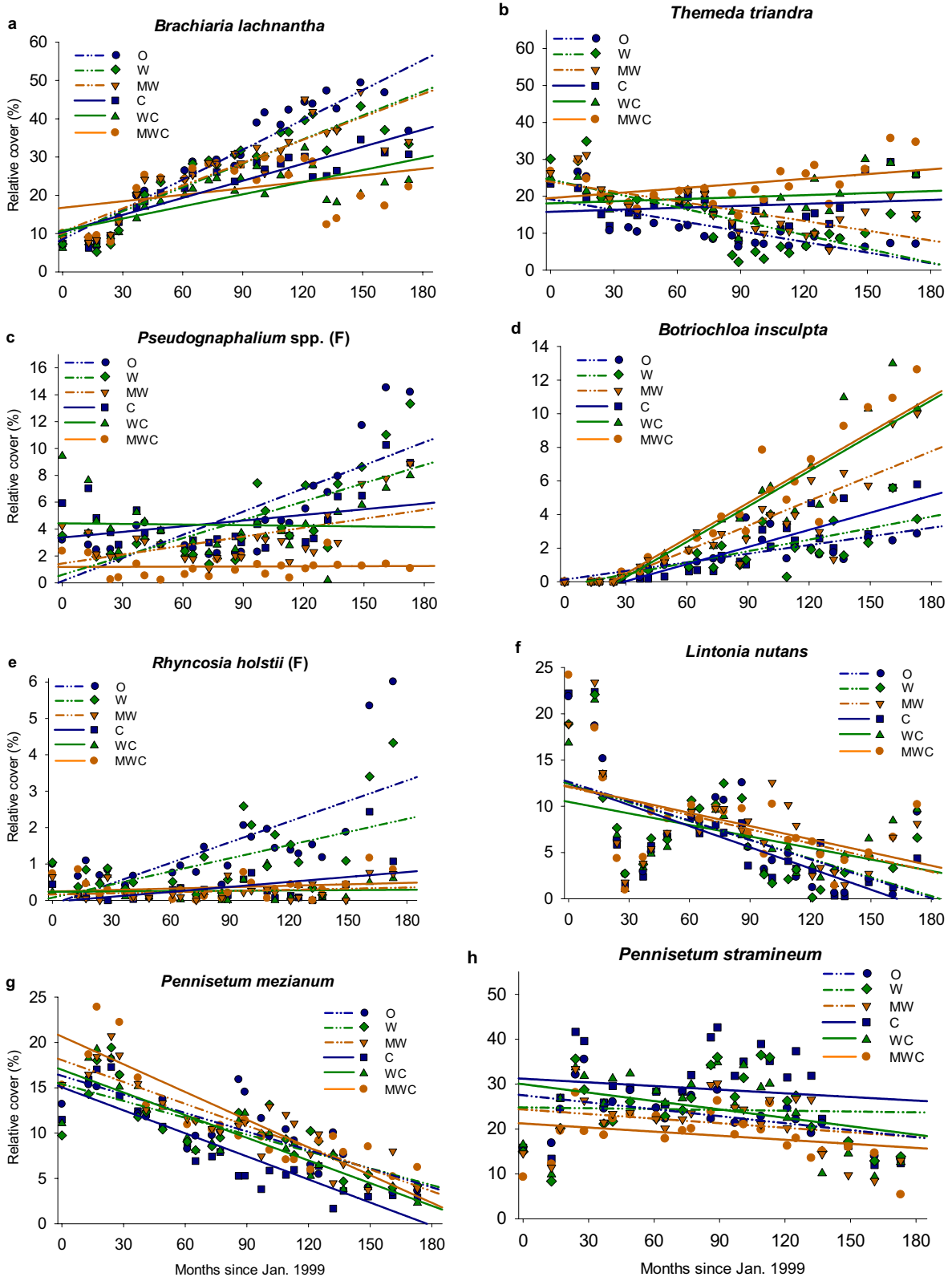


FIG. 2. Relative cover of plant species over time (1999–2013). All are grass species except the two species names followed by the notation “(F)”. Abbreviations are C, cattle allowed; W, meso-herbivore wildlife allowed; M, mega-herbivores allowed; and O, all large herbivores excluded.

