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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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1	Native and domestic browsers and grazers reduce fuels, fire temperatures, and acacia-ant
2	mortality in an African savanna
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16 Abstract

17 Despite the importance of fire and herbivory in structuring savanna systems, few replicated 18 experiments have examined the interactive effects of herbivory and fire on plant dynamics. In 19 addition, the effects of fire on associated ant-tree mutualisms have been largely unexplored. We 20 carried out small controlled burns in each of 18 herbivore treatment plots of the Kenya Long-21 term Exclosure Experiment (KLEE), where experimentally excluding elephants has resulted in 22 42% greater tree densities. The KLEE design includes six different herbivore treatments that 23 allowed us to examine how different combinations of megaherbivore wildlife, mesoherbivore 24 wildlife, and cattle affect fire temperatures and subsequent loss of ant symbionts from Acacia 25 trees. Before burning, we quantified herbaceous fuel loads and plant community composition. 26 We tagged all trees, measured their height and basal diameter, and identified the resident ant 27 species on each. We recorded weather conditions during the burns and used ceramic tiles painted 28 with fire-sensitive paints to estimate fire temperatures at different heights and in different 29 microsites (under versus between trees). Across all treatments, fire temperatures were highest at 30 0-50cm off the ground and hotter in the grass under trees than in the grassy areas between trees. 31 Plots with more trees burned hotter than plots with fewer trees, perhaps because of greater fine 32 woody debris. Plots grazed by wildlife and by cattle prior to burning had lower herbaceous fuel 33 loads and experienced lower burn temperatures than ungrazed plots. Many trees lost their ant 34 colonies during the burns. Ant survivorship differed by ant species, and at the plot level was 35 positively associated with previous herbivory (and lower fire temperatures). Across all 36 treatments, ant colonies on taller trees were more likely to survive, but even some of the tallest 37 trees lost their ant colonies. Our study marks a significant step in understanding the mechanisms 38 that underlie the interactions between fire and herbivory in savanna ecosystems.

40 Keywords: herbivory, Laikipia, Kenya, mutualism, *Acacia drepanolobium, Crematogaster,*41 *Tetraponera*, livestock, cattle, elephants

42

43 Introduction

44 Fire and herbivory are important drivers in savanna systems, playing key roles in structuring 45 tree-grass coexistence (reviewed in Sankaran et al. 2005, 2008), landscape heterogeneity 46 (Fuhlendorf and Engle 2004, Kerby et al. 2007, Waldram et al. 2008, Allred et al. 2011), forage 47 quantity and quality (Sensenig et al. 2010), and plant productivity (Holdo et al. 2007). Although 48 it is well-documented that both fire (Mapiya et al. 2008, Levick et al. 2009, Trollope 2011) and 49 herbivory (McNaughton et al. 1988, Levick et al. 2009) independently affect savanna 50 ecosystems, there is increasing interest in understanding their potentially interactive effects on 51 tree and grass dynamics. A variety of modeling approaches (Baxter and Getz 2005, van 52 Langevelde 2003, Holdo et al. 2009) and empirical studies (Dublin et al. 1990, Moncrieff et al. 53 2008) have suggested that fire may interact with grazing and browsing in complex ways (Collins 54 and Smith 2006) to create systems that are dynamic and non-equilibrial (Bond 2005), changing 55 at various scales in space and time (Archibald et al. 2005, Gillson 2004). 56 Understanding the mechanisms underlying how fire and herbivory interact with changes in 57 tree cover in particular has both important theoretical and applied implications, since variation in 58 savanna woody cover affects livestock production, wildlife conservation, predator-prev 59 interactions, nutrient cycling, and carbon storage (Bond 2005, Riginos and Grace 2008, Scholes

- and Archer 1997, van Auken 2000, Angassa and Baars 2000). In particular, there is a lack
- 61 controlled replicated experimental studies that quantify a) the separate and combined effects of
- 62 domestic and native herbivores on fuel loads and fire temperatures, and b) the separate and

