Herbivore effects on productivity vary by guild: cattle increase mean productivity while wildlife reduce variability

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Abstract. Wild herbivores and livestock share the majority of rangelands worldwide, yet few controlled experiments have addressed their individual, additive, and interactive impacts on ecosystem function. While ungulate herbivores generally reduce standing biomass, their effects on aboveground net primary production (ANPP) can vary by spatial and temporal context, intensity of herbivory, and herbivore identity and species richness. Some evidence indicates that moderate levels of herbivory can stimulate aboveground productivity, but few studies have explicitly tested the relationships among herbivore identity, grazing intensity, and ANPP. We used a long-term exclosure experiment to examine the effects of three groups of wild and domestic ungulate herbivores (megaherbivores, mesoherbivore wildlife, and cattle) on herbaceous productivity in an African savanna. Using both field measurements (productivity cages) and satellite imagery, we measured the effects of different herbivore guilds, separately and in different combinations, on herbaceous productivity across both space and time. Results from both productivity cage measurements and satellite normalized difference vegetation index (NDVI) demonstrated a positive relationship between mean productivity and total ungulate herbivore pressure, driven in particular by the presence of cattle. In contrast, we found that variation in herbaceous productivity across space and time was driven by the presence of wild herbivores (primarily mesoherbivore wildlife), which significantly reduced heterogeneity in ANPP and NDVI across both space and time. Our results indicate that replacing wildlife with cattle (at moderate densities) could lead to similarly productive but more heterogeneous herbaceous plant communities in rangelands.

Key words: aboveground net primary productivity; defaunation; ecosystem function; Kenya Long-term Exclosure Experiment; KLEE; livestock.

Introduction

Aboveground net primary production (ANPP; the amount of aboveground plant biomass accumulated over a given period of time) is a fundamental property of any ecosystem and can drive patterns in species diversity and composition (Mittelbach et al. 2001), as well as secondary and tertiary productivity (Coe et al. 1976, McNaughton et al. 1991, Donihue et al. 2013). Although factors such as productivity potential, grazing pressure, and plant adaptation to grazing are known to influence the relationship between herbivory and productivity (Milchunas and Lauenroth 1993, Anderson et al. 2007), our understanding of how herbivore identity shapes this relationship is poor. The role of herbivore identity is potentially significant because grasslands and savannas typically support diverse wild herbivore communities that, in many cases, have been partially or completely replaced by a different and less diverse assemblage of

domestic herbivores (du Toit et al. 2012, Veblen et al. 2016). The impacts of herbivores on productivity may depend on the herbivore species in question, even for species with superficially similar diets.

There are a number of reasons that wild and domestic herbivores may have divergent effects on productivity. First, domestic livestock are often stocked at higher densities than wild large herbivores, creating higher herbivory pressure (Prins 1992). Second, wild herbivore communities often include a more diverse suite of herbivores, which may spread grazing pressure across a greater diversity of forage species (Kartzinel et al. 2015). Third, different defoliation patterns (e.g., cropping height and selectivity, or the timing, duration, and frequency of grazing) among different herbivores may have different physiological and demographic consequences for forage species. Finally, different large herbivores can have divergent effects on herbaceous plant community composition and diversity (Veblen and Young 2010, Kanga et al. 2011, Bagchi et al. 2012, Porensky et al. 2013, Young et al. 2013, Veblen et al. 2016) that may in turn affect productivity.

In grassland and savanna ecosystems, the effects of herbivory on productivity are particularly complex

because herbivores can remove large amounts of herbaceous biomass, and, depending on the nature of this removal (e.g., timing or intensity) as well as other contextual factors, either stimulate or suppress herbaceous production (McNaughton 1979, Turner et al. 1993). On the one hand, defoliation by large mammalian herbivores can decrease overall grass productivity by reducing photosynthetic tissue and available plant nutrients, and these effects can persist across seasons (Muthoni et al. 2014) and years (Gill 2007). On the other hand, plants may compensate for herbivore damage by increasing growth rates (Strauss and Agrawal 1999, Knapp et al. 2012), and under certain circumstances herbivory may even stimulate added growth (overcompensation) and increase plant fitness (Paige and Whitham 1987, Agrawal 2000). The idea that plants can compensate or overcompensate for herbivory has fueled some debate (McNaughton 1983, Paige and Whitham 1987, Belsky et al. 1993). Compensation is now generally recognized to occur in relatively productive grasslands where self-shading by ungrazed, standing dead biomass (rank vegetation) can reduce productivity (Oesterheld and McNaughton 1991, Morgan and Lunt 1999), but few manipulative field studies have investigated how different levels and types of herbivory can influence compensatory dynamics.

In addition to having potentially different effects on mean productivity, different types of herbivores may also have contrasting effects on both spatial and temporal heterogeneity in productivity. Grazing by large herbivores, both wild and domestic, has the potential to either increase spatial heterogeneity in vegetation structure (Cid and Brizuela 1998, Olofsson et al. 2008) or homogenize it (Adler and Lauenroth 2000), and spatial heterogeneity may interact with herbivore-driven feedbacks to influence productivity. At the scale of individual feeding stations, for example, herbivores often preferentially graze in the same patches, keeping accumulated biomass low and nutrient cycling rates high (McNaughton 1984, Aguiar and Sala 1999), while other ungrazed patches become rank (Bailey et al. 1998) and presumably less productive. Moderate densities of herbivores are thought to create such patch-scale structural heterogeneity, while high herbivore densities are thought to create more homogenous vegetation structure (Cid and Brizuela 1998, de Knegt et al. 2008). However, few studies have explicitly measured the effects of different herbivores on spatial and temporal heterogeneity in productivity.

We asked how three different guilds of herbivores impact productivity across space and time using two techniques (multi-spectral satellite telemetry and on-the-ground clipping of caged plots) in a long-term exclosure experiment in an African savanna ecosystem. Specifically, we asked how mean and variance in aboveground net primary productivity, standing biomass, and normalized difference vegetation index values (NDVI; a correlate of productivity; Justice et al. 1985) were affected by cattle and different types of wild herbivores, separately and in combination.

METHODS

Study site

The Kenya Long-term Exclosure Experiment (KLEE) is located at the Mpala Conservancy (36°52′ E, 0°17′ N) in Laikipia County, Kenya. The study area is underlain with black cotton soils, poorly drained vertisols with high (>50%) clay content (Ahn and Geiger 1987). Black cotton savannas are widespread in East Africa, covering hundreds of thousands of km^2. Ninety-seven percent of the tree canopy cover in KLEE is *Acacia drepanolobium* Sjost. (Young et al. 1998), and total tree canopy cover averages 15–25%. Five grass species (*Pennisetum mezianum* Leeke, *P. stramineum* Peter, *Themeda triandra* Forssk., *Lintonia nutans* Stapf., and *Brachiaria lachnantha* (Hochst.) Stapf) make up 85% of herbaceous cover (Porensky et al. 2013). The site is located on virtually flat topography at an elevation of 1,810 m above sea level. The absence of distinct runoff or run-on areas, coupled with the relatively low plant diversity, makes this an ideal system to examine the effects of different herbivores on plant production independent of other factors. For 2010, 2011, and 2012 (the years on which the present study is focused), annual rainfall at the site was 579 ± 16, 1,003 ± 30, and 785 ± 9 mm/yr, respectively (mean ± 1 SE across the three experimental blocks). Although September–December of 2010 was relatively dry, most of the data collection period was wetter than normal; long-term (1998–2013, $N = 16$ yr) mean annual rainfall is 616 ± 48 mm/yr.

