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Native and domestic browsers and grazers reduce fuels, fire temperatures, and acacia ant mortality in an African savanna

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Abstract. Despite the importance of fire and herbivory in structuring savanna systems, few replicated experiments have examined the interactive effects of herbivory and fire on plant dynamics. In addition, the effects of fire on associated ant–tree mutualisms have been largely unexplored. We carried out small controlled burns in each of 18 herbivore treatment plots of the Kenya Long-term Exclosure Experiment (KLEE), where experimentally excluding elephants has resulted in 42% greater tree densities. The KLEE design includes six different herbivore treatments that allowed us to examine how different combinations of megaherbivore wildlife, mesoherbivore wildlife, and cattle affect fire temperatures and subsequent loss of ant symbionts from *Acacia* trees. Before burning, we quantified herbaceous fuel loads and plant community composition. We tagged all trees, measured their height and basal diameter, and identified the resident ant species on each. We recorded weather conditions during the burns and used ceramic tiles painted with fire-sensitive paints to estimate fire temperatures at different heights and in different microsites (under vs. between trees). Across all treatments, fire temperatures were highest at 0–50 cm off the ground and hotter in the grass under trees than in the grassy areas between trees. Plots with more trees burned hotter than plots with fewer trees, perhaps because of greater fine woody debris. Plots grazed by wildlife and by cattle prior to burning had lower herbaceous fuel loads and experienced lower burn temperatures than ungrazed plots. Many trees lost their ant colonies during the burns. Ant survivorship differed by ant species and at the plot level was positively associated with previous herbivory (and lower fire temperatures). Across all treatments, ant colonies on taller trees were more likely to survive, but even some of the tallest trees lost their ant colonies. Our study marks a significant step in understanding the mechanisms that underlie the interactions between fire and herbivory in savanna ecosystems.

Key words: Acacia drepanolobium; *cattle;* Crematogaster; *elephants; herbivory; Kenya; Laikipia; livestock; mutualism;* Tetraponera.

Introduction

Fire and herbivory are important drivers in savanna systems, playing key roles in structuring tree–grass coexistence (reviewed in Sankaran et al. 2005, 2008), landscape heterogeneity (Fuhlendorf and Engle 2004, Kerby et al. 2007, Waldram et al. 2008, Allred et al. 2011), forage quantity and quality (Sensenig et al. 2010), and plant productivity (Holdo et al. 2009). Although it is well documented that both fire (Mapiye et al. 2008, Levick et al. 2009, Winston and Trollope 2011) and herbivory (McNaughton et al. 1988, Levick et al. 2009) independently affect savanna ecosystems, there is increasing interest in understanding their potentially interactive effects on tree and grass dynamics. A variety of modeling approaches (van Langevelde 2003, Baxter and Getz 2005, Holdo et al. 2009) and empirical studies (Dublin et al. 1990, Moncrieff et al. 2008) have suggested that fire may interact with grazing and browsing in complex ways (Collins and Smith 2006) to create systems that are dynamic and nonequilibrial (Bond and Keeley 2005), changing at various scales in space and time (Gillson 2004, Archibald et al. 2005).

Understanding the mechanisms underlying how fire and herbivory interact with changes in tree cover in particular has both important theoretical and applied implications, since variation in savanna woody cover affects livestock production, wildlife conservation, predator–prey interactions, nutrient cycling, and carbon storage (Scholes and Archer 1997, Angassa and Baars 2000, van Auken 2000, Bond and Keeley 2005, Riginos and Grace 2008). In particular, there is a lack of controlled replicated experimental studies that quantify (1) the separate and combined effects of domestic and

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native herbivores on fuel loads and fire temperatures and (2) the separate and combined effects of fire and subsequent herbivory on the survival of savanna trees. We address the former and describe the experimental design that will be used to test the latter.

A number of previous results have provided partial evidence for these interactions. For example, there is some evidence from African savannas (Hobbs 1996, O'Connor et al. 2011), North American grasslands (van Auken 2000), and Australian savannas (Leonard et al. 2010) that preburn grazing decreases fire frequencies and intensities. This suggests feedback loops between herbivory and fire that current models of savanna dynamics do not include (Sankaran et al. 2004). However, most existing information on the relationship among herbivores, herbaceous fuel load, and fire behavior is based on anecdotal observations (Nader et al. 2007), studies involving only domesticated herbivores (Savadogo et al. 2007, Gambiza et al. 2008, Davies et al. 2010), studies that do not control or monitor preburn grazing (Kerby et al. 2007), or those lacking replication (Leonard et al. 2010).

