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Spatial scales influence long-term response of herbivores to prescribed burning in a savanna ecosystem

Duncan M. Kimuyu[A,B,F], Ryan L. Sensenig[B,C], Robert M. Chira[D],
John M. Githaiga[D] and Truman P. Young[B,E]

[A]School of Natural Resources and Environmental Studies, Karatina University,
  PO Box 1957-10101, Karatina, Kenya.
[B]Mpala Research Centre, PO Box 555-10400, Nanyuki, Kenya.
[C]Department of Biological Sciences, Goshen College, Goshen, IN 46526, USA.
[D]School of Biological Sciences, University of Nairobi, PO Box 30197-00100, Nairobi, Kenya.
[E]Department of Plant Sciences, University of California, Davis, CA 95616, USA.
[F]Corresponding author. Email: dkimuyu@gmail.com

Abstract. Both wild and prescribed fire in savanna ecosystems influence habitat use by herbivores by creating or maintaining spatial and temporal heterogeneity in forage quality and vegetation cover. Yet little is known about how spatial scales influence long-term persistence of fire effects. We examined changes over a 6-year period in herbivore preference for experimentally burned patches that varied in spatial extent and grain. Avoidance for the burns by elephants and preference for the burns by impala and Grant's gazelle decreased significantly. For the rest of the species (zebra, eland, oryx, hartebeest, warthog and hare), there were no significant changes in preference for the burns. Changes in preference for the burned areas depended on the spatial extent and grain of the burn, with intermediate-size (9-ha) burns and large (8-ha) patchy burns being more preferred 6–7 years after fire. Grain, but not the spatial extent of the burned area, influenced changes in grass height. Fire resulted in a delayed reduced tree density irrespective of the spatial scale of the burn. Results of this study indicate that, depending on the scale of fire prescription, the impacts of fire on herbivores may last longer than previous studies suggest.

Additional keywords: dung survey, fire frequency, habitat heterogeneity, Laikipia, patchiness, tree cover.

Introduction

Landscape heterogeneity is an important element in savanna ecosystems (Parr and Brockett 1999). It affects ecosystem function (Christensen 1997; Wiens 2002; Turner and Chapin 2005; Porensky and Veblen 2012) and to a great extent influences the persistence (Parr and Brockett 1999; du Toit 2003; Fuhlendorf *et al.* 2006; Fraterrigo *et al.* 2009; Fahrig *et al.* 2011; Miyashita *et al.* 2012), distribution (Morales and Ellner 2002) and movement patterns (Christensen 1997; Wiens 1997; Barraquand and Benhamou 2008) of herbivores in savanna landscapes. Hence, both natural processes and management interventions that create or maintain spatial and temporal heterogeneity are increasingly being promoted as ways to achieve biodiversity conservation goals and sustainability of ecosystem function (Benton *et al.* 2003; Fahrig *et al.* 2011; Kisel *et al.* 2011).

In most savanna ecosystems, fire has played a predominant role in creating and maintaining landscape heterogeneity, either by influencing pasture quality and productivity (Parr and Brockett 1999; Gureja and Owen-Smith 2002; Archibald *et al.* 2005; Sensenig *et al.* 2010) or by changing tree cover (Sankaran *et al.* 2005; Higgins *et al.* 2007; Bond 2008; Holdo *et al.* 2009). Fire

increases forage quality by removing moribund herbage material and stimulating highly nutritious fresh growth with higher concentrations of some nutrients such as nitrogen, phosphorus, potassium, magnesium and copper (Van de Vijver *et al.* 1999; Laclau *et al.* 2002; Eby *et al.* 2014). The effects of fire on tree cover can be categorised as either immediate effects, such as heat-induced stress, damage or mortality on trees (first-order effects), or delayed effects resulting from post-fire interaction of direct fire effect and other factors, such as drought and herbivory (second-order effects) (Ryan and Elliot 2005; Reinhardt and Dickinson 2010). Although some of the effects of fire on forage quality are ephemeral, declining within a few months (Van de Vijver *et al.* 1999; Eby *et al.* 2014), the effects of fire on forage digestibility, leaf stem ratio and tree cover may persist for longer periods after fire (Van de Vijver *et al.* 1999).