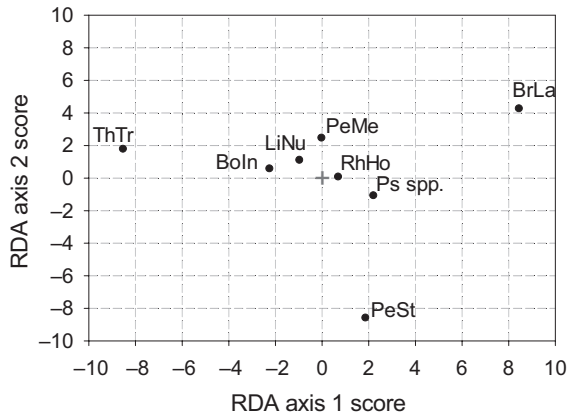


FIG. 3. Species plotted by first and second RDA axis scores. Only species that had RDA axis 1 or RDA axis 2 scores $\geq|0.5|$ are displayed. Abbreviations are Boln, *Bothriochloa insculpta*; BrLa, *Brachiaria lachnantha*; LiNu, *Lintonia nutans*; PeMe, *Pennisetum mezianum*; PeSt, *Pennisetum stramineum*; Ps spp., *Pseudognaphalium* + *Helichrysum* spp.; RhHo, *Rhynchosia holstii*; ThTr, *Themeda triandra*.

The LMM of RDA axis 2 scores revealed transient temporal trends that differed significantly among herbivore treatments (cattle \times wildlife \times time treatment effect, $F_{2,408} = 6.54$, $P = 0.0016$), but patterns were not as strongly directional as those of RDA axis 1 (Appendix S5a). For axis 2, the magnitude of differences among treatments varied throughout the sample period, with treatments converging somewhat in the final sampling periods (Appendix S5b). In particular, a strong increasing effect of cattle only (C) and decreasing effect of total exclusion (O) treatments appeared at month 86, a major drought period, but treatments partially converged again in the most recent sample periods. Rainfall \times treatment differences were significant ($P < 0.05$) for both RDA axes (Appendix S3), and the role of rainfall will be explicitly examined in a subsequent paper.

Plant community response to grazing intensity

Plant community composition (as represented by RDA axis 1 scores) was strongly related to both residual plant biomass (a measure of herbivore utilization) and total pin hits; further, the RDA axis 1 scores of the six herbivore treatments were ordered according to decreasing grazing intensity: removal of cattle, followed by removal of wildlife guilds (Fig. 1b; $R^2 = 0.92$, $P = 0.003$). RDA axis 1 scores also revealed simple additive effects of cattle and wildlife on plant community composition (Figs. 4 and 5). Specifically, removal of cattle and reduction of wildlife guilds (2, 1, or 0) each increased RDA scores such that $O > W > MW > C > WC > MWC$ (Table 3; LMM cattle effect, $F_{1,10} = 32.9$, $P = 0.0002$; wildlife effect, $F_{2,10} = 7.1$, $P = 0.012$; cattle \times wildlife interaction, $F_{2,10} = 0.04$, $P = 0.97$).

Positive plant species responses to herbivore removal

Of the eight species that scored highly ($\geq|0.5|$) on RDA axes 1 or 2, three species both were positively related to RDA axis 1 score (Fig. 3) and responded positively to the removal of large herbivores: *B. lachnantha*, *Pseudognaphalium* spp., and *R. holstii* (one grass and two forbs, respectively). Although cattle and wildlife each suppressed cover of these plant species, the three species did differ with respect to whether they responded more strongly to cattle vs. wildlife.

Brachiaria lachnantha attained the greatest cover when grazing pressure (Figs. 1b and 5) was lowest. Removal of cattle grazing in particular increased *B. lachnantha* cover (Fig. 2a; LMM cattle effect, $F_{1,10} = 10.4$, $P = 0.009$; final timestep LMM cattle effect, $F_{1,10} = 5.7$, $P = 0.04$; Appendix S3), and this effect intensified over time (Fig. 2a; LMM cattle \times time interaction, $F_{1,407} = 85.8$, $P < 0.0001$). By the end of the sampling period, *B. lachnantha* cover was 36% higher in plots without cattle and was the dominant species in these treatments. Wildlife removal also contributed to increased *B. lachnantha* cover over time (wildlife \times time interaction, $F_{2,407} = 12.0$, $P < 0.0001$; Appendix S3), though did not have a significant main effect ($P = 0.48$).

