ARTICLE

Wild herbivores and cattle have differing effects on postfire herbaceous vegetation recovery in an African savanna

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Abstract

Fire and herbivory have profound effects on vegetation in savanna ecosystems, but little is known about how different herbivore groups influence vegetation dynamics after fire. We assessed the separate and combined effects of herbivory by cattle and wild meso- and megaherbivores on postfire herbaceous vegetation cover, species richness, and species turnover in a savanna ecosystem in central Kenya. We measured these vegetation attributes for five sampling periods (from 2013 to 2017) in prescribed burns and unburned areas located within a series of replicated long-term herbivore exclosures that allow six different combinations of cattle and wild meso- and megaherbivores (elephants and giraffes). Vegetation cover (grasses, mainly) and species richness were initially reduced by burning but recovered by 15–27 months after fire, suggesting strong resilience to infrequent fire. However, the rates of recovery differed in plots accessible by different wild and domestic herbivore guilds. Wildlife (but not cattle) delayed postfire recovery of grasses, and the absence of wildlife (with or without cattle) delayed recovery of forbs. Herbivory by only cattle increased grass species richness in burned relative to unburned areas. Herbivory by cattle (with or without wildlife), however, reduced forb species richness in burned relative to unburned areas. Herbivory by wild ungulates (but not cattle) increased herbaceous species turnover in burned relative to unburned areas. Megaherbivores had negligible modifying effects on these results. This study demonstrates that savanna ecosystems are remarkably resilient to infrequent fires, but postfire grazing by cattle and wild mesoherbivores exerts different effects on recovery trajectories of herbaceous vegetation.

KEYWORDS
cattle–wildlife interaction, exclosures, fire–herbivory interaction, grass/forb balance, prescribed burning, pyrodiversity, species turnover

INTRODUCTION

African grassland and savanna ecosystems are among the most flammable ecosystems in the world (Ramo et al., 2021) and support the largest aggregations and greatest diversity of large mammalian herbivores in the world, including both domestic and native ungulates. In these ecosystems, fire and herbivory are widely recognized as the major top-down regulators of vegetation structure and composition (Anderson, 2006; Bond & Keeley, 2005; Carpio et al., 2015; Milchunas et al., 1988; Rutherford & Powrie, 2013; Van Beest et al., 2010; Van Langevelde et al., 2003). Informed by the long history of fire and grazing in African savannas (Anderson, 2006; Milchunas et al., 1988; Van Langevelde et al., 2003), fire and herbivory prescriptions have become important management interventions in these systems (Odadi et al., 2017; Trollope, 2011). As a result, both the separate and interactive effects of fire and herbivory have been extensively studied (e.g., Allred et al., 2011; Anderson, 2006; Bodí et al., 2014; Charles et al., 2017; Eby et al., 2014; Edwards et al., 2010; Fuhlendorf et al., 2009; Laclau et al., 2002; Porensky, Bucher, et al., 2013; Scheiter et al., 2012; Starns et al., 2020; Van Coller et al., 2018).

The effects of fire and large mammalian herbivores in savannas are especially profound within the herbaceous layer. These effects can be analogous in many ways (Bond & Keeley, 2005), though there are also fundamental, important differences (Archibald & Hempson, 2016). For example, both drivers may open microsites for the establishment of otherwise uncommon plants (especially forbs) by removing rank (grass) growth (Olff & Ritchie, 1998; Porensky, Wittman, et al., 2013; Riginos et al., 2018), which also increases net productivity (Charles et al., 2017; Eby et al., 2014). On the other hand, herbivores are more selective consumers than fire and may favor growth of nonpalatable plants at the expense of more palatable species (Van Beest et al., 2010; Veblen & Young, 2010).