Mpala Conservancy is managed for both wildlife conservation and livestock production, with mean stocking rates of 0.10–0.14 cattle/ha. Wild ungulates commonly found at the study site include the mesoherbivores plains zebra (*Equus burchelli* Gray), Grant's gazelle (*Gazella [Nanger] grantii* Brooke), hartebeest (*Alcelaphus buselaphus* Pallas), eland (*Taurotragus oryx* Pallas), and oryx (*Oryx gazella beisa* L.), as well as the megaherbivores elephant (*Loxodonta africana* Blumenbach), and reticulated giraffe (*Giraffa camelopardalis* L.). Total biomass-density (kg/km^2) of large wild ungulates is approximately one-third of cattle biomass-density, and large wild ungulate biomass density is split almost evenly between megaherbivores and mesoherbivore wildlife (Veblen et al. 2016; Appendix S1: Table S1). Because giraffes are strict browsers of woody species, we consider elephants the main megaherbivores for the purposes of herbaceous productivity analyses. However, we retain giraffes in our model because they may also have indirect effects on understory vegetation by altering shading or competitive dynamics. In addition to these larger herbivores, one small antelope, steinbuck (*Raphicerus campestris* Thunberg), a strict browser, occurs in the area and is able to access all experimental treatment plots (Young et al. 2005). Wildlife in this region are present year-round and do not undergo large seasonal migrations.

Experimental design

Kenya Long-term Exclosure Experiment was established in 1995 and consists of three replicate blocks, each containing six 200 × 200 m treatment plots. The replicate blocks are 70–200 m apart. The experiment uses semipermeable barriers to allow access by different combinations of cattle (C), mesoherbivore wildlife 15–1,000 kg (W), and megaherbivores (M). Each of the following six treatments is replicated across the three blocks: C, W, WC, MW, MWC, and O. The capital letters indicate which herbivores are allowed access (e.g., O allows no herbivores >15 kg, W allows mesoherbivore wildlife >15 kg, but no cattle or megaherbivores, and MWC allows megaherbivores, mesoherbivore wildlife, and cattle). There are also a number of smaller vertebrate and invertebrate herbivores that are not excluded, including rodents, birds, and grasshoppers. Long-term patterns of dung deposition in the KLEE plots indicate that (1) treatments are >90% effective at excluding targeted species and (2) experimental fences do not deter wild herbivores from using the plots intended to be accessible to them (see Young et al. 1998 for more details).

Individually herded groups of 100–120 head of cattle are grazed in C, WC, and MWC plots for several hours on each of two to three consecutive days, typically three to four times per year. The precise number of grazing days and timing of grazing 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 both private and communal properties in the region, where livestock graze in one general area for several days at a time until forage is depleted and then move on to a different area until the forage recovers. The landscape is not fenced into paddocks, but rather herders guide livestock so that the entire range undergoes similar episodic grazing throughout the year. The effective stocking rate of plots is similar to the moderate overall ranch stocking rate (0.10–0.14 cattle/ha; Odadi et al. 2007). Natural fires in this system are rare, and fire has not been an active part of this ecosystem since the 1950s (Okello et al. 2008; R. L. Sensenig, *personal communication*).

Data collection

Herbaceous standing biomass and ANPP.—Each of the 18 4-ha KLEE treatment plots is demarcated into 16 subplots, 50 × 50 m (Young et al. 1998). We randomly selected one of these subplots in each plot, excluding subplots that were being used for other experiments or that included former cattle corrals (bomas), which develop into uniquely productive glades (Veblen 2012). In the center of the selected 50 × 50 m subplot, we created a square grid of 49 1 × 1 m quadrats separated by 3 m (4 m on center).

We performed a clipping experiment in each of the 18 plots from February 2010 to September 2012, clipping every 123 ± 1 d (~4.1 months) using a moveable cage method (McNaughton et al. 1996). On the first clipping date (February 2010), three randomly selected quadrats were clipped of vegetation to ground level, and 1 × 1 × 1 m metal cages were installed over three other, randomly selected quadrats. Cages were covered with 5-cm chicken wire, and 1-cm mesh screen was installed over the bottom 0.3 m of each cage to deter rodent entry into the cages. Cages were secured to the ground using stakes and mallets. Soil was packed around each cage perimeter to seal any gaps between the cage and the ground. On the second clipping date (June 2010), vegetation within the three caged quadrats was clipped. At the same time, three other randomly selected uncaged quadrats were clipped. The three cages were then installed over three new, randomly selected (unclipped) quadrats, and the entire procedure was repeated at each clipping date. We did not re-clip any 1 × 1 m quadrat over the duration of the study. We chose to use a constant time interval between clipping events because rainfall is variable and unpredictable at the site, making it difficult to clip before and after a growing season.

Clipped material was collected in mesh bags made of mosquito netting. Bags were air dried until they reached constant weight (<3 d), and then weighed using manual hanging scales. Bag weights were subtracted from total weights to obtain dry biomass estimates. Clipped biomass included both green herbaceous material and standing dead herbaceous material, but excluded tree and shrub biomass. It was difficult to separate current season (<123 d old) standing dead from older standing dead material, so we included all standing dead material when weighing biomass. We note that our study occurred during a relatively wet period following a drought. Standing biomass increased steadily during the study (see *Results*) and little standing dead material developed during each sampling period.

For analyses, we calculated mean uncaged standing biomass for each time interval within each KLEE treatment plot (average of three uncaged quadrats per plot and sampling date). For each time interval, we then calculated mean monthly ANPP as mean caged standing biomass at time t − mean uncaged standing biomass at time t − 1/number of months since previous sampling date. Quadrats were not paired, so ANPP was calculated at the plot scale. Due to spatial variability and our small number of sub-samples per plot, our data included both positive and negative production values; in other words, despite caging to reduce the effects of mammalian herbivory, the three caged quadrats sampled at time t sometimes had less biomass than the three (different) uncaged quadrats sampled at time t − 1 (see Bork and Werner 1999 for similar results/issues).

To assess temporal variability for both ANPP and standing biomass, we calculated the absolute value of change between adjacent sampling dates for each response variable. To obtain estimates of spatial variability in uncaged standing biomass within each sample period, we

calculated standard errors around the mean value for each plot ($N = 3$ quadrats per sampling date). We could not calculate spatial variability in ANPP within plots because we had only one ANPP value per plot × sampling date.

