

## ARTICLE

# At high stocking rates, cattle do not functionally replace wild herbivores in shaping understory community composition

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## Funding information

National Geographic Society, Grant/Award Numbers: 4691-91, 9106-12, 9986-16; National Science Foundation, Grant/Award Numbers: LTREB BSR 03-16402, LTREB BSR 08-16453, LTREB BSR 12-56004, LTREB BSR 19-31224, LTREB BSR 97-07477; Rufford Foundation, Grant/Award Number: 27451-1; Smithsonian Institution, Grant/Award Number: James Smithsonian Fund; University of Leeds Centre for Climate, Grant/Award Number: Climate Research Bursary Award

**Handling Editor:** Neil H. Carter

## Abstract

Over a quarter of the world's land surface is grazed by cattle and other livestock, which are replacing wild herbivores, potentially impairing ecosystem structure, and functions. Previous research suggests that cattle at moderate stocking rates can functionally replace wild herbivores in shaping understory communities. However, it is uncertain whether this is also true under high stocking rates and the effects of wild herbivore on plant communities are moderate, enhanced, or simply additive to the effects of cattle at high stocking rates. To evaluate the influence of cattle stocking rates on the ability of cattle to functionally replace wild herbivores and test for interactive effects between cattle and wild herbivores in shaping understory vegetation, we assessed herbaceous vegetation in a long-term enclosure experiment in a semi-arid savanna in central Kenya that selectively excludes wild mesoherbivores (50–1000 kg) and megaherbivores (elephant and giraffe). We tested the effects of cattle stocking rate (zero/moderate/high) on herbaceous vegetation (diversity, composition, leafiness). We also tested how those effects depend on the presence of wild mesoherbivores and megaherbivores. We found that herbaceous community composition (primary ordination axis) was better explained by the presence/absence of herbivore types than by total herbivory, suggesting that herbivore identity is a more important determinant of community composition than total herbivory at high cattle stocking rates. The combination of wild mesoherbivores and cattle

stocked at high rates led to increased bare ground and annual grass cover, reduced perennial grass cover and understory leafiness, and enhanced understory diversity. These shifts were weaker or absent when cattle were stocked at high stocking rates in the absence of wild mesoherbivores. Megaherbivores tempered the effects of cattle stocked at high rates on herbaceous community composition but amplified the effects of high cattle stocking rate on bare ground and understory diversity. Our results show that cattle at high stocking rates do not functionally replace wild herbivores in shaping savanna herbaceous communities contrary to previous findings at moderate stocking rates. In mixed-use rangelands, interactions between cattle stocking rate and wild herbivore presence can lead to non-additive vegetation responses with important implications for both wildlife conservation and livestock production.

#### KEYWORDS

biodiversity conservation, cattle stocking rate, elephant, forb, grass, herbaceous plant communities, Kenya Long-term Exclosure Experiment, livestock–wildlife interactions, rangeland ecology

## INTRODUCTION

Cattle and other livestock graze more than a quarter of the Earth's land surface (Steinfeld et al., 2006) and are estimated to comprise >90% of the world's non-human mammalian biomass (Bar-On et al., 2018). Across the world's rangelands, including African savannas, livestock continues to replace large wild herbivores (>50 kg), potentially with negative impacts on ecosystem structure and function (Hempson et al., 2017; du Toit & Cumming, 1999). Understanding how plant communities respond to partial or complete replacement of large wild herbivores by livestock requires knowledge of (i) the extent to which and at what stocking rates livestock can functionally replace large wild herbivores and, (ii) in mixed-use rangelands, whether the effects of wild and domestic herbivores are simply additive to those of livestock grazing, or whether large wild herbivores moderate or amplify the effects of livestock on vegetation. This understanding is critical in rangeland management for maintaining plant diversity and predicting plant community responses to ecological restoration and herbivore reintroductions. Shifts in rangeland plant communities are also important because associated changes in forage quality and quantity can affect the abundance and diversity of large wild herbivore (Olf et al., 2002), as well as livestock grazing (Odadi et al., 2011).

In grasslands, including African savannas, grazing and/or browsing wild herbivores affect understory plant biomass (Staver et al., 2019), productivity (Frank et al., 2016), diversity (Koerner et al., 2018; Porensky et al., 2013), species composition (Veblen et al., 2016) and

plant functional traits (van der Plas et al., 2016). The consequences of wildlife extirpation for understory vegetation may be dependent on climate and the identity of the species lost or the species remaining, either wild or domestic (Burkpile et al., 2017; Burns et al., 2009; Goheen et al., 2013; van der Plas et al., 2016; Staver & Bond, 2014). Domestic herbivores also affect understory community composition, diversity, biomass (e.g., Pakeman et al., 2019; Seymour et al., 2010; Veblen et al., 2016), and productivity (Charles et al., 2017), and can reduce ecosystem structure and function in ways that are mediated by climate, grazing regime, and herbivore identity (Cingolani et al., 2005; Eldridge et al., 2016, 2018; Liu et al., 2015; O'Connor et al., 2010; Young et al., 2013). Several studies have examined the effects of livestock stocking rates on vegetation diversity and community composition (e.g., Pakeman et al., 2019; Porensky et al., 2016; Seymour et al., 2010). In contrast to only investigating presence versus absence of livestock (e.g., Charles et al., 2017; Koerner et al., 2018; Porensky et al., 2013; Veblen et al., 2016), studying the effects of different livestock stocking rates better allows us to understand and adjust the management of globally dominant domestic herbivores to meet biodiversity conservation objectives.

Livestock at a particular stocking rate could functionally compensate for wild herbivore losses in shaping plant communities if: (i) livestock diets mirror the collective diets of the assemblage of wild herbivores lost (Cingolani et al., 2014); (ii) plant communities respond primarily to total herbivory (not herbivore identity),

which remains comparable following replacement of wild herbivores by livestock (Perevolotsky & Seligman, 1998; Veblen et al., 2016); and/or (iii) domestic and wild herbivores have similar non-consumptive effects on vegetation (e.g., trampling or nutrient addition via defecation). These effects overpower consumptive effects. If these criteria are not fulfilled, the replacement of wild herbivores by livestock would lead to plant community shifts. For example, if livestock stocking rates are increased to the point that the total herbivory by domestic and wild herbivores exceeds the herbivore pressure with which the ecosystem coevolved, plant communities can cross thresholds to assume functionally different states. There is ample evidence that rangeland vegetation can be characterized by threshold dynamics and herbivory (i.e., the consumption of plants by livestock, wild herbivores, or both) can drive shifts among states (Bestelmeyer et al., 2015; Briske et al., 2003; Vetter, 2005).

Generally, we lack studies that experimentally tested the effects of large wild herbivores in the context of more than two livestock stocking rates (i.e., presence versus absence) on understory vegetation. Previous work from our study system in central Kenya identified strong impacts of cattle presence on understory plant successional dynamics, diversity, and community stability (Porensky et al., 2013; Riginos et al., 2018; Veblen & Young, 2010). Veblen et al. (2016) showed that savanna understory plant community composition (measured using primary ordination axis scores) was explained more by total herbivory than herbivore identity, and cattle at moderate densities appeared to functionally replace the resident large wild herbivore assemblage in shaping understory vegetation. However, whether this pattern persists at higher cattle stocking rates, or how the effects of high cattle stocking rates interact with the presence of native herbivore, is unknown. Investigating the effects of increasing cattle stocking rates is important because rangelands in this region, particularly those that are communally managed, are stocked at higher rates than the moderate stocking rates evaluated by Veblen et al. (2016) (Crego et al., 2020; Wells, Kimuyu, et al., 2021).