In addition, these drivers often interact with each other through complex feedback loops to influence vegetation dynamics (Collins & Calabrese, 2012; Holdo et al., 2009; Midgley et al., 2010; Novellie & Kraaij, 2010; Starns et al., 2020). For example, the high-quality regrowth and reduced cover in previously burned areas attract herbivores (pyric herbivory) due to improved pasture quality and reduced perceived predation risk (Eby et al., 2014; Kimuyu et al., 2017; Riginos & Grace, 2008; Sensenig et al., 2010). This intensifies grazing pressure and nutrient cycling in burns, sometimes maintaining pastures in a productive, short-cropped, highly nutritive state long after fire (Ainalis et al., 2006; Archibald & Hempson, 2016; Aremu et al., 2007). Intensive herbivory in previously burned areas may also slow down or even arrest biomass recovery (resilience) in both woody (LaMalfa et al., 2019; Raffaele et al., 2011; Silva et al., 2014) and grass-dominated ecosystems (Archibald, 2008; Donaldson et al., 2018; Starns et al., 2020; Yoganand & Owen-Smith, 2014), thereby reducing the frequency and intensity of subsequent fires (Starns et al., 2020). While demonstrations of these feedback loops have become an important part of ecological literature, our understanding of how these interactions persist through time and affect ecosystem resilience is limited to just a few studies (Collins & Calabrese, 2012; Midgley et al., 2010; Novellie & Kraaij, 2010; Starns et al., 2020).

Even less studied is how relationships between fire, herbivory, and ecosystem resilience are dependent upon different herbivore groups. Even though domestic and wild ungulates share many savannas and other grass-dominated rangeland ecosystems, we do not know how these different ungulate guilds, individually and in combination, influence postfire vegetation structure and species richness and species turnover. Such information is critical for predicting the ecological consequences of removal or loss (local extirpation or extinction) of different herbivore species or guilds from fire-prone/fire-dependent savanna landscapes and their replacement with livestock.

Here, we report our investigations into the separate and combined effects of cattle and wild ungulates on recovery of herbaceous vegetation cover and changes in species richness and species turnover in a multiuse savanna ecosystem in central Kenya. For the purposes of this study, we define the "recovery" of a burned subplot as the attainment of pasture conditions similar to those in the unburned control subplots. We hypothesized that, because attraction of ungulates to burned areas should reinforce the initial effects of fire on vegetation, it would take longer for herbaceous vegetation to recover in burned plots that are accessible to herbivores than burned plots where herbivores are excluded. Second, we hypothesized that postfire grazing by both wildlife and cattle would slow recovery more than grazing by either cattle or wildlife alone. Lastly, we hypothesized that, since cattle movement is controlled by herders while wildlife movement is largely ad libitum, their grazing in the burned plots would have dissimilar effects on herbaceous vegetation.

METHODS

Study area

The study was conducted in the Kenya Long-term Exclosure Experiment (KLEE) located at Mpala Research Centre (MRC) in Laikipia County, Kenya

(0°17′ N, 37°52′ E). The 20,000-ha MRC integrates wildlife conservation with livestock production. The area has a semiarid climate with an average annual rainfall of 550–600 mm. The rainfall pattern is weakly trimodal, with a distinct dry season in December–March. The average monthly rainfall records at the study plot during the study period are as shown in Appendix S1: Figure S1. The study site is underlain with high clay "black cotton" soil (vertisol). Vegetation structure is classified as wooded savanna, with *Acacia drepanolobium* accounting for 97% of woody cover (Young et al., 1997). The understory vegetation is relatively homogeneous and is dominated by five grass species: *Pennisetum mezianum*, *P. stramineum*, *Themeda triandra*, *Lintonia nutans*, and *Brachiaria lachnantha* (Young et al., 1997). Common forbs in the system include *Helichrysum* (*Pseudognaphalium*) sp., *Aspilia pleuriseta*, *Commelina* spp., and *Solanum* spp. (Supplement 1 in Porensky, Bucher, et al., 2013).

Native large mammalian herbivore species at the study site include two megaherbivores, elephant (*Loxodonta africana*) and reticulated giraffe (*Giraffa camelopardalis reticulata*), and a rich mesoherbivore fauna: plains zebra (*Equus quagga*), Grevy's zebra (*Equus grevyi*), Grant's gazelle (*Gazella granti*), buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*), hartebeest (*Alcelaphus buselaphus*), oryx (*Oryx beisa*), bush duiker (*Sylvicapra grimmia*), and steinbuck (*Raphicerus campestris*). Cattle (*Bos indicus*), the predominant domestic herbivore in this system, occur at a greater biomass density than wild herbivores and graze the landscape episodically through rotational herding (Charles et al., 2017; Veblen et al., 2016; Wells et al., 2022). Stocking density of cattle at MRC has ranged between 0.1 and 0.2 cattle ha^{-1} (Odadi et al., 2007).