Ant mutualisms may mediate fire–herbivore interactions. Symbiotic ant species that reside on *Acacia drepanolobium* trees are effective in reducing browsing by megaherbivores (Madden and Young 1992, Palmer et al. 2008*a*, Martins 2010, Stanton and Palmer 2011), increasing individual tree fitness (Palmer and Brody 2007, Goheen and Palmer 2010, Palmer and Brody 2013), and stabilizing tree cover across the landscape (Goheen and Palmer 2010). To the extent that fire may weaken or destroy ant colonies (Palmer et al. 2008*b*), it may lead to subsequent shifts in ant species composition or declines in ant abundance across the landscape, either of which could make trees in burned areas more susceptible to browsing and the destructive effects of elephants, with subsequent cascades to other herbivore and plant guilds.

In order to tease apart these complex dynamics among diverse herbivores (wild and domestic, grazing and browsing), fire, savanna grasses, trees, and acacia ants, we implemented prescribed burns inside the replicated Kenya Long-term Exclosure Experiment (KLEE) in early 2013. By experimentally burning within different herbivore treatments, we were able to simultaneously test the effects of a diverse guild of herbivores on woody and herbaceous fuel loads and fire temperatures and will be able to quantify how postburn foraging by herbivores may be responsible for the delayed mortality of larger trees after a fire. To our knowledge, this is the first fully crossed, replicated, field experiment that independently manipulates fire and multiple guilds of domestic and wild large herbivores (but see Collins and Smith 2006, Collins and Calabrese 2012, Koerner and Collins 2014).

We address the following questions: (1) how do different guilds of herbivores indirectly affect burn temperatures by influencing woody and herbaceous fuel loads, (2) what are the patterns of ant colony survival after burning, and (3) do differences in ant colony survival and subsequent shifts in ant species composition or occupancy correlate with herbaceous fuel loads and burn temperatures?

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; 1810 m above sea level). This plant community overlies high clay black cotton soils and is representative of similar ecosystems that occur extensively throughout eastern and southern Africa. Rainfall averages 550–600 mm at our study site and is weakly trimodal, with a distinct dry season from December to March.

The whistling thorn tree, *Acacia drepanolobium*, accounts for 97% of woody cover at our study site (Young et al. 1998). At some branch nodes, *A. drepanolobium* produces hollow swollen thorns that serve as ant domatia. The trees also produce extrafloral nectaries at the bases of leaves to nourish symbiotic ants (Hocking 1970, Huntzinger et al. 2004). At our study site, each tree is occupied by one of four species of ants: *Crematogaster mimosae*, *C. sjostedti*, *C. nigriceps*, or *Tetraponera penzigi*. These ant species differ in various aspects of their behavior, including the average size and number of trees they occupy, their relative competitive abilities, their benefits to host trees (Young et al. 1997, Stanton and Palmer 2011), and their behavioral responses to fire. During a fire, *C. nigiceps* and *C. mimosae* evacuate domatia and take refuge in insulated cracks in the soil (Jaffe and Isbell 2009; T. Palmer, *personal communication*), reoccupying the tree after the fire. *Tetraponera penzigi* do not leave their domatia, and *C. sjostedi* take refuge in holes on tree stems, often created by *Cerambycidae* larvae (Palmer et al. 2008*a*).

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, C), wildlife (large mammals 15–1000 kg, W), and megaherbivores (elephants and giraffes, M). There are 18 plots, each 200 × 200 m, representing three replicate blocks of each of six combinations of large herbivores (Fig. 1). For details of the experimental design, see Young et al. (1998).

Controlled burns

In February and March 2013, we burned one 30 × 30 m subplot in each of the 18 4-ha KLEE plots (Fig. 1). Each burn therefore covered 2.25% of each plot. These subplots were situated within each plot using the following criteria: (1) subplots were located along the plot boundary that was most accessible for fire-fighting equipment, (2) local sources of landscape heterogeneity (e.g., termite mounds and old livestock enclosure sites)

were avoided, and (3) we attempted to select subplots that were similar with respect to the density and size structure of *Acacia drepanolobium* trees (>1 m tall). Understory composition was similar across these sites (see Young et al. 1998) with the exception of the plots excluding all large herbivores, which have experienced increases in forb cover and shifts in the relative abundances of the five dominant grass species due to KLEE treatment effects.