To test this experimentally, we assessed herbaceous vegetation in the Kenya Long-term Exclosure Experiment (KLEE; here, for 25 years), which enabled us to test the individual and interactive effects of wild mesoherbivores (50–1000 kg), megaherbivores (elephant and giraffe), and cattle at three stocking rates (zero/moderate/high). Our objectives were to investigate: (1) the extent to which cattle at high stocking rates functionally replace the loss of large wild herbivores (wild mesoherbivores and megaherbivores), and (2) whether the effects of large wild herbivores on savanna vegetation moderate, enhance, or are simply additive to the effects of cattle at moderate and high stocking rates.

## MATERIALS AND METHODS

### Study site

We conducted this study in KLEE plots at Mpala Research Centre (0°17' N, 36°52' E, 1800 masl) in Laikipia, Kenya. Kenya is a biodiversity hotspot, where keeping livestock plays an important role in livelihoods and culture (Sundaresan & Riginos, 2010). Rainfall at the site is weakly trimodal with a pronounced dry season from December to March. From 2001 to 2019, annual rainfall averaged 613 mm year<sup>-1</sup> (range: 421–1009 mm year<sup>-1</sup>, annual coefficient of variation: 27%). Rainfall totals over the March–May “wet season” prior to sampling were 393, 210, and 204 mm in 2018, 2019, and 2020, respectively (2018–2020 mean: 225 mm; Appendix S1: Figure S1). Soils are poorly drained vertisols with high clay content (>40%) known as “black cotton.” This type of soils are widespread across Africa and other vertisols cover >100 million hectares across the continent (Ahmad, 1996). The overstory of this savanna ecosystem is dominated by *Acacia drepanolobium* (syn. *Vachellia drepanolobium*, 97% of the canopy; Young et al., 1997), while five perennial grass species comprise 85% of herbaceous understory cover (Porensky et al., 2013). Mpala Research Centre is managed for both wildlife conservation and livestock production, where cattle are the main domestic animal. The grazing lands for livestock cover 80% of Kenya’s area and account for >12% of gross domestic product (Allan et al., 2017).

### Experimental design

The KLEE plots, established in 1995, use barriers to control access to 200 × 200 m (4-ha) treatment plots by three herbivore guilds in different combinations: wild megaherbivores (“M”, elephant and giraffe), wild mesoherbivores (“W”, 50–1000 kg), and cattle (“C”). There are three replicate blocks, each consisting of six treatments (18 plots in total): (1) “MWC” (accessed by megaherbivores, wild mesoherbivores, and cattle), (2) “MW” (accessed by megaherbivores and wild mesoherbivores), (3) “WC” (accessed by wild mesoherbivores and cattle), (4) “W” (accessed only by wild mesoherbivores), (5) “C” (accessed only by cattle), (6) “O” (excludes cattle, wild mesoherbivores, and megaherbivores). The treatment plots accessible to cattle are typically grazed by 100–120 mature Boran cows *Bos indicus* (sometimes with calves and/or bulls) for 2–3 days (2 h day<sup>-1</sup>) within a 2-week period, 3–4 times per year. The timing and number of grazing days depend on the availability of forage and reflect typical grazing regimes of ranches in the region, wherein

cattle graze in an area for several days before being moved to allow that area to recover.

Each of the treatment plots accessible to cattle (MWC, WC, C) contains a  $50 \times 50$  m (0.25-ha or 1/16 of the plot) subplot (established in 2008), in which the same cattle herd is grazed for a further 30 min following the initial 2-h grazing period in the wider plot to achieve an approximately five-fold increase in cattle stocking rate compared to the wider plot (Appendix S1: Figures S2 and S3). These three additional treatments are named: (1) MWCh, (2) WCh, and (3) Ch, where “h” denotes high cattle stocking rate. We note that “grazing” also involves trampling and nutrient cycling effects (Sitters et al., 2020). Grazing behavior can also be affected by the time of the day and the presence of other herbivores (Odadi et al., 2017). As cattle only access individual plots a few times per year, responses of most large wild herbivores are unlikely to be due to direct interaction with cattle or herders. Fire has not been used as a management tool in this ecosystem for over 50 years, and is rarely used by other ranches in the region. Natural-ignition fires have not occurred in decades. See Young et al. (1997, 2018) for further details of the experimental design.

## Data collection

To assess understory vegetation, we sampled herbaceous plants during May–August in 2018, 2019, and 2020. We measured aerial cover every 10 m by counting the number of pins of a 10-point pin frame (vertical pins separated by 5 cm) hit by each species (maximum one hit per pin per species). For the main six treatments (O, C, W, WC, MW, MWC), we sampled 10 transects each measuring  $100 \text{ m}^2$  within the central hectare of the 18 4-ha treatment plots, recording pin hits every 20 m for a total of 50 sites. We further subsampled pin hits and leaf versus stem hits for the five dominant species (*Brachiaria lachnantha*, *Themeda triandra*, *Pennisetum stramineum*, *Pennisetum mezianum*, and *Lintonia nutans*) by sampling four of 10 transects (second, fourth, sixth, and eighth transects) totalling 20 sites. For the  $50 \times 50$  m high cattle stocking rate subplots (Ch, WCh, MWCh), we ran four 40-m transects (leaving a 10-m buffer along two sides to minimize edge effects of the 4-ha plot), recording pin hits every 10 m for a total of 16 sites. Leaf versus stem pin hits were only recorded at eight sites (second and fourth transects).

To estimate total herbivory, we used camera traps. We deployed one Browning Strike Force HD Pro X camera in each of the 27 plots (three replicates of nine treatments) between 23 May 2019 and 26 May 2020. Cameras

were secured to a tree 80 cm above the ground, avoiding treeless glades that occur throughout the landscape, and ensuring a view unobstructed by woody vegetation within the detection zone. Cameras were programmed to take three images per trigger (1 s apart) with a 1-min delay between triggers. Cameras were checked every 2–3 weeks to download images, replace batteries, and ensure cameras were operational. Camera traps were operational for an average of 364 ( $\pm 2$  SE, range: 340–374) trap nights. Each camera’s detection area is  $275 \text{ m}^2$  calculated as  $(\text{detection angle} \times 360^{-1}) \times \pi \times \text{detection range}^2$ , where detection angle is in degrees and detection range in meters. For further details of the camera trap methodology, see Wells, Kirobi, et al. (2021). We calculated the total annual herbivory as

$$\sum \text{body mass} \times \text{number of individuals} \times \text{duration} \\ \times \text{detection area}^{-1} \times \text{trap night}^{-1} \times 365.25,$$

for each species where the duration is in hours (each image corresponds to 1 min). We included all 16 herbivore species heavier than 2 kg, which comprised of elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), plains zebra (*Equus quagga*), Grevy’s zebra (*Equus grevyi*), eland (*Taurotragus oryx*), buffalo (*Syn- cerus caffer*), hartebeest (*Alcelaphus buselaphus*), oryx (*Oryx beisa*), Grant’s gazelle (*Nanger granti*), impala (*Aepyceros melampus*), ostrich (*Struthio camelus*), duiker (*Sylvicapra grimmia*), steenbok (*Raphicerus campestris*), warthog (*Phacochoerus africanus*), hare (*Lepus* spp.), and cattle. Although the total herbivory metric was calculated for a single 12-month period, this period was representative of average annual rainfall at the site (Appendix S1: Figure S1).