Persistence of fire-induced heterogeneity likely depends on post-fire herbivory feedback. Burned areas generally attract high densities of herbivores owing to increased forage quality and greater predator visibility (Moe and Wegge 1997; Moe *et al.* 2009; Valeix *et al.* 2009; Sensenig *et al.* 2010; Eby *et al.* 2014). Herbivores thus attracted to burns may reinforce the initial impact of fire by maintaining pastures in short-cropped highly

nutritious condition for a long time after fire or maintaining low tree and herbaceous cover, hence greater visibility. Although herbivore preference for burned areas is widely documented, most of the studies tend to be short-lived (Zavala and Holdo 2005; Sensenig *et al.* 2010; Eby *et al.* 2014; Green *et al.* 2015) and only a few studies report long-term dynamics of herbivore preference for burned areas. Understanding temporal dynamics in herbivore response to fire is essential for development of fire prescriptions in savanna ecosystems.

Individual species vary greatly in their habitat requirements; hence, it is reasonable to expect that long-term dynamics in herbivore response to burned areas vary across species. For example, species-specific differences in nutritional require-ments, often driven by individual bodyweight and digestive physiology (hindgut versus foregut fermenters), could predict temporal dynamics in preference for burns. Also, because the spatial scales at which animals perceive landscape heterogene-ity vary greatly across species (Ritchie 1998; Sensenig *et al.* 2010; Allred *et al.* 2011), we might expect diverse responses to burns at different scales. Two elements of spatial scale are important in understanding herbivores' response to landscape heterogeneity: the extent (the overall area that is burned) and grain (the size of individual burned patches). Both extent and grain may have important implications for herbivore attraction to (or avoidance of) previously burned patches, and hence can influence the post-fire grazing pressure and persistence of the initial effects of fire.

By implementing a unique set of controlled burns of different spatial extents (81, 9 and 1 ha) and grain (patchy and continuous) in areas with similar soil type and rainfall intensity, Sensenig (2007) demonstrated strong effects of spatial scale on attraction (or avoidance) of different herbivore species to burned areas within the first 2 years after burning. However, information regarding long-term persistence of these initial preference patterns for burned areas is generally lacking. We resurveyed these burns 6–7 years after fire: (i) to examine how preference patterns by different herbivore species had changed over time; (ii) to examine the effect of spatial scale on such preference patterns; and (iii) to examine correlations between tree cover and grass height and preference for the burned plots. The unique design of this experiment allowed us to test, for the first time, the influence of spatial scales on the long-term persistence of fire effects. This information could be useful in informing fire prescriptions to achieve a range of ecological and management goals.

Materials and methods

Study area

We conducted the present study on four ranches in Laikipia, Kenya: Mpala, Jessel, Segera and Ol Pejeta. All four ranches are located in the Laikipia Plateau on the dry leeward side of Mount Kenya at an altitude of 1800 m above sea level (see Fig. S1 available as online supplementary material). The area receives a weakly trimodal rainfall averaging 500–700 mm annually, with a distinct dry season in December to March. The common wildlife species on the four ranches include elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*), plains zebra (*Equus burchelli*),

Grevy's zebra (*Equus grevyi*), Defassa waterbuck (*Kobus ellipsiprymnus*), oryx (*Oryx beisa*), hartebeest (*Alcelaphus buselaphus*), warthog (*Phacochoerus africanus*), Grant's gazelle (*Gazella granti*), impala (*Aepyceros melampus*), Thomson's gazelle (*Eudorcas thomsonii*), steinbuck (*Raphicerus campes-tris*) and hare (*Lepus* spp.). Management of the four ranches is similar in many ways, including integration of livestock pro-duction (mainly cattle (*Bos indicus*)) with wildlife conservation and application of prescribed burning. Our study plots were all located in homogeneous heavy clay (black cotton) vertisols. The overstorey in this system is dominated by *Acacia drepanolobium* trees, which make up 97% of the woody vegetation (Young *et al.* 1997). Minor woody species include *Balanites aegyptica*, *Rhus natalensis* and *Acacia mellifera*. The herbaceous layer is domi-nated by the perennial grass species *Pennisetum stramineum*, *P. mezianum*, *Themeda triandra*, *Brachiaria lachnantha* and *Lintonia nutans*, and common herbs include *Aspilia pleuriseta*, *Commelina* spp., *Solanum incanum* and *Pseudognaphalium* sp. (Porensky *et al.* 2013, suppl. 1).

