Synergistic effects of long-term herbivory and previous fire on fine-scale heterogeneity of prescribed grassland burns

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Abstract. Grassland and savanna ecosystems, important for both livelihoods and biodiversity conservation, are strongly affected by ecosystem drivers such as herbivory, fire, and drought. Interactions among fire, herbivores and vegetation produce complex feedbacks in these ecosystems, but these have rarely been studied in the context of fuel continuity and resultant fire heterogeneity. We carried out 36 controlled burns within replicated experimental plots that had allowed differential access by wild and domestic large herbivores since 1995 in a savanna ecosystem in Kenya. Half of these were reburns of plots burned 5 yr previously. We show here that the fine-scale spatial heterogeneity of fire was greater in plots (1) previously burned, (2) accessible to large herbivores, and especially (3) these two in combination. An additional embedded experiment demonstrated that even small experimental burn-free patches can have strong positive effects on tree saplings, which experienced less damage during controlled burns and quicker postfire recovery. This work highlights the importance of simultaneously examining the interactions between fire and herbivory on fuel heterogeneity, which can have important impacts on the growth of woody saplings in savanna grasslands.

Key words: Acacia drepanolobium*; Africa; fire; fuel; grassland; herbivory; Kenya; rangeland; savanna; spatial heterogeneity.*

INTRODUCTION

In many terrestrial ecosystems worldwide, herbaceous-dominated communities persist where more woody-dominated vegetation could be supported by soil and climate conditions. The difference between potential and actual vegetation is often driven by abiotic and biotic consumers—fire and herbivores—and consequent feedback interactions with these control mechanisms (Bond and Keeley 2005). Interactions among herbaceous vegetation, woody vegetation, and consumers play out dramatically in savannas, which are defined by the coexistence of trees and grasses, and characterized by their potential for alternative states of either grass- or tree-dominated vegetation reinforced by fire and herbivory (Sankaran et al. 2008, Touboul et al. 2018). There have been an increasing number of studies of how interactions among fire, herbivores, and vegetation in these ecosystems influence the landscape-scale heterogeneity of tree-grass ratios (Higgins et al. 2000, Sankaran et al. 2008, Holdo et al. 2009, Hempson et al. 2019, Johansson et al. 2020) and grass fuel loads (Bielski et al. 2018, Starns et al. 2019). Fewer examine how these interactions affect fine-scale landscape heterogeneity (Blackhall et al. 2017), despite the assertion that spatial heterogeneity in turn engenders landscape-level diversity (Pickett and Cadenasso 1995, Stein et al. 2014) and resilience to future disturbance (Koontz et al. 2019). These questions are made even more critical by increasing global encroachment of woody species into grassland ecosystems, reducing livestock production and wildlife habitat (Wilcox et al. 2018, Buisson et al. 2019).

Synergistic effects of fire and grazing on fuel loads

A growing body of literature has focused on separate and interactive influences of fire and herbivory on grass biomass and fuel loads, which may influence behavior of subsequent fires. For example, by increasing

heterogeneity in grass fuel loads, both herbivores (e.g., Adler et al. 2001, Parsons and Dumont 2003) and fire (e.g., Fuhlendorf and Engle 2001) may separately influence subsequent fire temperature and spatial patterns. Herbivores are known to increase the heterogeneity of vegetation at both larger (between-patch) and smaller (within-patch) spatial scales, often via the creation of bare patches (Taylor et al. 1994, Porensky et al. 2013). Different fire frequencies and severities can also promote heterogeneity of vegetation, as has been observed in systems ranging from tallgrass prairie to mixed-conifer forest (Gibson et al. 1990, Safford and Stevens 2017).

In addition to the separate effects of fire and grazing on fuel heterogeneity, interactions between fire and herbivory, described as "pyric herbivory," can influence subsequent fuel loads and landscape-scale spatial complexity (Fuhlendorf et al. 2009). Intense herbivory can decrease fuel load, in turn decreasing fire temperatures and continuity, even to the extent of suppressing fire completely (Liedloff et al. 2001, Kimuyu et al. 2014, Johansson et al. 2020). Herbivores often preferentially forage within burned areas, although different herbivore groups may use burned areas differently (Klop et al. 2007, Sensenig et al. 2010, Allred et al. 2011). This pattern of focused grazing can create synergistic or positive feedbacks on grass biomass when postfire herbivory decreases fuel loads and continuity more than fire or grazing alone (Kirkpatrick et al. 2011, Blackhall et al. 2017, Donaldson et al. 2018). This synergistic effect on the heterogeneity of fuel loads in turn has been hypothesized to strongly decrease future fire temperatures and spread rates, although these patterns have rarely been empirically tested (Starns et al. 2019). Alternatively, selective grazing by herbivores may influence herbaceous composition, promoting taller unpalatable grasses that subsequently support little herbivory and are maintained by regular fire (Donaldson et al. 2018, Hempson et al. 2019).

Spatial scales and within-burn heterogeneity

The interactions between fire and herbivory on fuel loads and fire impacts are likely dependent on the spatial scales of these processes (Collins and Smith 2006, Kimuyu et al. 2017). Most studies have examined fire–herbivory impacts on fuel loads at intermediate to landscape-level scales (Waldram et al. 2008, Hempson et al. 2019). For example, at large spatial scales (tens of meters), mega-herbivores such as rhinos increase burn heterogeneity by maintaining large grazing lawns devoid of fine dead fuels (Waldram et al. 2008, Donaldson et al. 2018), and combinations of patch-burning and grazing management have been used to promote landscape-scale heterogeneity in prairie and heathland systems (Parr and Brockett 1999, Vandvik et al. 2005).