Experimental design

The KLEE design consists of eighteen 4-ha plots with semipermeable barriers that allow or exclude different combinations of cattle (C), wild mesoherbivores (W: hereafter mesoherbivores, 15–1000 kg; duiker and steinbuck and smaller herbivores not excluded); and wild megaherbivores (M: hereafter megaherbivores). In total, there are six herbivore treatments, each of which is replicated over three experimental blocks. The treatments are as follows: (1) plots excluding all herbivores >15 kg ("O"); (2) plots allowing only cattle access ("C"); (3) plots accessible to only mesoherbivores ("W"); (4) plots allowing access by both cattle and mesoherbivores ("WC"); (5) plots allowing access by mesoherbivores and megaherbivores ("MW"); and (6) plots accessible to mesoherbivores, megaherbivores, and cattle ("MWC").

For details on the KLEE experimental design, see Young et al. (1997).

Cattle are regularly herded into the designated KLEE plots (i.e., C, WC, and MWC) three to four times per year. During each cattle run, 100–120 head of cattle are herded in each of these plots for 2 h for 2–3 days depending on forage availability. These cattle runs are designed to reflect the moderate stocking rates at MRC and similar properties across our study region (Odadi et al., 2007). This grazing regime reflects typical livestock management strategies for the region where cattle graze the landscape episodically through individual herding of herds of similar size, with residence time in each location being determined by forage availability (Veblen et al., 2016). To maintain similar cattle-stocking rates between burned and unburned areas during cattle runs, cattle access to each burned subplot was limited to ~2% of the total time they accessed each herbivory treatment plot, similar to the proportion of the burned subplot area in the whole plot area (Odadi et al., 2017). However, cattle-feeding rate during these cattle runs was expected to be greater in burned than unburned areas (Odadi et al., 2017). Wildlife visitation and use of burns and nonburns was ad libitum, and the trends that have been documented through camera traps (Odadi et al., 2017).

In each of the 18 KLEE herbivory treatment plots, a 30 × 30-m subplot was subjected to controlled burning during February–March 2013 (described in detail in Kimuyu et al., 2014). In addition, for each of the 18 herbivory treatment plots, a 30 × 30-m area was demarcated in the unburned matrix for use as a control (nonburn) subplot. Both the burned and nonburned subplots were located in areas with similar tree density and size structure. We avoided areas with known sources of heterogeneity, such as termite mounds and old livestock enclosure sites.

Data collection

We sampled herbaceous vegetation once in June–July 2012 (prior to the burns in early 2013), and thereafter every June–July of each year from 2013 to 2017 (3, 15, 27, 29, and 51 months after burn). For each fire treatment subplot, we placed a 10-point pin frame at each of three equally spaced sampling stations along each of three 25-m line transects located 5 m apart (nine frames, 90 pins per subplot). We recorded the total contacts on each pin with herbaceous vegetation by each species ("pin hits"). We used the pin-hit data to estimate aerial cover (as number of hits per pin), species richness, and turnover. An earlier study in KLEE (Veblen et al., 2016) has shown that the number of pin hits is strongly

correlated with herbaceous biomass, so our pin-hit data are a good representative of actual herbaceous biomass.

We analyzed total grass cover and total forb cover both combined and separately but could not attribute the effects of the mesoherbivore treatment on the vegetation (or individual plant species) to the different species within the mesoherbivore guild. The diverse mesoherbivore community is composed of species with different dietary niches, yet only proximally assessed (Kartzinel et al., 2015), and in any case, herbivores were excluded as groups in some of the KLEE treatments. We note that giraffes do not feed on vegetation less than 0.5 m from the ground (Young & Isbell, 1991), so the megaherbivore effects on herbaceous vegetation can be attributed to elephants.

Our estimation of species turnover accounted for species abundance distributions in measuring the compositional change over time (Hallett et al., 2016). Calculations of species turnover were implemented using the codyn package version 20.5 (Hallett et al., 2016).

Statistical analysis

We analyzed herbaceous vegetation cover (pin hits) and species richness using generalized linear mixed models (GLMMs) in the glmmTMB package (Brooks et al., 2017) and species turnover using linear mixed models (LMMs) with the "lmer" function in the LmerTest package (Kuznetsova et al., 2017). For both GLMMs and LMMs, we specified fire treatment (burn vs. nonburn), herbivory treatment (O, W, MW, C, WC, and MWC), and time since burning (i.e., June–July surveys conducted in 2013 [3 months after fire], 2014 [15 months after fire], 2015 [27 months after fire], 2016 [39 months after fire], and 2017 [51 months after fire], and their interactions as the fixed effects). Blocks, herbivore plots nested within blocks, and fire treatment subplots nested within the

herbivore plots (blocks/herbivore plots/fire treatment subplots) were included as the random effects.