Pseudognaphalium spp. also responded positively to protection from herbivores (Figs. 3 and 2c). Throughout the sample period *Pseudognaphalium* spp. cover increased in response to the removal of wildlife herbivory (Fig. 2c; LMM wildlife effect, $F_{2,10} = 5.7$, $P = 0.02$; wildlife \times time interaction, $F_{2,407} = 6.2$, $P = 0.002$; Appendix S3), particularly by mega-herbivores (Tukey tests comparing number of guilds, 0 vs. 1, $P = 0.8$; 0 vs. 2, $P < 0.05$; 1 vs. 2, $P < 0.05$). By the end of the sample period, protection from meso-herbivore wildlife had increased *Pseudognaphalium* spp. cover by 65% and protection from both mega-herbivore and meso-herbivore wildlife increased cover by 158%. *Pseudognaphalium* spp. also responded substantially to the removal of cattle, albeit more slowly; by the end of the sample period, protection from cattle had increased cover of *Pseudognaphalium* spp. by 102% (Fig. 2c; LMM cattle \times time effect,

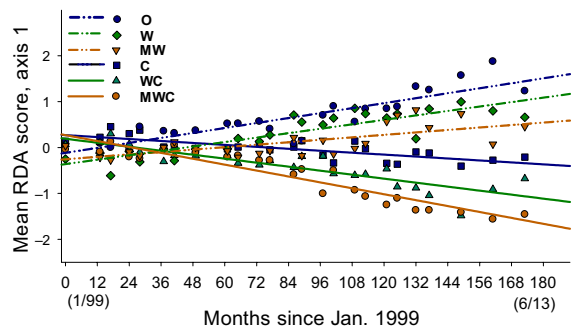


FIG. 4. RDA axis 1 scores for herbivore treatments over time (1999–2013). Abbreviations are C, cattle allowed; W, meso-herbivore wildlife allowed; M, mega-herbivores allowed; and O, all large herbivores excluded.