However, we have little information addressing how fire–herbivore interactions affect the heterogeneity of fuel loads at finer spatial scales (i.e. <1–2 m, the feeding station scale), or their consequences. Even at fine scales,

herbivore-introduced heterogeneity may create discontinuous surface fuels (Shea et al. 1996, Blackhall et al. 2017), which could in turn result in lower fire temperatures and more heterogeneous burns (Kerby et al. 2007).

Local heterogeneity and tree-grass interactions

Herbivore–fire effects on grass biomass at the scale of feeding station can also contribute important insights to understanding how fire and grazing influence tree survival of young saplings. Both herbivory and fire can shape savanna composition by shifting the balance between trees and grasses (Sankaran et al. 2008), and tree saplings are particularly susceptible to negative effects of browsing (e.g., Levick et al. 2009, Maclean et al. 2011, Porensky and Veblen 2011) and to mortality or top-kill by fire (Grady and Hoffmann 2012). In addition to the direct effects of herbivores, grazing-driven decreases in fuel load may mitigate the damage caused by fire on young trees. In particular, within-patch heterogeneity may decrease overall fire intensity and leave small unburned patches that allow individual saplings to better survive, grow, and eventually escape fire.

To better understand how herbivory and fire interact to modify fuel loads at small spatial scales, with concomitant impacts on tree seedling survival, we examined spatial burn patterns of prescribed fires in the Kenya Long-term Exclosure Experiment (KLEE). This experiment has manipulated the presence and absence of three guilds of large herbivores, cattle, meso-wildlife, and mega-herbivores, in six different combinations since 1995. After several decades of fire exclusion in this ecosystem, fire was reintroduced in prescribed burns in 30 × 30 m KLEE subplots in 2013 and again in 2018. We investigated the interactive effects of prefire disturbance, herbivory, and previous burn on spatial patterns of burning within plots, using a controlled replicated experimental design. We hypothesized that fires in plots with higher herbivory pressure and in previously burned plots burn a lower proportion of the plot (H1). We also hypothesized that fires in plots with herbivores and previous fire burn more heterogeneously, with smaller burned patches and more frequent spatial transitions between burned and unburned patches (H2). We further hypothesized that these two effects are synergistic (H3): that the herbivory-driven differences in burned area and heterogeneity are greater in previously burned plots (which are more attractive to herbivores) than plots burned a single time. Lastly, we experimentally tested the consequences of burn heterogeneity on woody vegetative response to fire by monitoring selected saplings within a subset of the controlled burns for which we had either clipped the surrounding herbaceous vegetation or not. We hypothesized that saplings located within even small clipped patches (1 m diameter) experience lower fire severity (proportion burned) (H4a), and consequently have higher aboveground survival rates and are larger postfire (H4b).

Study Site and Methods

Study site and species

This research was carried out in *Acacia drepanolobium* wooded savanna on the Laikipia Plateau, Kenya (36°52′ E, 0°17′ N; 1,810 m above sea level). This plant community overlies high-clay "black cotton" soils (vertisols) and is representative of similar ecosystems that occur extensively throughout eastern and southern Africa. Annual rainfall averages 550–600 mm at our study site, and is weakly trimodal, with a distinct dry season in December–March.

Five grass species (*Brachiaria lachnantha* (Hochst.) Stapf, *Pennisetum mezianum* Leeke, *P. stramineum* Peter, *Themeda triandra* Forssk., and *Lintonia nutans* Stapf.) make up 85% of herbaceous cover (Porensky et al. 2013). More than 90% of the tree canopy cover in KLEE is *Acacia drepanolobium* Sjost., and total tree canopy cover averages 15–25%. The size structure of *A. drepanolobium* is strongly left skewed, with large numbers of small (<80 cm tall) individuals that are of indeterminate age, due to their ability to resprout after fire or herbivory (Young et al. 1997).

The Kenya Long-term Exclosure Experiment (KLEE) is located at the Mpala Research Centre. Since 1995, we have been manipulating the presence and absence of three guilds of large herbivores: livestock (cattle), wildlife (large mammals 15–1,000 kg), and mega-herbivores (elephants and giraffes). There are 18 plots, each 200 × 200 m, in three replicate blocks (North, Central, South). Semipermeable barriers exclude different combinations of cattle, meso-herbivore wildlife > 15 kg, and mega-herbivores (elephants and giraffes). The two-level cattle manipulation (with cattle [C] or without cattle) is crossed with a three-level wildlife manipulation (both mega-herbivores and meso-herbivore wildlife [MW]; meso-herbivores allowed but mega-herbivores excluded [W]; or both mega- and meso-herbivore wildlife excluded). Crossing these treatments results in six herbivore treatments, each of which is replicated over the three blocks: O (no large herbivores), C, W, WC, MW, and MWC (see Fig. 1; for more detail of the KLEE design, see Young et al. 1997).

Controlled burns

In February–March 2013 we burned one 30 × 30 m subplot in each of the 18 4-ha KLEE plots (see Kimuyu et al. 2014). In February 2018, we re-burned these subplots, and burned an additional subplot in each KLEE plot (36 burns total; Fig. 1). In addition to the 36 burns, 18 unburned control plots were established in 2013. For each set of burn and control plots, we selected subplots that were similar with respect to the density and size structure of larger *Acacia drepanolobium* trees (>1 m tall).