## Statistical analyses

All statistical analyses were performed using R version 3.6.2 (R Core Team, 2019). To test how the understory plant community was responding to treatments and total herbivory, we assessed community composition and quantified plant diversity metrics (effective number of species, evenness, and dominance).

To assess herbaceous community composition, we performed an unconstrained ordination in the *boral* package version 1.9 (Hui, 2016) on relative abundance data by fitting a latent variable model (negative binomial with log-link, no fixed effects, and random effect of year), using Bayesian Markov Chain Monte Carlo (MCMC) parameter estimation. Model-based methods have several advantages over, and have been shown to outperform,

distance-based approaches to ordination, such as non-metric multidimensional scaling (Warton et al., 2015). We ran one MCMC chain of MCMC method for  $10^5$  iterations, and discarded the first  $10^4$  iterations as burn-in and thinned by removing one out of every 90 iterations for a total of 1000 posterior samples. We used very weakly informative priors with normal distributions, mean zero, and variance 10. We assessed model convergence by visualizing MCMC chain traces and using Geweke diagnostics (Hui, 2016) and ensured that residuals met model assumptions (Appendix S1: Figure S4). Prior to diversity and ordination analyses, species observed in <5% of samples (plots within years) were excluded (c.f., Veblen et al., 2016), leaving 51 taxa (48 species and three multi-species genera) of the original 81 taxa (78 species and three multi-species genera).

We used the *vegan* package version 2.5-6 (Oksanen et al., 2019) to calculate Shannon–Wiener diversity index,  $H'$ , which we converted to “effective number of species” (the number of equally likely elements needed to produce the diversity value,  $H'$ ) by taking  $\exp(H')$ , to facilitate interpretation (Jost, 2007). We calculated evenness by taking  $H'/H'_{\max}$ , and assessed dominance using the Berger–Parker dominance index,  $D$  (relative cover of the most abundant species; Berger & Parker, 1970).

To evaluate the individual and interactive effects of the presence of wild mesoherbivore, presence of megaherbivore, and cattle stocking rate on understory vegetation, we employed linear mixed-effects models (LMMs) to model the effects of herbivore treatment on (1) primary and secondary community ordination axes (latent variables 1 and 2); (2) absolute cover of species groups (life forms: grass, forb; life histories: annual, perennial); (3) species-specific relative cover; (4) species-specific and across-species leaf-to-stem ratio (leaf:stem); and (5) diversity metrics (effective number of species, evenness, and dominance). We implemented LMMs in the *glmmTMB* package version 1.0.1 (Brooks et al., 2017). To distinguish between individual and interactive effects of herbivore types, we coded cattle (none/moderate/high), wild mesoherbivores (presence/absence), megaherbivores (presence/absence), and interactive terms  $\text{cattle} \times \text{mesoherbivores}$  and  $\text{cattle} \times \text{megaherbivores}$  as fixed effects. Metrics derived from pin hits (absolute/relative cover) were scaled to correct for the unbalanced sampling effort; namely, (i) 16 versus 50 sampling locations in high cattle stocking rate and all other treatments, respectively, and (ii) subsampling of dominant species. We normalized the data of these metrics using square root transformation.

To evaluate the effects of total herbivory on understory vegetation, we used LMMs to test the relationship between total pin hits and the five sets of response variables of herbaceous plant as listed above. Second-order

polynomial functions were implemented when their fit had  $p < 0.05$ .

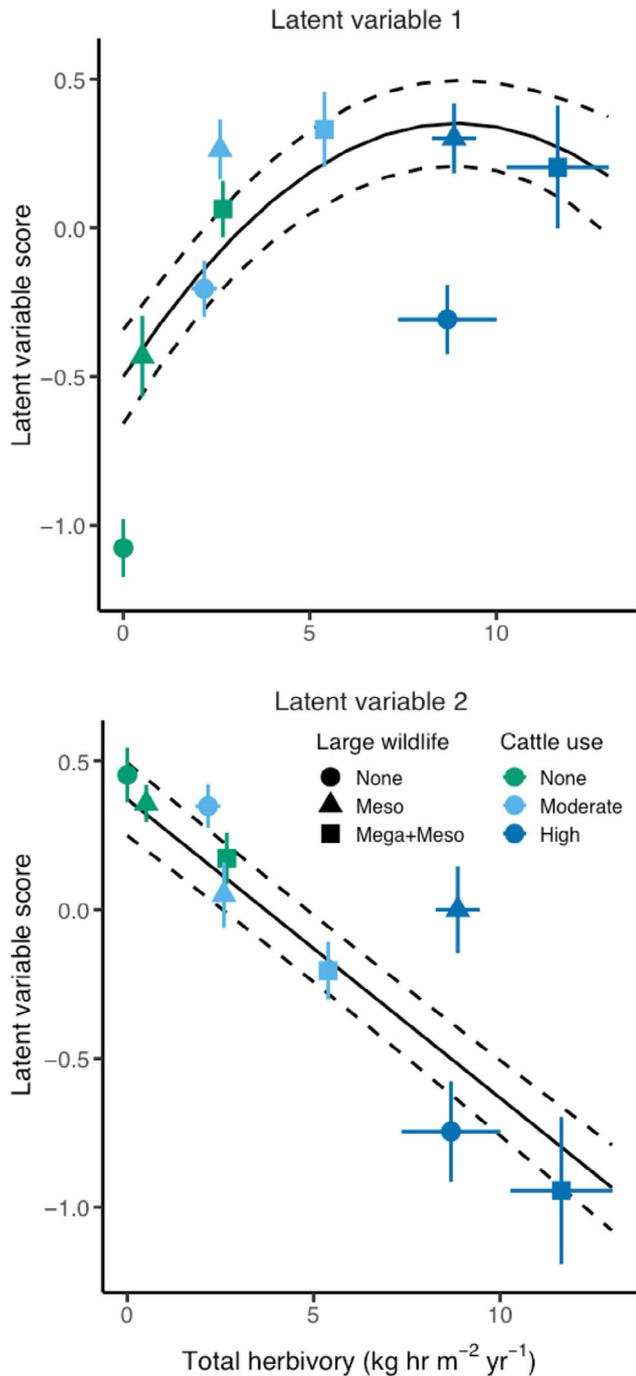
We performed model selection using Akaike’s information criterion (AIC) to compare herbivore-identity and total-herbivory approaches to modeling herbaceous plant responses. We compared LMMs for the following three predictors: (1) total herbivory using a linear or second-order polynomial function; (2) herbivore identity using the presence/absence of the three types of herbivore (cattle, wild mesoherbivores, and megaherbivores); (3) herbivore identity, as in model 2, but including cattle–mesoherbivore and cattle–megaherbivore interactions. In all LMMs, we coded block nested within year (2018/2019/2020) as the random effect. As we were comparing herbivore-identity and total-herbivory approaches to modeling herbaceous community composition, we did not explore the effects of the covariates included in each model.

## RESULTS

### Understory community composition is primarily shaped by herbivore identity, not total herbivory, at high cattle stocking rates

Understory community composition, represented by primary ordination axis (represented by latent variable 1) was affected by both herbivore treatments and total herbivory (Figure 1). The treatments without high cattle stocking rates showed a similar relationship with total herbivory to that reported by Veblen et al. (2016). However, two lines of evidence suggest that high cattle stocking rate, as included in the present study, was the principal driver of understory community composition. First, model selection showed that herbivore identity (presence/absence of herbivore types) was a more important predictor of herbaceous community composition (represented by latent variable 1) than total herbivory (Table 1). Second, treatments with high cattle stocking rates separated from other treatments in the ordination biplots, particularly along the secondary ordination axis, were largely driven by annual grasses (Figure 2). The primary and secondary ordination axes (represented by latent variables 1 and 2, respectively) explained 58% of the variation in herbaceous community composition and explained more of the variation of rarer species (Appendix S1: Figure S5).