Normalized difference vegetation index.—We collected GPS points from the corners of each of the 18 experimental plots using a Trimble Juno 3B GPS unit (Trimble Navigation Ltd., Sunnyvale, CA, USA). These GPS points were imported into QGIS 1.8.0 (QGIS Development Team 2012), which was used for all analysis of satellite data. GPS points were then overlaid on Pan-sharpened multispectral Quickbird satellite images taken in November 2009, May 2011, and July 2013 with 0.6-m spatial resolution. We visually checked each GPS point for accuracy against visible vertices of KLEE plot fences. If necessary, GPS points were manually adjusted so that they were more accurately located at the four corners of each of the 18 plots. Using these corner points and the point-to-polygon function in QGIS, we created separate images of each of the 18 plots for 2009, 2011, and 2013. NDVI from the satellite imagery was calculated as NIR − R/NIR + R (Tucker 1979).

We masked out the extent of any glades (see *Methods: Data collection*) before calculating NDVI values. We determined and recorded GPS locations of glades based on predominant vegetation, especially the lack of *A. drepanolobium* and the dominance of *P. stramineum* and *Hibiscus flavifolius* (Veblen 2012). After excluding glades, we were left with an average of 102,535 ± 2,337 (SE) NDVI values (pixels) per treatment plot. We extracted the mean, maximum, minimum, range (maximum–minimum), and standard deviation of the NDVI values of each experimental plot for each sampling date. We used maximum, minimum, range, and standard deviation values (one of each per plot and sampling date) to assess spatial variability in NDVI. We assessed temporal variability in mean NDVI at the plot scale by calculating the absolute value of changes between adjacent sampling dates.

Statistical analysis

We used analysis of covariance (ANCOVA) to (1) establish that herbivore exclusion treatments created a gradient of herbivore utilization and (2) determine whether uncaged standing biomass, ANPP, and NDVI were linearly related while controlling for block effects. We ran four related models: (1) herbivore biomass-density, block, and herbivore biomass-density × block as predictors of standing biomass; (2) standing biomass, block, and standing biomass × block as predictors of ANPP; (3) standing biomass, block, and standing biomass × block as predictors of NDVI; and (4) ANPP, block, and ANPP × block as predictors of NDVI. We estimated herbivore biomass-density for each experimental treatment using data from local wildlife aerial surveys conducted in 1999, 2001, and 2003–2005 (Appendix S1: Table S1; Veblen et al. 2016, Georgiadis et al. 2007). Before running

each model, we averaged measurements across all time steps in each KLEE plot (per model $N = 18$).

We used linear mixed models (LMMs) to ask how different experimentally manipulated groups of herbivores (cattle, mesoherbivore wildlife, and megaherbivores) affected standing biomass, ANPP, NDVI, and spatial and temporal variability associated with these parameters. Random factors included block and plot nested within block, and we used a compound symmetry covariance structure to address the nonindependence of repeated surveys within the same plots. Fixed effects included cattle (yes/no), mesoherbivore wildlife (yes/no), megaherbivores (yes/no), cattle × mesoherbivore wildlife, and cattle × megaherbivores. This model structure allowed us to isolate the individual and interactive effects of different herbivore guilds. Because we expected pre-survey rainfall to have strong impacts on biomass in this system (Porensky et al. 2013), we included rainfall as a fixed covariate in LMMs. For clipping dates from June 2010 onward, we calculated mm of rain since the previous survey. For the initial clipping date (February 2010) and the three NDVI dates, we calculated mm of rain over the previous four months. For mean, minimum, maximum, and range of NDVI (but not temporal variability or standard deviation of NDVI), we also standardized values within each sampling period to minimize rainfall-, atmosphere-, and image processing-induced variability. To standardize, we calculated the maximum of the 18 observed NDVI values (one per plot) measured within each sample period. We then divided all 18 values by this maximum value. We used a similar LMM structure to ask how herbivore biomass-density affected temporal variation in standing biomass and ANPP. In these models, we used the same random factors and covariance structure as above, but used herbivore biomass-density instead of herbivore guilds as our fixed effect.

Analyses were conducted in R 3.0.1 using the nlme package (Pinheiro et al. 2015). Response values were transformed and variance-weighted when necessary to meet model assumptions. Results are reported as untransformed means ± 1 SE except where noted.

RESULTS

Relationships among standing biomass, ANPP, and NDVI

Herbaceous standing biomass decreased as herbivore biomass-density increased (Fig. 1a; $R^2 = 0.82$, $F_{1,12} = 50.2$, $P < 0.0001$), supporting the idea that herbivore treatments create a gradient of herbivory. Standing biomass was highest in the total exclusion (O) treatment and generally decreased with the addition of herbivore guilds as follows: O = W > MW > C > WC = MWC. ANPP and mean NDVI both increased as standing biomass decreased (Fig. 1b, c; ANPP, $R^2 = 0.61$, $F_{1,12} = 18.68$, $P = 0.001$; NDVI, $R^2 = 0.57$, $F_{1,12} = 3.55$, $P = 0.08$),
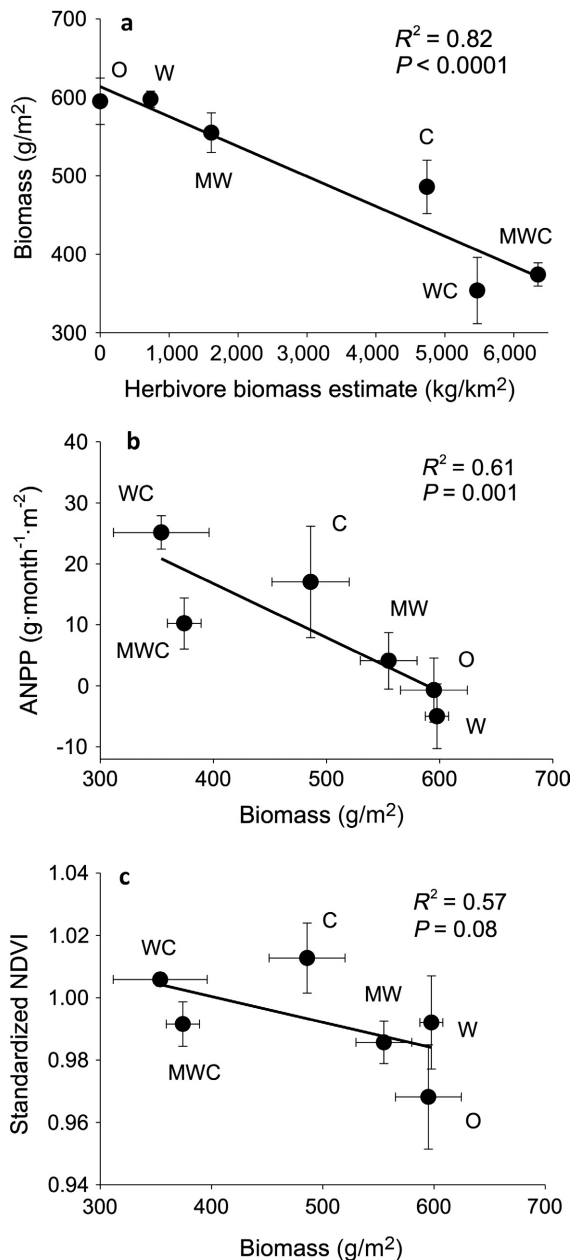
FIG. 1. Relationships among (a) estimated herbivore biomass-density and standing biomass, (b) standing biomass and ANPP, and (c) standing biomass and NDVI. For each herbivore treatment, herbivore biomass-density was estimated from local aerial surveys conducted in 1999, 2001, and 2003–2005 (Georgiadis et al. 2007, Veblen et al. 2016). Mean ± 1 SE of three replicates per treatment ($N = 18$ plots; value for each plot averaged over all available time steps). Abbreviations are C, cattle allowed; W, mesoherbivore wildlife allowed; M, megaherbivores allowed; and O, all large herbivores excluded.