We refrained from grazing cattle in the KLEE plots for five months (one rainy and one dry period) prior to the burns. In early 2013, we estimated herbaceous fuel loads by harvesting all aboveground herbaceous biomass in three randomly located 1 × 1 m quadrats adjacent to each designated burn plot. This material was air dried to constant mass and weighed. Every tree (all size classes) in each burn plot was permanently tagged and its height and stem diameter measured at 15 cm (for trees >1 m tall) or at the base (for trees <1 m tall). A total of 4304 trees were tagged and measured (mean per plot, 240; range, 130–359). In addition, the species identity of each tree's resident ant was recorded, as was evidence of the presence of stem-boring cerambycid beetle damage.

In 2011, we documented the effects that elephants had on *Acacia drepanolobium* densities by carrying out surveys in each of the 18 KLEE plots, six of which allowed elephants and 12 of which did not (see Fig. 1). We counted all trees within three 100 × 4 m transects (1200 m^2 total per plot). Trees were categorized into height classes: <1.00 m, 1.00–1.99 m, 2.00–2.99 m, 3.00–3.99 m, and ≥4.00 m). We did not survey the burn subplots for fine woody debris before the burns, so instead we documented the general relationship between tree density and fine woody debris. In July 2013, along 10 of the same (unburned) transects surveyed for tree density in 2011, we collected and weighed all fine woody debris (FWD; dead woody material on the ground with diameters <2.0 cm) within 1 m of each transect line (a 100 × 2 m transect).

We monitored fire temperatures with ceramic tiles painted with Tempilac (LA-CO Industries, Elk Grove Village, Illinois, USA) paints. We used paints designed to melt at each of the following six temperatures: 80°C (175°F), 150°C (300°F), 260°C (500°F), 400°C (750°F), 510°C (950°F), and 620°C (1150°F). We placed 18 tiles in each burn plot: two in each of three grassy areas away from trees and four on each of three separate, randomly chosen trees. In each open grassy sampling location, we placed one tile on the ground (under any leaf litter present) and attached one to a piece of rebar at 50–60 cm above the ground. At each tree, we placed one tile on the ground (under any leaf litter present) and attached three tiles to the tree, one at 100 cm, one at 180–200 cm, and one at 270–300 cm above the ground.

Firebreaks were established between 13 January and 6 February 2013. A 1–2 m wide swath was slashed to a vegetation height of 5–10 cm. In addition, for many

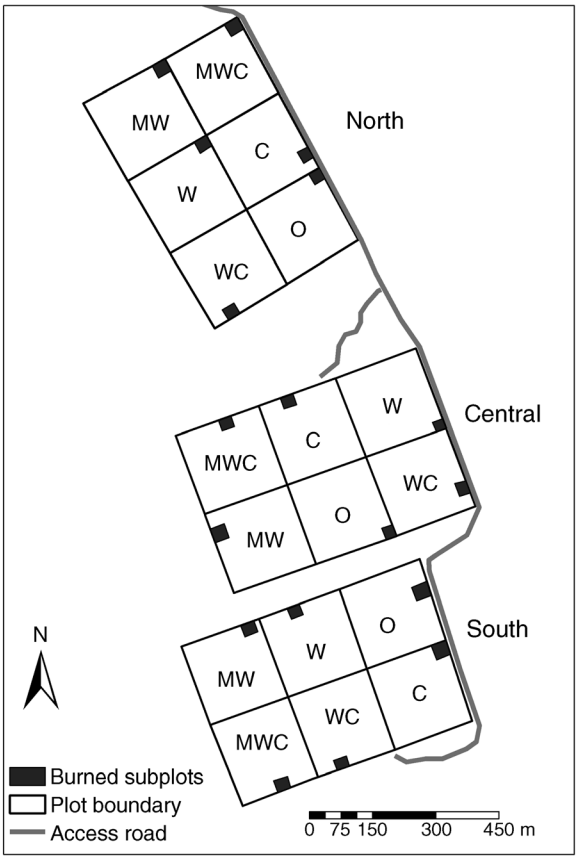

FIG. 1. Schematic of the Kenya Long-term Exclosure Experiment (KLEE) plots and the burned subplots (solid squares) within each. The letters inside each plot indicate the large herbivores allowed: C, cattle; M, megaherbivores (elephants and giraffes); W, nonmegaherbivore wildlife >15 kg; O, all large herbivores excluded.

subplots, either an access road or cleared fence lines provided firebreaks. Over a period of three days (28 February–2 March 2013), a single burn was completed in each of the 18 subplots. Burn boundaries were wetlined and then back-burned to create 5–10 m of firebreak along downwind edges. The interiors of all plots were burned using head fires with two technicians simultaneously lighting the upwind edges to create a perimeter ring fire. Flame heights ranged from less than 1 m to a maximum of 3–4 m. From first ignition to the end of the burn, each lasted between 8 and 13 minutes (two-thirds of the burns were 9–11 minutes). All burns consumed virtually all of the understory vegetation (save some tussock bases) and fine woody debris. Each day's burning began at ~08:00 (07:47–08:06) and finished approximately midday (11:17–12:15).