Experimental plots

Data for the present study were collected from a series of experimental burn plots established in 2004 and 2005 as part of the Scale and Fire Ecology (SAFE) project that used fire to manipulate landscape heterogeneity at different spatial scales (Sensenig *et al.* 2010). A total of 18 plots were burned at the end of the dry season, just before the long rains, in February–March in 2004 and 2005. The 18 plots varied in both their extent (total area) and their grain (finest scale of resolution). Total burn extent varied at three levels: 1, 9 and 81 ha. Each size class was burned at two levels of grain: 'continuous' and 'patchy'. The patchy burns consisted of a quasi-random pattern of burned patches interspersed with unburned patches whereas the con-tinuous burns consisted of a continuous block of burned area (Fig. S2). A complete set of treatments was implemented in 2004 and two or three replicates per treatment were added in 2005, except for the 81-ha patchy burn, which was not replicated owing to the rigorous burning protocol. In total, there were four 81-ha, four 9-ha and three 1-ha continuous burns, and one 81-ha, three 9-ha and three 1-ha patchy burns (Table S1). To maximise treatment independence, all burned plots were at least 1 km apart. See Sensenig *et al.* (2010) for more details.

Data collection

Dung counts were used to compare presence of herbivores in the burned plots and in the unburned matrix. Although there have been concerns about the use of dung counts as measures of mammal densities (Fuller 1991), including evidence for sea-sonality and habitat effects on decomposition rates (Vernes 1999; Nchanji and Plumptre 2001; Rivero *et al.* 2004), there is ample evidence from our study system (Augustine 2003; Augustine *et al.* 2003; Young *et al.* 2005; Riginos 2015) and elsewhere (Altendorf *et al.* 2001; Marques *et al.* 2001; Blake 2002; Rasmussen *et al.* 2005; Daniels 2006; Lunt *et al.* 2007) that dung counts are robust for comparing relative habitat use by large mammals within a species, habitat type and rainfall period. In the present study, dung counts were used as relative assays of animal presence, within a homogeneous habitat patch. For these

purposes, it appears that dung counts are reliable measures in this ecosystem (Augustine *et al.* 2003; Young *et al.* 2005).

Dung counts were conducted along four 4 m-wide fixed transects located at intervals of 20 m in 1-ha burns, 40 m in 9-ha burns and 200 m in 81-ha burns. To estimate wildlife presence in unburned areas near the treatments, two control transects were laid out perpendicular to each burned plot extending 200, 400 and 1200 m into the unburned matrix in the 1-, 9- and 81-ha burns respectively.

Dung was surveyed throughout each transect, recorded by species and subsequently crushed to avoid recounting in the next survey. Dung piles for all major herbivore species could be identified to species in the field, with two exceptions. The dung of cattle and buffalo could not be distinguished, and were counted together. The dung of plains and Grevy's zebras also could not be distinguished from each other and were grouped together as 'zebra'. However, plains zebra far outnumbered Grevy's zebra in the study system during the study period, so zebra dung counts are essentially plains zebra.

During the first surveys (in 2006, 1–2 years after the fire), four dung surveys were conducted (Sensenig *et al.* 2010), whose results were averaged in the present study. A single survey was conducted during the second round of surveys (in 2011, 6–7 years after the fire). To account for differences in dung accumulation time, we used preference index rather than absolute counts to compare the two survey periods (see *Data analyses* section).

Two of the 18 burned plots were excluded from analysis in this study because they had undergone significant managerial manipulations. One of these (1-ha continuous) had been reburned (accidental fire), whereas a cattle 'boma' (corral) had been constructed on the other one (9-ha continuous) (Table S1).

To test for correlations between tree density (index of tree cover) and grass height (index of grass cover and quality) and preference for the burns, we measured grass height and counted trees along transects in the burns and unburned areas. Previous work has demonstrated that grass height in this system is negatively correlated with crude protein and positively correlated with acid detergent fibre (ADF) (Sensenig 2007); hence, changes in grass height could be indicative of changes in forage quality (Arsenault and Owen-Smith 2002; Pavlů *et al.* 2006). Measurements on grass height were done at 15-m intervals along each of the dung transects. For tree density, we counted all trees along a 10-m-wide belt transect running through the entire length of the burned plot and extending into the unburned matrix for an equal length. We also measured individual heights of each tree within the belt transects.

Data analyses

For each herbivore species, burn preference index was calculated as the ratio of dung density in burned areas divided by the dung density in both burned and unburned area. Preference index ranges from 0 to 1, where 0 indicates complete avoidance, 1 indicates complete preference for burned areas, and 0.5 indicates equal use of burns and unburned areas. The use of preference indices instead of absolute dung count values helps to: (i) minimise seasonality effects such as differential dung decomposition; (ii) account for potential landscape variability in wildlife abundance; and (iii) allow comparisons to be made