suggesting a positive response of ANPP and NDVI to biomass removal by herbivores. Our two measures of productivity (satellite-based NDVI and quadrat-based ANPP, estimated at different times) were positively, but not significantly correlated with each other ($R^2 = 0.49$,

$F_{1,12} = 2.39$, $P = 0.15$). For all four models, interactions between block and predictors of interest were not significant (all $P > 0.20$).

Standing biomass

Over all nine sample periods (every four months from February 2010 to September 2012), plots to which cattle had access (C, WC, and MWC) had an average of 31% lower standing biomass than plots without cattle (O, W, and MW), and plots to which mesoherbivore wildlife had access (W, WC, MW, and MWC) had 13% less biomass than plots without mesoherbivore wildlife (O and C; significant main effects of cattle and mesoherbivore wildlife; Figs. 2a and 3a, Table 1). The effect of mesoherbivore wildlife on biomass was greater in plots with cattle (20% reduction in plots with cattle vs. 4% reduction in plots without cattle; significant interaction between cattle and mesoherbivore wildlife; Fig. 2a, Table 1). Similarly, the effect of cattle on biomass was greater when mesoherbivore wildlife were present (37% when mesoherbivore wildlife were present vs. 18% reduction when mesoherbivore wildlife were absent; Fig. 2a). Rainfall had a strong, positive relationship with standing biomass (Fig. 3a, c; $F_{1,143} = 16.0$, $P = 0.0001$), and biomass generally increased through this time of relatively high rainfall. Megaherbivores did not have significant effects on standing biomass (Fig. 2a, Table 1).

Mesoherbivore wildlife and megaherbivores, but not cattle, marginally reduced temporal variability in standing biomass (marginally significant main effects of mesoherbivore wildlife and megaherbivores; Fig. 2b, Table 1). The effects of mesoherbivore wildlife and megaherbivores on temporal variability in standing biomass did not depend on cattle presence (interaction $P > 0.7$; Table 1). In contrast to temporal variability, spatial variability in standing biomass was not affected by herbivore treatments (all $P > 0.25$). Surveys following rainier periods tended to have marginally higher temporal variability (i.e., more change in biomass since the previous survey; Fig. 3a, c; $F_{1,125} = 3.12$, $P = 0.08$) and higher spatial variability ($F_{1,125} = 2.98$, $P = 0.09$).

Mean productivity

Results from productivity cage and NDVI measurements followed similar patterns. Productivity cage measurements revealed that while ANPP per month was very low or even negative in plots without cattle, in plots with cattle it averaged 10–25 $g \cdot m^{-2} \cdot month^{-1}$ (1,200–3,000 $kg \cdot ha^{-1} \cdot yr^{-1}$). The presence of cattle enhanced ANPP by about 18 $g \cdot m^{-2} \cdot month^{-1}$ (Figs. 2c and 3b, Table 1). The positive effect of cattle on ANPP was weaker when megaherbivores were also present (C and WC > MWC; significant interaction between cattle and megaherbivores; Fig. 2c, Table 1). In contrast to cattle, mesoherbivore wildlife had no significant effects on ANPP (Table 1).
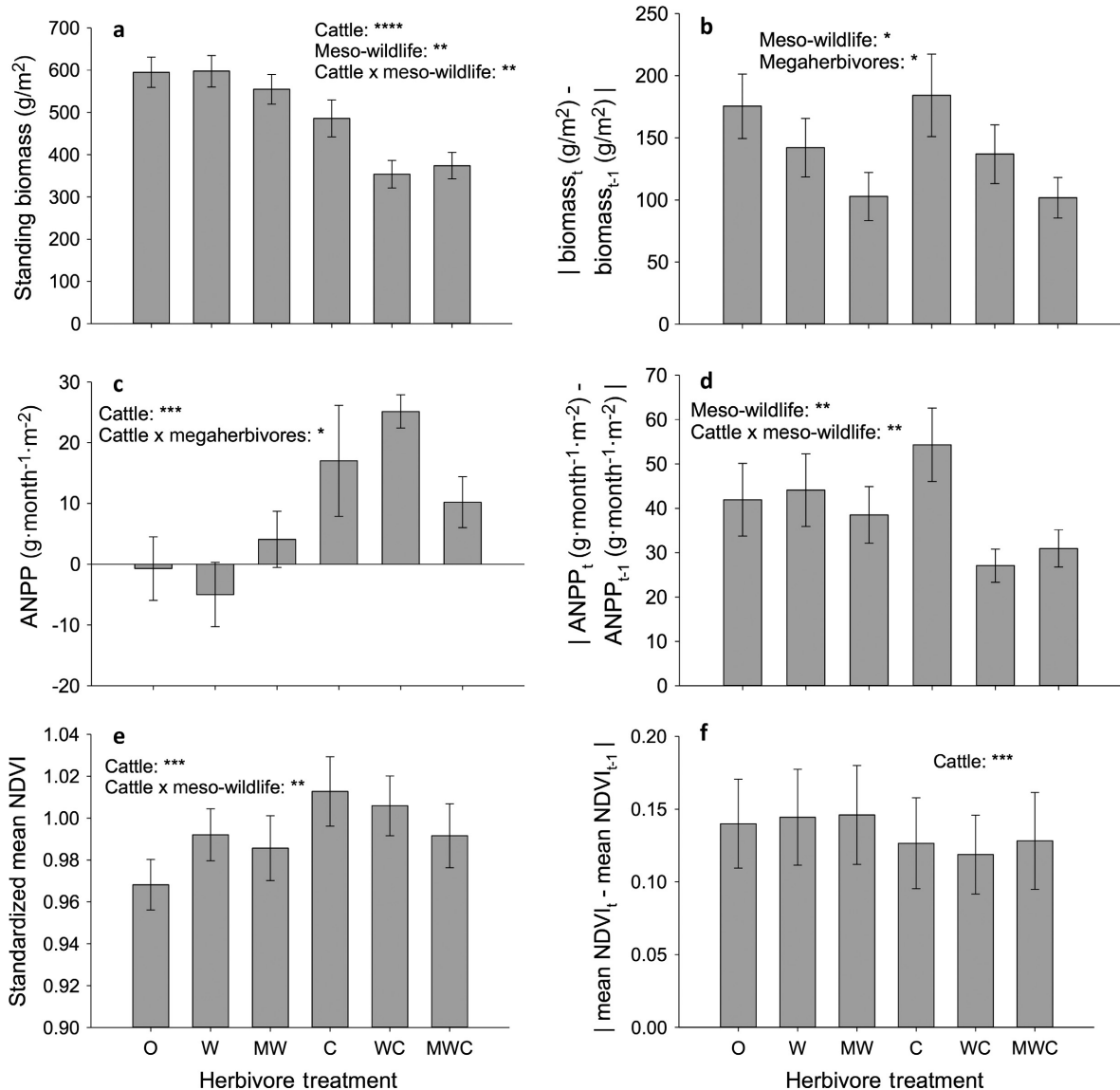
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FIG. 2. Impacts of long-term herbivore treatments on (a) standing biomass, (b) temporal variability in standing biomass, (c) ANPP, (d) temporal variability in ANPP, (e) standardized NDVI, and (f) temporal variability in NDVI. Mean ± 1 SE of three replicates per treatment ($N = 18$ plots; value for each plot averaged over all available time steps). Significant main and interactive effects of herbivore guilds, calculated from linear mixed models, are indicated above each graph. Abbreviations are C, cattle allowed; W, mesoherbivore wildlife allowed; M, megaherbivores allowed; and O, all large herbivores excluded. * $P < 0.10$, ** $P < 0.05$, *** $P < 0.01$, and **** $P < 0.001$.