We implemented GLMMs for species richness, overall herbaceous cover, and cover of grasses and forbs separately using generalized Poisson error distribution with log link. When necessary, we incorporated dispersion and zero inflation structures into GLMMs to improve model fit. We checked GLMMs for typical model misspecification problems (i.e., dispersion, zero inflation, and uniformity) in the DHARMa package (Hartig, 2022). For LMMs, we checked model assumptions using diagnostic residual plots. Based on these diagnostics, all GLMMs and LMMs fitted met the requisite model assumptions.

For LMMs, we constructed analysis of variance (ANOVA) tables with Satterthwaite's method for denominator df using the "anova" function in the LmerTest package. For GLMMs, we constructed analysis of deviance tables with Type II Wald χ^2 tests using the function "Anova" in the car package (Fox & Weisberg, 2018). We accepted statistical significance at $p < 0.05$. We used the "emmeans" function in the emmeans package (Lenth, 2020) to separate means for statistically significant interactions between fire and herbivory or for significant main effect of herbivory when appropriate. All analyses were performed in R version 4.0.2 (R Core Team, 2020).

RESULTS

In the five vegetation surveys conducted during the study period (2013–2017) on 18 burn and 18 control plots, we recorded a total of 18,955 pin hits on 70 herbaceous plant species (24 grasses and 46 forbs) (Appendix S1: Table S1). There were multiple significant effects of fire, herbivory, time since burn, and their interactions on various vegetation variables (Table 1) reported below.

TABLE 1 Generalized linear mixed models and linear mixed models results for the effects of fire, herbivory, or time since burning on herbaceous vegetation cover, species richness, and turnover.

Independent variable	Dependent variable	χ^2	*p*-value
Fire × Herbivory × Time interaction	Overall herbaceous vegetation	37.82	0.09
Fire × Herbivory × Time interaction	Total grass cover	35.03	0.020
Fire × Herbivory × Time interaction	Total forb cover	49.4	<0.001
Fire × Herbivory interaction	Overall herbaceous species richness	11.59	0.041
Fire × Herbivory interaction	Grass species richness	12.15	0.03
Fire × Herbivory interaction	Forb species richness	20.57	0.001
Fire × Herbivory interaction	Total species turnover	12.15	0.042

Note: See Appendix S1: Table S1 for a summary of all the main effects and interactions that were tested.

Changes in postfire herbaceous vegetation cover

The effects of fire on absolute cover of overall herbaceous vegetation, total grasses, and total forbs were influenced by fire × herbivory × time interactions (all $\chi^2 > 35.00$, all $p < 0.02$; Figure 1a–c). Overall herbaceous vegetation cover was 26%–57% lower (all $p < 0.005$) in burns than nonburns in all herbivory treatments during the first sampling period, approximately 3 months after fire (Figure 1a). Thereafter, overall herbaceous cover returned to control values within the next 15 months after fire, except in those plots accessible to wildlife, where the recovery was delayed until 27 months after fire. Total grass cover (which accounted for the great majority of overall herbaceous cover) mirrored these patterns except for the cattle plot, where there was no significant difference in grass cover between burns and nonburns during the study period except for the fourth sampling period at 39 months after fire (Figure 1b). Absolute cover of forbs was also initially lower in burns than nonburns (although sometimes nonsignificantly), but recovery patterns were the converse of those for grasses. Forb cover quickly recovered in plots accessible to wildlife but was delayed for up to 39 months in plots from which wildlife was excluded (i.e., O, C; Figure 1c).

Changes in postfire herbaceous vegetation species richness

Species richness of overall herbaceous vegetation, and grasses and forbs separately, was not significantly influenced by three-way interactions among fire, herbivory, and period, that is, no significant temporal effects of time since fire (all: $\chi^2 < 19.00$, all $p > 0.52$). Although a two-way interaction between fire and herbivory was significant for overall herbaceous vegetation species richness ($\chi^2 = 11.59$, $p = 0.041$), post hoc analysis did not reveal significant fire treatment differences in species richness (all $p > 0.072$) in any of the six herbivory treatments (Figure 2a). However, in the cattle-only plots (C), grass species richness was 18% greater ($p = 0.039$) and forb species richness 38% lower ($p = 0.019$) in burns than nonburns (Figure 2b,c).