At the beginning of the study, plots differed in grass cover, forb cover, and bare ground due to the previous
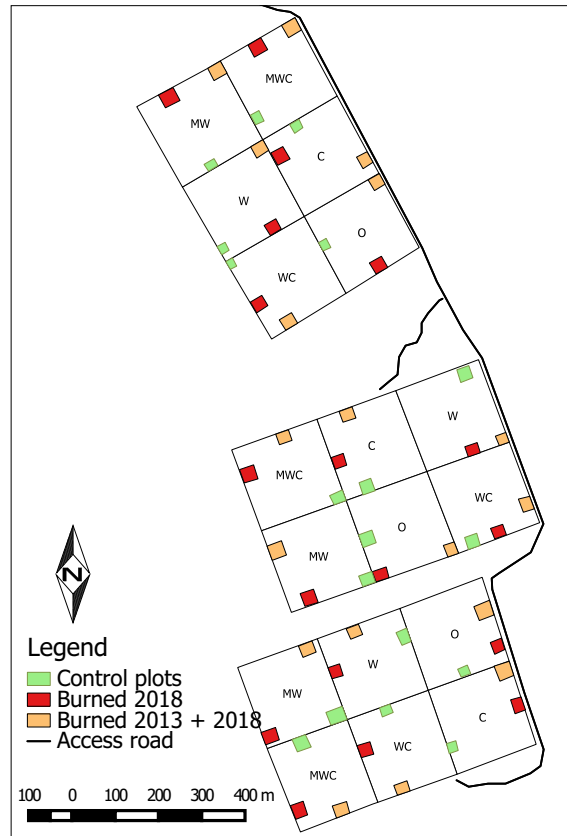

Fig. 1. Layout of the Kenya Long-term Exposure Experiment (KLEE) plots and prescribed burn subplots. Burned 2013 + 2018 indicates plots that were burned in both 2013 and 2018; burned 2018 were burned only in 2018; and control plots are the unburned references. Letters refer to the herbivory treatments: all large herbivores excluded (O), cattle only (C), meso-wildlife only (W), meso-wildlife and cattle (WC), mega- and meso-wildlife (MW), mega- and meso-wildlife and cattle (MWC).

herbivory and fire treatments. These differences were significantly associated with KLEE herbivore treatments, but not the 2013 burn treatments (Appendix S1: Table S1). The KLEE treatments also differed somewhat in understory composition (e.g., forb/grass ratio, Appendix S1: Table S1), but these differences were not significant. Aerial cover measured in the KLEE plots in mid-2017 was strongly correlated with the biomass from clips (from the sub-plots designated for their first burn in 2018) in the week before the burns ($r^2 = 0.56$, $F_{1,16} = 19.9$, $P = 0.0004$).

We refrained from grazing cattle in the KLEE plots for five months prior to the burns to ensure sufficient fuel loads. The 2013 burns were preceded by a modest rainfall season (806 mm over the preceding 12 months) while the 2018 burns were proceeded by drier period (446 mm).

Firebreaks for the 2018 burns were established in the weeks preceding the burns. A 1–2 m wide swath was

slashed to a vegetation height of 5–10 cm. For some subplots, either an access road or cleared fence line provided firebreaks. Over a period of five days (19–23 February 2018), we carried out all 36 burns, between 08:00 and 13:00 each day. Plots with higher fuel loads tended to be burned earlier in the day (during more moderate wind, temperature, and humidity conditions) for logistical and safety reasons. Burn boundaries were wet-lined and then "black lined" to create 5–10 m of firebreak along downwind edge and 2–5 m breaks along the flanks. The interiors of all plots were burned using a strip head-fire ignition pattern. Due to discontinuous fuel loads in some subplots, we spot-lit head fires for the larger (>5 m^2) unburned grass patches and fingers not burned by the original head fire, to ensure that the burn was carried out across the entire area. Due to both the non-random timing of burns and the spot-lighting of large patches, our estimates below of treatment effects (differences) on area burned and heterogeneity are likely to be conservative.

Spatial patterns of burn

To quantify the effects of herbivory and previous burn on proportion of area burned (H1) and burn heterogeneity (H2), we laid six parallel regularly spaced 30-m line-intercept transects within each of the 36 burned subplots. We surveyed three similar transects in each of the 18 control subplots. On each transect, we recorded the interception lengths for the following patch types: charred understory, bare ground, and unburned grass. To minimize the chance that areas that were bare after the fires had actually been covered before the burn by overhead grasses, bare sections of 20 cm or less in length that were embedded in char or grass were not counted as bare. These line-intercepts were used to compute average percent area of burned grass, unburned grass, and bare ground (H1) for each of the 36 burns and for the 18 control plots. We considered unburned grass separately for this analysis to determine whether differences in proportion of the plot burned were solely from pre-burn differences in bare ground, or additional patches of vegetation that could have burned but did not.

To test the heterogeneity of the burn (H2), we combined bare ground and unburned grass into a single "unburned" type and calculated average unburned patch length along transects and frequency of transitions between burned and unburned patches for each of the 36 burns (c.f. Sheffer et al. 2013). This lumping allowed us to investigate spatial patterns of all areas that could provide refugia for vegetation (including tree saplings; see *Sapling clearing experiment*).