Rainfall had a marginally significant positive relationship with productivity cage ANPP (Fig. 3b, c; $F_{1,125} = 3.46$, $P = 0.07$). Similarly, the difference in standing biomass between times t and $t - 1$ in uncaged plots (i.e., ANPP minus consumption) was positively related to rainfall ($F_{1,125} = 2.92$, $P = 0.09$). Unlike ANPP, however, this difference was similar across all herbivore treatments (all $P > 0.4$). That is, although herbivore treatments consistently differed in standing biomass and ANPP, they did not differ in the accumulation of biomass from one sample period to the next. This suggests that

during years 16–18 of this long-term experiment, herbivore-driven differences in ANPP were offset by differences in consumption (i.e., treatments with more production also experienced more consumption).

Similar to our productivity cage findings, standardized mean NDVI, a recognized correlate and metric of productivity, was also higher in plots where cattle were present compared to plots where cattle were absent (Fig. 2e, Table 1). Mesoherbivore wildlife alone did not have a significant effect on NDVI, but the effect of cattle on NDVI was significantly weaker when mesoherbivore

TABLE 1. Linear mixed model results (F, df = 1,10, and P, in parentheses) for the effects of different groups of herbivores (cattle, mesoherbivore wildlife, and megaherbivores) on standing biomass, ANPP, NDVI, and spatial and temporal variability associated with these parameters.

Category	Response	Model fixed factors				
		Cattle	Mesoherbivores	Megaherbivores	Cattle × meso-herbivores	Cattle × mega-herbivores
Mean	standing biomass	**55.6 (<0.001)**	**5.20 (0.05)**	0.03 (0.92)	**5.54 (0.04)**	1.26 (0.29)
	cage-based ANPP	**15.8 (0.003)**	0.11 (0.74)	0.27 (0.61)	1.24 (0.74)	**4.65 (0.06)**
	standardized NDVI	**14.3 (0.004)**	1.51 (0.25)	2.22 (0.17)	**4.91 (0.05)**	0.33 (0.58)
	biomass accumulation(ANPP-consumption)	0.04 (0.84)	0.42 (0.53)	0.69 (0.43)	0.14 (0.72)	0.05 (0.83)
Spatial variability	standing biomass SD	0.97 (0.35)	1.3 (0.28)	0.02 (0.89)	0.007 (0.94)	0.001 (0.97)
	NDVI SD	1.37 (0.27)	**5.16 (0.05)**	**5.58 (0.04)**	0.64 (0.45)	0.86 (0.38)
	NDVI standardized range	2.11 (0.18)	**14.6 (0.003)**	**8.99 (0.01)**	0.5 (0.49)	0.58 (0.46)
	NDVI standardized max	2.27 (0.16)	**14.3 (0.004)**	**25.1 (0.0005)**	0.82 (0.39)	0.29 (0.60)
	NDVI standardized min	2.51 (0.14)	**5.28 (0.04)**	0.38 (0.55)	0.30 (0.60)	1.05 (0.33)
Temporal variability	standing biomass	0.01 (0.93)	**3.88 (0.08)**	**3.60 (0.09)**	0.02 (0.89)	0.15 (0.70)
	cage-based ANPP	0.04 (0.8)	**5.74 (0.04)**	0.01 (0.91)	**7.15 (0.02)**	0.90 (0.37)
	NDVI	**16.2 (0.002)**	0.11 (0.75)	2.09 (0.18)	2.21 (0.17)	0.95 (0.35)

Notes: Random factors included block and plot nested within block, and we used a compound symmetry covariance structure to address the nonindependence of repeated surveys within the same plots. Fixed effects in our models included cattle (C), meso-herbivore wildlife (W), megaherbivores (M), cattle × mesoherbivore wildlife, and cattle × megaherbivores. Significant main and interactive effects of herbivore guilds ($P < 0.10$) are indicated in bold.

wildlife were also present (C > WC and MWC; Fig. 2e; significant interaction between cattle and mesoherbivore wildlife; Table 1). Megaherbivores had no significant effects on mean NDVI (Table 1).

Spatial variation in productivity

We did not calculate spatial variation in ANPP in productivity cages because our experimental design only allowed us to calculate one value per time period in each experimental plot. However, spatial variability in NDVI (measured as standard deviation among the 102,535 ± 2,337 SE pixels within each plot, each pixel 0.6 × 0.6 m) was 10% lower when mesoherbivore wildlife were present vs. absent and 19% lower when both mesoherbivore wildlife and megaherbivores were present (Fig. 4a, Table 1). Cattle had no significant main effect on spatial variability in NDVI, and effects of wildlife were not altered by cattle presence (interaction $P > 0.27$; Table 1). Rainier periods tended to be associated with more spatial variability ($F_{1,35} = 4.07$, $P = 0.051$).

Analysis of the range of NDVI values for each plot (the maximum–minimum NDVI observed across the 102,535 ± 2,337 SE pixels per plot, each pixel 0.6 × 0.6 m) further emphasized the role of wildlife in reducing spatial variability. Across the three time steps, the range of NDVI values was 25% smaller when mesoherbivore wildlife were present vs. absent and 32% smaller when both mesoherbivore wildlife and megaherbivores were present (significant main effects of mesoherbivore wildlife and megaherbivores; Fig. 4b, Table 1). Cattle had no significant effects on NDVI range (main effect and interaction $P > 0.18$; Table 1).