The relative importance of herbivore identity and total herbivory varied across vegetation metrics. Total herbivory was a better predictor ( $\Delta\text{AIC} > 2$ ) of bare ground, leafiness (leaf:stem), evenness, absolute covers of annual and perennial forbs, and perennial grasses.



**FIGURE 1** Responses of understory herbaceous community composition represented by latent variable model ordination axes 1 and 2. Regressions of ordination axes on total herbivory (means  $\pm$  1 SE). Fitted means (solid lines) and standard errors (dashed lines) of linear mixed models ( $n = 81$ ). “Meso” = accessible to wild mesoherbivores (50–1000 kg); “mega” = accessible to megaherbivores (elephant, giraffe); “none” = no wild mesoherbivores/megaherbivores

Meanwhile, herbivore identity was a better predictor of total herbaceous cover, annual grass cover, the effective number of species, and dominance (Table 1). Detailed

statistical results are presented in Appendix S1: Tables S1 and S2.

### The effects of cattle and large wild herbivores on the understory community are non-additive

Megaherbivores moderated the effects of cattle on understory community composition at both moderate and high stocking rates (Figures 1 and 2). This was evidenced by the combined effects of cattle and megaherbivores on the primary ordination axis (represented by latent variable 1), being weaker than the sum of their individual effects (megaherbivores  $\times$  cattle, moderate:  $Z = -2.4$ ,  $p = 0.02$ , high:  $Z = -3.3$ ,  $p < 0.001$ ).

Bare ground was positively related to total herbivory and was minimal in the absence of cattle (Figure 3; Appendix S1: Table S2). The combined effects of cattle at high stocking rates and wild mesoherbivores increased bare ground 96% more than the sum of their individual effects (mesoherbivores  $\times$  cattle, high:  $Z = 2.8$ ,  $p = 0.004$ ). This led to over three times as much bare ground in the two treatments accessible to both mesoherbivores and cattle at high stocking rates compared to all other treatments. The total herbaceous cover was negatively related to total herbivory, exhibiting a quadratic response (Figure 3; Appendix S1: Table S2), but no interactive effects between domestic and wild herbivores on the total cover were detected (Appendix S1: Table S1).

Increasing total herbivory was associated with declines in absolute covers of perennial grasses, perennial forbs, and annual forbs (Figure 4a; Appendix S1: Table S2). Compared to the sum of their individual effects, the combined effects of cattle and wild mesoherbivores reduced perennial grass cover more (mesoherbivores  $\times$  cattle, high:  $Z = -3.0$ ,  $p = 0.003$ ) and perennial forb cover less (mesoherbivores  $\times$  cattle, high:  $Z = 6.3$ ,  $p < 0.001$ ; Figure 4a and Appendix S1: Figure S6). This led to 11% and 28% lower covers for perennial grasses and forbs, respectively, in the two treatments accessible to both wild mesoherbivores and cattle at high stocking rates compared to the seven other treatments. Species-specific treatment effects on the relative cover and its relationship with total herbivory for plant functional groups and the eight most common species are shown in Figure 4a and Appendix S1: Tables S1 and S2, Figure S7.

Understory leafiness (leaf:stem) exhibited a quadratic response to total herbivory, where leafiness increased under increasing herbivory when total herbivory was below  $5 \text{ kg h m}^{-2} \text{ year}^{-1}$ , but decreased as herbivory increased beyond that level. Interactive effects between cattle and wild mesoherbivores were evident in that

**TABLE 1** Model selection comparing total herbivory and herbivore identity (presence/absence [P/a] of herbivore types) as predictors of herbaceous community composition (represented by the ordination axes, latent variables 1 and 2), species diversity metrics (effective number of species, evenness, and dominance), bare ground, total aerial cover, covers of annual/perennial grasses/forbs, and leafiness (measured by leaf-to-stem ratio). The “TH/ID” column indicates whether “TH” for total herbivory or “ID” for herbivore identity was the more important predictor ( $\Delta AIC > 2$ );  $n = 81$