All spatial metrics from burned plots were analyzed with ANOVA, testing the effects of herbivore treatments in a 2 × 3 × 2 complete factorial design (two cattle treatments [C, no cattle]; three wildlife treatments [MW, W, no wildlife]; times burned [single burn, reburn]). We additionally included block as a fixed effect, because

there is a known rainfall gradient among blocks, and this is more conservative than using random effects (Dixon 2016). To test how the effects of re-burning differed by herbivore treatment (H3), we included terms for the two-way interactions between cattle and wildlife, cattle and times burned, and wildlife and times burned in these models. To analyze unburned control data (H1), we used an ANOVA model with a 2 × 3 factorial design of cattle treatments and wildlife treatments, with the additional fixed block effect.

Sapling clearing experiment

In each O, C, MW, and MWC plot (12 plots total), two *A. drepanolobium* saplings were selected prior to the burn, paired for similar size (total saplings = 24; three replicate pairs per treatment). All saplings were between 20 and 80 cm tall. We clipped understory vegetation to ground level and cleared all litter within a 50 cm radius around one randomly selected sapling of each pair to create a burn-free patch. For each sapling we measured prefire height and widest diameter of canopy (Appendix S1: Fig. S1E and F).

To test the effects of these small cleared patches on burn intensity (H4), we monitored fire temperatures with ceramic tiles painted with Tempilac paints (LA-CO Industries, Elk Grove Village, Illinois, USA). We used paints designed to melt at each of the following six temperatures: 79°C (175°F), 107°C (225°F), 149°C (300°F), 204°C (400°F), 260°C (500°F), and 316°C (600°F). We placed two tiles at each sapling: one tile on the ground, and one attached to a piece of rebar at 50–60 cm above the ground. In one sapling plot (MW in the Central block), we mistakenly did not place temperature tiles. After the burns, we collected the ceramic tiles and scored them for the highest temperature class of paint melted by the fire, which provides a lower boundary on the fire temperature at that location. If none of the paints melted, a default of 25°C was used for analysis (mean air temperature at the time of the burns was 25.7 °C). We averaged the temperature score for the tile on the ground and the tile at 50–60 cm height to get a mean fire temperature score for each sapling, which was used for all analyses.

To test the effects of small cleared patches on micro-site fire severity (H4), we measured on each sapling the proportion of total stem length with no spines remaining. (Spines are more readily burned off completely, and so make a readily quantifiable measure of burn severity). Two weeks after burning and after the start of the rainy season, we surveyed each sapling for live growth, either new leaves or coppicing shoots, and measured height and widest diameter of canopy. Saplings were resurveyed for live growth height and canopy size again in June 2018, four months after the burns.

To test whether saplings within clipped patches experienced lower fire intensity and severity (H4a), we analyzed fire temperatures and percentage of spines

remaining with ANOVA, testing the effects of herbivore treatment and clipping treatment in a 2 × 2 × 2 complete factorial design (two cattle treatments [C, no cattle]; two wildlife treatments [MW, no wildlife]; two clipping treatments [clipped, unclipped]), with block as a fixed effect (Dixon 2016). Interaction terms were not significant (all $P > 0.4$), so were not included in the model. To test the effects of fire intensity on postfire sapling condition (H4b), sapling top-kill and resprouting were split into four mutually exclusive categories: survived aboveground (no top-kill), resprouted by March, resprouted by June (but not yet in March), did not resprout (died), and analyzed using ordinal linear regression with temperature as the predictor. Sapling postfire size (H4b) was analyzed with ANOVA testing the effects of mean fire temperature, and including prefire size as a covariate (with separate models for each of March height, March canopy width, June height, and June canopy diameter).

All analyses were done in R version 3.6.0 using plyr and tidyverse packages for data structuring, the MASS package for analyses, and ggplot2 and cowplot packages for figures (Venables and Ripley 2002, Wickham 2011, 2016, Wickham et al. 2019, R Core Team 2019, Wilke 2019).

Results

Percentage of area burned

The average proportion of area burned in all 36 plots was 73% (range 25–99%). Proportion of unburned grass ranged from 0% to 33%, and the proportion of bare ground ranged from 1% to 51%. Plots with more herbivores experimentally allowed had less area burned and more unburned grass cover remaining (Fig. 2A), even with the additional lighting of larger unburned patches. The effects of both cattle and wildlife on proportion of area burned depended on whether the plot had been previously burned (Appendix S1: Table S2; times burned × cattle $F_{1,24} = 12.7$, $P = 0.002$; times burned × wildlife $F_{2,24} = 4.9$, $P = 0.02$). In plots burned in 2018 for the first time, the proportion of burned area was not significantly affected by cattle or wildlife treatment (cattle $F_{1,10} = 2.5$, $P = 0.15$; wildlife $F_{2,10} = 1.7$, $P = 0.23$). However, in plots burned in 2013 and reburned in 2018, both cattle and wildlife decreased proportion burned (cattle $F_{1,10} = 64.6$, $P < 0.001$; wildlife $F_{2,10} = 28.5$, $P < 0.001$). A Tukey post-hoc test indicated that burned area in reburned plots with only meso-herbivores (W and WC) and in reburned plots with meso- and mega-herbivores (MW and MWC) was significantly lower than in reburned plots with no wildlife (O and C; both differences $P < 0.001$). Block effects were also significant ($F_{2,24} = 8.1$, $P = 0.002$), with the average proportion burned decreasing from north to south.