between herbivore species and across different sampling periods. To examine changes in preference of the burned areas across the two surveys, separate β regression models (Ferrari and Cribari-Neto 2004) were fitted for each species using the 'betareg' package in *R* (R Development Core Team 2009). Beta regression is a form of generalised linear models that assumes that the response variable is β-distributed and occurs in a continuous unit scale with a bounded range. To convert the preference values from open unit range (values occur between 0 and 1 with possibility of obtaining a value that is either 0 or 1) to a bounded unit range (values occur between 0 and 1 but no possibility of obtaining a value that is either 0 or 1), the following rescaling transformation was applied: $y' = [y(N - 1) + s]/N$, where s is a constant between 0 and 1 (serving as a prior from a Bayesian standpoint), and N is the sample size (Smithson and Verkuilen 2006). To test for changes in preference over time, we first fitted a global model including interaction between species and survey period. We then tested for the species-specific changes by fitting separate models for each species. In both approaches, we included plot ID as a fixed effect to control for differences across plots. To test whether species-specific changes in preference for the burns over time were influenced by digestive physiology and bodyweight, we fitted separate models including interactions between digestive physiology, bodyweight and the survey period. We then tested for the interactive effects of spatial extent and grain of the burns on changes in preference for the burns over time. Finally, to identify factors driving preference for the burns, we built a candidate set of 432 generalised linear models with the following predictors and their first-order interactions: grass height, tree height class (trees taller than 0.8 m and trees shorter than 0.8 m) and herbivore species. We then ranked these models using corrected Akaike Information Criterion (AIC$_C$) to obtain the most parsimonious model (Burnham and Anderson 2002).

Results

A total of 131 556 dung piles were counted during the initial four surveys completed 1–2 years after burning and 75 536 during the single later survey completed 6–7 years after burning. Data for nine herbivores species were analysed, of which four were hindgut fermenters (elephant (3900 kg), zebra (275 kg), warthog (69 kg), and hare (2 kg)) and five were foregut fermenters (eland (475 kg), oryx (205 kg), Grant's gazelle (55 kg), hartebeest (144 kg), impala (53 kg) – bodyweights obtained from Sensenig *et al.* (2010)). Cattle (whose movements are largely dictated by herders) and buffalo (whose dung could not be distinguished from cattle dung) were not included in dung analyses. Thomson's gazelle and Defassa waterbuck were also excluded from analyses because they occurred in relatively low densities and were completely absent in at least 25% of all the burned plots. Giraffe and steinbuck, the only two pure browsers in this study system, were also excluded from analyses because this study was primarily focused on herbivores' response to fire-induced grass heterogeneity.

Changes in preference for the burned areas

Herbivores still preferred burned areas, even 6–7 years after fire. Overall preference for the burns decreased by only 3% (from
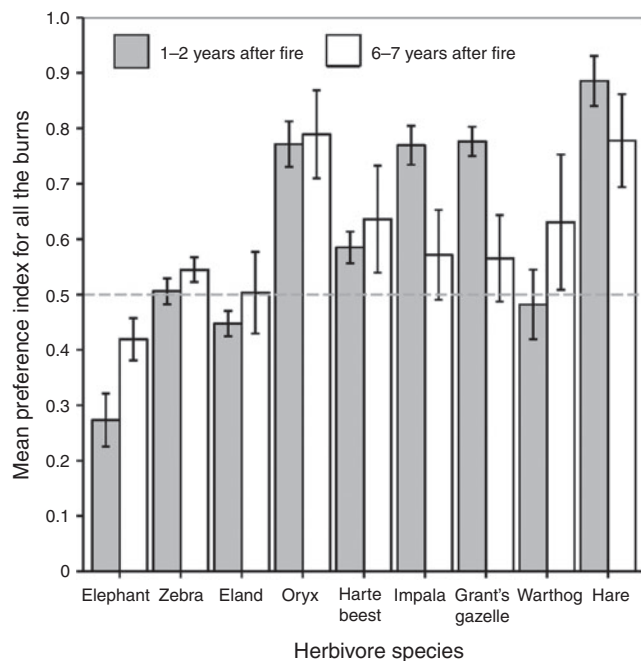
0.61 to 0.59) between the initial surveys (1–2 years after the burns) and the second survey (6–7 years after the burn). However, this obscures greater species-specific responses, which included both significant increases and decreases in preference. After controlling for plot effect (different grain and spatial extent), preference for the burns by different species varied significantly between the two survey periods (Table S2*a*: species × survey period: $P = 0.023$).