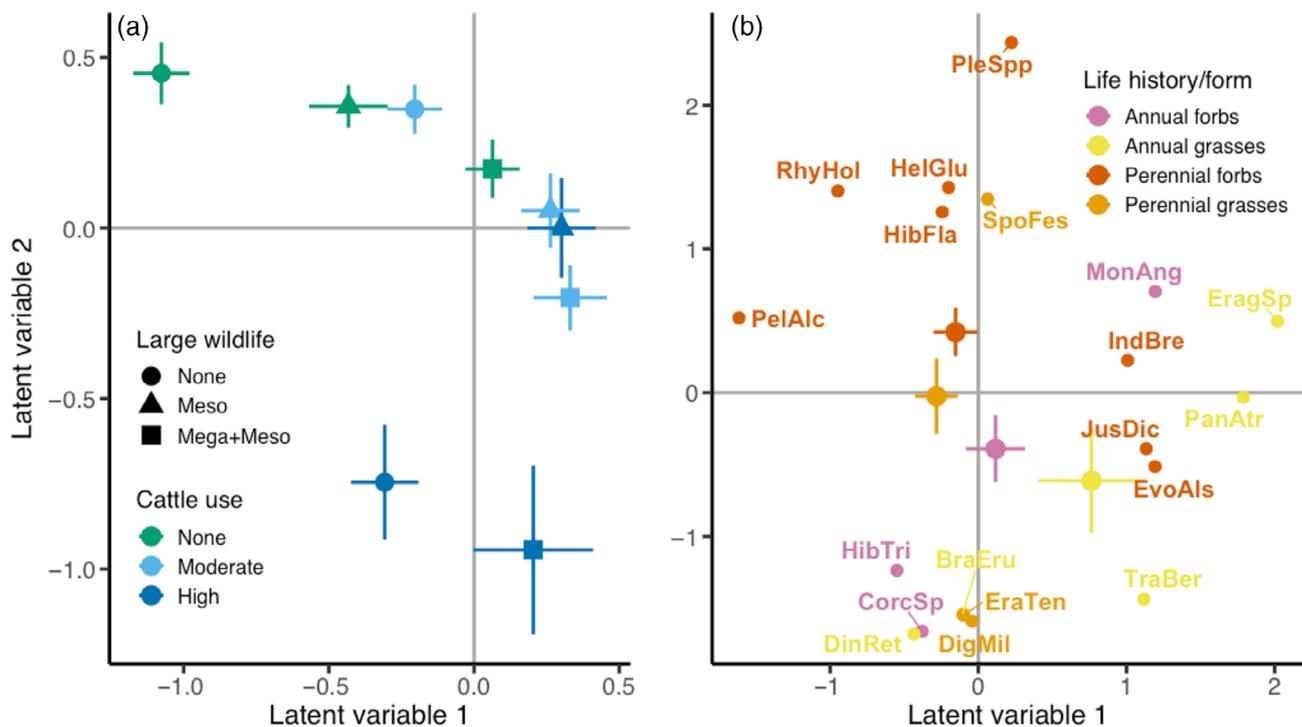
Variable	Model	df	AIC	TH/ID
Latent variable 1 (primary ordination axis)	$\sim \text{cattle}(P/A) \times \text{mega}(P/A) + \text{cattle}(P/A) \times \text{meso}(P/A) + (1 \text{year/block})$	9	55.2	ID
	$\sim \text{cattle}(P/A) + \text{mega}(P/A) + \text{meso}(P/A) + (1 \text{year/block})$	7	66.9	
	$\sim \text{poly}(\text{total herbivory}, 2) + (1 \text{year/block})$	6	116.3	
Latent variable 2 (secondary ordination axis)	$\sim \text{total herbivory} + (1 \text{year/block})$	5	99.5	TH
	$\sim \text{cattle}(P/A) + \text{mega}(P/A) + \text{meso}(P/A) + (1 \text{year/block})$	7	123.9	
	$\sim \text{cattle}(P/A) \times \text{mega}(P/A) + \text{cattle}(P/A) \times \text{meso}(P/A) + (1 \text{year/block})$	9	125.0	
Bare ground	$\sim \text{total herbivory} + (1 \text{year/block})$	5	472.6	TH
	$\sim \text{cattle}(P/A) + \text{mega}(P/A) + \text{meso}(P/A) + (1 \text{year/block})$	9	493.1	
	$\sim \text{cattle}(P/A) \times \text{mega}(P/A) + \text{cattle}(P/A) \times \text{meso}(P/A) + (1 \text{year/block})$	7	493.3	
Total cover	$\sim \text{cattle}(P/A) + \text{mega}(P/A) + \text{meso}(P/A) + (1 \text{year/block})$	7	690.5	ID
	$\sim \text{cattle}(P/A) \times \text{mega}(P/A) + \text{cattle}(P/A) \times \text{meso}(P/A) + (1 \text{year/block})$	9	691.4	
	$\sim \text{poly}(\text{total herbivory}, 2) + (1 \text{year/block})$	6	693.5	
Annual forbs absolute cover	$\sim \text{total herbivory} + (1 \text{year/block})$	5	131.6	TH
	$\sim \text{cattle}(P/A) + \text{mega}(P/A) + \text{meso}(P/A) + (1 \text{year/block})$	7	141.2	
	$\sim \text{cattle}(P/A) \times \text{mega}(P/A) + \text{cattle}(P/A) \times \text{meso}(P/A) + (1 \text{year/block})$	9	144.5	
Annual grasses absolute cover	$\sim \text{cattle}(P/A) + \text{mega}(P/A) + \text{meso}(P/A) + (1 \text{year/block})$	7	238.5	ID
	$\sim \text{cattle}(P/A) \times \text{mega}(P/A) + \text{cattle}(P/A) \times \text{meso}(P/A) + (1 \text{year/block})$	9	238.1	
	$\sim \text{total herbivory} + (1 \text{year/block})$	5	241.2	
Perennial forbs absolute cover	$\sim \text{poly}(\text{total herbivory}, 2) + (1 \text{year/block})$	6	242.4	TH
	$\sim \text{cattle}(P/A) \times \text{mega}(P/A) + \text{cattle}(P/A) \times \text{meso}(P/A) + (1 \text{year/block})$	9	256.4	
	$\sim \text{cattle}(P/A) + \text{mega}(P/A) + \text{meso}(P/A) + (1 \text{year/block})$	7	268.9	
Perennial grasses absolute cover	$\sim \text{total herbivory} + (1 \text{year/block})$	5	162.3	TH
	$\sim \text{cattle}(P/A) \times \text{mega}(P/A) + \text{cattle}(P/A) \times \text{meso}(P/A) + (1 \text{year/block})$	9	164.5	
	$\sim \text{cattle}(P/A) + \text{mega}(P/A) + \text{meso}(P/A) + (1 \text{year/block})$	7	165.0	
Leafiness (leaf-to-stem ratio)	$\sim \text{poly}(\text{total herbivory}, 2) + (1 \text{year/block})$	6	349.2	TH
	$\sim \text{cattle}(P/A) \times \text{mega}(P/A) + \text{cattle}(P/A) \times \text{meso}(P/A) + (1 \text{year/block})$	9	358.2	
	$\sim \text{cattle}(P/A) + \text{mega}(P/A) + \text{meso}(P/A) + (1 \text{year/block})$	7	366.7	
Effective number of species	$\sim \text{cattle}(P/A) \times \text{mega}(P/A) + \text{cattle}(P/A) \times \text{meso}(P/A) + (1 \text{year/block})$	9	278.8	ID
	$\sim \text{cattle}(P/A) + \text{mega}(P/A) + \text{meso}(P/A) + (1 \text{year/block})$	7	284.9	
	$\sim \text{poly}(\text{total herbivory}, 2) + (1 \text{year/block})$	6	289.6	

(Continues)

TABLE 1 (Continued)

Variable	Model	df	AIC	TH/ID
Evenness	$\sim \text{poly}(\text{total herbivory}, 2) + (1 \text{year/block})$	6	-204.4	TH
	$\sim \text{cattle}(P/A) \times \text{mega}(P/A) + \text{cattle}(P/A) \times \text{meso}(P/A) + (1 \text{year/block})$	9	-158.2	
	$\sim \text{cattle}(P/A) + \text{mega}(P/A) + \text{meso}(P/A) + (1 \text{year/block})$	7	-155.3	
Dominance	$\sim \text{cattle}(P/A) \times \text{mega}(P/A) + \text{cattle}(P/A) \times \text{meso}(P/A) + (1 \text{year/block})$	9	584.1	ID
	$\sim \text{total herbivory} + (1 \text{year/block})$	5	594.1	
	$\sim \text{cattle}(P/A) + \text{mega}(P/A) + \text{meso}(P/A) + (1 \text{year/block})$	7	601.0	

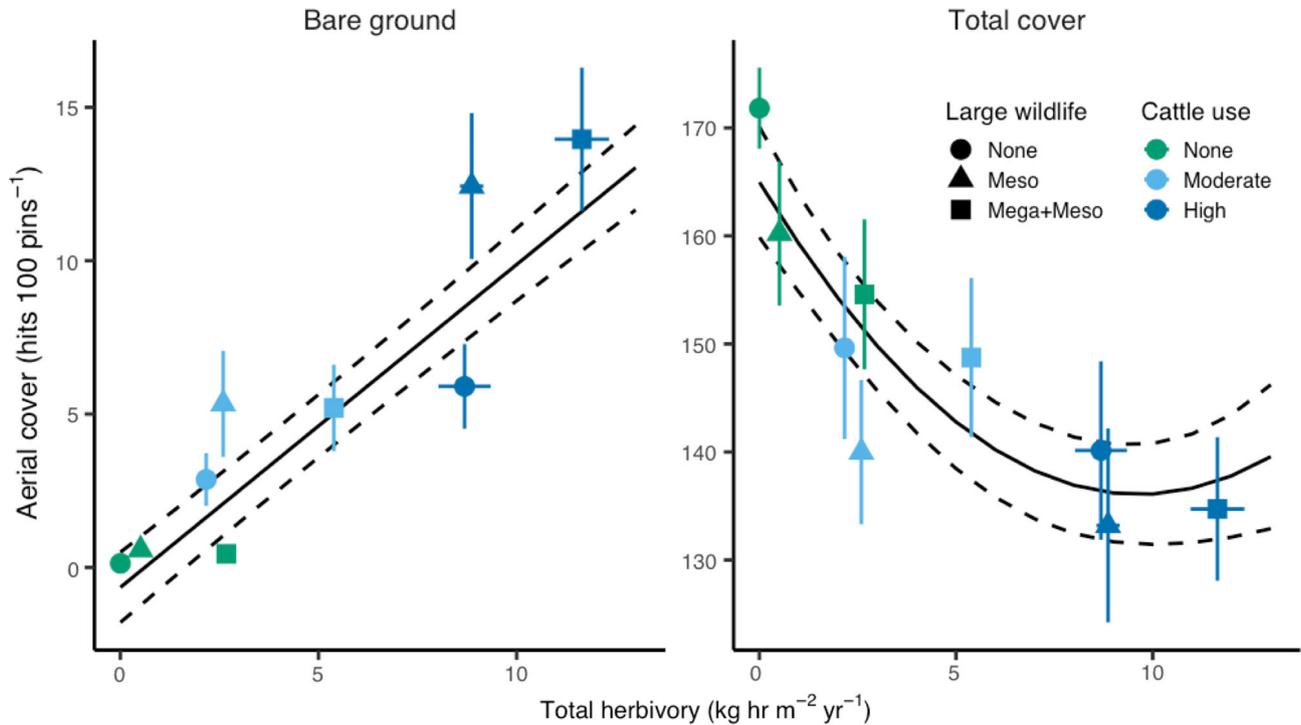
Abbreviation: AIC, Akaike's information criterion.



