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RESEARCH ARTICLE

Wild and domestic savanna herbivores increase smaller vertebrate diversity, but less than additively

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Abstract

1. Cattle and other livestock graze more than a quarter of the world's terrestrial area and are widely regarded to be drivers of global biodiversity declines. Studies often compare the effects of livestock presence/absence but, to our knowledge, no studies have tested for interactive effects between large wild herbivores and livestock at varying stocking rates on small-bodied wild vertebrates.
2. We investigated the effects of cattle stocking rates (none/moderate/high) on the diversity of wildlife 0.05–1,000 kg using camera traps at a long-term exclosure experiment within a semi-arid savanna ecosystem in central Kenya. In addition, by selectively excluding wild 'mesoherbivores' (50–1,000 kg) and 'megaherbivores' (>1,000 kg; elephant and giraffe), we tested whether the presence of these two wild herbivore guilds (collectively, 'larger wild herbivores') mediates the effect of cattle stocking rate on habitat use and diversity of 'smaller wildlife' (mammals ranging between 10 and 70 cm shoulder height and birds).
3. Our results show that cattle enhance alpha diversity of smaller wildlife (with or without larger wild herbivore presence) and of all wildlife 0.05–1,000 kg (with or without megaherbivore presence), by altering vegetation structure. However, for smaller wildlife, this effect is less pronounced in the presence of larger wild herbivores, which also shorten grass. In the absence of cattle, mesoherbivore-accessible sites showed higher alpha diversity of smaller wildlife than sites excluding mesoherbivores.
4. Smaller wildlife habitat use was increased by high cattle stocking rates and wild mesoherbivores more in the presence of the other.
5. *Synthesis and applications*. Our findings imply that grazing, whether by livestock or wildlife, can enhance local savanna wildlife diversity. The biodiversity benefits of localised increases in herbivory are likely to be due to shortened grass and associated visibility improvements (for predator avoidance/foraging). This suggests

that land managers can increase local biodiversity by shortening grass, with wild or domestic herbivores (or both), at least in patches within a taller grass matrix.

KEYWORDS
biodiversity conservation, cattle stocking rate, ecological restoration, elephant, grazing intensity, livestock–wildlife interactions, savanna ecosystems, spatio-temporal heterogeneity

1 | INTRODUCTION

Over a quarter of the Earth's land surface is grazed by cattle and/or other domestic animals (Steinfeld et al., 2006). Livestock comprise >90% of the planet's non-human mammalian biomass (Bar-On et al., 2018). Wildlife populations are declining globally (Brondizo et al., 2019) and livestock grazing is generally considered to be detrimental to biodiversity (Asner et al., 2004; Crego et al., 2020). Across the world's rangelands, including African savannas, livestock continue to replace wildlife, potentially with negative impacts on ecosystem structure and function (du Toit & Cumming, 1999; Hempson et al., 2017). A global review showed that livestock grazing suppresses a broad spectrum of wild mammals and birds (Schieltz & Rubenstein, 2016). However, few of these studies considered mammals 1–50 kg, such as primates and suids, despite their conservation importance and potential to harbour zoonotic pathogens (Hoffman et al., 2017; Johnson et al., 2020). Although many studies investigating wildlife responses to livestock grazing have examined birds (e.g. Fletcher et al., 2010; Malm et al., 2020), examples from African ecosystems are uncommon (Ogada et al., 2008)—a general symptom of the paucity of research from the Global South. Crucially, there are few comparisons of multiple livestock stocking rates (Briske et al., 2011).

Another understudied but potentially important influence is that of large wild herbivores in shaping interactions between livestock and small-bodied wildlife. This could occur via trophic cascades, for example, the shortening of herbaceous vegetation by livestock can reduce prey species densities, resulting in suppression of predators (e.g. rodents and snakes; Keesing & Young, 2014). Wild herbivores of different sizes have distinctive effects on plant functional composition in savannas (van der Plas et al., 2016), and vegetation consumption by large wild herbivores can affect densities or habitat use of small-bodied wildlife (e.g. white rhinoceroses *Ceratotherium simum* benefitting impalas *Aepyceros melampus*, Cromsigt & te Beest, 2014). Small-bodied wildlife also respond to vegetation structure (e.g. birds; Duchardt et al., 2018), which is shaped by both domestic and large wild herbivores in mixed-use rangelands. In mixed-use systems, additive effects may occur where grazing by large wild herbivores amplifies the cattle grazing effect, as both herbivore types reduce the height and shift the composition of herbaceous vegetation (Veblen et al., 2016). In the case of small mammals that are suppressed by cattle grazing via herbaceous cover reduction, the effect of cattle stocking rates on small mammal habitat use would be dampened if large wild herbivores and cattle supress each other to such an extent that herbaceous cover is unchanged.

Alternatively, if wildlife responds to changes in tree density, the presence of ecosystem-engineering megaherbivores may mediate (enhance/buffer) the effect of cattle stocking rate by thinning the overstorey. Megaherbivores (e.g. elephant *Loxodonta africana*) can also buffer the negative impacts of cattle on wild ungulates (Kimuyu et al., 2017; Young et al., 2005), likely by altering cattle grazing behaviour (Odadi et al., 2011), which in turn impacts herbaceous vegetation, because cattle forage less when elephant are present (Veblen et al., 2016).

Our objectives were to investigate: (a) how cattle stocking rate affects alpha (local) diversity of wildlife 0.05–1,000 kg, and (b) whether cattle stocking rate effects on diversity and habitat use by smaller wild vertebrates (mammal and bird species 10–70 cm shoulder height [s.h.]) are mediated by the presence of 'mesoherbivores' (50–1,000 kg) and 'megaherbivores' (elephant and giraffe *Giraffa camelopardalis*)—collectively termed 'larger wild herbivores'. Such information can guide land management decisions that promote biodiversity in mixed-use rangelands, while maintaining productive and economically viable livestock systems to feed a growing human population.