Three species (elephant, eland and warthog) avoided the burns (preference index less than 0.5) during the first surveys but only elephants avoided the burns during the second survey (Fig. 1). Even so, avoidance of the burns by elephant decreased by 38% between the first survey and the second survey (Table S2*b*: $P = 0.011$). However, preference for the burns by Grant's gazelle decreased by 13% between the first and the second survey (Table S2*b*: $P = 0.028$), and impala's preference for the burns tended to decrease (Table S2*b*: $P = 0.073$). For the rest of species (zebra, eland, oryx, hartebeest, warthog and hare), we did not find significant changes in preference (or avoidance) for the burned areas (Table S2*b*).

Influence of bodyweight and digestive physiology

Changes in preference (or avoidance) for the burns between the two survey periods depended on individual species bodyweight (Table S3*a*: bodyweight × survey period: $P = 0.029$) but not significantly on digestive physiology (Table S3*a*, gut type × survey period: $P = 0.17$). Although preference for the burns was inversely correlated with herbivore bodyweight

during both survey periods (Fig. 2, Table S3*b*), this relationship was stronger 1–2 years after the burns (first survey; $r^2 = 0.74$; $Z = -4.25$, $P < 0.001$) than 6–7 years after the burns (second survey; $r^2 = 0.48$; $Z = -2.74$, $P = 0.006$).
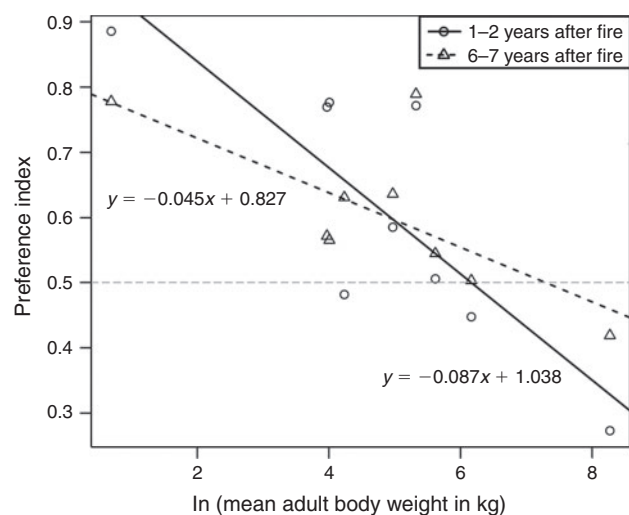
Effects of spatial extent and grain of the burns

Changes in overall preference for the burned areas between the first and the second survey period depended on both spatial extent and the grain of the burned plots (Table S4: survey × extent × grain: $Z = 10.58$, $P = 0.001$). Preference for the largest patchy burns (81-ha patchy) increased, thus becoming the most preferred burn 6–7 years after fire, whereas preference for 81-ha continuous burns and all the intermediate-size burns (9-ha, both continuous and patchy) remained essentially unchanged (Fig. 3). The smallest burns (1-ha) shifted from being preferred to avoided, with a 21 and 18% reduction in preference index for patchy and continuous burns respectively. Overall, the change in herbivore preferences between 1–2 years and 6–7 years after fire was significantly positively correlated with burn diameter ($r^2 = 0.71$; $F_{1,4} = 9.81$, $P = 0.03$).

Differences in grass height and tree density between the burned and unburned areas

Although the burned plots were initially set up in areas with similar tree density to the surrounding matrix (Sensenig 2007), the density of taller trees (>0.8 m) in burned areas decreased by 42% over the 6–7-year period after the fire, resulting in significantly fewer trees in the burned than unburned areas (Fig. 4*a*: $F_{1,20} = 12.28$, $P = 0.002$). However, the density of smaller trees (less than 0.8 m) increased in burned areas relative to unburned areas, albeit not significantly (Fig. 4*b*: $F_{1,20} = 0.41$, $P = 0.53$). For both height classes, there were no significant effects of the spatial extent or grain of the burn tree density (Table S5).

Average grass height was significantly shorter in burned areas (14.2 ± 1.3 cm) than unburned areas ($31.4 + 2.0$ cm) during the first survey ($F_{1,30} = 51.42$, $P < 0.001$). During the

Fig. 1. Changes in individual species' preference for the burned areas between the initial sampling period (1–2 years after fire) and the second sampling period (6–7 years after fire). Values less than 0.5 indicate avoidance, values greater than 0.5 indicate preference, while 0.5 indicates equal presence in burned and unburned areas. Error bars represent standard error bars.