The effect of cattle on proportion of unburned vegetation remaining in the burned plots also differed between the single burn and reburned plots (Fig. 2A; interaction $F_{1,24} = 5.5$, $P = 0.03$). In plots burned for the first time, the higher proportion of unburned grass in plots with cattle herbivory was not significant ($F_{1,10} = 1.9$, $P = 0.2$), but in reburned plots, plots with cattle herbivory had four times more unburned grass remaining than those without cattle herbivory ($F_{1,10} = 41.6$, $P < 0.001$). Across both first and second burns, wildlife treatment had a significant effect on unburned grass remaining ($F_{2,24} = 5.4$, $P = 0.01$). Plots with meso- and mega-herbivores had 2.5 times more unburned grass remaining than plots with no herbivores (Tukey post-hoc, $P = 0.01$), with intermediate levels of unburned grass in plots with only meso-herbivores, which were marginally significantly different from plots with no herbivores ($P = 0.05$).

In the unburned control plots, proportion of grass cover was lower in plots with cattle present (Appendix S1: Table S1; $F_{1,10} = 13.1$, $P = 0.005$). Additionally, grass cover in controls differed by wildlife treatment ($F_{2,10} = 4.1$, $P = 0.049$); a Tukey post-hoc test revealed that grass cover in plots with both meso- and mega-herbivores was significantly lower than grass cover in plots with meso-herbivores only ($P = 0.043$), with grass cover in plots with no wild herbivores intermediate to those two (Fig. 2A).

Heterogeneity of burn

The average length of unburned area along the transect line in the burned plots ranged from 0.4 m to 3.5 m, and differed significantly depending on herbivory and previous burn. The effect of cattle on unburned patch length differed between the single burn and previously burned plots (Fig. 2B; interaction $F_{1,24} = 6.6$, $P = 0.02$). In plots burned for the first time there was no significant difference in unburned patch length between plots with cattle and plots without cattle ($F_{1,10} = 0.83$, $P = 0.39$), but in reburned plots, the average unburned patch length was twice as long in plots with cattle compared to plots without cattle ($F_{1,10} = 9.4$, $P = 0.01$). There was also indication of a similar interaction between wildlife and reburning (interaction $F_{2,24} = 3.1$, $P = 0.06$), with no difference between wildlife treatments in single burn plots ($F_{2,10} = 0.22$, $P = 0.8$), but previously burned plots without wildlife had less than one-half the unburned patch lengths than previously burned plots with either meso-herbivores or meso- and mega-herbivores ($F_{2,10} = 3.3$, $P = 0.08$). There was also an overall block effect ($F_{2,24} = 4.2$, $P = 0.03$).

The average frequency of transitions between burned and unburned areas ranged from 0.02 transitions/m (nearly continuous burns) to 0.9 transitions/m (heterogeneous burns), and differed significantly depending on herbivory ($F_{1,24} = 5.5$, $P = 0.03$). Transition frequency in plots with cattle was 25% higher than in plots without cattle (Fig. 2C). Transition frequency also differed by wildlife treatment ($F_{2,24} = 8.3$, $P = 0.002$). In plots with only
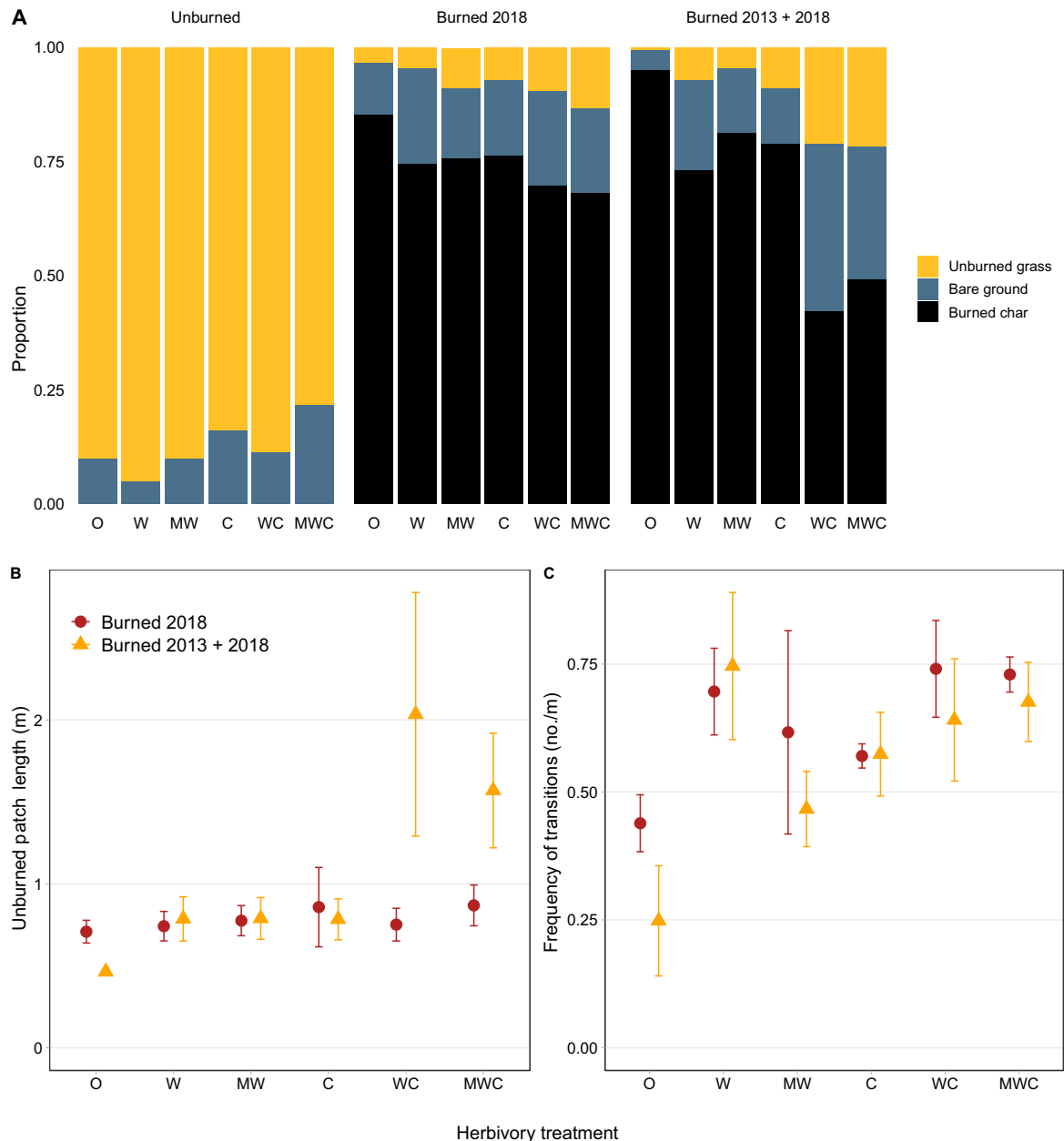
FIG. 2. Spatial patterns of burn. (A) Average proportion of plot with burned char (black), unburned grass (yellow), and bare ground (blue). Plots are grouped by their fire history (unburned controls, plots burned only in 2018, and plots burned in 2013 and reburned in 2018) and by their herbivory treatment. (B) Unburned patch length (mean ± SE) and (C) frequency of transitions between burned and unburned patches (mean ± SE) by herbivory treatment and fire history. The unburned patches in B and C include both unburned grass and bare ground. The unburned controls location nearby the burns provides an unbiased estimate of pre-burn conditions for plots burned in 2018 only.