2 | MATERIALS AND METHODS

2.1 | Study area

We conducted this study in the Kenya Long-term Exclosure Experiment (KLEE) plots at Mpala Research Centre (0°17′N, 36°52′E, 1,800 m a.s.l.) in Laikipia, Kenya, where livestock-keeping has long played an important role for livelihoods and culture. Rainfall at KLEE is weakly trimodal with a pronounced dry season December–March. Between 2001 and 2019, annual rainfall averaged 613 mm/year (range: 421–1,009 mm/year, inter-annual coefficient of variation: 27%). Soils are poorly drained vertisols with high clay content (>40%) known as 'black cotton'. Black cotton soils are widespread across Africa and, with other vertisols, cover >100 million hectares across the continent (Ahmad, 1996). The overstorey of this savanna ecosystem is dominated by *Acacia drepanolobium* (syn. *Vachellia drepanolobium*, 97% of the canopy; Young et al., 1998), while five perennial grass species comprise 85% of the herbaceous understorey (Porensky et al., 2013). Mpala Research Centre is managed for both wildlife conservation and livestock production. Cattle are the main domestic animal, stocked at moderate densities of 10–15 cattle/km^2 (Veblen et al., 2016). Livestock grazing lands cover 80% of Kenya's area and account for >12% of gross domestic product (Allan et al., 2017).

2.2 | Experimental design

The KLEE plots, established in 1995, use fences to control access to 200 × 200 m (4-ha) treatment plots by three herbivore types—wild mesoherbivores (50–1,000 kg, 'W'), megaherbivores (elephant and giraffe, 'M') and cattle ('C')—in different combinations. There are three replicate blocks, each consisting of six treatments (18 plots in total): (a) 'MWC' (accessed by megaherbivores, mesoherbivores and cattle), (b) 'MW' (accessed by megaherbivores and mesoherbivores), (c) 'WC' (accessed by mesoherbivores and cattle), (d) 'W' (accessed by mesoherbivores only), (e) 'C' (accessed by cattle only), (f) 'O' (excludes megaherbivores, mesoherbivores and cattle). Mesoherbivores are excluded from O and C plots by a 2.3-m tall 11-strand fence of alternating live and ground wires, the lowest (ground) wire being at ground level. This fence is easily permeable to species <70 cm s.h., but excludes ostriches *Struthio camelus*, and may partially exclude spotted hyaenas *Crocuta crocuta* and striped hyaenas *Hyaena hyaena* (both ≥70 cm s.h., but both caught on camera traps in O and C plots on few occasions). All species mass and height categories are based on mean adult body mass and shoulder heights, respectively, from Kingdon et al. (2013).

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 hr/day) within a 2-week period, three to four times per year. The timing and number of grazing days depends on forage availability and reflects 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. For these six treatments, we selected one of four 50 × 50 m (0.25-ha or 1/16 of the plot) subplots within the central hectare of each of the eighteen 4-ha treatment plots for wildlife and vegetation monitoring. In cattle-accessible plots, the subplot closest to the higher-cattle-stocking-rate subplots (described below) was selected to maximise comparability with moderate-cattle-stocking-rate plots, while subplots were randomly selected in plots excluding cattle (the experimental layout is illustrated in Figure S1).

Each of the treatment plots accessible to cattle (MWC, WC, C) contains a 50 × 50 m subplot at a corner/edge established in 2008. Here, the same cattle herd is grazed for a further 30 min following the initial 2-hr grazing period in the wider plot, to achieve an approximately fourfold increase in cattle stocking rate compared to the wider plot (Figure S2). These three additional treatments are named: (a) MWCh, (b) WCh and (c) Ch, where 'h' denotes high cattle stocking rate. We note that 'grazing' also involves trampling, which is a considerable cause of disturbance. Grazing behaviour can also be altered by time of day and the presence of other herbivores (Odadi et al., 2017). Because cattle only access individual plots a few times per year, responses of most wildlife 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, if at all. See Young et al. (1998) and Young et al. (2018) for further details of the experimental design.

2.3 | Data collection

To assess wildlife habitat use, between 23 May 2019 and 26 May 2020, we deployed one camera trap (Browning Strike Force HD Pro X) in each of the twenty-seven 50 × 50 m subplots (three replicates of nine treatments). Cameras were secured to a tree 80 cm above the ground, avoiding glades, and ensuring a view unobstructed by woody vegetation within the detection zone to eliminate detectability issues due to trees and shrubs. To avoid bias towards any particular species, we did not specifically target animal trails. 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 (±2 *SE*, range: 340–374) trap nights. Vegetation in the cameras' detection zones was not cleared. Although this increased false trigger rates, potential biases due to animals' attraction/repulsion towards clearing-induced shorter vegetation were avoided. Each camera's detection area is 275 m^2 (11% of the subplot area), calculated as: $(\textit{detection angle}*360^{-1})*\pi*(\textit{detection range})^2$, where detection angle is in degrees and detection range in metres.

We measured two covariates that could affect wildlife habitat use: grass height and tree density (Riginos & Grace, 2008; Soto-Shoender et al., 2018). Grass height was measured every 2–3 weeks in three locations within each camera's detection zone (2 m in front of the camera) using a Robel pole—the resulting metric correlates with grass biomass (Robel et al., 1970). The density of *A. drepanolobium* trees taller than 2 m was assessed in each of the 27 subplots using four 10 × 40 m belt transects. Because fence maintenance can influence tree density, we excluded a 10-m wide buffer on the two sides of subplots located in a corner of the 4-ha main plots and excluded an identical buffer in all other subplots. Images were managed using the CAMTRAPR package version 2.0.3 (Niedballa et al., 2016) in R version 3.6.2 (R Core Team, 2019).