Fig. 2. Relationship between herbivores' bodyweight and their preference for the burns during the first sampling period and the second sampling period. Bodyweights were obtained from Sensenig *et al.* (2010).

second survey, there were no longer significant differences ($F_{1,30} = 0.14$, $P = 0.71$) between burned and unburned areas in grass height. Changes in grass height in the burned plots between the first and the second survey period depended on the grain (Table S6: grain × survey interaction: $F = 4.74$, $P = 0.04$), but not the spatial extent of the burns (Table S6: $F = 0.52$, $P = 0.60$). For continuous burns, grass height increased significantly between the two survey periods (Fig.5a)

Fig. 3. Changes in overall preference of burns of different spatial extents (1-, 9- and 81-ha) and grain (continuous and patchy).

$F = 6.10$, $P = 0.02$), but there were not significant changes in patchy burns (Fig. 5b; $F = 0.69$, $P = 0.43$).

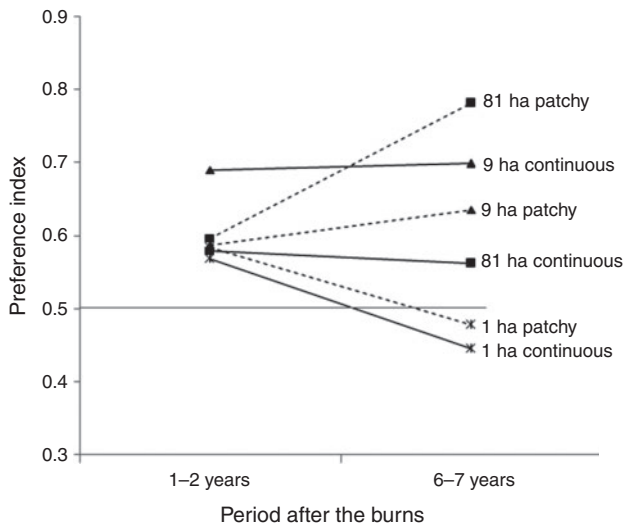*Effects of trees and grass on preference for the burned plots*

From 432 candidate models testing the independent or interactive effects of grass height and tree density (trees shorter than 0.8 m and trees taller than 0.8 m) on preference for the burns by individual species, the best-fitting model (Akaike weight $wi = 0.51$) included only the main effects of grass height (Table S7). Overall preference for the burns was negatively correlated with grass height (ratio in burned vs unburned plots).
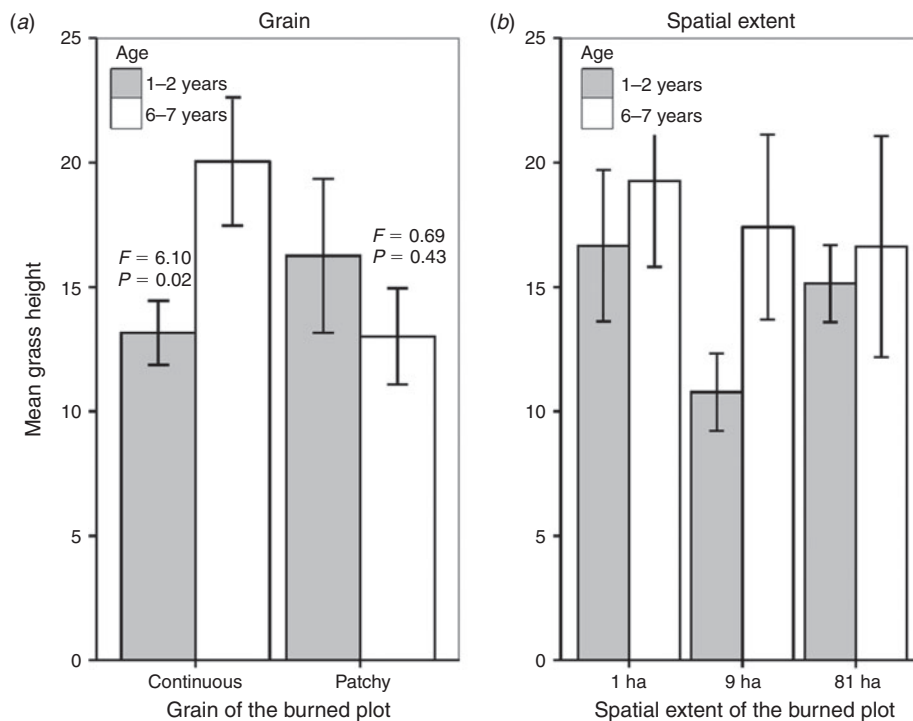
Discussion

This study provides evidence that herbivores' response to fire-induced heterogeneity persists for at least 6 years after fire. However, this response varied across individual species (in some systematic ways) and depended on the spatial scale (extent and grain) at which the burning was implemented. Intermediate-size (9-ha) burns and large (81-ha) patchy burns were most preferred 6–7 years after fire whereas small burns (1-ha both patchy and continuous) were the least preferred. Grain, but not the spatial extent of the burned area, influenced changes in grass height. Fire resulted in a delayed reduced tree density irrespective of the spatial scale of the burn.