Results also held for independent analyses of minimum and maximum NDVI (Fig. 4c). Across the three time steps, maximum NDVI values were 6% lower when mesoherbivore wildlife were present and 14% lower when both mesoherbivore wildlife and megaherbivores were present (Table 1). Mesoherbivore wildlife, but not mega-herbivores, increased minimum NDVI values by 13% (Table 1). Cattle had no significant effects on maximum or minimum NDVI (Table 1). Rainier periods had significantly higher maximum NDVI values, even after within-image standardization ($F_{1,35} = 10.5$, $P = 0.003$).

Temporal variation in productivity

Temporal variability in productivity cage ANPP was significantly lower when mesoherbivore wildlife and both cattle and mesoherbivore wildlife were present (significant main effect of mesoherbivore wildlife and interaction between mesoherbivore wildlife and cattle; Fig. 2d, Table 1). Cattle had no significant main effect on temporal variability (Table 1), and the effects of megaherbivores and cattle × megaherbivores were also nonsignificant (Table 1). In contrast, herbivore biomass was not a significant predictor of temporal variation in ANPP ($F_{1,14} = 0.10$, $P = 0.76$) or standing biomass ($F_{1,14} = 0.56$, $P = 0.47$).

Cattle reduced temporal variability in NDVI by 13% (Fig. 2f, Table 1). Neither mesoherbivore wildlife nor megaherbivores had significant effects on temporal variability in NDVI (Table 1). Rainier periods were associated with significantly more temporal change in NDVI ($F_{1,17} = 292$, $P < 0.0001$).
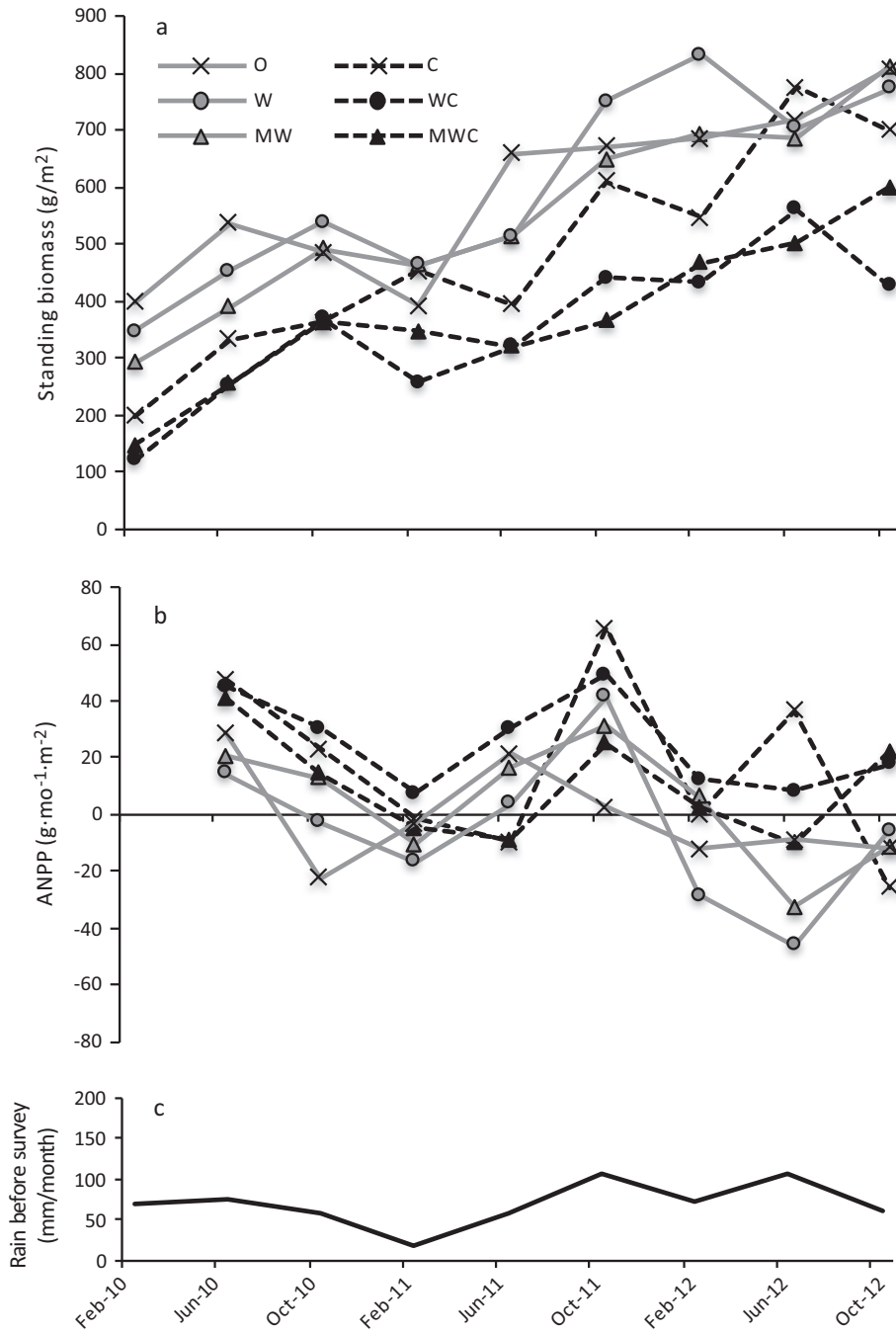
FIG. 3. Temporal patterns in (a) standing biomass, (b) ANPP, and (c) rainfall for the six herbivore treatments. Each point represents the mean of three replicates. Abbreviationsa are C, cattle allowed; W, mesoherbivore wildlife allowed; M, megaherbivores allowed; and O, all large herbivores excluded. Rainfall values for each survey date represent cumulative rainfall during the four months preceding the survey.

DISCUSSION

Our results provide experimental evidence that wildlife and cattle can have unique, additive, and interactive effects on aboveground net primary productivity in an African savanna. In our experiment, mean productivity, measured both via ANPP and NDVI, was negatively associated with standing biomass and generally increased in response to increasing herbivore biomass-density, driven primarily by cattle presence. In contrast, variability in ANPP and NDVI were mostly driven by specific types of herbivores, with wild herbivores constraining variability more than

cattle. Our results suggest that replacing wildlife with cattle at similar biomass-densities could lead to similarly productive, but more heterogeneous rangelands.

Herbivore pressure and standing biomass

In line with previous studies from this experiment (Veblen et al. 2016), our results suggest a strong gradient of herbivory in which MWC ≈ WC > C > MW > W ≈ O (Fig. 1). Cattle and mesoherbivore wildlife each reduced standing biomass, and the effects of these two herbivore groups were greater than additive; that is, each reduced standing biomass more when the other was also present (Figs. 1 and 2). This may be a result of facilitation between cattle and wildlife. During rainy periods, cattle in KLEE have been shown to put on more weight in plots shared with wildlife (Odadi et al. 2011), and conversely, cattle presence has been shown to increase wildlife use during rainy periods (Kimuyu et al., *unpublished manuscript*). Since our study focused on a relatively rainy three-year period, the net effect of cattle and wildlife on each other may have been facilitative, resulting in greater forage removal in shared plots. Facilitation among herbivores, which usually occurs when one species or guild improves the quality and/or production of forage for others, has been observed in other savanna systems (Arsenault and Owen-Smith 2002, Waldram et al. 2008). The standing biomass patterns we observed over three years of the KLEE study are generally consistent with herbaceous cover patterns over 14 years of the study, although the longer chronosequence indicated only additive, not interactive, effects of mesoherbivore wildlife with cattle (Veblen et al. 2016) perhaps because the longer chronosequence integrates times of facilitative (wet conditions) and competitive (dry conditions) cattle–wildlife interactions (Odadi et al. 2011).