2.4 | Data analyses

All statistical analyses were performed in R. We excluded all domestic species and all wild species that comprised fewer than five detections per 100 trap nights, to avoid biases induced by very rare species. This left 27 species, of which 25 (93%) were 0.05–1,000 kg (i.e. excluding elephant and giraffe; Table 1; Figure S3). We used the VEGAN package version 2.5-6 (Oksanen et al., 2019) to calculate Shannon–Wiener diversity (H'), which we converted to

TABLE 1 Phylogenetic and dietary characteristics of wildlife species recorded in this study in sufficient numbers for analysis (for full list, see Figure S3)

Type	Common name	Scientific name	Order	Family	Diet
Mega-herbivores ($n = 2$)	African elephant	*Loxodonta africana*	Proboscidea	Elephantidae	Mixed feeder
	Giraffe	*Giraffa camelopardalis*	Artiodactyla	Giraffidae	Browser
Meso-herbivores ($n = 6$)	Plains zebra	*Equus quagga*	Perissodactyla	Equidae	Grazer
	Common eland	*Taurotragus oryx*	Artiodactyla	Bovidae	Mixed feeder
	Beisa oryx	*Oryx beisa*	Artiodactyla	Bovidae	Grazer
	Hartebeest	*Alcelaphus buselaphus*	Artiodactyla	Bovidae	Grazer
	Grant's gazelle	*Nanger granti*	Artiodactyla	Bovidae	Mixed feeder
	African buffalo	*Syncerus caffer*	Artiodactyla	Bovidae	Grazer
	Common ostrich	*Struthio camelus*	Struthioniformes	Struthionidae	Omnivore
Smaller mammals ($n = 9$)	Common duiker[a]	*Sylvicapra grimmia*	Artiodactyla	Bovidae	Browser
	Steenbok[a]	*Raphicerus campestris*	Artiodactyla	Bovidae	Browser
	Common warthog[a]	*Phacochoerus africanus*	Artiodactyla	Bovidae	Grazer
	Cape hare[a]	*Lepus capensis*	Lagomorpha	Leporidae	Grazer
	Olive baboon[a]	*Papio anubis*	Primate	Cercopithecidae	Omnivore
	Northern lesser galago (bushbaby)[a]	*Galago senegalensis*	Primate	Galagidae	Omnivore
	Serval[a]	*Leptailurus serval*	Carnivora	Felidae	Carnivore
	Black-backed jackal[a]	*Canis mesomelas*	Carnivora	Canidae	Omnivore
Birds ($n = 9$)	Helmeted guineafowl[a]	*Numida meleagris*	Galliformes	Numididae	Omnivore
	Crested francolin[a]	*Dendroperdix sephaena*	Galliformes	Phasianidae	Omnivore
	Yellow-necked francolin[a]	*Pternistis leucoscepus*	Galliformes	Phasianidae	Omnivore
	Cattle egret[a]	*Bubulcus ibis*	Pelecaniformes	Areidae	Insectivore
	Black-bellied bustard[a]	*Lissotis melanogaster*	Otidiformes	Otididae	Omnivore
	Buff-crested bustard[a]	*Lophotis gindiana*	Oditiformes	Otididae	Omnivore
	Superb starling[a]	*Lamprotornis superbus*	Passeriformes	Sturnidae	Insectivore
	Northern white-crowned shrike[a]	*Eurocephalus ruppelli*	Passeriformes	Laniidae	Insectivore
Larger carnivores ($n = 2$)	Spotted hyaena	*Crocuta crocuta*	Carnivora	Felidae	Carnivore
	Striped hyaena	*Hyaena hyaena*	Carnivora	Felidae	Omnivore

[a]'Smaller wildlife' = mammal and bird species 10–70 cm shoulder height able to access all treatments unimpeded.

'effective number of species' by taking $exp^{H'}$ (Jost, 2007). Treatment effects on the effective number of species were investigated for these 25 species 0.05–1,000 kg (only for the six treatments accessible to wild mesoherbivores) and for 16 species whose access to O, C and Ch subplots appears unaffected by the 11-strand fence that excludes larger wild herbivores. We term these 16 species (all 10–70 cm s.h.) 'smaller wildlife'. We use shoulder height to define smaller wildlife because warthogs *Phacochoerus africanus* (65 cm s.h., 70 kg) have a larger body mass than taller species excluded by the 11-strand fence (e.g. Grant's gazelle *Nanger* (*Gazella*) *granti*, 85 cm s.h., 52 kg). Habitat use by larger mammals (>50 kg; zebra *Equus quagga*, eland *Taurotragus oryx*, oryx *Oryx beisa*, hartebeest *Alcelaphus buselaphus*, Grant's gazelle, elephant, giraffe) has already been investigated at this site using dung surveys (Kimuyu et al., 2017). Therefore, we focussed particularly on two groups of wildlife whose responses to herbivore treatments are difficult to capture using dung surveys: (a) 'smaller mammals' (defined here as species 10–70 cm s.h.; distinguished from small mammals, because some species are relatively large e.g. warthogs), (b) 'birds' (bird species <50 kg living/foraging primarily on the ground that trigger camera traps). A third group, 'larger carnivores' (spotted and striped hyaena), was excluded from analyses due to potential fence permeability effects.