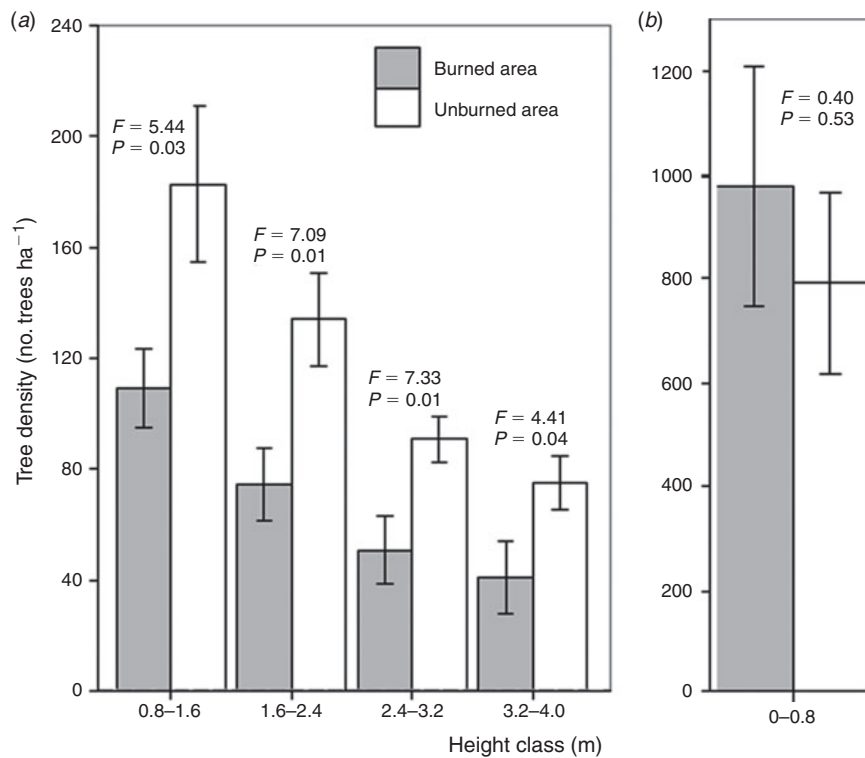*Long-term response of herbivores to fire*

Three mechanisms may explain the observed long-term preference by herbivores for burned sites. The first mechanism relates to herbivores maintaining burned areas as grazing lawns.

Fig. 4. Changes in average grass height between the first survey (1–2 years) and the second survey (6–7 years), in just the burned areas for burns of different (*a*) grain (continuous and patchy); and (*b*) spatial extent (1, 9 and 81 ha). Error bars represent standard error bars.

Fig. 5. Differences in the density of trees in burned areas relative to unburned areas for trees (*a*) taller than 0.8 m; and (*b*) shorter than 0.8 m. Error bars represent standard error bars.

Because burned areas attract large numbers of herbivores (Klop *et al.* 2007; Sensenig *et al.* 2010; Greene *et al.* 2012; Riginos *et al.* 2012; Eby *et al.* 2014), their preferential foraging in burns may maintain the herbaceous vegetation in short and nutritious state for a long time after fire. However, most studies on post-fire forage quality suggest that this increase in forage palatability is transient, lasting for only up to a year (Batmanian and Haridasan 1985; Van de Vijver *et al.* 1999; Green *et al.* 2015). Although the present study did not compare forage quality directly (i.e. crude protein or ADF) between burned and unburned sites 6–7 years after fire, a large decrease in the quality of post-fire regrowth was recorded within the first year after burning (Sensenig *et al.* 2010). Consistent with this, there were no significant differences in grass height between burned and unburned plots 6–7 years after fire. This suggests the observed long-term preference patterns are not likely to be primarily driven by forage quality.

A more plausible explanation for the observed long-term preference for the burned areas may be changes in vegetation cover. Fire modifies habitat structure either by directly reducing tree and shrub cover (Van Langevelde *et al.* 2003; Bond 2008; Staver *et al.* 2009) or indirectly through intensifying browsers' impact on trees in burned sites (Holdo *et al.* 2009; Staver *et al.* 2009; Gordijn and Ward 2014). In the current study system, browsers (particularly elephants) appear to interact synergistically with fire to reduce the densities of the mono-dominant *Acacia drepanolobium* trees (Okello *et al.* 2008; Wahungu *et al.* 2010; Wahungu *et al.* 2011; Pringle *et al.* 2015). In either case,

there was a large (>40%) reduction in the density of tall (>0.8 m) *Acacia drepanolobium* trees in the burned plots in the current study (Fig. 4*a*). As most of the large wild herbivores in the study system prefer more open areas (lower tree densities) owing to enhanced ability to detect predators (Augustine *et al.* 2011; Riginos 2015), it is likely that this reduction in tree cover is continuing to draw herbivores to previous burns long after the effect of fire on forage quality has faded.