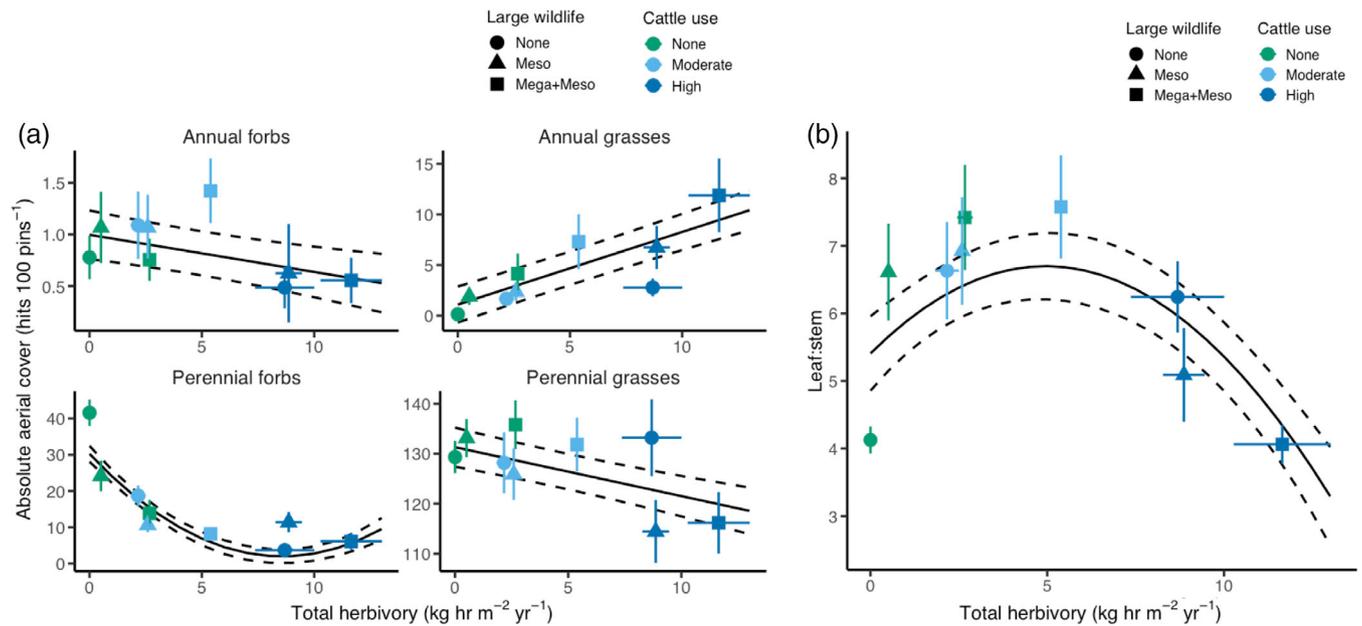
**FIGURE 2** Biplots of understory herbaceous community composition represented by latent variable model ordination axes 1 and 2. Treatments responses (a) and latent variable coefficients for species (smaller points) and life history and life form groups (b; larger points; means  $\pm 1$  SE). “Meso” = accessible to wild mesoherbivores (50–1000 kg); “mega” = accessible to megaherbivores (elephant, giraffe); “none” = no wild mesoherbivores/megaherbivores. Only species with coefficients  $> |1|$  for either latent variable are shown. BraEru = *Brachiaria eruciformis*, CorcSp = *Corchorus* sp., DigMil = *Digitaria milanjaniana*, DinRet = *Dinebra retroflexa*, EraTen = *Eragrostis tenuifolia*, EragSp = *Eragrostis* sp., EvoAls = *Evolvulus alsinoides*, HelGlu = *Helichrysum (Pseudognaphalium) glumaceum*, HibFla = *hibiscus flavifolius*, HibTri = *H. trionum*, IndBre = *Indigofera brevicalyx*, JusDic = *Justicia diclipteroideis*, MonAng = *Monsonia angustifolia*, PanAtr = *Panicum atosanguineum*, PelAlc = *pelargonium alchemilloides*, PleSpp = *Plectranthus* spp., RhyHol = *Rhynchosia holstii*, SpoFes = *Sporobolus festivus*, TraBer = *tragus bertonianus*

understory leafiness was increased by the combined effect of cattle and wild mesoherbivores less strongly than by the sum of their individual effects, at both moderate and high stocking rates (mesoherbivores  $\times$  cattle, moderate:  $Z = -2.2$ ,  $p = 0.04$ , high:  $Z = -3.6$ ,  $p < 0.001$ ; Figure 4b). Species-specific treatment effects on understory leafiness for the five most common species are shown in Appendix S1: Table S3, Figure S8.

Wild mesoherbivores and cattle had positively synergistic effects on understory diversity (measured as the effective number of species, evenness, and dominance), particularly at high stocking rates (Figure 5). The combined effects of wild mesoherbivores and cattle at high stocking rates on the effective number of species (mesoherbivores  $\times$  cattle, high:  $Z = 3.2$ ,  $p = 0.002$ ) and evenness (mesoherbivores  $\times$  cattle, high:  $Z = 4.3$ ,