Images taken 1 hr apart were treated as independent detections (Soto-Shoender et al., 2018). To evaluate the effects of treatments and environmental covariates (grass height and *A. drepanolobium* density) on wildlife habitat use, we employed beta-distributed generalised linear mixed models using the glmmTMB package version 1.0.1 (Brooks et al., 2017). Prior to modelling, habitat use was standardised and rescaled by converting independent detections per trap night, first to an open unit interval (0,1) by taking $y' = (y - a)^*(b - a)^{-1}$, where a and b are the minima and maxima, respectively, from the data, then compressing to remove 0s and 1s by taking $y'' = [y'(N - 1) + 0.5]*N^{-1}$, where N is the sample size (Smithson & Vercuilen, 2006). We examined proportional effects in the rescaled standardised data, which do equal the proportional effect in the unscaled values.

To separate the individual and interactive effects of herbivore types, we coded the interaction terms mesoherbivores(yes/no)*cattle(none/moderate/high) and megaherbivores(yes/no)*cattle(none/moderate/high) as fixed effects. In order to assess intra-annual dynamics (i.e. month effects), we coded grass height*month as fixed effect and plot as a random effect to account for temporal non-independence. When analysing treatment effects on all species groups combined, species-nested-within-plot (to account for repeated measures when averaging monthly) or block (to account for spatial block effects when averaging annually) were coded as random effects. A Gaussian linear mixed model was employed to test treatment effects on grass height, crossing treatment effects with month and coding plot as a random factor to account for temporal non-independence. Analysis of variance (ANOVA) was used to test treatment effects on *A. drepanolobium* density. When using Gaussian models, we visually checked normality and homoscedasticity of residuals. We did not perform model selection. Herbaceous vegetation can influence detectability, so we also ran the diversity and habitat use analyses on a subset of the data (December 2019 to January 2020) when grass height was not significantly affected by treatments (cattle, moderate, $Z = -1.5$, $p = 0.14$, high, $Z = -0.33$, $p = 0.74$; mesoherbivores, $Z = -0.65$, $p = 0.52$; megaherbivores, $Z = -1.5$, $p = 0.12$). We also analysed smaller mammal habitat use and responses to vegetation after excluding carnivores (servals *Leptailurus serval*, jackals *Canis mesomelas*) to assess their influence (Table S1).

3 | RESULTS

We recorded a total of 6,672 independent detections of 49 mammal and bird species (45 wild and four domestic) over 9,841 trap nights. Among the 27 wildlife species that each accounted for greater than five detections per 100 trap nights, 25 species (0.05–1,000 kg; 75% of total detections; $n = 4{,}972$) remained after excluding megaherbivores. The 16 smaller wildlife species (53% of total detections; $n = 3{,}527$) represented a wide range of phylogenetic and dietary characteristics (Table 1).

3.1 | Species diversity

Considering all 25 wildlife species 0.05–1,000 kg, alpha diversity (effective number of species) increased by 18% (equivalent to more than two species, $Z = 2.31$, $p = 0.02$) and 26% (more than three species, $Z = 3.26$, $p = 0.001$) in moderate- and high cattle stocking rate plots respectively (Figure 1). Compared to plots excluding cattle and larger wild herbivores, diversity of the 16 small-bodied wild species 10–70 cm s.h. (i.e. excluding ostrich, striped hyaena and spotted hyaena) was 55% higher (almost four species, $Z = 4.49$, $p < 0.001$) in plots with high cattle stocking rates, but not significantly higher in plots with moderate cattle stocking rates ($Z = 1.69$, $p = 0.09$). Compared to plots excluding cattle and larger wild herbivores, plots accessible to wild mesoherbivores had 25% (equivalent to at least one species, $Z = 1.99$, $p = 0.05$) more diverse communities of smaller wildlife, but the effect of megaherbivores was not significant ($Z = 1.58$, $p = 0.11$). For the December–January subset (which accounts for grass-induced detectability issues), the effects of moderate cattle stocking rates ($Z = 0.06$, $p = 0.95$)

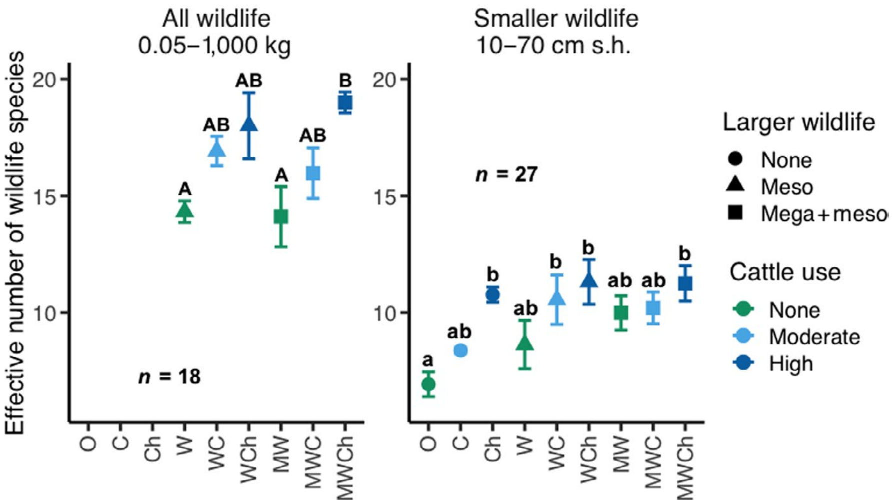

FIGURE 1 Diversity (effective number of species) responses to treatments for all wildlife 0.05–1,000 kg and smaller wildlife [10–70 cm shoulder height (s.h.)] able to access all treatments unimpeded ($M \pm 1$ SE). ‘C’ = only cattle allowed (moderate); ‘Ch’ = only cattle allowed (high); ‘W’ = wild mesoherbivores allowed; ‘M’ = megaherbivores (elephant, giraffe) allowed; ‘O’ = cattle, mesoherbivores and megaherbivores excluded. Beta-distributed linear mixed models (species groups modelled separately): *habitat use* ~ $M*C + W*C + (1|Block)$. Treatments sharing letters are not significantly different ($p > 0.05$) based on Tukey's post hoc tests. The Tukey results indicate that significant pairwise differences in smaller wildlife diversity were not detected between the eight treatments accessible to cattle and/or larger wild herbivores

and mesoherbivores ($Z = 0.26$, $p = 0.79$) were not significant, but high cattle stocking rates still increased smaller wildlife diversity (effective number of species) by 60% (three species, $Z = 2.62$, $p = 0.01$; Table S2).