Species turnover

There were no significant three-way interactive effects of fire, herbivory, and time since burning on total species turnover, appearance, and disappearance (all $\chi^2 < 15.32$,
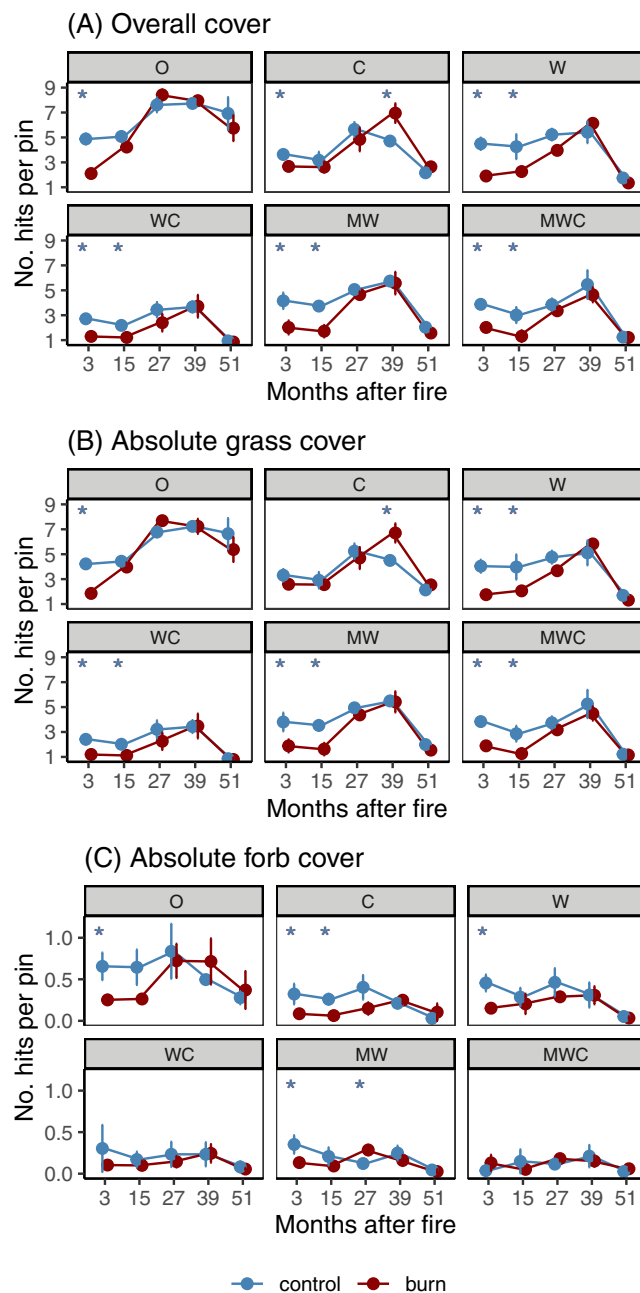

FIGURE 1 Effects of fire, herbivory, and time (in months) since fire on herbaceous vegetation cover (number of hits per pin). Letters in each panel denote the herbivore groups that are allowed in each plot: C, cattle; W, wild mesoherbivores; M, megaherbivores; and O, no large herbivores. Error bars represent SEs. For each sampling period, significant differences between burned and unburned plots are denoted by asterisks.