63 combined effects of fire and subsequent herbivory on the survival of savanna trees. This paper 64 addresses the former, and describes the experimental design that will be used to test the latter. A number of previous results have provided partial evidence for these interactions. For 65 66 example, there is some evidence from African savannas (Hobbs 1996, O'Connor et al. 2011), 67 North American grasslands (van Auken 2000), and Australian savannas (Leonard et al. 2010) 68 that pre-burn grazing decreases fire frequencies and intensities. This suggests feedback loops 69 between herbivory and fire that current models of savanna dynamics do not include (Sankaran et 70 al. 2004). However, most existing information on the relationship among herbivores, herbaceous 71 fuel load, and fire behavior is based on anecdotal observations (Nader et al. 2007), studies 72 involving only domesticated herbivores (Savadogo et al. 2007; Gambiza et al. 2008; Davies et 73 al. 2010), studies that do not control or monitor pre-burn grazing (Kerby et al. 2007), or those 74 lacking replication (Leonard et al. 2010).

75 Ant mutualisms may mediate fire-herbivore interactions. Symbiotic ant species that reside on 76 Acacia drepanolobium trees are effective in reducing browsing by mega-herbivores (Madden 77 and Young 1992, Palmer et al 2010a, Martins 2010, Stanton and Palmer 2011), increasing 78 individual tree fitness (Palmer and Brody 2007, Goheen and Palmer 2010, Palmer and Brody 79 2013) and stabilizing tree cover across the landscape (Goheen and Palmer 2010). To the extent 80 that fire may weaken or destroy ant colonies, it may lead to subsequent shifts in ant species 81 composition, or declines in ant abundance across the landscape, either of which could make trees 82 in burned areas more susceptible to browsing and the destructive effects of elephants, with 83 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

86 prescribed burns inside the replicated Kenva Long-term Exclosure Experiment (KLEE; see 87 below) in early 2013. By experimentally burning within different herbivore treatments, we were 88 able to simultaneously test the effects of a diverse guild of herbivores on woody and herbaceous 89 fuel loads and fire temperatures, and (in the future) quantifying how post-burn foraging by 90 herbivores may be responsible for the delayed mortality of larger trees after a fire. To our 91 knowledge, this is the first fully crossed, replicated field experiment that independently 92 manipulates fire and multiple guilds of domestic and wild large herbivores (but see Collins and 93 Smith 2006, Collins and Calabrese 2012, Koerner and Collins, in press). 94 In this paper we address the following questions: a) how do different guilds of herbivores

95 indirectly affect burn temperatures by influencing woody and herbaceous fuel loads, b) what are 96 the patterns of ant colony survival after burning, and c) do differences in ant colony survival and 97 subsequent shifts in ant species composition or occupancy correlate with herbaceous fuel loads 98 and burn temperatures?

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100 **Study Site and Methods**

101 Study site and species

102 This research was carried out in *Acacia drepanolobium* wooded savanna on the Laikipia Plateau, 103 Kenya (36°52'E, 0°17'N; 1810m asl). This plant community overlies high-clay 'black cotton' 104 soils and is representative of similar ecosystems that occur extensively throughout eastern and 105 southern Africa. Rainfall averages 550-600mm at our study site, and is weakly trimodal, with a 106 distinct dry season in December-March.

The whistling-thorn tree, Acacia drepanolobium, accounts for 97% of woody cover at our 108 study site (Young et al. 1997). At some branch nodes, A. drepanolobium produces hollow

109 swollen thorns that serve as ant domatia. The trees also produce extrafloral nectaries at the bases 110 of leaves to nourish symbiotic ants (Hocking, 1970, Huntzinger et al. 2004). At our study site, 111 each tree is occupied by one of four species of ants: Crematogaster mimosae, C. sjostedti, C. 112 *nigriceps*, or *Tetraponera penzigi*. These ant species differ in various aspects of their behavior, 113 including the average size and number of trees they occupy, their relative competitive abilities, 114 their benefits to host trees (Young et al. 1997, Stanton and Palmer 2011), and their behavioral 115 responses to fire. During a fire, Crematogaster nigiceps and C. mimosae evacuate domatia and 116 take refuge in insulated cracks in the soil (T. Palmer, pers. comm.; Jaffe and Isbell 2009), re-117 occupying the tree after the fire. Tetraponera penzigi do not leave their domatia, and C. sjostedi 118 take refuge in holes on tree stems, often created by Cerambycidae larvae (Palmer et al. 2008b). 119 The Kenya Long-term Exclosure Experiment (KLEE) is located at the Mpala Research 120 Centre. Since 1995, we have been manipulating the presence and absence of three guilds of 121 large herbivores: livestock (cattle), wildlife (large mammals 15-1000kg), and mega-herbivores 122 (elephants and giraffes). There are 18 plots, each 200m x 200m, representing three replicate 123 blocks of each of six combinations of large herbivores (Figure 1). For details of the 124 experimental design, see Young et al. (1997).