On each burn day we periodically recorded air temperature, wind temperature, and relative humidity (Appendix B). Air temperatures during the burns ranged from 15° to 28°C, increasing during the course of each day. Winds ranged from 3.5 to 12.5 km/h, increasing during the course of each day. Relative humidity ranged

TABLE 1. ANOVA for the effects of cattle, wildlife, and block on the densities of trees >1 m tall, mean herbaceous fuel loads, and mean minimum fire temperatures across all tile locations (heights).

		Tree density		Herbaceous fuel load		Minimum temp	
Source	df	*F*	*P*	*F*	*P*	*F*	*P*
Block	2	9.32	0.0004	7.41	0.008	3.74	0.055
Cattle	1	0.33	0.57	28.7	0.0002	6.91	0.022
Wildlife	2	6.14	0.004	9.95	0.003	3.65	0.058
Error	48						

Notes: Tree density data are from the overall plots, not the burn subplots, which were selected to reduce variation in tree density. Mean fuel loads and minimum fire temperatures are from burn subplots.

from 80% to 30%, declining during the course of each day.

To quantify the presence or absence of acacia ants in the first week after the burns, we carried out a survey of trees in the burned plots for a random subset of 30–50 tagged trees in each plot. Data on the fate of individual trees in the burns could not be collected at that time because rains had not yet fallen that would result in either a flush of leaves from aboveground shoots or the coppicing of top-killed trees. (These data will be reported in subsequent publications).

At the same time, we collected the ceramic tiles and scored them for the lowest temperature class of paint melted by the fire (minimum fire temperature). If none of the paints melted, a default of 20°C (air temperature) was used for analysis. For 12 tiles (<4% of the total), the higher temperature paints were charred and not readable. These may have been the hottest tiles; all but one were at ground level, and nine out of these 11 were under trees. This represented 17% of the tiles at ground level under trees, and our minimum temperature estimates for these locations should be considered conservative.

Statistical analyses

Tree densities, mean herbaceous fuel loads, mean fire temperatures, and ant survivorship (percentage of trees retaining their ants) were calculated for each of the 18 burns and were analyzed with ANOVA (including block as a fixed effect; N, C, and S for North, Central, and South blocks), testing the effects of herbivore treatments in a 2 × 3 complete factorial design (two cattle treatments [C, no cattle] crossed with three herbivore treatments [MW, W, no wildlife]). Interaction terms were not significant, so were not included in the model.

Correlations were calculated among tree density, mean fire temperature, and fine woody debris. Correlations between herbaceous fuel loads and minimum fire temperatures were calculated separately for each of the three blocks (which differed significantly in tree densities and mean herbaceous fuel loads; Table 1) and the overall pattern tested with a Fisher's combined probability test.

Ant colony survivorships (proportion of trees retaining their ant colonies) within ant species were calculated for tree size classes that were relatively consistent for mean survivorship and had sufficient sample sizes to estimate proportions reliably. Ant colony survivorships were compared with chi-square contingency tests.

RESULTS

Before the burns, experimental exclusion of mega-herbivores (elephants and giraffes) had resulted in 42% more trees >1 m tall (1257 trees/ha) than in plots where all large wildlife was allowed access (884 trees/ha). In addition, there were significant block effects, with trees becoming less dense in blocks farther north (Table 1). Our attempts to reduce these sources of variation in tree density in selecting our burn subplots were only partly successful. Although the number of trees >1 m tall did not significantly differ across our wildlife treatments in our selected burn subplots ($P = 0.34$), there remained significant differences across blocks ($P = 0.002$).

At ground level, minimum temperatures were on average 18°C higher under trees than in open grassy areas. On trees, fire temperatures declined with greater height from the ground (Fig. 2a). Even at 3 m, however, more than half the tiles reached temperatures of at least 80°C. In grassy areas between trees, fire temperatures were nearly as high at 0.5 m as at ground level (Fig. 2a).