all $F < 0.77$, all $p > 0.75$). However, a two-way interaction between fire and herbivory was significant for total species turnover ($\chi^2 = 12.15$, $F = 2.39$, $p = 0.042$). Total turnover was significantly higher (both $p < 0.035$) in burns than nonburns in the wildlife-only treatments (MW and W; Figure 3).
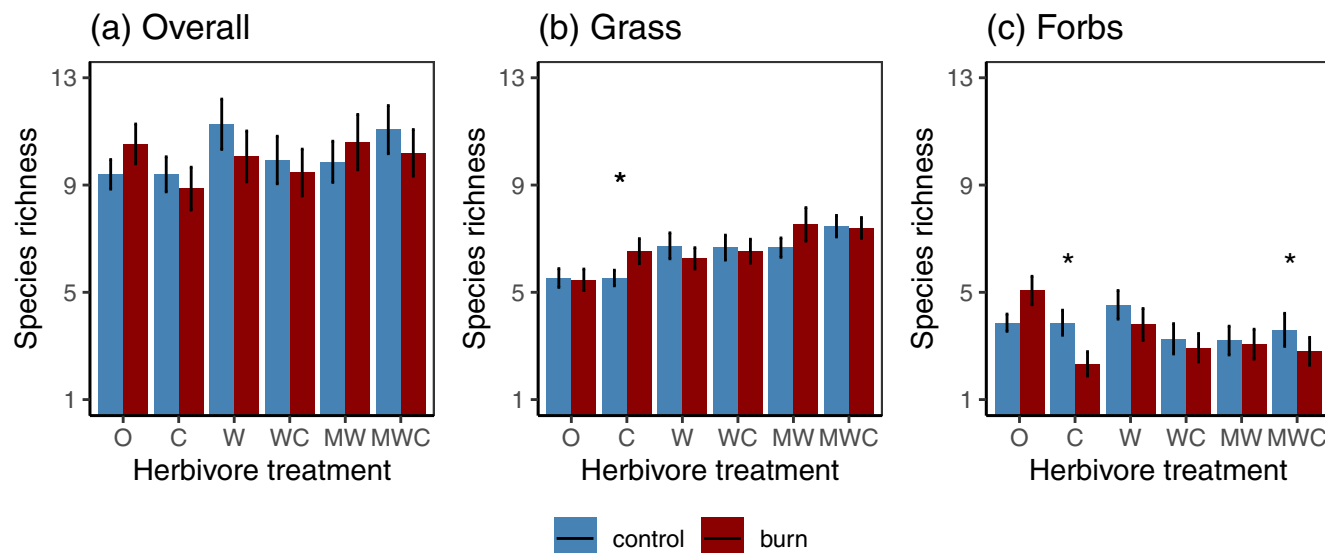
FIGURE 2 Effects of fire and herbivory on herbaceous species richness. Letters on the *x*-axis denote the herbivore groups that are allowed in each plot: C, cattle; W, wild mesoherbivores; M, megaherbivores; and O, no large herbivores. Error bars represent SEs. For each herbivore treatment, significant differences between burned and unburned plots are denoted by asterisks.
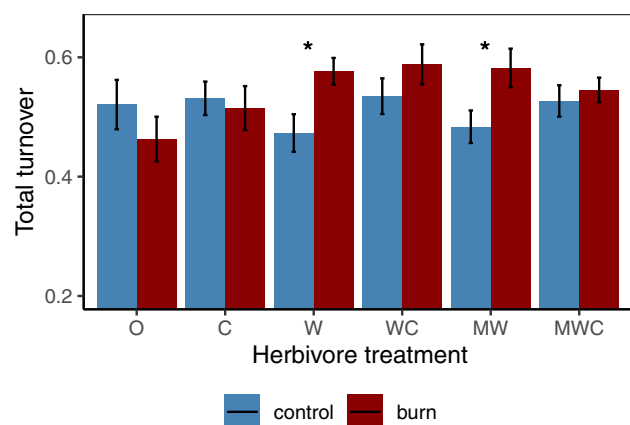

FIGURE 3 Effects of fire and herbivory on herbaceous species turnover. Letters on *x*-axis denote the herbivore groups that are allowed in each plot: C, cattle; W, wild mesoherbivores; M, megaherbivores; and O, no large herbivores. Error bars represent SEs. For each herbivore treatment, significant differences between burned and unburned plots are denoted by asterisks.

DISCUSSION

We assessed the separate and combined effects of postfire herbivory by cattle and wild mesoherbivores with and without megaherbivores on herbaceous vegetation recovery in a multiuse African savanna rangeland ecosystem. Wild herbivores, but not cattle, maintained overall herbaceous and grass cover lower in burned plots than unburned plots while enhancing forb recovery after fire. Cattle increased grass species richness but reduced forb species richness in burns relative to the nonburns. Our

study thus reveals that vegetation response to fire differs depending on postfire herbivory pressure, the vegetation response variable, and the time elapsed after fire.