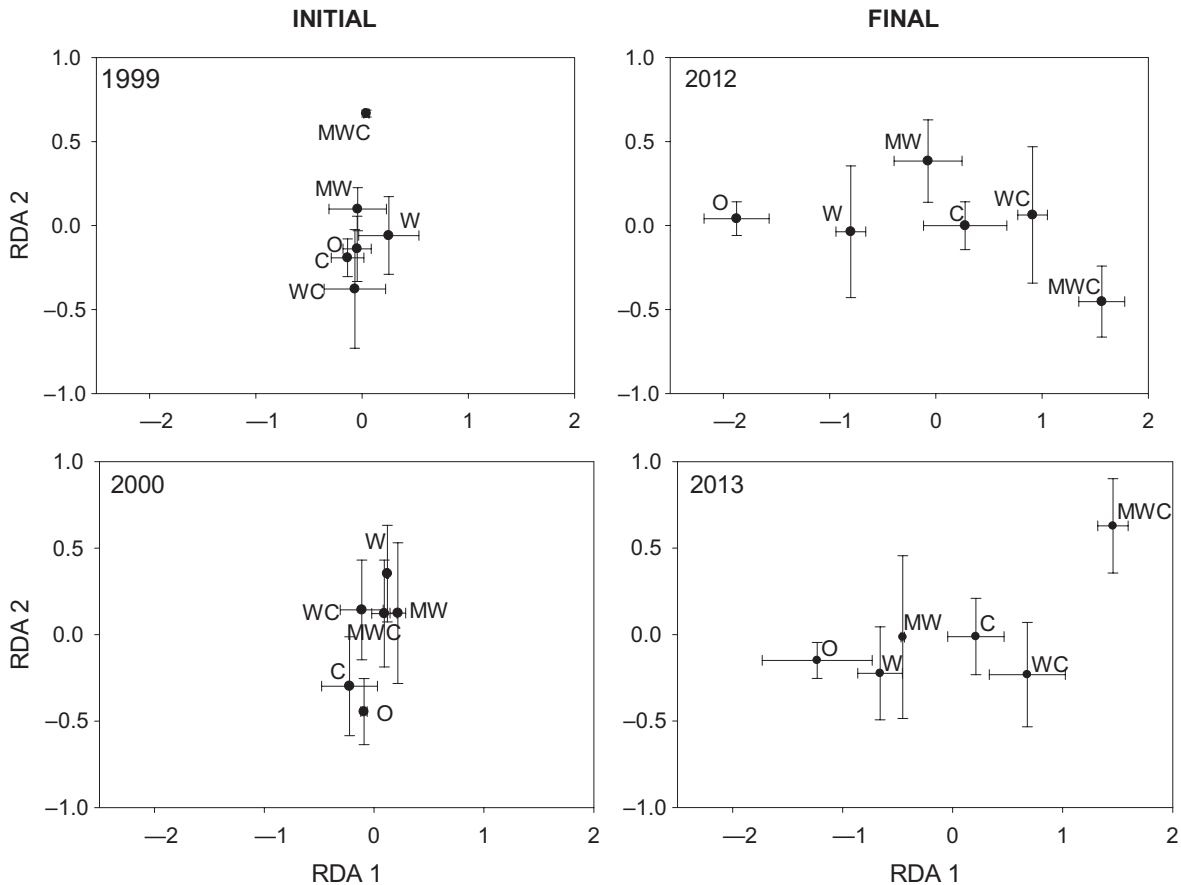


FIG. 5. RDA axis 1 and 2 scores for herbivore treatments during the first (1999, 2000) and final (2012, 2013) two sampling periods (of 25 total). Values are mean \pm 1 SE across three replicates of each treatment. Abbreviations are C, cattle allowed; W, meso-herbivore wildlife allowed; M, mega-herbivores allowed; and O, all large herbivores excluded.

TABLE 3. LMM Tukey post-hoc results (at $P = 0.05$ level) for RDA axis 1 scores.

	Mean RDA score	SE	Tukey
Wildlife treatment effect			
2 wildlife guilds	0.25	0.08	A
1 wildlife guilds	0.05	0.08	A
0 wildlife guilds	-0.31	0.07	B
Cattle treatment effect			
Cattle presence	0.35	0.06	A
Cattle absence	-0.35	0.06	B

Notes: Shared letters indicate no significant differences within a treatment effect.

$F_{1,407} = 54.3$, $P < 0.0001$; final time step LMM cattle effect, $F_{1,10} = 9.4$, $P = 0.01$; Appendix S3).

By the end of the sample period, removal of cattle grazing had increased cover of the second forb, *R. holstii*, by 340% (Fig. 2e; LMM cattle effect, $F_{1,10} = 13.8$, $P = 0.004$; final time step LMM cattle effect, $F_{1,10} = 31.3$, $P = 0.0002$; Appendix S3) and removal of all wildlife herbivory increased it by 350% (Fig. 2e; LMM wildlife

effect, $F_{2,10} = 4.0$, $P = 0.053$; final time step LMM wildlife effect, $F_{2,10} = 9.2$, $P = 0.006$; Appendix S3). Both cattle and wildlife contributed to divergence among treatments over time (Fig. 2e; LMM cattle \times time interaction, $F_{1,407} = 15.1$, $P = 0.0001$; LMM wildlife \times time interaction, $F_{2,407} = 7.1$, $P = 0.0009$).

For all three species, cattle \times wildlife interaction effects on cover were not significant for the full model that included all time steps. Similarly, cattle \times wildlife interaction effects were not significant for final cover of *B. lachmantha* or *Pseudognaphalium* spp. However, there was a significant cattle \times wildlife interaction for final cover of *R. holstii* (Appendix S3) due to a reduced cattle effect in the presence of mega-herbivores.

Negative plant species responses to herbivore removal

Three grass species were negatively correlated with RDA axis 1 score (Fig. 3) and responded negatively to reductions in grazing pressure (Fig. 1b): *T. triandra*, *B. insculpta*, and *L. nutans*. Release from cattle and wildlife herbivory each were associated with reduced cover of these plant species, but the three species differed

with respect to whether they responded more strongly to cattle vs. wildlife. For all three species there were no significant cattle \times wildlife interaction effects (Appendix S3).