125 Controlled burns

In February/March 2013 we burned one 30m x 30m subplot in each of the eighteen 4ha KLEE plots (Figure 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 (>1m 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.

136 We refrained from grazing cattle in the KLEE plots for five months (one rainy and one dry 137 period) prior to the burns. In early 2013, we estimated herbaceous fuel loads by harvesting all 138 aboveground herbaceous biomass in three randomly-located 1m x 1m quadrats adjacent to each 139 designated burn plot. This material was air dried to constant weight and weighed. Every tree 140 (all size classes) in each burn plot was permanently tagged, and its height and stem diameter 141 measured at 15cm (for trees above 1m tall) or at the base (for trees less than 1m tall). A total of 142 4304 trees were tagged and measured (mean per plot: 240, range: 130-359). In addition, the 143 species identity of each tree's resident ant was recorded, as was evidence of the presence of 144 cerambycid beetle damage (stem-boring).

145 In 2011, we documented the effects that elephants had on *Acacia drepanolobium* densities by 146 carrying out surveys of in each of the 18 KLEE plots, six of which allowed elephants and 12 of which did not (see Figure 1). We counted all trees within three 100m x 4m transects $(1200m^2)$ 147 148 total per plot). Trees were categorized into height classes: <1.00m, 1.00-1.99m, 2.00-2.99m, 149 3.00-3.99m, and >4.00m). We did not survey the burn subplots for fine woody debris before the 150 burns, so instead we documented the general relationship between tree density and fine woody 151 debris. In July 2013, along ten of the same (unburned) transects surveyed for tree density in 152 2011, we collected and weighed all fine woody debris (FWD; dead woody material on the 153 ground with diameters <2.0cm) within 1m of each transect line (a 100m x 2m transect).

154 We monitored fire temperatures with ceramic tiles painted with TempilacTM paints. We used 155 paints designed to melt at each of the following six temperatures: 80°C (175°F), 150°C (300°F), 156 260°C (500°F), 400°C (750°F), 510°C (950°F), and 620°C (1150°F). We placed 18 tiles in each 157 burn plot: two in each of three grassy areas away from trees, and four on each of three separate, 158 randomly chosen trees. In each open grassy sampling location, we placed one tile on the ground 159 (under any leaf litter present), and attached one to a piece of rebar at 50-60cm above the ground. 160 At each tree, we placed one tile on the ground (under any leaf litter present), and attached three 161 tiles to the tree, one at 100cm, one at 180-200cm and one at 270-300cm above the ground. 162 Firebreaks were established between 13 January and 6 February 2013. A 1-2m wide swath 163 was slashed to a vegetation height of 5-10cm. In addition, for many subplots either an access 164 road or cleared fence-lines provided firebreaks. Over a period of three days (28 February-2 165 March 2013), a single burn was completed in each of the 18 subplots. Burn boundaries were 166 wet-lined and then back-burned to create 5-10 meters of firebreak along downwind edges. The 167 interiors of all plots were burned using head-fires with two technicians simultaneously lighting 168 the upwind edges to create a perimeter ring fire. Flame heights ranged from less than a meter to a 169 maximum of 3-4 meters. From first ignition to the end of the burn, each lasted between 8 and 13 170 minutes (2/3 of the burns were 9-11 minutes). All burns consumed virtually all of the understory 171 vegetation (save some tussock bases) and fine woody debris. Each day's burning began at ~8am 172 (7:47-8:06) and finished ~midday (11:17-12:15). 173 On each burn day we periodically recorded air temperature, wind temperature, and relative

humidity (Appendix B). Air temperatures during the burns ranged from 15-28°C, increasing
during the course of each day. Winds ranged from 3.5 to 12.5 km/hr, increasing during the

course of each day. Relative humidity ranged from 80-30%, declining during the course of eachday.