Differences in mean minimum fire temperatures were associated with wildlife treatment, cattle treatments, and block effects (Table 1). Analysis of the data on preburn tree density revealed that the block effects in fire temperatures were strongly associated with the densities of trees >1 m tall (but not smaller trees). The more trees (>1 m), the hotter the fire ($r^2 = 0.63$, $P < 0.001$; Fig. 2b). Herbaceous fuel loads were not significantly correlated with the densities of trees ($r^2 = 0.04$, $P = 0.45$). Fine woody debris was found almost entirely directly beneath larger trees and was strongly correlated at the transect level with tree density in unburned plots ($r^2 = 0.83$, $P = 0.0002$, Fig. 2c).

After controlling for block effects (strongly correlated with tree density) mean minimum fire temperatures were also positively correlated with mean herbaceous fuel loads across plots ($P < 0.01$). Both mean herbaceous fuel loads and mean minimum fire temperatures were significantly affected by herbivore treatments (Table 1). Herbaceous fuel loads were lower and fires burned

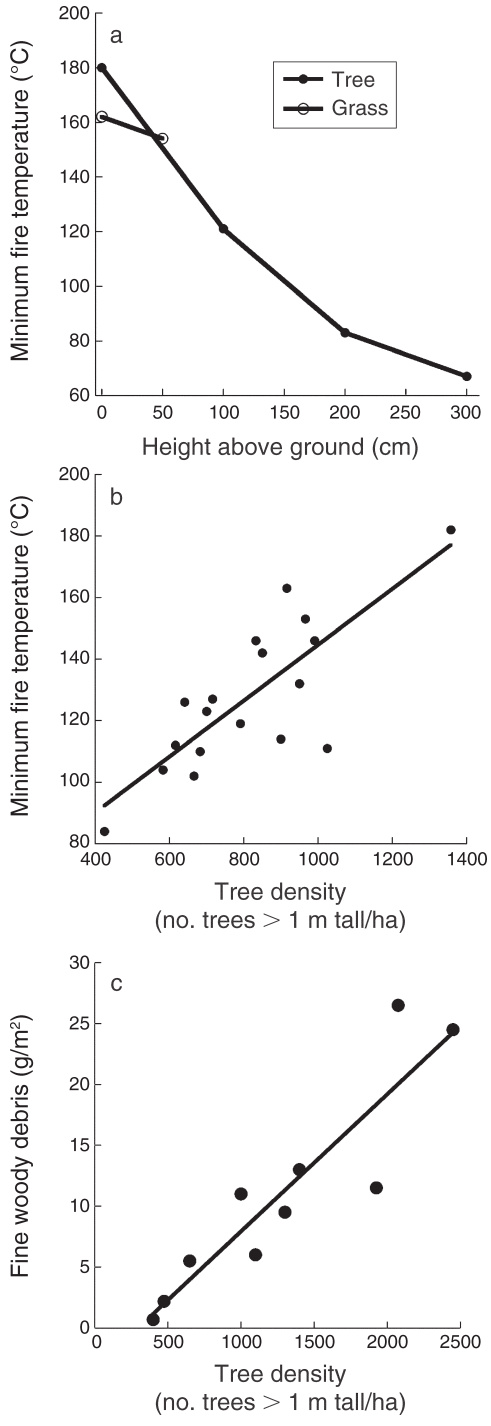

FIG. 2. (a) Mean minimum fire temperature as a function of height aboveground for tiles placed at two heights in grassy areas away from trees and for tiles placed beneath and at different height in trees. (b) Mean minimum fire temperatures as a function of the preburn density of trees >1 m tall. (c) The abundance of fine woody debris (<2 cm diameter) as a function of the density of tree >1 m tall along transects in unburned areas.

cooler in plots to which cattle had access (C < O, WC < W, and MWC < MW) and in plots to which more wildlife guilds had access (MW < W < O and MWC < WC < C, Fig. 3).

Across all ant species, survivorship on trees was negatively correlated with mean herbaceous fuel load and mean minimum fire temperature across herbivore treatments for trees 1–2 m tall (herbaceous fuel load, $r^2 = 0.71$, $P = 0.04$; temperature, $r^2 = 0.73$, $P = 0.03$), but not for trees 2–4 m tall (both $P > 0.50$).

Before the burns, virtually all trees >50 cm tall were inhabited by ants. After burning, trees <50 cm tall were often burned completely aboveground, and trees <1 m tall were almost all uninhabited by ants a week after the fire, many of them having all their swollen thorns burned off (D. M. Kimuyu and T. P. Young, *personal observations*).