Alpha diversity was negatively correlated with grass height (wildlife 0.05–1,000 kg, $Z = -4.41$, $p < 0.001$; wildlife 10–70 cm s.h., $Z = -3.12$, $p = 0.002$; Figure 2) but not significantly correlated with *A. drepanolobium* density (wildlife 0.05–1,000 kg, $Z = 1.59$, $p = 0.11$; wildlife 10–70 cm s.h., $Z = -0.58$, $p = 0.56$).

3.2 | Wildlife habitat use

Habitat use of smaller wildlife (smaller mammals and birds) was not significantly affected by cattle alone (moderate, $Z = 1.53$, $p = 0.13$; high, $Z = -0.32$, $p = 0.75$) or wild mesoherbivores alone ($Z = 0.36$, $p = 0.72$), but was increased 60% more in plots accessible to both mesoherbivores and cattle (high) than expected by summing their individual effects (mesoherbivores × scattle, high, $Z = 2.36$, $p = 0.02$; Figure 3). There were no significant treatment effects for December–January (Table S2).

Similarly, smaller mammal habitat use was not significantly affected by cattle (moderate, $Z = 1.53$, $p = 0.13$; high, $Z = -0.32$, $p = 0.75$), wild mesoherbivores ($Z = 0.36$, $p = 0.72$) or megaherbivores ($Z = -1.90$, $p = 0.06$) but, during December–January, was significantly reduced by megaherbivores ($Z = -4.34$, $p < 0.001$) and cattle at high stocking rates ($Z = -3.66$, $p < 0.001$). Smaller mammal habitat use was impacted more positively in plots accessible to both wild mesoherbivores and cattle (high) than expected by summing their individual effects (mesoherbivores × cattle, high, overall, 298%, $Z = 2.20$, $p = 0.03$; December–January, 155%, $Z = 0.81$, $p = 0.001$). The effect of high cattle stocking rates on ground bird habitat use was not significant overall ($Z = 1.84$, $p = 0.06$) or during December–January ($Z = 0.67$, $p = 0.50$). Habitat use by birds peaked over the 2 months following cattle use (Figure 4).

Species-specific treatment responses are illustrated in Figure S4 and Table S3.

3.3 | Vegetation

Grass was significantly shorter in plots grazed by cattle at different time-scales at moderate stocking rates (averaged monthly, 33%

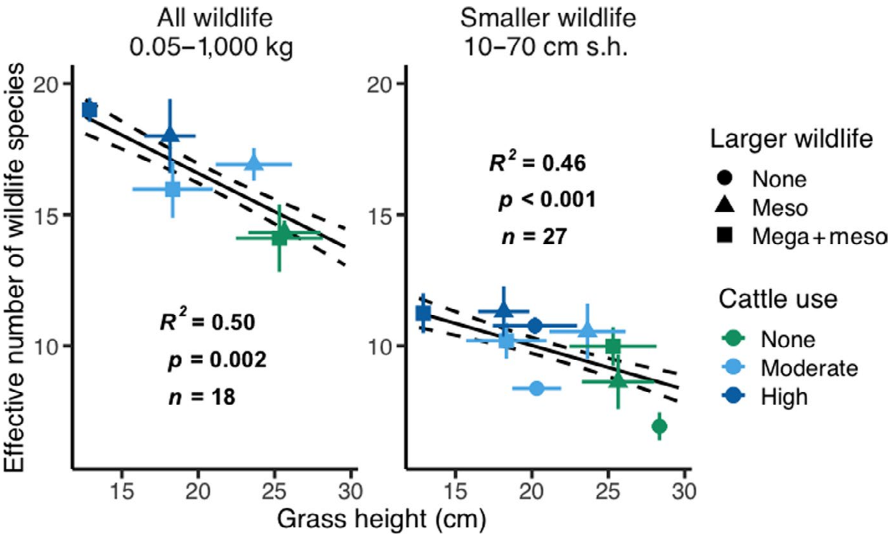

FIGURE 2 Diversity (effective number of species) correlations with annually averaged grass height for all wildlife 0.05–1,000 kg and smaller wildlife [10–70 cm shoulder height (s.h.)] able to access all treatments unimpeded ($M \pm 1$ *SE*). Fitted means (solid lines) and standard errors (dashed lines) of Gaussian linear mixed models (species groups modelled separately): *diversity ~ grass height* + (1|*Block*). R^2 = marginal R^2. 'Meso' = accessible to wild mesoherbivores (50–1,000 kg); 'Mega' = accessible to megaherbivores (elephant, giraffe); 'None' = no wild mesoherbivores/megaherbivores