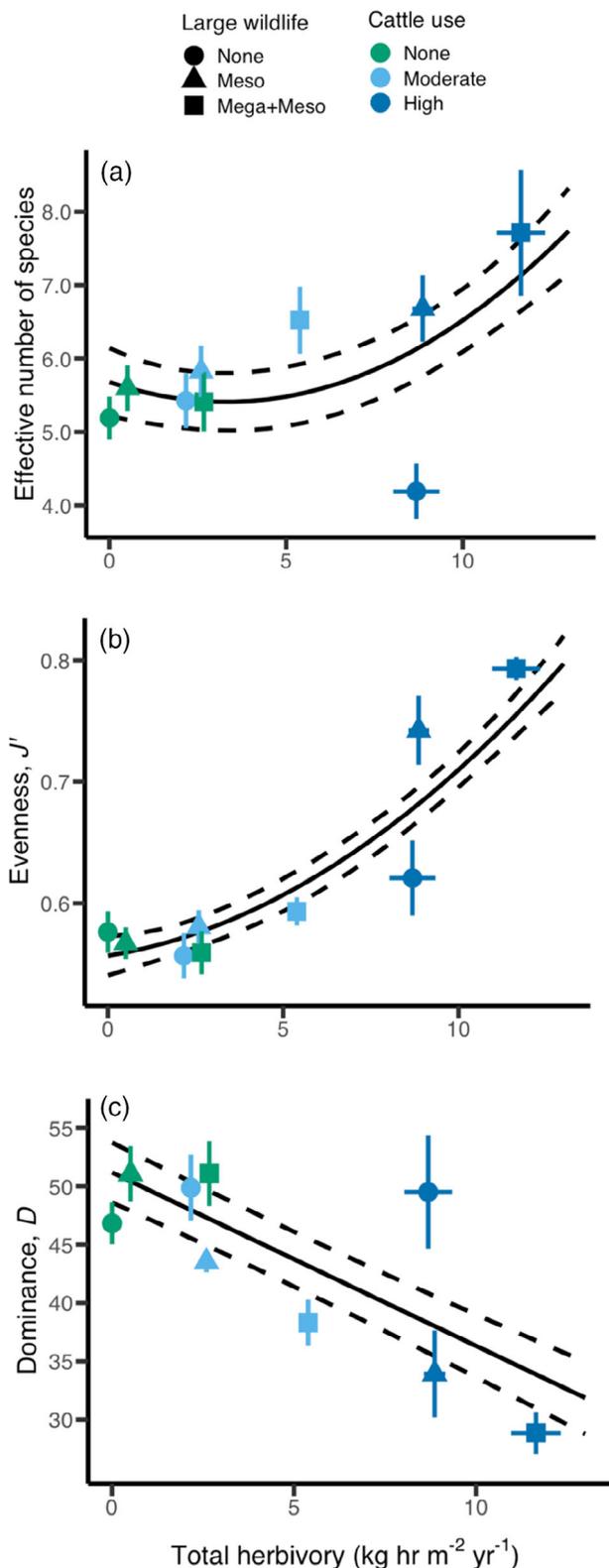
**FIGURE 3** Responses of total herbaceous cover and bare ground to treatments and total herbivory (means  $\pm$  1 SE). Fitted means (solid lines) and standard errors (dashed lines) of linear mixed models ( $n = 81$ ). “Meso” = accessible to wild mesoherbivores (50–1000 kg); “mega” = accessible to megaherbivores (elephant, giraffe); “none” = no wild mesoherbivores/megaherbivores



**FIGURE 4** Relationships between total herbivory and both herbaceous cover and “leafiness” (measured by leaf:Stem) of understory plants. Regressions of the absolute covers of annual forbs, annual grasses, perennial forbs, perennial grasses (a), and leaf:Stem (b) on total herbivory (means  $\pm$  1 SE). Fitted means (solid lines) and standard errors (dashed lines) of linear mixed models ( $n = 81$ ). “Meso” = accessible to wild mesoherbivores (50–1000 kg); “mega” = accessible to megaherbivores (elephant, giraffe); “none” = no wild mesoherbivores/megaherbivores

$p < 0.001$ ) of the herbaceous community was greater than the sum of their individual effects. This led to 32% (equivalent to almost two species) and 33% higher

diversity and evenness, respectively, in the two treatments accessible to both wild mesoherbivores and cattle at high stocking rates compared to the seven other



**FIGURE 5** Treatment responses and regressions on total herbivory for diversity (a, b), and Berger–Parker dominance (c; means  $\pm$  1 SE). Fitted means (solid lines) and standard errors (dashed lines) of linear mixed models ( $n = 81$ ). “Meso” = accessible to wild mesoherbivores (50–1000 kg); “mega” = accessible to megaherbivores (elephant, giraffe); “none” = no wild mesoherbivores/megaherbivores

treatments. The reduction of understory dominance by the combined effects of cattle and wild mesoherbivores was also stronger than the sum of their individual effects (mesoherbivores  $\times$  cattle, moderate:  $Z = -2.4$ ,  $p = 0.02$ , high:  $Z = -4.5$ ,  $p < 0.001$ ), leading to a 29% lower dominance in treatments accessible to both wild mesoherbivores and cattle than all other treatments.

## DISCUSSION

Although individual effects of large wild herbivores and livestock on herbaceous vegetation are well documented (Frank et al., 2016; Koerner et al., 2018; Pakeman et al., 2019; van der Plas et al., 2016; Porensky et al., 2016; Seymour et al., 2010; Staver et al., 2019), to our knowledge, this study provides the first experimental evidence of the separate and combined effects of wild herbivores and cattle at more than two stocking rates (i.e., more than simply presence versus absence) on vegetation. After 11 years of high cattle stocking rate treatments (24 years after the exclosures were established), the data showed that the understory community composition was primarily shaped by herbivore identity rather than total herbivory and the effects of cattle stocking rate interacted with the presence of large wild herbivores (mesoherbivores and megaherbivores). Wild mesoherbivores amplified the effects of high cattle stocking rates in terms of increasing bare ground and reducing perennial grass cover, while they tempered the positive effects of high cattle stocking rates on increasing understory leafiness. The quadratic response of leafiness to total herbivory suggests that forage quality peaks at intermediate herbivory. These changes in forage quantity and quality have important implications for both large wild herbivore conservation and cattle production. Understanding these non-additive interactions between cattle and large wild herbivores will aid in managing mixed-use rangelands and implementing ecological restoration and/or rewilding globally. Notably, the measured effects and interactions may differ in areas with different large wild herbivore assemblages or different spatio-temporal patterns of herbivory.

### Cattle at high stocking rates do not functionally replace large wild herbivores in shaping understory community composition

Herbivore identity was more important than total herbivory in explaining understory plant community composition when including high cattle stocking rates (Table 1).

Cattle at high stocking rates shifted the understory plant community in quantitatively different ways from large wild herbivores or moderate cattle stocking rates, and in ways that were not predicted by total herbivory alone (Figure 1). In a previous study of the same exclosure experiment that did not consider high cattle stocking rates, Veblen et al. (2016) concluded that cattle at moderate stocking rates functionally replace large wild herbivores, and that total herbivory was the primary driver of plant community composition. Our results are consistent with those of Veblen et al. (2016) when disregarding high cattle stocking rate treatments. However, our findings provide a strong caveat to those of Veblen et al. (2016), suggesting a threshold of cattle grazing intensity exists beyond which their impacts change, akin to thresholds documented in other rangelands (Bestelmeyer et al., 2015; Briske et al., 2003; Vetter, 2005). In other words, cattle stocked at moderate rates were able to mimic herbivory by the assemblage of large wild herbivores, but unique effects of cattle on understory community composition became apparent at high cattle stocking rates. As each herbivore species has a unique morphology and dietary profile (Table 1 in Veblen et al., 2016), albeit with some overlap (Kartzinel et al., 2015), increased prevalence of any one herbivore species, wild or domestic, may cause understory community composition to shift in ways that are not governed by total herbivory (Tóth et al., 2016). This suggests that an increase in the density of any single herbivore, domestic or wild, may shift understory plant communities in specific ways that are otherwise muted when the species is at moderate densities. Further research would be required to confirm this. However, at moderate stocking rates, the ability of cattle to mimic the effects of an assemblage of large wild herbivores on understory vegetation may also be because their relative consumption of grasses and forbs reflects the overall relative consumption of grasses and forbs by the grazers, mixed feeders, and browsers represented in the large wild herbivore assemblage.