178 To quantify the presence or absence of Acacia ants in the first week after the burns, we 179 carried out a survey of trees in the burned plots for a random subset of 30-50 tagged trees in each 180 plot. Data on the fate of individual trees in the burns could not be collected at that time because 181 rains had not yet fallen that would result in either a flush of leaves from above-ground shoots or 182 the coppicing of top-killed trees. (These data will be reported in subsequent publications). 183 At the same time, we collected the ceramic tiles and scored them for the lowest temperature 184 class of paint melted by the fire ("minimum fire temperature"). If none of the paints melted, a 185 default of 20°C (air temperature) was used for analysis. For 12 tiles (<4% of the total), the 186 higher-temperature paints were charred, and not readable. These may have been the hottest tiles; 187 all but one were at ground level, and 9 out of these 11 were under trees. This represented 17% of 188 the tiles at ground level under trees, and our minimum temperature estimates for these locations 189 should be considered conservative.

190

191 Statistical analyses

Tree densities, mean herbaceous fuel loads, mean fire temperatures, and ant survivorship (% of trees retaining their ants) were calculated for each of the 18 burns and were analyzed with ANOVA (including Block as a fixed effect), testing the effects of herbivore treatments in a 2x3 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.

198	Correlations were calculated among tree density, mean fire temperature, and fine woody
199	debris. Correlations between herbaceous fuel loads and minimum fire temperatures were
200	calculated separately for each of the three blocks (which differed significantly in tree densities
201	and mean herbaceous fuel loads; Table 1), and the overall pattern tested with a Fisher's
202	combined probability test.
203	Ant colony survivorships (proportion of trees retaining their ant colonies) within ant species
204	were calculated for tree size classes that were a) relatively consistent for mean survivorship, and
205	b) had sufficient sample sizes to estimate proportions reliably. Ant colony survivorships were
206	compared with Chi-square contingency tests (Vasserstats).
207	
208	Results
209	Before the burns, experimental exclusion of mega-herbivores (elephants and giraffes) had
210	resulted in 42% more trees >1m tall (1257 trees/ha) than in plots where all large wildlife was
211	allowed access (884 trees/ha). In addition, there were significant block effects, with trees
212	
	becoming less dense in blocks farther north (Table 1). Our attempts to reduce these sources of
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 213 214 215 216 217 	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 (see above) were only partly successful. Although the number of trees >1m 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
 213 214 215 216 217 218 	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 (see above) were only partly successful. Although the number of trees >1m 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

219 (Figure 2a). Even at 3m, 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(Figure 2a).

222 Differences in mean minimum fire temperatures were associated with wildlife treatment, 223 cattle treatments, and block effects (Table 1). Analysis of the data on pre-burn tree density 224 revealed that the block effects in fire temperatures were strongly associated with the densities of trees >1m tall (but not smaller trees). The more trees (>1m), the hotter the fire ($r^2 = 0.63$, F = 225 226 27.8, p < 0.001; Figure 2b). Herbaceous fuel loads were not significantly correlated with the densities of trees ($r^2 = 0.04$, F = 0.6, p = 0.45). Fine woody debris was found almost entirely 227 228 directly beneath larger trees, and was strongly correlated at the transect level with tree density in unburned plots ($r^2 = 0.83$, F = 39.0, p = 0.0002, Figure 2c). 229

230 After controlling for block effects (strongly correlated with tree density) mean minimum fire 231 temperatures were also positively correlated with mean herbaceous fuel loads across plots (p < p232 0.01). Both mean herbaceous fuel loads and mean minimum fire temperatures were significantly 233 affected by herbivore treatments (Table 1). Herbaceous fuel loads were lower and fires burned 234 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) (Figure 3). 235 236 Across all ant species, survivorship on trees was negatively correlated with mean herbaceous 237 fuel load and mean minimum fire temperature across herbivore treatments for trees 1-2m tall (herbaceous fuel load: $r^2 = 0.71$, F = 9.7, p = 0.04; temperature: $r^2 = 0.73$, F = 10.9, p = 0.03), but 238 239 not for trees 2-4 m tall (both p > 0.50).

Before the burns, virtually all trees greater than 50 cm tall were inhabited by ants. After
burning, trees less than 50cm tall were often burned completely aboveground, and trees less than

1m tall were almost all uninhabited by ants a week after the fire, many of them having all theirgalls burned off (DMK and TPY, pers. obs.).