Long-term attraction of herbivores could also relate to changes in forage composition after fire. Fire may facilitate the growth of palatable species (Greene *et al.* 2012) or increase species diversity (Savadogo *et al.* 2007) by creating open microsites for plant establishment (Morgan 1998; Pourreza *et al.* 2014), altering the soil environment (Marion *et al.* 1991; Neff *et al.* 2005) and triggering germination of seed-banking species (Keeley 1991; Brown and van Staden 1997; Crosti *et al.* 2006). This increase in floristic diversity may result in higher density and diversity of faunal assemblage (Elliott *et al.* 2011). In addition, herbivores attracted to the burns may also promote floristic diversity through intensive grazing or trampling, which creates open microsites in the same way as fire (Porensky *et al.* 2013). Although the present study did not investigate compositional dynamics of herbaceous vegetation, an increase in abundance of *Themeda triandra* with respect to three other dominant grasses in this system (*Pennisetum mezianum*, *P. stramineum* and *Brachiaria lachnantha*) was recorded earlier in the study (Sensenig 2007). Burning breaks seed dormancy in *Themeda triandra*, promoting its post-fire recruitment (Baxter and Van Staden 1994; Baxter *et al.* 1994).

Although *Themeda triandra* has a lower crude protein content than the three other dominant grasses in this system (Sensenig 2007), it is a preferred grass species for herbivores (Novellie and Kraaij 2010).

Influence of bodyweight and digestive physiology

Extending the timeframe of previous studies (Wilsey 1996; Sensenig *et al.* 2010; Riginos *et al.* 2012; Eby *et al.* 2014), we found that the bodyweight of herbivores is a significant predictor of preference for burns even 6–7 years after fire. However, the observed decrease in the strength of the relationship between preference for the burns and bodyweight suggests a trend towards herbivores being less discriminating between burned and unburned areas over time (both positively and negatively).

Although small herbivores prefer the green flushes that emerge immediately after fire, and may exclusively feed in burned areas, large herbivores have to strike a balance between feeding on high-quality but limited forage in burns and feeding on readily available but less nutritious forage in unburned areas. Thus, as forage regrows towards preburn status and becomes less nutritious, the burns may become less attractive to small herbivores but more attractive (or less avoided) by large herbivores. This argument is also supported by the trend towards increase in preference for burns by hindgut fermenters (which require a higher quantity and can tolerate lower-quality forage for the same body size) and decrease in preference for foregut fermenters (which require a lower quantity but high-quality forage; Sensenig *et al.* 2010).

Influence of spatial scale

We found evidence in support of the idea that long-term attraction of herbivores to burned areas depends on the spatial scale of the fire treatment. There was a trend towards intermediate-sized (9-ha) burns being attractive to herbivores for the longest time (see Fig. 3). Also, long-term preference for burns with the largest spatial extent (81 ha) diverged depending on the grain, with patchy burns becoming more preferred over time and continuous burns not showing pronounced changes over time. The observed avoidance for small-size burns can be explained by the lack of adequate resources to support large densities of herbivores. Even though a substantial number of herbivores may visit small burns, a lower amount of dung in burned compared with unburned area suggests that herbivores spend disproportionately less time in the burns. Although the mechanism for this scale-mediated effect is not clear from this study, our findings support the idea that spatial scales, particularly spatial extent and grain, influence the response of large herbivores to heterogeneity in the landscape, and hence fire–herbivory interactions.

Conclusions

Our results demonstrate that fire can exert lasting effects in the landscape and that the longevity of herbivore response to fire depends on the spatial scale at which fire is applied. Also, different herbivore species respond to burning differently, with some species avoiding burns generally, others preferring burns more during early successional stages and others preferring burns more during later successional stages. Future work should focus on elucidating the mechanism driving the observed long-term preference patterns. As a recommendation to managers interested in promoting herbivore diversity, it would be more beneficial implementing several interspersed burns of intermediate size than one big or small burn. However, these results are highly contingent on post-fire grazing and browsing intensity and therefore should be interpreted with caution.

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