Themeda triandra attained its greatest cover under the highest grazing pressure (Figs. 1b and 5). In plots protected from all large herbivores, *T. triandra* cover decreased by 71% (from 24% to 7% cover). Removal of cattle reduced *T. triandra* percent cover (Fig. 2b; LMM cattle effect, $F_{1,10} = 12.7$, $P = 0.005$; final time step LMM cattle effect, $F_{1,10} = 25.3$, $P = 0.0005$; Appendix S3), and this effect intensified over time (Fig. 2b; LMM cattle \times time interaction, $F_{1,407} = 126.4$, $P < 0.0001$). By the final sample period, the removal of cattle had reduced *T. triandra* cover by 56% (from 27% to 12%). The removal of wildlife also showed marginally significant negative effects on *T. triandra* cover (Fig. 2b; LMM wildlife effect, $F_{2,10} = 3.6$, $P = 0.07$; wildlife \times time interaction, $F_{2,407} = 2.0$, $P = 0.14$; Appendix S3).

Cover of *B. insculpta* decreased in response to reduced wildlife herbivory (Fig. 2d; LMM wildlife effect, $F_{2,10} = 6.3$, $P = 0.02$; wildlife \times time interaction, $F_{2,407} = 15.8$, $P < 0.0001$; Appendix S3), and by the final sample period, cover was 62% lower in plots with no wildlife. By the final sample period, exclusion of cattle grazing also had decreased cover of *B. insculpta* by 42% (Fig. 2d; LMM cattle \times time effect, $F_{1,407} = 18.3$, $P < 0.0001$; final time step LMM cattle effect, $F_{1,10} = 5.6$, $P = 0.04$; Appendix S3).

The third grass species, *L. nutans*, decreased in response to reduced wildlife herbivory (Fig. 2f; LMM wildlife effect, $F_{2,10} = 6.3$, $P = 0.02$; Appendix S3). However, despite wildlife-driven divergence of treatments over time (wildlife \times time interaction, $F_{2,407} = 7.8$, $P = 0.0005$), trajectories were non-linear (Fig. 2f), and there was no significant effect of wildlife by the final sampling period (final time step LMM wildlife effect, $F_{2,10} = 2.2$, $P = 0.80$; Appendix S3). There were no significant effects of cattle on *L. nutans* (Fig. 2f; LMM cattle effect, $F_{1,10} = 0.2$, $P = 0.7$; cattle \times time effect, $F_{1,407} = 2.2$, $P = 0.14$).

Plant species that responded to interactions among herbivore guilds and rainfall

The grass *P. mezianum* was only very weakly correlated with RDA axis 1 (Fig. 3), but responded positively to release from cattle grazing over time (Fig. 2g; LMM cattle \times time interaction, $F_{1,407} = 11.3$, $P = 0.0009$). It showed no other statistically significant responses to herbivore treatments (Fig. 2g; Appendix S3). Similarly, its congener, *P. stramineum*, which showed a moderate correlation to RDA axis 1, was not significantly affected by herbivore treatments (Fig. 2h; Appendix S3). Each of these two species was most strongly correlated with RDA axis 2. (Fig. 3), suggesting that divergence among treatments for these species was most strongly driven by significant

transient interactions among wildlife, cattle, and rainfall prior to sampling (Appendix S3).

DISCUSSION

In African savannas, domestic livestock have partially or completely replaced a diverse array of wild ungulate herbivores across millions of hectares, but the consequences of this broad-scale conversion for understory plant communities are poorly known. In our semi-arid study system, we found surprisingly similar, additive effects of domestic cattle (at moderate densities) and native wild herbivores on understory plant community composition, though individual plant species exhibited distinct and contrasting responses to herbivory. These results suggest considerable functional redundancy between cattle and a suite of native wild ungulates (including grazers, browsers, and mixed feeders) with respect to impacts on understory plant community composition, but also demonstrate that for individual plant species, impacts of a single livestock species are not functionally identical to a diverse group of native herbivores.

Are cattle ecological surrogates for a multispecies native ungulate community?