Wildlife, but not cattle, significantly retarded the recovery of overall herbaceous cover

Fire consumes and initially lowers cover of overall herbaceous vegetation, grasses, and forbs (Figure 1a–c). Our results demonstrate that in the absence of herbivores, overall herbaceous cover (grasses mainly) can recover from the direct effects of fire by the 15th month after fire, as this vegetation is not grazed and or browsed by large herbivores. However, the presence of herbivores can slow down such recovery to up to 27 months after fire. One possibility for the delay in recovery was that the herbivores would be so attracted to burns that they would create an alternative stable state in the form of "grazing lawns." Such lawns could take one of two forms. First, there could be a conversion to a new plant species composition dominated by low stoloniferous species, like (in our ecosystem) *Pennisetum*, *Cynodon*, and *Digitaria* spp. (Augustine, 2003; Augustine et al., 2011; Veblen & Young, 2010). We found no such conversion. Second, herbivores can maintain grazing lawns in a plant species composition similar to adjacent nonlawn vegetation (which they did) but kept in a low (and palatable) state, which our results show they did not. Therefore, herbivores merely delayed but did not prevent recovery

of vegetation structure to the levels in the unburned controls.

These findings are consistent with other studies conducted elsewhere (Archibald, 2008; Donaldson et al., 2018; Starns et al., 2020), although those studies did not distinguish between different herbivore guilds. We demonstrated that the delayed recovery of overall herbaceous vegetation cover differed depending on the herbivore guilds that had access to burned patches. There were fundamental differences in the effects of cattle versus wild ungulates, with wild ungulates causing longer recovery periods than cattle, especially for grasses. It is not clear why herbivory by cattle alone did not have a similar retarding effect, especially since cattle occur at five to 10 times greater biomass densities than wildlife (Porensky, Bucher, et al., 2013). One suggestion is that cattle diets are very different from those of wildlife (e.g., less preference for fire-adapted species), but this does not appear to be the case (Odadi et al., 2007; Veblen et al., 2016). Second, the episodic nature of cattle access to these plots, between periods of absence, could have enabled overall herbaceous vegetation cover and grass cover to recover to preburn levels more quickly. Other studies have reported that even temporary pasture rests can enhance vegetation recovery from the effects of fire (Boughton et al., 2016; Gittins et al., 2011; Letnic, 2004). Lastly, we constrained the cattle herds to fixed grazing durations in the burned subplots, limiting their ability to suppress grass regrowth, although we did observe that they ate more quickly in these plots (Odadi et al., 2017) and also noted significant cattle effects in grass species richness in burned plots (see below). In any case, the episodic and controlled cattle-grazing regime in the KLEE experiment is simulative of grazing management in the study ecosystem (Odadi et al., 2007; Veblen et al., 2016). Thus, these findings are possible indicators of the effect that the current cattle-grazing regimes can have on vegetation response to fire compared to the impact of ad libitum grazing by wildlife.

Forb cover was delayed only in plots from which wildlife was excluded

In contrast to the overall vegetation recovery patterns discussed previously, which were mainly driven by grasses, forb cover recovered quickly in plots accessible to wildlife in similar ways to nongrazed plots. Forb recovery was, however, delayed in plots from which wildlife was excluded (C), while there was no significant difference between burned and nonburned subplots in plots grazed by both cattle and wild herbivores (WC, MWC) during the whole study period (Figure 1c).

Curiously, this meant that forb recovery was slower in plots accessible to cattle only, even though cattle are primarily grazers. However, cattle in our system do eat a wide variety of forbs (Odadi et al., 2007). The most likely explanation for this pattern could be that grasses compete strongly with forbs and that in plots where grass recovery was impeded (as in the wild herbivore plots), forbs were released from this competition, whereas in the cattle plots, forb recovery was suppressed possibly due to shading or established dominance by rank growth, grasses (Borer et al., 2014; Czarniecka-Wiera et al., 2019; Eskelinen et al., 2022). This facilitation effect would require that the direct effect of wildlife on the regeneration of forbs through selective grazing (note that the wildlife guild was dominated by mixed feeders, e.g., impala) was less than the suppression of forbs by grasses. However, these effects were only evident in plots accessible to wildlife and from which cattle were excluded. The nonsignificant forb response to fire in plots grazed by both cattle and wild herbivores may be due to the fact that the intense herbivory in these plots led to a similar reduction in forb cover in both burns and nonburns, that is, forb cover was so low even in the nonburned subplots that further reductions were not measurable.