244 For trees >1m, the proportion of trees occupied by ants in the first week after the burns 245 increased with tree height, but even trees >5m tall sometimes had no detectable ant presence 246 (Figure 4). Ant survival also differed significantly by ant species, even after controlling for tree 247 size (Table 4). Tetraponera colonies rarely survived fire (12%). Crematogaster mimosa and C. 248 nigiceps had relatively high survivorships (68-91%), and C. sjostedti had intermediate 249 survivorship (37-68%). Among trees originally occupied by C. sjostedti, those that had evidence 250 of cerambycid beetle stem boring were significantly more likely to retain their ant colonies than 251 those that did not have beetle damage (Chi-square = 33.66, P < 0.001). This benefit was most 252 pronounced in smaller trees (Figure 5). Lepisota canescens, a ground-dwelling ant species that is 253 not otherwise observed on A. drepanolobium, was found on 13 out of 595 resurveyed trees after 254 the burns and in one case was observed removing ant brood from a burned tree.

255

256 Discussion

257 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 grassland, at least for the controlled burns we carried out in Feb-Mar 2013. Minimum fire temperatures were strongly and positively associated with densities of *A. drepanolobium* trees >1m tall (Figure 2a). In the plots overall, mega-herbivores 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), reduce fire temperatures by reducing the densities of trees.

267 Why did subplots with greater densities of tall trees (but not small trees) burn hotter? We 268 suggest two possibilities. First, grass biomass tends to be higher under trees. Although our 269 subplot surveys failed to reveal a positive relationship between tree density and herbaceous fuel 270 load, the relatively small sample size of herbaceous biomass (three quadrats per subplot) may not 271 have picked up on the tree biomass under trees. Perhaps more likely, the hotter fires in subplots 272 with more trees may have been due to the fine woody debris that collects under and around these 273 trees. We did not survey fine woody debris in the burn subplots prior to burning, but our survey 274 across the broader KLEE plots did show a strong positive relationship between tree density and 275 fine woody debris. Such fine woody debris was essentially lacking after the burns, presumably 276 consumed by fire.

277 In addition, both herbaceous fuel loads and fire temperatures were reduced in plots grazed by 278 livestock and/or wild herbivores (Figure 4). The fact that we found significant effects of previous 279 cattle grazing even after resting the plots for one growing (wet) season demonstrates that the 280 influence of grazing on herbaceous fuel loads and fire behaviour extends beyond the immediate 281 effect of grazers removing current season's plant growth. Consistent with the observation that 282 grass biomass is higher under A. drepanolobium trees (Riginos et al. 2009) and perhaps also 283 because of fine woody debris, we found greater ground-level fire temperatures under trees than 284 away from trees. This is also likely to put trees at greater risk of fire damage.

285 *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

288 vulnerability of symbiotic ants to fire varied greatly across the four ant species in our study 289 (Appendix A). The high colony survival of C. nigiceps and C. mimosae may be attributable to 290 colonies of these species rapidly evacuating domatia downwind of fire, and taking refuge in 291 insulated cracks in the soil (T. Palmer, pers. comm.), presumably returning after the fire. 292 Although C. sjostedti take refuge in holes created by Cerambycidae larvae on tree stems, these 293 holes are rare among trees with <4.0 cm stem diameter (usually <2 m tall trees) (Palmer *et al.* 294 2013), which are most vulnerable to ground fire. In this study, most C. sjostedti colonies 295 occupying short trees without these holes succumbed to fire (Figure 5). Tetraponera penzigi, 296 which had the lowest colony survival, usually inhabits shorter trees and does not evacuate 297 colonies in the event of fire, both of which make them more vulnerable to the high ground fire 298 temperatures. The two ant species that exhibited the greatest survival after fire (C. nigiceps and 299 C. mimosae) are also the two species that are most effective in aggressively defending trees 300 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 on which most resident ant species depend for nourishment (Hocking 1970). Conversely, we expect trees that have lost their ant colonies to be eventually 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 in this study site,
most of the tall trees (>2 m) are able to survive the immediate effects of fire, but there was an