For trees >1 m, the proportion of trees occupied by ants in the first week after the burns increased with tree height, but even trees >5 m tall sometimes had no detectable ant presence (Fig. 4). Ant survival also differed significantly by ant species, even after controlling for tree size (Table 2). *Tetraponera* colonies rarely survived fire (12%). *Crematogaster mimosa* and *C. nigiceps* had relatively high survivorships (68–91%), and *C. sjostedti* had intermediate survivorship (37–68%). Among trees originally occupied by *C. sjostedti*, those that had evidence of cerambycid beetle stem boring were significantly more likely to retain their ant colonies than those that did not have beetle damage (chi-square = 33.66, $P < 0.001$). This benefit was most pronounced in smaller trees (Fig. 5). *Lepisota canescens*, a ground-

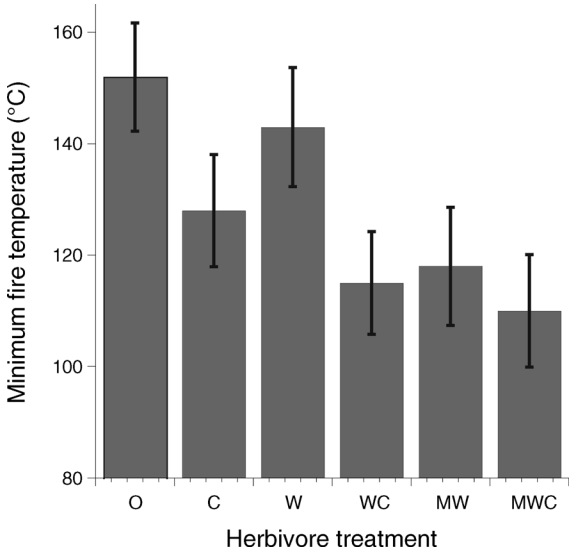

FIG. 3. Mean minimum fire temperatures as a function of herbivore treatment. Plots with cattle burned cooler than plots without cattle, and plots with more native herbivore guilds burned cooler than plots with fewer (MW, MWC < W, WC < O, C). See Fig. 1 caption for herbivore treatments. Bars represent one standard error.

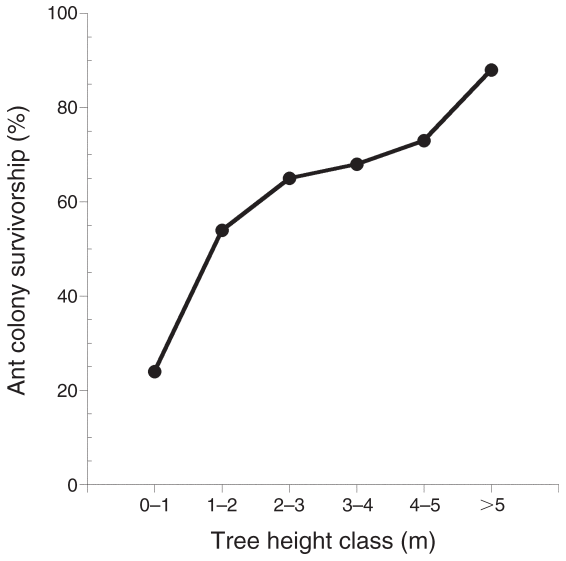

FIG. 4. Ant survivorship as a function of *A. drepanolobium* tree size across all ant species. This does not include trees completely consumed by the fire, of which there were many in the 0–1 m height class.

dwelling ant species that is not otherwise observed on *A. drepanolobium*, was found on 13 out of 595 resurveyed trees after the burns and in one case was observed removing ant brood from a burned tree.

DISCUSSION

Fire temperatures and herbivory

It appears that both browsing and grazing herbivores, both wild and domestic, can have significant effects on fire temperatures in this *A. drepanolobium* wooded savanna, at least for the controlled burns we carried out in February and March 2013. Minimum fire temperatures were strongly and positively associated with densities of *A. drepanolobium* trees >1 m tall (Fig. 2b). In the plots overall, megaherbivores have dramatically reduced densities of these trees. Although we successfully controlled for this variance across wildlife treatments in our selection of burn subplots, there was still considerable variation, mostly associated with block effects, resulting in different fire temperatures. These data strongly suggest that the presence of large herbivores (particularly elephants), reduces fire temperatures by reducing the densities of trees.