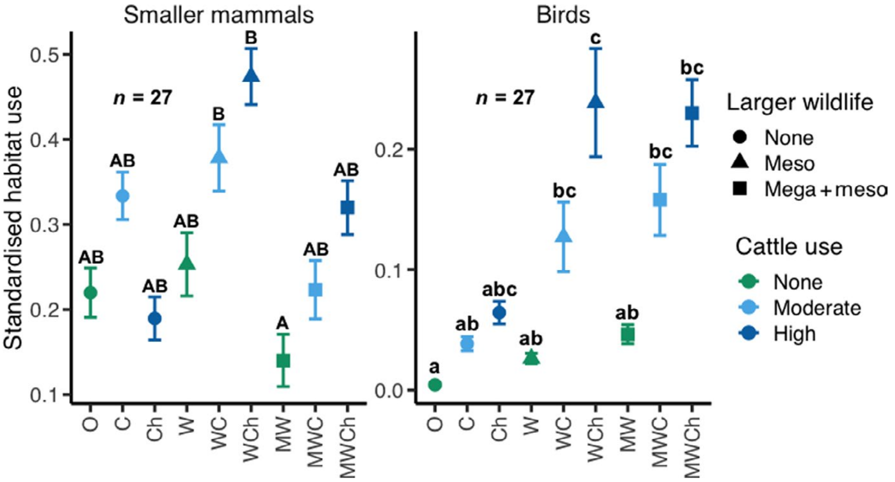

FIGURE 3 Treatment effects on species group habitat use ($M \pm 1$ *SE*; scales differ). Habitat use is standardised and rescaled by converting images per trap night to an open unit interval (0,1) then compressing to remove 0s and 1s. 'C' = only cattle allowed (moderate); 'Ch' = only cattle allowed (high); 'W' = wild mesoherbivores allowed; 'M' = megaherbivores (elephant, giraffe) allowed; 'O' = cattle, mesoherbivores and megaherbivores excluded. Beta-distributed linear mixed models (species groups modelled separately): *habitat use ~ M*C + W*C* + (1|*Block*). Treatments sharing letters are not significantly different ($p > 0.05$) based on Tukey's post hoc tests

or 11 cm, $Z = -3.10$, $p = 0.002$; averaged annually, 28% or 8 cm, $Z = -3.39$, $p < 0.001$) and high stocking rates (averaged monthly, 54% or 18 cm, $Z = -5.14$, $p < 0.001$; averaged annually, 30% or 9 cm, $Z = -3.65$, $p < 0.001$). Similarly, grass was significantly shorter in plots accessible to wild mesoherbivores when averaged monthly (23% or 8 cm, $Z = -2.18$, $p = 0.03$) but not annually (10% or 3 cm, $Z = -2.18$, $p = 0.21$). Monthly averaged grass height was reduced in plots accessible to cattle and megaherbivores more than expected based on

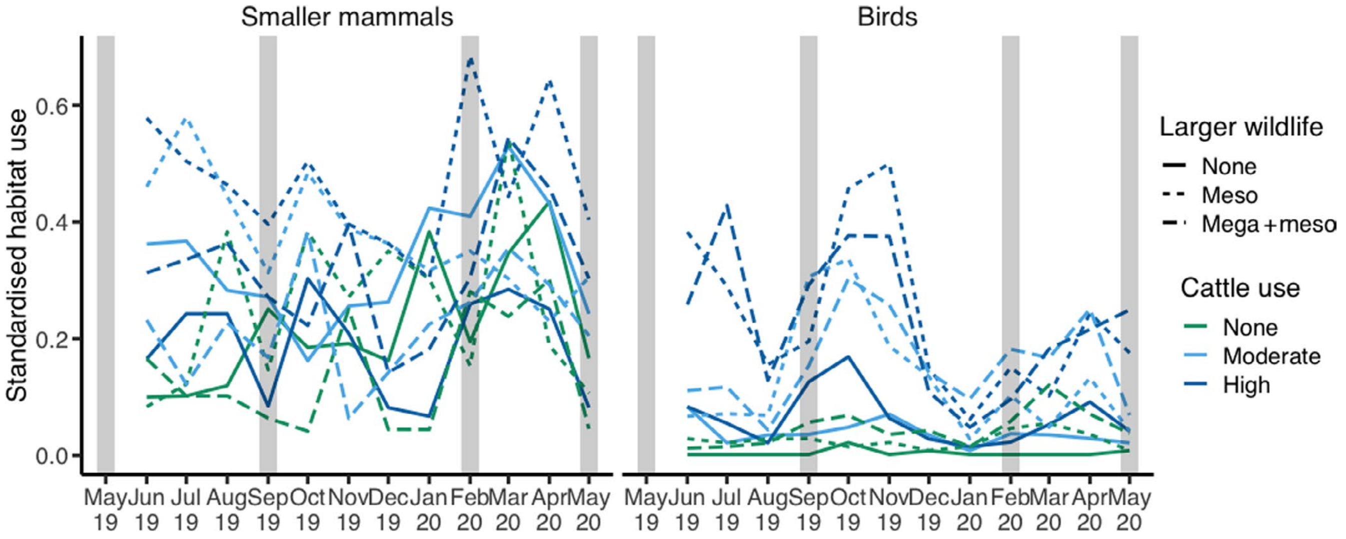

FIGURE 4 Monthly mean habitat use by treatment for four species groups. Habitat use is standardised and rescaled by converting images per trap night to an open unit interval (0,1) then compressing to remove 0s and 1s. Grey bars indicate cattle grazing events. 'Meso' = accessible to wild mesoherbivores (50–1,000 kg); 'Mega' = accessible to megaherbivores (elephant, giraffe); 'None' = no wild mesoherbivores/megaherbivores