311 unexpected increase in the number of large trees toppled by elephants and killed (Sensenig, 312 unpubl data) and a striking decline in the density of larger trees (Okello et al. 2008) in burn sites 313 relative to unburned areas in the years following burning. This suggests several possibilities: a) 314 fire has a delayed direct effect on tree mortality, b) fire makes trees more susceptible to elephant 315 damage, or c) elephants respond to fire in a way that increases their impact on trees. We know 316 that elephants preferentially select A. drepanolobium trees from which ants have been 317 experimentally removed (Goheen and Palmer 2010). Do elephant similarly attack trees that have 318 lost their ant colonies through fire? Continued monitoring of our experimental design can test the 319 interaction between fire and elephants and whether ants mediate this interaction.

320 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, Goheen et al. 2010, Maclean et al. 2011). This research suggests two additional indirect pathways: wild and domestic large herbivores affect burn temperatures that could affect post-fire tree demography (to be revealed in later surveys) and fire also affects the ant symbionts on which these trees depend.

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).

334 These data also have implications of the conservation of large mammals in savanna 335 ecosystems. Although the impacts of herbivory are analogous to the impacts of fire in their 336 removal of herbaceous biomass (Bond and Keeley 2005), they have very different effects on 337 long-term tree and grass cover and community ecological interactions. Our data suggest that an 338 additional cost of the loss of meso- and megafaunal wildlife is that it increases savanna fuel loads 339 and fire temperatures (see also Gill et al. 2009). This results in increased symbiotic ant mortality 340 and likely other expressions of increased fire severity. There are parallels to the dynamics of 341 some of the coniferous forests in the western United States, where human intervention (there, in 342 the form of fire suppression) has also increased the likelihood of high-severity fires (Moore et al. 343 1999, Savage and Mast 2005). In our system, the replacement of native grazers by cattle only 344 partly compensates for the loss of large mammal biodiversity, reducing the herbaceous fuels, but 345 not the woody fuels released 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 multi-trophic interactions and herbivore-fire feedbacks that are likely to play out in fascinating ways.

350

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359	Riginos, and K. Caylor.
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362 References

1 ~ .

- Allred, B. W., S. D. Fuhlendorf, D. M. Engle, R. D. Elmore. 2011. Ungulate preference for
- burned patches reveals strength of fire-grazing interaction. Ecology and Evolution 1:132-144.
- 365 Angassa, A. and R. M. T. Baars. 2000. Ecological condition of encroached and non-encroached
- 366 rangelands in Borana, Ethiopia. African Journal of Ecology 38:321-328.
- Archibald, S., W. J. Bond, W. D. Stock, D. H. K. Fairbanks. 2005. Shaping the landscape: Firegrazer interactions in an African savanna. Ecological Applications 15:96-109.
- Bachelet, D, J. M. Lenihan, C. Daly, and R. P. Neilson. 2000. Interactions between fire, grazing
 and climate change at Wind Cave National Park, SD. Ecological Modelling 134:229-244.
- 371 Baxter, P. W. J. and W. M. Getz. 2005. A model-framed evaluation of elephant effects on tree
- and fire dynamics in African savannas. Ecological Applications 15:1331-1341.
- Bond, W. J. and J. E. Keeley. 2005. Fire as a global 'herbivore': the ecology and evolution of
 flammable ecosystems. Trends in Ecology and Evolution 20:387-394.
- Collins, S. L. and L. B. Calabrese. 2012. Effects of fire, grazing and topographic variation on
 vegetation structure in tallgrass prairie. Journal of Vegetation Science 23:563–575.
- 377 Collins, S. L. and M. D. Smith. 2006. Scale-dependent interaction of fire and grazing on
- 378 community heterogeneity in tallgrass prairie. Ecology 87:2058–2067.

379	Diamond, J. M., C. A. Call, N. Devoe. 2009. Effects of targeted cattle grazing on fire behavior of
380	cheatgrass-dominated rangeland in the northern Great Basin, USA. International Journal of
381	Wildland Fire 18:944-950.

- 382 Dublin, H. T., A. R. E. Sinclair, and J. McGlade. 1990. Elephants and fire as causes of multiple
- 383 stable states in the Serengeti-Mara woodlands. Journal of Animal Ecology 59:1147-1164.
- 384 Ellair, D. P. and W. J. Platt. 2013. Fuel composition influences fire characteristics and

understorey hardwoods in pine savanna. Journal of Ecology 101:192-201.