Why did subplots with greater densities of tall trees (but not small trees) burn hotter? We suggest two possibilities. First, grass biomass tends to be higher under trees. Although our subplot surveys failed to reveal a positive relationship between tree density and herbaceous fuel load, the relatively small sample size of herbaceous biomass (three quadrats per subplot) may not have picked up on the tree biomass under trees. Perhaps more likely, the hotter fires in subplots with more trees may have been due to the fine woody debris that collects under and around these trees. We did not survey fine woody debris in the burn subplots prior to burning, but our survey across the broader KLEE plots did show a strong positive relationship between tree density and fine woody debris (Fig. 2c). Such fine woody debris was essentially lacking after the burns, presumably consumed by fire.

In addition, both herbaceous fuel loads and fire temperatures were reduced in plots grazed by livestock and/or wild herbivores (Fig. 3). The fact that we found significant effects of previous cattle grazing even after resting the plots for one growing (wet) season demonstrates that the influence of grazing on herbaceous fuel loads and fire behavior extends beyond the immediate effect of grazers removing current season's plant growth. Consistent with the observation that grass biomass is higher under *A. drepanolobium* trees (Riginos et al. 2009) and perhaps also because of fine woody debris, we found greater ground-level fire temperatures under trees than away from trees. This is also likely to put trees at greater risk of fire damage.

Fire and symbiotic acacia ants

One of our key findings is the indirect effect that herbivores have on ant mortality due to fire, mediated by browser and grazer effects on tree densities and herbaceous fuel loads. The vulnerability of symbiotic ants to fire varied greatly across the four ant species in our study (Appendix A). The high colony survival of *C. nigiceps* and *C. mimosae* may be attributable to colonies

TABLE 2. Ant survivorship on trees of different heights (percentage of trees of a given height occupied by a given ants species that retained their ant colony).

Tree height	*N*	*Tetraponera*	*Crematogaster nigiceps*	*C. mimosae*	*C. sjostedti*	Chi-square	*P*
1–2 m	132	5% (1/24)	91% (20/22)	70% (37/53)	37% (10/27)	44.52	<0.0001
2–4 m	372	13% (7/52)	82% (23/28)	75% (122/163)	52% (65/124)	69.98	<0.0001
≥4 m	91	0% (0/5)	no data	68% (26/38)†	68% (30/47)	8.91	0.01
Chi-square		2.18	0.23	0.22	1.05		
P		0.34	0.63	0.64	0.31		

Note: N is the number of trees. The ratios in parentheses are the number of trees occupied by ants that retained their ant colony divided by the number of trees that had an ant colony to begin with. The chi-square tests to the right compare ant colony survivorships within tree height classes across ant species. The chi-square tests on the bottom compare ant colony survivorships across tree height classes within ant species.

† The estimate for *C. mimosae* on taller trees includes four trees whose surviving ants in treetops could not be reliably identified to species.

of these species rapidly evacuating domatia downwind of the fire front and taking refuge in insulated cracks in the soil (T. Palmer, *personal communication*), presumably returning after the fire. Although *C. sjostedti* take refuge in holes created by *Cerambycidae* larvae on tree stems, these holes are rare among trees with <4.0 cm stem diameter (usually <2 m tall trees; Palmer et al. 2013), which are most vulnerable to ground fire. In this study, most *C. sjostedti* colonies occupying short trees without these holes succumbed to fire (Fig. 5). *Tetraponera penzigi*, which had the lowest colony survival, usually inhabits shorter trees and does not evacuate colonies in the event of fire, both of which make them more vulnerable to the high ground fire temperatures. The two ant species that exhibited the greatest survival after fire (*C. nigiceps* and *C. mimosae*) are also the two species that are most effective in aggressively defending trees against herbivory (Palmer and Brody 2007).

Our prescribed burns caused significant ant colony mortality, especially on smaller trees. It is possible that there will be further reductions in ant occupancy in the future if trees in burns are physiologically stressed and produce fewer of the extrafloral nectaries upon which most resident ant species depend for nourishment (Hocking 1970). Conversely, we expect trees that have lost their ant colonies to eventually be colonized by founder queens or by colony expansion from nearby trees. Long-term monitoring will reveal such colonization and whether there are spatially explicit or species-specific patterns to such recolonization.