meso-wildlife, transition frequencies were 60% higher than in plots with no wildlife (Tukey post-hoc test, $P = 0.001$) and 38% higher in meso- and mega-wildlife plots than in plots with no wildlife (Tukey post-hoc test, $P = 0.04$). Transition frequency also differed significantly by block ($F_{2,24} = 5.0$, $P = 0.01$), but not between the single burn and reburned plots ($F_{1,24} = 2.1$, $P = 0.16$).

Sapling response to fire

Mean fire temperature adjacent to the experimental saplings (averaged from ground level and 50 cm above ground height) was higher in unclipped treatments than clipped treatments (Fig. 3A; 142°C vs 90°C; $F_{1,16} = 5.2$, $P = 0.04$). Temperature was also higher in plots without
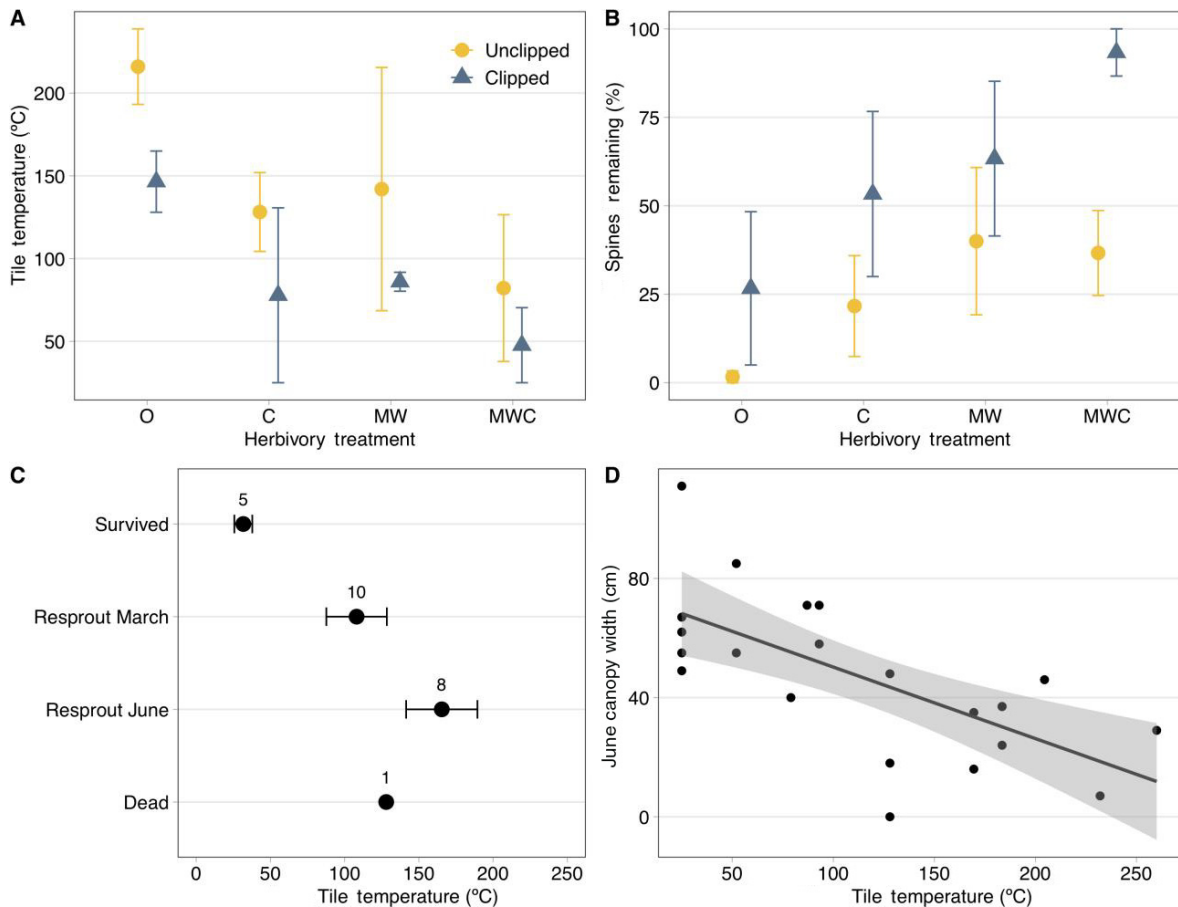
FIG. 3. Fire intensity and severity by clipped or unclipped treatment in four herbivory treatments and sapling responses to mean fire temperature. (A) Mean fire temperature, averaged from temperature at ground level and 50 cm height (mean ± SE). (B) Percentage of saplings' stems with spines remaining (mean ± SE). (C) Differences in fire temperature experienced by saplings that survived aboveground, survived belowground and resprouted by March, survived belowground and resprouted by June, and died (mean ± SE). Numbers indicate sample size for each survival class. (D) Postfire sapling width in June, with linear regression and 95% confidence intervals.