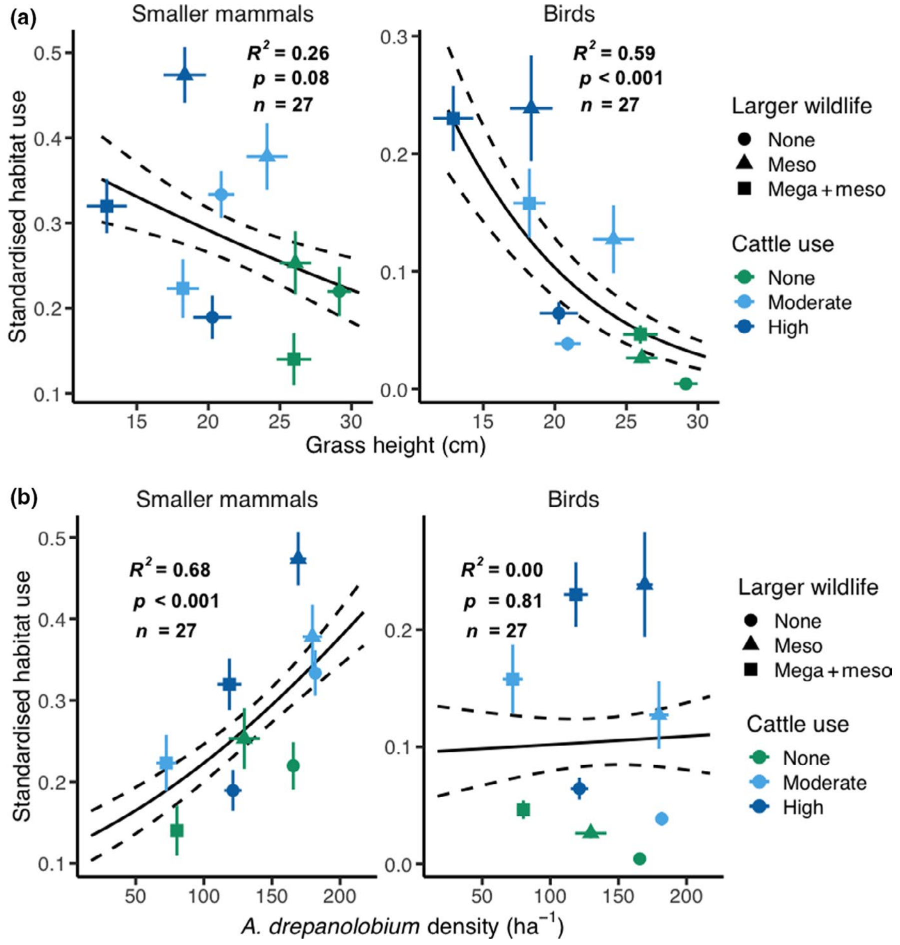

FIGURE 5 Species group habitat use correlations with annually averaged grass height (a) and *Acacia drepanolobium* density (b) ($M \pm 1$ *SE*; scales differ). Habitat use is standardised and rescaled by converting images per trap night to an open unit interval (0,1) then compressing to remove 0s and 1s. Fitted means (solid lines) and standard errors (dashed lines) of beta-distributed linear mixed models (species groups modelled separately): *habitat use ~ grass height* + (1|*Block*). R^2 = marginal R^2. 'Meso' = accessible to wild mesoherbivores (50–1,000 kg); 'Mega' = accessible to megaherbivores (elephant, giraffe); 'None' = no wild mesoherbivores/megaherbivores

summing their individual effects, at both moderate and high cattle stocking rates (megaherbivores × cattle, moderate, 46% or 15 cm, $Z = -3.07$, $p = 0.03$; high, 35% or 12 cm, $Z = -2.35$, $p = 0.02$). These relationships were not significant when averaging annually (megaherbivores × cattle, moderate, 20% or 6 cm, $Z = -1.68$, $p = 0.09$; high, 18% or 5 cm, $Z = -1.56$, $p = 0.12$).

Acacia drepanolobium density was reduced 29% by megaherbivores ($F = 9.06$, $p = 0.008$), but not significantly affected by cattle ($F = 0.18$, $p = 0.83$) or wild mesoherbivores ($F = 0.02$, $p = 0.88$). Only 19% of the variation in tree density was related to treatments, while over 60% of the variation in grass height was explained by treatments.

3.4 | Vegetation correlates of wildlife habitat use

Across all smaller wildlife (smaller mammals and birds), habitat use declined with increasing grass height when averaged monthly ($Z = -3.58$, $p < 0.001$) or over the entire year ($Z = -6.60$, $p < 0.001$). The statistical significance of this relationship depended on temporal scale in smaller mammals (monthly: $Z = -2.81$, $p = 0.01$, annual: $Z = -1.76$, $p = 0.08$) and birds (monthly: $Z = -5.10$, $p < 0.001$, annual: $Z = -4.93$, $p < 0.001$; Figure 5a).

Habitat use across all smaller wildlife was positively correlated with *A. drepanolobium* density ($Z = 2.13$, $p = 0.03$). *Acacia drepanolobium* density was positively correlated with smaller mammal habitat use ($Z = 3.98$, $p < 0.001$), but did not significantly correlate with ground bird habitat use ($Z = 0.24$, $p = 0.81$; Figure 5b).

Species-specific responses to vegetation are illustrated in Figure S5 and Table S4.

4 | DISCUSSION

We present experimental evidence that cattle at moderate and high stocking rates increase alpha diversity of wildlife 0.05–1,000 kg. Both cattle (at high and, to a lesser extent, moderate stocking rates) and larger wild mammalian herbivores (mesoherbivores and, to a lesser extent, megaherbivores) increase diversity and, in some cases, habitat use of smaller wildlife (10–70 cm s.h.). These effects on smaller wildlife may be due to factors such as increased visibility and predator avoidance (due to altered vegetation structure) and/or trophic cascades.

A trade-off exists between predation risk and food availability in savannas. Larger bodied species are less vulnerable to predation (Hopcraft et al., 2012) and, for smaller species, shorter grass can lower predation risk by increasing visibility (Riginos, 2015). This may explain the preference for more heavily grazed plots by smaller mammals and birds. Similarly, preference by ostriches for treatments with megaherbivore-induced tree density loss may also reflect predation avoidance (we assume that the effects of megaherbivores are primarily due to elephant because giraffe do not feed on the herbaceous layer and have a comparatively minor effect on tree density).