Grass species richness was greater and forb species richness lower in burns than nonburns, in plots grazed by cattle

In contrast to the results for overall herbaceous cover, cattle did have significant effects on the overall species richness of burned plots (assessed across all surveys). Plots accessible to cattle showed significant differences between burns and nonburns, with grass species richness being higher in burned C plots and forb species being lower in burned C and MWC plots (Figure 2a–c). This parallels our previous research that examined the effect of interaction of drought and herbivory on forbs species richness, where only cattle plots showed significant changes, that is, increases in richness (Porensky, Wittman, et al., 2013). It is not clear why wildlife, which had significant effects on forb cover (above), did not significantly affect forb species richness, or why cattle shifted overall species richness without significantly affecting forb cover. We suggest that in cattle plots, the dominance of grasses led to more vegetation (grass) heterogeneity but, in turn, suppressed forb recovery (Czarniecka-Wiera et al., 2019; Marriotte et al., 2013). However, in the case of burned plots accessible to wildlife, high herbivory pressure, especially grazing on grasses, led to a reduction in grass species richness and created opportunities for other vegetation species to regrow. This facilitation effect of

grazing pressure for subordinate vegetation species has also been noted under drought–grazing interactions (Porensky, Bucher, et al., 2013) and likely facilitated the recovery of forbs to the levels in nonburns.

Species turnover was higher in burns than nonburns in wildlife treatments

It is not surprising, given all the differences in herbaceous cover and species richness, that species turnover was greater in some plots. Here the pattern was restricted to plots with wildlife only (i.e., in W and MW, but not MWC; Figure 3). This suggests that whatever increases in turnover in burned versus unburned plots caused by wildlife were offset by the effects of cattle. This could be through cattle suppressing habitat utilization by most of the wild herbivores at the study system, thereby modulating their effect (Kimuyu et al., 2017; Young et al., 2005).

Summary of separate and combined effects of cattle and wild ungulates on postfire vegetation

In this ecosystem, wild herbivores delay postfire grass recovery, and in this way, they initiate a guild-specific facilitation of forb recovery after fire. On the other hand, the current cattle-grazing regime facilitates grass recovery, both in terms of cover and species richness, and has a negative effect on forb recovery via the establishment of dominance by grass species. Megaherbivores (elephants, mainly, with respect to herbaceous vegetation) have no significant effects in how most of the measured metrics responded to grazing by cattle and or wild mesoherbivores. This wide diversity of the effects of herbivores in postburn vegetation underscores similar complexities in other systems (Collins & Calabrese, 2012; Smith et al., 2016) and other aspects of this system (Porensky, Wittman, et al., 2013; Riginos et al., 2018; Veblen et al., 2016).

Implications for savanna management in context of resilience

This fire- and herbivore-adapted ecosystem appears to be resilient to the combination of both, despite transient delaying effects of both cattle and wild herbivores, separately and especially in combination, on various metrics of herbaceous vegetation. Landscape heterogeneity produced by patch burning under herbivory (pyrodiversity) has been proposed as a desirable benefit of rangeland

burning, maximizing biodiversity while maintaining or even improving livestock foraging (Fuhlendorf et al., 2009). The temporal extent of these benefits, however, is limited by rapid postfire vegetation recovery in our ecosystem. The observation that postfire herbivory (pyric herbivory) delays this recovery suggests that the combination of fire and large-mammal herbivory maximizes these landscape benefits through time (Starns et al., 2020). In our system, it appears that wild herbivores are more effective than cattle at maintaining postfire landscape heterogeneity, at least for a few years. In this case, the presence or absence of megaherbivores may only have negligible additional or counteractive effects.

Given that our metrics all returned to nonburn levels within less than 5 years after fire, it is possible that repeat burning, at this interval or longer, may have little effect on the herbaceous layer, barring long-term depletion of belowground resources, as has been found in some woody systems experiencing repeated fires (Pratt et al., 2014). However, our results leave opens the possibility that at higher fire frequencies (at shorter time scales), these complex interactions among fire and wild and domestic ungulates, swards that are both burned and grazed may be more effectively maintained in a more nutritious, more productive state of regenerating grasses than under either alone. We are currently testing this possibility.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT
Data (Masudi et al., 2024) are available in Figshare at https://doi.org/10.6084/m9.figshare.25242787.v2.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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