cattle than those with cattle (154°C vs 84°C; $F_{1,16} = 9.2$, $P = 0.008$) and higher in plots with all wildlife than those without any wildlife (142°C vs 85°C; $F_{1,16} = 4.8$, $P = 0.04$).

Saplings in the clipping treatment had spines remaining on more than twice as much stem length than those in the unclipped treatment (59% vs 25%; Fig. 3B; $F_{1,18} = 8.5$, $P = 0.009$). Stem length with spines remaining was also more than double in plots with wildlife than plots without wildlife (58% vs 26%; $F_{1,18} = 7.7$, $P = 0.01$), and was 56% higher (although not significantly) on saplings in plots with cattle than those without cattle (51% vs 33%; $F_{1,18} = 2.4$, $P = 0.14$).

Although all but one of the saplings survived the burn, there was a range of postfire responses, with saplings either surviving aboveground (not top killed), being top killed and resprouting by March, being top killed and resprouting by June, or not resprouting. Saplings in these different categories had experienced significantly different fire temperatures (Fig. 3C; $t_{18} = 2.7$, $P = 0.007$). Saplings that survived above-ground had experienced a mean fire temperature of 32°C, those that resprouted by March had experienced a mean fire temperature of 108°C, and those that resprouted in June had experienced a mean fire temperature of 165°C. The sapling that did not resprout had experienced a mean fire temperature of 128°C.

In March, sapling canopy width was negatively correlated with mean tile temperature, (Appendix S1: Fig. S1C, $F_{1,20} = 6.0$, $P = 0.02$), as was sapling height (Appendix S1: Fig. S1D, $F_{1,20} = 7.2$, $P = 0.01$). The negative correlation between mean tile temperature and canopy width persisted in June (Fig. 3D, $F_{1,20} = 16.6$, $P < 0.001$), although the relationship with height became nonsignificant (Appendix S1: Fig. S1F; $F_{1,20} = 3.1$, $P = 0.1$). Neither prefire height nor canopy width were significant covariates in any of our models (all $P > 0.4$).

DISCUSSION

Our experimental design allowed us to uniquely demonstrate that fine-scale fire heterogeneity in this savanna ecosystem is a richly complex consequence of the interactive drivers of previous fire and large wild and domestic herbivores, and that even small-scale heterogeneity has consequences for sapling success in the face of fire.

Herbivory and previous fire decrease burn severity and increase heterogeneity

Evidence from our experimental exclosures demonstrates that long-term use by herbivores increased plot-level burn heterogeneity and decreased burn severity in patches that were burned. However, the strength of these effects depended strongly on previous fire history: the effect of herbivores on proportion of the plot burned and unburned patch length was stronger in plots that had previously been burned. This pattern is consistent with observations of focal grazing (pyric herbivory) by herbivores in burned areas (Klop et al. 2007, Sensenig et al. 2010), creating in this case a synergistic effect between burn history and herbivory. Given the long-term nature of our experiment, it is also possible that long-term herbivory effects are also driving the responses to reburning, for example, via shifts in understory vegetation composition (Veblen et al. 2016). Contrary to our expectations, a single previous burn did not decrease area burned or increase small-scale burn heterogeneity unless grazers were also present. In ungrazed plots, the 5-yr window between fires was apparently sufficient for reaccumulation of fuels. The previous burn actually may have led to more severe and homogenous fires, by promoting the accumulation of a continuous layer of fine fuels. This parallels findings by Staver et al. (2009) that the combination of fire and browsing is required to affect savanna tree densities.