Trophic cascades may also be responsible for the preference of cattle treatments by birds (Dennis et al., 2008), particularly cattle egrets (*Bubulcus ibis*), galliforms and passerines. Birds' responses to grazing are well known to be species- and site-specific, often mimicking that of small mammals but, contrary to our findings, most studies show that grazing suppresses gallinaceous birds (Briske et al., 2011). The preference by omnivorous/insectivorous bird species for higher-cattle-stocking-rate plots in this study may be due to greater success catching invertebrates due to visibility or more abundant invertebrates attracted by increased cattle dung. Cattle egrets' habitat use unsurprisingly coincided with cattle (and buffalo *Syncerus caffer*) presence. By contrast, habitat use by galliforms (helmeted guineafowl *Numida meleagris*, crested francolin *Dendroperdix sephaena*, yellow-necked francolin *Pternistis leucoscepus*) peaked over the 2 months following cattle use (Figure 4), when herbaceous vegetation is beginning to respond to October rainfall, but before grass height peaks in December–January (Figure S6). As their activity peak does not coincide with the months of shortest grass, our results suggest that galliforms are tracking seeds or invertebrates proliferating in cattle plots in response to vegetation growth. A global review suggests that grazing tends to reduce arthropod diversity (due to unintentional predation/disturbance, reduced resource base and changes in vegetation), but can increase arthropod diversity if benefits of grazing-induced heterogeneity compensate for the overall decrease in resources (van Klink et al., 2015). The high cattle stocking rate effect on diversity and habitat use of smaller wildlife persisted during December–January, suggesting that the positive effects of grazing are not solely due to detectability effects of grass height, but also suggests that diversity and habitat use are responding in a lagged way to short grass in preceding months.

Our results also show that the effects of cattle and wild mesoherbivores on smaller wildlife diversity are less than additive, so the impacts of each are less in the presence of the other. Wild mesoherbivores (and to a lesser extent megaherbivores) increase alpha diversity of smaller mammals, but less so where cattle are present, particularly at high cattle stocking rates. Similarly, cattle increase smaller mammal diversity, but less so in the presence of wild mesoherbivores (and megaherbivores). The general pattern of wildlife dampening the effects of cattle mirrors the trend of elephant mitigating the effects of cattle in this system (Kimuyu et al., 2017; Sitters et al., 2020).

Correlations between grass height/tree density and diversity/habitat use suggest that vegetation structure plays an important role in mediating treatment effects on smaller vertebrates. The importance of vegetation structure has also been demonstrated for small-bodied wildlife elsewhere (e.g. birds, Duchardt et al., 2018). The observed contrasting responses of steenboks *Raphicerus campestris* and duikers *Sylvicapra grimmia* (also black-bellied bustard *Lissotis melanogaster* and buff-crested bustard *Lophotis gindiana*) to grass height and tree density, demonstrate that even sympatric morphologically and functionally similar species can show differing responses to the same environmental variables.

Other factors can influence wildlife habitat use in savannas, including soil and foliar nutrient content. Cattle grazing can reduce soil carbon/nitrogen and grass nitrogen—effects that are reversed by megaherbivore presence over the long term (Sitters et al., 2020). Soil and foliar nutrients are also well known to be influenced by tree canopies (Sitters et al., 2020), but we were not able to test the influence of soil/foliar nutrients as we did not measure these variables. There are several other limitations of the experiment, such as restricted range of soil, vegetation and cattle stocking rate gradients, as well as grass-induced detectability issues. We attempted to address detectability issues by analysing the December–January subset, which gave similar results in general for diversity. The negative effects of high cattle stocking rates and megaherbivores on smaller mammal habitat use during December–January suggest that these two effects may be masked by grass-induced detectability effects. The degree of influence of other biases, such as observed patterns being restricted to this particular time of year, is unclear.

While the KLEE has demonstrated that cattle generally suppress other large herbivores via forage reduction (Kimuyu et al., 2017), our results suggest that smaller vertebrates may be more sensitive to structural differences in vegetation induced by wild and domestic herbivores. The effects of grazing may also depend on whether it enhances spatio-temporal heterogeneity, the importance of which has been recognised in rangelands (Fynn et al., 2016). The study design generates heterogeneity at different scales by creating areas of taller/shorter grass and higher tree density than the surrounding matrix, while creating smaller shorter grass areas within the main 4-ha plots through high cattle use. More heavily grazed patches may offer better foraging opportunities, refugia from predators and ease of locomotion, only within a matrix of taller grass habitat with higher prey abundance.

To our knowledge, this study provides the first experimental evidence that larger wild herbivores (mesoherbivores and megaherbivores) mediate the effects of cattle stocking rate on alpha diversity and habitat use of smaller wild vertebrates. Our results demonstrate that grazing, whether by cattle (at both moderate and high stocking rates) or larger wild herbivores, can increase alpha diversity of smaller wildlife (10–70 cm s.h.) in savannas, at least at small spatial scales. Consequently, savanna rangeland managers may be able to increase the diversity of wildlife (particularly smaller vertebrates) through grazing by domestic or wild herbivores. The positive effects of grazing on local wildlife diversity may depend on the state of the surrounding habitat. This work also has implications beyond tropical savannas. The role of larger wild herbivores in mediating livestock grazing effects will be an important consideration in rewilding efforts globally, where livestock cohabit with reintroduced wildlife.

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AUTHORS' CONTRIBUTIONS

H.B.M.W., T.P.Y., A.J.D. and L.C.S. designed the methodology; H.B.M.W. collected and analysed the data and led the writing of the manuscript; H.B.M.W., D.M.K., W.O.O., T.P.Y., A.J.D. and L.C.S. contributed critically to the drafts. All the authors approved for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.7m0cfxpsw (Wells et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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