Mean productivity

Across all herbivore treatments, both measures of mean productivity, ANPP in the field and satellite-derived NDVI, were negatively related to standing biomass, indicating a positive relationship between biomass removal and productivity. The greatest differences in biomass-density, standing biomass, and mean productivity were all related to cattle presence. There are nearly three times as many cattle as total wildlife in this ecosystem (Fig. 1a), and it is therefore difficult to disentangle effects of grazing pressure from effects of cattle grazing and cattle management. It is possible that differences in grazing patterns and timing of grazing between cattle and wildlife were the primary drivers of mean ANPP results. For example, intermittent herbivory caused by periodic cattle grazing may have led to the high levels of aboveground productivity in the cattle-accessible plots. Compensatory regrowth is hypothesized to increase with time between grazing events (Oesterheld and McNaughton 1991), as well as with high nutrient inputs and intermittent patterns of herbivory (Augustine and McNaughton 1998). However, wildlife in
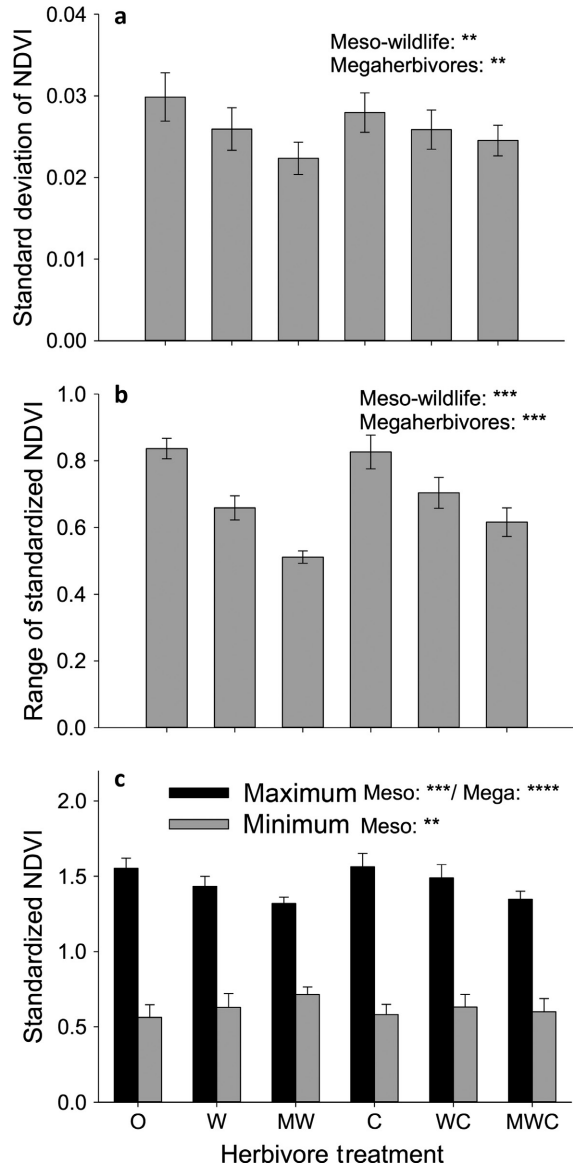

FIG. 4. Impacts of long-term herbivore treatments on spatial variability in NDVI values: (a) standard deviation of NDVI, (b) range of NDVI, and (c) maximum and minimum NDVI. Values for (b) and (c) were standardized based on the maximum NDVI value for each sampling date. Mean ± 1 SE of three replicates per treatment ($N = 18$ plots; value for each plot averaged over all available time steps). Significant main and interactive effects of herbivore guilds, calculated from linear mixed models, are indicated above each graph. Abbreviations are C, cattle allowed; W, mesoherbivore wildlife allowed; M, megaherbivores allowed; and O, all large herbivores excluded. * $P < 0.10$, ** $P < 0.05$, *** $P < 0.01$, and **** $P < 0.001$.

this system are also intermittently abundant depending on season and recent rainfall patterns in the region (T. P. Young, *personal observation*), and it is difficult to say which guild (cattle, mesoherbivore wildlife, or megaherbivores) is present most intermittently. Moreover, our results suggest that wildlife and cattle grazing had qualitatively

similar impacts on mean productivity (Figs. 1 and 2). We therefore hypothesize that differences between livestock and wildlife effects on mean primary productivity are driven primarily by differences in grazing intensity, rather than herbivore type.

Several factors may help to explain similarities between the effects of cattle and wildlife on mean productivity. First, although wildlife in this system includes a diverse set of species, wildlife biomass-density is dominated by plains zebras, which are functionally similar to cattle (primarily grazers that are not highly selective) and consume many of the same grass species (Kartzinel et al. 2015). Thus, the apparent similarity between the impacts of cattle and wildlife may be driven largely by foraging similarities between cattle and zebras. Secondly, herbivore effects on ANPP may be mediated by differences in plant community composition, which are themselves strongly driven by total herbivore pressure rather than herbivore identity (Veblen et al. 2016). It is possible that certain grass species that are more abundant in plots with higher grazing pressure may have higher productivity than other species that dominate the plots with lower total grazing pressure.

Our results indicate that the herbaceous community in this system is able to fully compensate for moderate herbivory by increasing ANPP. Biomass accumulation in uncaged plots (difference in standing biomass between times t and $t-1$, or the net of ANPP minus consumption) was similar across herbivore treatments, indicating that herbivore-driven differences in consumption were offset by differences in production (and vice versa). Compensatory regrowth following herbivory has been widely documented (McNaughton 1979, Maschinski and Whitham 1989, Gadd et al. 2001, Peinetti et al. 2001) and has been hypothesized to have evolved as a strategy to limit reductions in plant fitness caused by loss of photosynthetic capacity or reproductive units (Belsky et al. 1993, Strauss and Agrawal 1999). Additional mechanisms for compensatory regrowth following herbivory, such as increased nutrient cycling, have also been hypothesized (De Mazancourt et al. 1998, 1999). An additional, simpler explanation for high-biomass systems such as the one studied here may be that compensatory regrowth occurs when herbivory releases plants (especially grasses) from self-shading, especially by dead standing leaves (McNaughton 1979). Our results are similar to findings in the Serengeti, where plants displayed the most positive growth rates at moderate grazing levels (McNaughton 1979, 1985). Other research from Kruger National Park, an ecosystem with similar average wildlife biomass (1,750 kg/km^2 vs. our 1,611 kg/km^2; du Toit et al. 2003), has demonstrated similar effects of herbivores on herbaceous ANPP (Knapp et al. 2012).