Understory plant community composition in the six different herbivore treatments diverged throughout the study period. Most of the variation in this divergence was strongly correlated with trends in residual plant biomass (which were indicative of grazing pressure). After accounting for the effects of temporal change, variation in understory plant community composition was dominated by variation in RDA axis 1, which was not correlated with any particular type of ungulate, but rather with herbivore pressure in general. Addition of any single herbivore guild (cattle, wildlife, or mega-herbivores) caused a shift along this axis proportional to that guild's removal of plant biomass. That cattle caused a greater shift than wildlife guilds composed of multiple species (i.e., greater effects in C than W or MW plots) appears to be explained by greater cattle stocking densities (see Table 1). At least in the context of overall herbaceous plant community composition, it appears that moderately stocked cattle are indeed largely the ecological equivalents of a native ungulate community comprised of grazers, browsers, and mixed feeders.

This apparent ecological similarity is surprising given the very different feeding strategies of cattle (mainly grazers) vs. the native wild herbivores (a mixture of grazers, browsers, and mixed feeders). We suggest that apparent equivalence could be due to several factors. First, although cattle are generally considered grazers (Everitt et al. 1981, Hanley and Hanley 1982, Bóo et al. 1993), their diets are not limited to grasses and in fact include forbs that are typically eaten by browsers and mixed feeders. In our system, cattle diets comprise 5–20% forbs, depending on season (Odadi et al. 2009). If cattle

feed on both grasses and forbs, and in proportion to their availability in the landscape (88% and 12%, respectively), their diets may be somewhat similar to a more diverse group of native herbivores' diets. Second, the wildlife guild included many zebra (fairly strict grazers; Kartzinel et al. 2015), but also included multiple other grazing, browsing, and mixed feeding species (Table 1; Kartzinel et al. 2015). Therefore, the wildlife guild may have a composite diet not unlike cattle, even if the diets of individual component species each differ from cattle. Third, if neither cattle nor wildlife are under intense inter- or intra-specific competition for forage, they all may focus on a few of the most palatable plants, making their diets more similar. Fourth, cattle and wild herbivores may have similar non-consumptive effects on plant communities, such as trampling of vegetation or nutrient addition via defecation.

Although our results present strong evidence for a prevailing role of grazing intensity, several other factors also may have driven shifts in plant community composition. First, because it is logistically impossible to test the effects of megaherbivores alone (i.e., in the absence of mesoherbivore wildlife), we cannot rule out the possibility that addition of mega-herbivores had indirect (non-grazing) effects on the herbaceous plant community (e.g., via alterations of woody cover or influence on cattle or mesoherbivore wildlife foraging). Nonetheless, the plant community shift associated with addition of megaherbivores was proportional to its reduction of herbaceous plant biomass (Fig. 1), consistent with the idea that grazing intensity was the chief driver of plant community composition. Second, we similarly cannot rule out the influence of small mammal herbivory on the plant community. Cattle and wildlife both reduce the abundance of the dominant small mammal, *Saccostomus mearnsi* (85% of all captures; Keesing and Young 2014), which consumes some of the same forage resources as large mammals. Thus, we would expect any effects of small mammals to mute the effects of the large herbivore treatments. Since we found significant net effects of cattle and wildlife on the plant community, it appears that any effects of small mammals are secondary to the effects of large mammals. Third, strong responses through time suggest that some aspects of plant community trajectories may reflect recovery from the heavier grazing the study site received prior to the initiation of our experiment. However, our study site has been grazed by livestock at varying intensities for millennia (Lane 2011) making it difficult to determine whether the most recent heavy grazing period or longer term grazing history would have the strongest influence on recent plant community trajectories.

Individual plant responses and incomplete ecological equivalence

Community change in our experimental treatments appears to be strongly driven by relative decreases in more palatable species (*B. lachnantha*, *R. holstii*) and