For *A. drepanolobium*, the loss or reduction of ant colonies could have far-reaching implications for the protection of the trees against herbivory. In previous burns near the study site, most of the tall trees (>2 m) were able to survive the immediate effects of fire, but there was an unexpected increase in the number of large trees toppled by elephants and killed (R. L. Sensenig, *unpublished data*) and a striking decline in the density of larger trees (Okello et al. 2008) in burn sites relative to unburned areas in the years following burning. This suggests several possibilities: (1) fire has a delayed direct effect on tree mortality, (2) fire makes trees more susceptible to elephant damage, or (3) elephants respond to fire in a way that increases their impact on trees. We know that elephants preferentially select *A. drepanolobium* trees from which ants have been experimentally removed (Goheen and Palmer 2010). Do elephant similarly attack trees that have lost their ant colonies through fire? Continued monitoring of our experimental design can test the interaction between fire and elephants and whether ants mediate this interaction.

Implications for management and conservation

We have previously demonstrated in this system that livestock and different guilds of wildlife have complex direct and indirect effects on the recruitment and survival of *Acacia drepanolobium* trees (Goheen et al. 2004, 2010, Maclean et al. 2011). This research suggests two additional indirect pathways: wild and domestic large herbivores affect burn temperatures that could affect postfire tree demography (to be revealed in later surveys), and fire also affects the ant symbionts on which these trees depend.

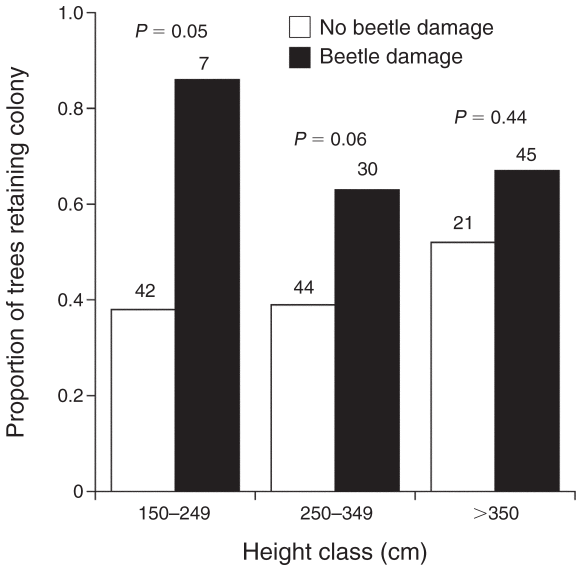

FIG. 5. Proportion of trees originally occupied by *Crematogaster sjostedti* that retained their ant colonies after the burns based on whether or not the tree had preburn evidence of damage by stem-boring cerambycid beetles. Beetle damage was rare in trees <250 cm tall.

Fire and grazing can be employed to achieve complementary range management goals (Kirkpatrick et al. 2011). For example, in the western United States, Diamond et al. (2009) demonstrated that targeted grazing and prescribed burning can reduce the biomass and cover of cheatgrass (*Bromus tectorum*), resulting in reductions in flame length and rate of spread in a system where fire is a recent (and damaging) anthropogenic disturbance. Integrated burning and grazing has also been used to manipulate habitat heterogeneity (Fuhlendorf and Engle 2004), to restore degraded habitats, and increase biodiversity (Fuhlendorf and Engle 2001).

These data also have implications for the conservation of large mammals in savanna ecosystems. Although the impacts of herbivory are analogous to the impacts of fire in their removal of herbaceous biomass (Bond and Keeley 2005), they have very different effects on long-term tree and grass cover and community ecological interactions. Our data suggest that an additional cost of the loss of meso- and megafaunal wildlife is that it increases savanna fuel loads and fire temperatures (see also Gill et al. 2009). This results in increased symbiotic ant mortality and likely other expressions of increased fire severity. There are parallels to the dynamics of some of the coniferous forests in the western United States, where human intervention (there, in the form of fire

suppression) has also increased the likelihood of high-severity fires (Moore et al. 1999, Savage and Mast 2005). In our system, the replacement of native grazers by cattle only partly compensates for the loss of large mammal biodiversity, reducing the herbaceous fuels, but not the woody fuels reduced by wildlife.

The results presented here are the first stage in a long-term monitoring program that will further elucidate the effects of fire and large mammal herbivory on each other and on the savanna ecosystem in which they occur. Already, we have documented both multitrophic interactions and herbivore–fire feedbacks that are likely to play out in fascinating ways.

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Supplemental Material

Appendix A

Ant survivorship (across all ant species) in different herbivore treatments (*Ecological Archives* A024-044-A1).

Appendix B

Air temperature, relative humidity, and wind speed with respect to time of day (*Ecological Archives* A024-044-A2).