It is important to note that cattle in this experiment were moderately stocked; in many parts of East Africa, cattle stocking rates far exceed those tested here, and time between grazing events is likely shorter. Under such very high levels of grazing intensity, plants may not be able to compensate for herbivory (Turner et al. 1993), reducing rangeland productivity.

When different herbivore treatments were examined in more detail, both metrics of productivity displayed hump-shaped responses to herbivore biomass-density, in line with the intermediate disturbance hypothesis (Grime 1973, Connell 1978). The highest productivity occurred at intermediate to high levels of herbivore biomass-density (WC and C; Fig. 2c, e). These results suggest that productivity may decline at the highest levels of herbivore biomass-density. Unlike both productivity metrics, uncaged standing biomass was similarly low in MWC and WC plots (Fig. 2a). Biomass accumulation results suggested that production matched consumption across treatments. Taken together, these results indicate that plots with all herbivore guilds (MWC) had lower per-animal biomass removal than plots with cattle and meso-herbivore wildlife but no megaherbivores (WC), and this lower removal was associated with somewhat lower ANPP. Reduced per animal use could be a consequence of lower forage quality or reduced availability of key forage resources in these plots due to the competitive effects of elephants (Young et al. 2005).

We have at least three reasons to believe that our ground-based ANPP results are robust or even conservative. First, we detected ANPP responses despite the fact that our caged and uncaged samples were not paired (and this potentially created more noise in our data). Secondly, we detected responses despite relatively long time intervals (4.1 months) between sampling dates that could have caused attenuation of large herbivore effects on productivity. Finally, ground-based ANPP estimates from this study align well with estimates from other, similar ecosystems. In the presence of cattle, mean ANPP (excluding woody plant production) ranged from 120 to 300 g·m^{-2}·yr^{-1} (1,200–3,000 kg·ha^{-1}·yr^{-1}). While it is possible that cage-based ANPP measurements can be affected by cage-induced light limitation, this study's ANPP estimate is similar to productivity estimates from both North American and Serengeti grasslands with comparable rainfall (Sala et al. 1988, 2012) and somewhat higher than estimates of herbaceous ANPP from an adjacent, less productive soil type (Augustine and McNaughton 2006).

Temporal and spatial variation

In contrast to our findings for mean productivity, which appear to be driven by cattle presence and/or grazing intensity, we found that variation in productivity and standing biomass across space and time were significantly affected by the identity of individual herbivore groups. Mesoherbivore wildlife and megaherbivores reduced spatial or temporal variability in multiple ecosystem traits, including ANPP and NDVI (Table 1, Figs. 2–4). Cattle had much weaker effects on variability, though cattle did reduce temporal variation in NDVI.

There are a number of reasons why wildlife might lead to more homogenous patterns of productivity than cattle. Wildlife are able to respond opportunistically to local rainfall events and increase their grazing activity where and

when primary productivity is high (Frank and McNaughton 1993, Young et al. 2005, Bonnet et al. 2010). This could reduce both spatial and temporal variation in productivity and standing biomass. It is also possible that the diverse set of wildlife species leads to a more evenly distributed spatial impact on the herbaceous layer, resulting in lower structural diversity at the foraging-patch scale and homogenizing productivity. Cattle are known to preferentially graze patches with high productivity or highly palatable plants and avoid less productive or palatable patches, creating a structural mosaic of patches (Senft et al. 1985, Cid and Brizuela 1998). Because grazing stimulates production in this system, patches that are more heavily grazed by this single herbivore species might be expected to be more productive than lightly grazed ones. The more diverse complement of wildlife species may have a more spatially diffuse impact on the herbaceous layer via a wider collective dietary breadth (Kartzinel et al. 2015) either because of differences in herbivore forage preferences or because of competitive foraging niche separation.

Temporal variability in productivity also appeared to be driven by particular herbivores. Somewhat surprisingly, we found that cattle reduced temporal variability in NDVI. Like wildlife, cattle graze in KLEE when forage availability is high. However, unlike wildlife, cattle are actively managed and their grazing is concentrated into relatively few grazing events per year. This study's productivity measurements were not synchronized temporally with cattle grazing events, yet mean NDVI values were consistently higher in cattle plots. Taken together, these facts suggest that cattle grazing affected plant productivity for several months after actual grazing episodes. In addition, we found that plots where both cattle and mesoherbivore wildlife were present exhibited reduced temporal variation in ANPP compared to plots with just cattle. This may be a result of facilitation between cattle and wildlife (see *Discussion: Herbivore pressure and standing biomass*). Increased mesoherbivore wildlife presence in cattle plots may make up for the relatively concentrated cattle grazing events, in turn further reducing temporal variation in ANPP.

We found little evidence to support the idea that differences in grazing pressure alone drove differences in variation in productivity. Herbivore biomass was not a significant predictor of temporal variation in ANPP or standing biomass.

Productivity cages vs. NDVI

Results obtained via on the ground measurements of understory vegetation were consistent with and comparable to remotely sensed NDVI results across space and time. However, it is important to note that productivity cage and NDVI measurements, although similar, represent slightly different aspects of aboveground productivity. While productivity cage measurements included both live and dead plant tissue, NDVI measures only active photosynthetic material. Because our ANPP measurements and NDVI measurements were taken in different years, we were not able to draw conclusions about the relationship between living and dead biomass in this system. In addition, NDVI measurements included both understory and overstory vegetation, whose contributions can independently impact NDVI measurements in savanna ecosystems (Archibald and Scholes 2007). Given the differences between NDVI and ground-based productivity estimates, it is encouraging that our results were broadly consistent across these two productivity metrics. It seems that different herbivores have relatively robust and predictable effects on multiple aspects of productivity in this system.

CONCLUSIONS

Our findings experimentally demonstrate that both the abundance and the identity of large mammalian herbivores can have profound impacts on primary production. These results contribute to our growing understanding of the ways in which livestock and wildlife may be more compatible than has traditionally been assumed. Although livestock and wildlife are often thought to compete (Prins 1992, Voeten and Prins 1999), we found that mean primary production was enhanced by the presence of cattle, while variation in primary production was minimized by mesoherbivore wildlife. Further, the impacts of these different guilds were complementary: While cattle were the primary drivers of higher mean productivity, mesoherbivore wildlife were the primary drivers of more spatially and temporally stable productivity. Although our results suggest a form of compatibility between livestock and wildlife, livestock are replacing wildlife in many African savanna systems. Our findings indicate that replacing wildlife with cattle, at moderate biomass-densities, may result in similarly productive systems, but that productivity may become more variable in space and time. Conversely, our results suggest that productivity does start to decline at the highest levels of herbivore biomass-density in our experiment, which are well below the levels currently occurring in most East African rangelands. A more thorough mechanistic understanding of why and how different herbivore guilds drive differences in productivity patterns will broaden our insights about the impacts of livestock and wildlife, separately and together, on savanna ecosystem functions.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1422/full

Data Availability

Data associated with this paper is available in figshare: https://dx.doi.org/10.6084/m9.figshare.3520172.v2