increases in less palatable species (*B. insculpta*, *L. nutans*; Odadi et al. 2013) with increasing herbivore pressure. Grazing (and reduction) of the more palatable species would automatically increase relative cover of the less palatable species (a simple mathematical result), but it is also possible that reduction of palatable species released the less palatable species from competition (Augustine and McNaughton 1998). A notable exception to the overall pattern was the dominant grass, *T. triandra*, which is highly palatable but responded negatively to herbivore removal (and the associated higher plant biomass). This is likely because it is a poor competitor (Groves et al. 2003), particularly when ungrazed (Fynn et al. 2005). Additionally, although unpalatable, the forb *Pseudognaphalium* increased with increasing protection from large herbivores. Thus, rather than being explained by palatability, some of our results may be better explained by growth–defense or competition–defense trade-off hypotheses (Lind et al. 2013 and references therein), which posit inherent trade-offs between tolerance to herbivory and either growth rate or competitive ability. For example, *B. lachnantha* and *R. holstii* may be more sensitive to grazing but good at producing above-ground biomass in the absence of grazing, while *B. insculpta* and *L. nutans* are more tolerant of herbivory at the cost of growth.

While most species responded to overall herbivory pressure, several species responded in different ways depending on herbivore types. *Brachiaria lachnantha* and *T. triandra* responded early, strongly, and persistently to the effects of cattle grazing, but less so to wildlife herbivory. *Pseudognaphalium*, *B. insculpta*, and *L. nutans* showed the opposite trend: strong, early response to wildlife herbivory, and a more gradual (or no) response to cattle grazing. For both groups of plants, responses to cattle and wild herbivores were in the same direction, which helps explain why overall herbivory pressure (regardless of herbivore identity) appeared to drive changes in overall plant community composition. Only one species, *R. holstii*, showed strong, early, and persistent responses to both cattle and wildlife. The two *Pennisetum* species, both of which are relatively unpalatable (Odadi et al. 2013), showed complex and transient responses to interactions among rainfall and different herbivore types (C. Riginos, et al., *unpublished manuscript*).

Our results suggest that cattle effects on herbaceous plant community composition might partially, but not fully, replicate those of native ungulates, and there are several possible reasons for these differences. First, individual plant species differed in their sensitivities to cattle vs. wild ungulate herbivory. Although such differences were not immediately obvious from our analyses of overall plant community composition (RDA), these subtle but important individual species differences may become more apparent or meaningful over time. Second, at our study site, and throughout rangelands worldwide, cattle are often stocked at higher rates (density over time)

than the native ungulates they replace or share the landscape with. Our results demonstrate that higher herbivory pressure is more impactful to herbaceous communities, both in terms of total biomass (Fig. 1b) and community composition (Fig. 4). Third, livestock and wild ungulates often show different habitat preferences and daily or seasonal movement patterns (Allred et al. 2013), which can in turn differently influence plant communities over the broader landscape. Fourth, even if cattle and wild herbivores have similar effects on the herbaceous community, they may have contrasting effects on the structure of the landscape because native herbivore communities include browsers and mixed feeders that can dramatically affect woody cover (Goheen et al. 2007, Moe et al. 2009, Maclean et al. 2011, Sankaran et al. 2013). This is particularly true for elephants that both browse and topple trees, and in turn can influence habitat use by other herbivores (Valeix et al. 2011, Riginos 2015).

Management implications

Despite many dietary, physiological, and behavioral differences among livestock and individual native ungulate species, our analysis suggests that in an herbivory-adapted savanna landscape, overall herbaceous plant community composition responds primarily to grazing pressure, rather than to the identity of individual herbivore species. This finding has potential implications for the management of rangeland systems. In particular, presence or absence of certain herbivore species or guilds is not necessarily associated with pervasive plant community changes or plant species extinctions (Veblen et al. 2015). Rather, our analyses suggest that both heavy grazing (by any type of herbivore) and the total absence of herbivory are the conditions most likely to effect major plant community changes. Therefore, a central focus of rangeland management should be to moderate the combined stocking densities of domestic and wild large herbivores. This is especially important in areas where current stocking densities of livestock far exceed historical densities of ungulate wildlife (e.g., African savannas and the Intermountain West of the USA; Mack and Thompson 1982, du Toit and Cumming 1999). Our results also suggest that areas that have been subject to one type of herbivore regime for a long time, for example, moderate grazing by cattle in the absence of one or more types of native wild ungulates, can maintain plant communities that are still well-suited to supporting a diverse, full complement of herbivore species. Overall, partial functional redundancy between cattle and native wild ungulates in their effects on herbaceous plant communities may help promote livestock–wildlife coexistence and conservation on multi-use lands.

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