### **Cattle stocking rate interacts with large wild herbivore accessibility to shape understory vegetation**

Under high cattle stocking rates, the negative effects of herbivory on forage quantity and quality were enhanced more than additively in the presence of wild mesoherbivores, as evidenced by more bare ground, lower perennial grass cover, and lower understory leafiness. Some understory community metrics also exhibited nonlinear relationships with total herbivory; relationships that are likely to share similar mechanisms to those

underlying interactive effects between cattle and large wild herbivores. For example, perennial forb cover was both nonlinearly related with total herbivory and reduced by high cattle stocking rates less in the presence of wild mesoherbivores (predominantly plains zebra *Equus quagga*; Figure 4a). These patterns are partly explained by perennial forbs (dominated by unpalatable *Helichrysum [Pseudognaphalium] glumaceum*) resisting further reductions in cover despite increased herbivore pressure (Appendix S1: Figure S7), possibly via compensatory growth or increased production of defensive chemicals that reduce palatability (Quintero & Bowers, 2013). Similarly, the relative cover of the palatable dominant perennial grass, *Brachiaria lachnantha*, decreased with total herbivory at a greater rate as herbivory increased (Appendix S1: Figure S7) and was impacted non-additively by interactions between cattle at high stocking rates and both wild mesoherbivores and megaherbivores. These patterns can be explained by (i) *B. lachnantha* being pushed beyond physiological thresholds as total herbivory was increased by wild and domestic herbivores (Appendix S1: Figure S7); or (ii) foraging behavior and dietary selectivity being altered by the presence of other herbivore species resulting in greater preference for *B. lachnantha* (Odadi et al., 2013).

The interactive effects between cattle at both moderate and high stocking rates and wild mesoherbivores on understory “leafiness” (leaf:stem) may be due to a combination of compensatory growth and differences in palatability between leaves and stems (Figure 4b). The positive effect of cattle on understory leafiness was dampened, where wild mesoherbivores were present. This suggests that herbivory of leaves (selected over stems due to greater palatability) by both wild and domestic animals begins to non-additively outweigh defoliation-enhanced leaf growth (McNaughton et al., 1983).

The interactions between cattle at high stocking rates and wild mesoherbivores in their effects on diversity (effective number of species and evenness; Figure 5) may, in part, be driven by herbivory-induced suppression of dominance (Koerner et al., 2018) and increased light availability (Borer et al., 2014). Globally, both of these are important determinants of understory species diversity in grasslands. Similarly, for annual grasses (Figure 4a), previous research suggests that such suppression of dominance can open up spaces that are subsequently colonized by non-dominant short-lived species such as annual grasses (Fynn & O’Connor, 2001; Porensky et al., 2013). Consequently, both diversity and annual grass cover may be influenced by the amount of bare ground. Cattle at high stocking rates increased bare ground non-additively, where mesoherbivores were present (Figure 3). This may have occurred because, beyond a

certain threshold of bare ground, animals (domestic and/or wild) increase their preference for bare patches for locomotion, exacerbating trampling, and/or bare patches become more difficult for plants to colonize. Dominance itself may be expected to rise with total herbivory as unpalatable species replace palatable species (Seymour et al., 2010; Vetter, 2005). However, more research is needed to test these hypothetical underlying processes and the relative influence of each component.

## Implications for management

Our findings echo those of other studies (Eldridge et al., 2016, 2018; Liu et al., 2015), highlighting the importance of considering the combined effects of domestic and wild herbivores, their identities, and their interactions in shaping understory plant communities in mixed-use rangelands. As understory community composition responded primarily to herbivore identity when high cattle stocking rates were included (Table 1), total herbivory by wild and domestic species may not be a useful predictor of herbaceous community composition when cattle densities are increased in mixed-use rangelands. Evidence of non-additive effects of cattle and large wild herbivores indicates that land managers must be mindful of interactive effects when adjusting cattle stocking rates. For example, in areas where wild mesoherbivores are present, increasing cattle stocking rates from moderate to high can lead to disproportionately lower the understory leafiness (Figure 4b) and more bare ground (Figure 3). Similarly, non-linear responses of understory community composition to total herbivory (Figure 1) indicate that the magnitude of the effect of increasing herbivore stocking rates depends on the existing level of herbivory.

When managing for understory diversity, increasing cattle stocking rates may increase or reduce diversity depending on the presence of large wild herbivores (Figure 5). While diversity declined when cattle were stocked at high rates in the absence of large wild herbivores, the combination of large wild herbivores and cattle at high stocking rates led to reduced dominance and increased species diversity and evenness. However, the plant species that benefitted most from this herbivore combination were annual grasses, mirroring other studies (Fynn & O'Connor, 2001; Porensky et al., 2013). Compared to perennial grasses, annual grasses in this system are less palatable, more ephemeral resource of forage, and less capable of resisting water erosion (Riginos & Herrick, 2010). Ultimately, our results suggest that cattle should preferably be stocked at moderate rates in mixed-use rangelands not only to minimize direct negative

impacts on large wild herbivores of conservation importance (Kimuyu et al., 2017), but also to avoid shifts in understory cover, community composition, forage quality, and soil erosion that are undesirable for both cattle production and conservation objectives. Importantly, our results support previous studies from this and other systems that suggest that moderate grazing by cattle does not cause effects that are unique or undesired by most land managers. However, there appears to be a threshold, between 2 and 10 kg h m<sup>-2</sup> year<sup>-1</sup> in our system (Appendix S1: Figure S3), at which the unique effects of a single species (in this case cattle) manifest in the understory plant community.

## ACKNOWLEDGMENTS

We thank Mpala Research Centre and its staff for logistical support. The KLEE plots were built and maintained by grants from the James Smithson Fund of the Smithsonian Institution (to A.P. Smith), The National Geographic Society (Grants 4691-91, 9106-12, and 9986-16), and the National Science Foundation (LTREB BSR 97-07477, 03-16402, 08-16453, 12-56004, 12-56034, and 19-31224). Funding for field equipment was received by H.B.M. Wells from The Rufford Foundation (Grant 27451-1) and the University of Leeds Centre for Climate's Climate Research Bursary Award. Additional financial support was provided through the Leeds Doctoral Scholarship to H.B.M. Wells. This research complies with the current laws of the country in which it was conducted (Kenya).

## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## AUTHOR CONTRIBUTIONS

Harry B. M. Wells, Lindsay C. Stringer, Andrew J. Dougill and Truman P. Young conceived and designed the methodology. Harry B. M. Wells collected and analyzed the data and led to the writing of the manuscript. Kari E. Veblen, Lauren M. Porensky, Corinna Riginos, Truman P. Young, Lindsay C. Stringer, and Andrew J. Dougill contributed critically to the drafts. All authors approved publication.

## DATA AVAILABILITY STATEMENT

Data (Wells, Porensky, et al., 2021) are available in Figshare: <https://doi.org/10.6084/m9.figshare.16615888.v3>.

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**How to cite this article:** Wells, Harry B. M., Lauren M. Porensky, Kari E. Veblen, Corinna Riginos, Lindsay C. Stringer, Andrew J. Dougill, Mathew Namoni, Jackson Ekedeli, and Truman P. Young. 2022. “At High Stocking Rates, Cattle Do Not Functionally Replace Wild Herbivores in Shaping Understory Community Composition.” *Ecological Applications* e2520. <https://doi.org/10.1002/eap.2520>