The frequency of transitions between burned and unburned patches was greater in plots with more large herbivores but did not differ by burn history. In this case, it appears that the pattern was primarily driven by transition frequencies being particularly low in plots where all herbivores were excluded, which tended to have more continuous and homogenous burns, likely due to the high pre-burn fuel load.

The effects of different herbivore groups were essentially additive. Despite previously observed differences in how herbivore guilds use burned areas (Sensenig et al. 2010), herbivory effects on fire heterogeneity were consistent across herbivore groups, with qualitative similarities between grazing by cattle and by wildlife. In this and other ways, cattle may act as "surrogate wildlife" for vegetation communities, fire dynamics, and heterogeneity in savanna systems (Veblen et al. 2016).

Our experiment demonstrates the consequences of a single fire reintroduction compared to the second of two burns and may differ in fundamental ways from systems with a longer history of repeated burning. Long periods of fire suppression in systems with historically frequent burn return intervals (i.e., high frequency fire regimes) can increase fuel accumulation and fire severity (Schoennagel et al. 2004). Prefire herbivory can be used as a management tool to decrease understory fuel loads before reintroducing fire (Fuhlendorf et al. 2009, Blackhall et al. 2017) or to control the impacts of wildfire (Nader et al. 2007). Our results suggest that herbivory impacts on fuel load and fire heterogeneity may be evident with as few as one additional fire event.

Patch-scale heterogeneity promotes sapling survival

We experimentally demonstrated the relevance of fine-scale fuel heterogeneity to sapling survival and size, which has implications for tree-grass interactions in this savanna system and for biodiversity conservation and rangeland management. The average unburned patch length in our plots ranged from approximately 0.5 m to 2 m; the clipped treatment of a 1 m diameter circle was consistent with this range of naturally occurring patches. Our clipping experiment demonstrated that, even at this 1-m scale, unburned patches create refugia of lower temperatures, which in turn promote aboveground sapling survival. Over time, these subtle differences in burn heterogeneity produced at the scale of the feeding station differences could lead to increases in tree abundance in savanna systems.

Clipping around saplings had a similar and additive effect to plot-level herbivory in reducing fire temperatures and fire damage to the saplings (increasing proportion of spines remaining on the stem). These small refugia of lower fire intensity and severity in turn promoted saplings' aboveground survival and size. Saplings of *A. drepanolobium* readily resprout and are resilient to fire (Pratt and Gwynne 1977, Okello et al. 2007, LaMalfa et al. 2019); almost all of the saplings in our experiment survived belowground. However, saplings that experienced lower local temperatures were more likely to survive aboveground. The process of resprouting after top-kill has energetic costs, and can leave saplings more vulnerable to future fire, herbivory, or drought (Clarke et al. 2013). In *Acacia drepanolobium*, the loss of spines can further decrease sapling protection from herbivory, including the physical protection from the spines (Milewski et al. 1991) and mutualistic protection from ant species (Stanton and Palmer 2011), which require intact hollow spines for their domatia. Finally, saplings that experienced lower local temperatures were larger postfire. For these saplings < 1 m tall, differences in size can determine the outcomes of their competitive interactions with surrounding grasses; growing above this herbaceous layer is important for both direct competition and surviving future grass-fueled fires (Higgins et al. 2000, LaMalfa et al. 2019).

The interaction between herbivores and fire can affect sapling growth in other ways, including prefire browsing legacy and postfire browse (Roques et al. 2001, LaMalfa 2019). Prefire browsing can affect sapling size, which in turn can influence postfire size (Grady and Hoffmann 2012). We selected saplings of as similar prefire sizes as possible across the herbivory treatments, and did not find a significant effect of prefire size in our models of postfire sapling size. Although we observed no evidence of browsing on the saplings we sampled in the four-month postfire window, postfire browse can be another important component of interacting fire and herbivore effects on saplings (Staver et al. 2009, O'Connor et al. 2019). On a longer time scale, preferential foraging by herbivores in burned areas could lead to higher direct browsing pressure on saplings (Midgley et al. 2010, Shannon et al. 2011, Pringle et al. 2015), although saplings that were less damaged by burning may be more resistant to postfire browsing.

Bush encroachment into grassland ecosystems is increasingly a problem worldwide, associated with changing herbivore communities and fire regimes and exacerbated by rising CO_2 levels. This encroachment is both promoted by and threatens livestock production and pastoral livelihoods, reduces large mammal biodiversity and has myriad other effects on ecosystem services (Hempson et al. 2017, Wilcox et al. 2018, Buisson et al. 2019). In contrast, fire and wildlife browsing generally suppress bush encroachment (Staver et al. 2009). We find that by increasing small-scale fire heterogeneity, wildlife may create refugia that promote sapling resprouting postfire, and consequently may have indirect positive effects on brushy species. While the basic drivers of woody encroachment and conversely, grassland maintenance have been well studied, we are still unravelling the complexities of their interactions (Fuhlendorf et al. 2009).

The research presented here experimentally demonstrates the importance of considering interactive effects of herbivory and fire as they influence small-scale heterogeneity in savanna grass fuel, leading to more heterogeneous burns. Furthermore, we show that even small unburned patches can serve as refugia for tree saplings, suggesting that attention to the spatial scale of pyric-herbivory warrants more attention in elucidating the complexity of tree–grass dynamics.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3270/suppinfo

Data Availability Statement

Data and code are available on Figshare (Werner 2020): https://doi.org/10.6084/m9.figshare.11861184