- Fuhlendorf, S. D. and D. M. Engle. 2004. Application of the fire-grazing interaction to restore a
 shifting mosaic on tallgrass prairie. Journal of Applied Ecology 41:604-614.
- Gambiza, J., B. M. Campbell, S. R. Moe, and I. Mapaure. 2008. Season of grazing and stocking
 rate interactively affect fuel loads in *Baikiaea plurijuga* Harms woodland in northwestern
 Zimbabwe. African Journal of Ecology 46:637-645.
- Gill, J. L., J. W. Williams, S. T. Jackson, K. B. Lininger, and G. S. Robinson. 2009. Pleistocene
 megafaunal collapse, novel plant communities, and enhanced fire regimes in North America.
 Science. 326,1100-1103.
- Goheen J. R., F. Keesing, B. F. Allan, D. Ogada, and R. S. Ostfeld. 2004. Net effects of large
 mammals on Acacia seedling survival in an African savanna. Ecology 85:1555-1561.
- Goheen, J. R. and T. M. Palmer. 2010. Defensive plant-ants stabilize megaherbivore-driven
- landscape change in an African savanna. Current Biology 20:1768-1772.
- 398 Goheen, J. R., T. M. Palmer, F. Keesing, C. Riginos, and T. P. Young. 2010. Large herbivores
- 399 facilitate savanna tree establishment via diverse and indirect pathways. Journal of Animal
- 400 Ecology 79:372-382.

- 401 Gillson, L. 2004. Evidence of hierarchical patch dynamics in an east African savanna?
 402 Landscape Ecology 19:883-894.
- Hayes, G. F., and K. D. Holl. 2003. Site-specific responses of native and exotic species to
 disturbances in a mesic grassland community. Applied Vegetation Science 6: 235-244.
- Hobbs, N. T. 1996. Modification of ecosystems by ungulates. Journal of Wildlife Management
 60:695-713.
- 407 Holdo, R. M., R. D. Holt, and J. M. Fryxell. 2009. Grazers, browsers, and fire influence the
 408 extent and spatial pattern of tree cover in the Serengeti. Ecological Applications 19:95-109.
- 409 Hocking, B. 1970. Insect associations with swollen thorn acacias. Transactions of the Royal
- 410 Entomological Society of London 122: 211-255.
- Huntzinger, P. M., R. Karban, T. P. Young and T. M. Palmer. 2004. Relaxation of induced
 indirect defenses of acacias following removal of mammalian herbivores. Ecology 85:609614.
- 414 Ingram, R. S., M. P. Doran and G. Nader. 2013. Planned herbivory in the management of
- 415 wildfire fuels. In: Herbivory, B. Barros (Ed.), ISBN: 978-953-51-1052-1; InTech, DOI:
- 416 10.5772/48673. http://www.intechopen.com/books/herbivory/planned-herbivory-in-the-
- 417 <u>management-of-wildfire-fuels</u>
- 418 Isbell, L. A. and T. P. Young. 2007. Interspecific and temporal variation in domatia contents of
- 419 the ant-plant Acacia drepanolobium, a staple food for patas monkeys (Erythrocebus patas) in
- 420 Laikipia, Kenya. American Journal of Primatology 69:1387-1398.
- 421 Jaffe K. E., and L. A. Isbell. 2009. After the fire: benefits of reduced ground cover for vervet
- 422 monkeys (*Cercopithecus aethiops*). American Journal of Primatology 71: 252-260.

423	Kerby, J. D., S. D. Funiendorf, and D. M. Engle. 2007. Landscape neterogeneity and fire
424	behavior: scale-dependent feedback between fire and grazing processes. Landscape Ecology
425	22:507-516.

1 D M F 1 2007 I

1

1 4

٠,

1 0

- 426 Kirkpatrick, J. B., J. B Marsden-Smedley, and S. W. J. Leonard. 2011. Influence of grazing and
- 427 vegetation type on post-fire flammability. Journal of Applied Ecology 48:642-649.
- Koerner, S. E. and S. L. Collins (in press). Interactive effects of grazing, drought, and fire on
 grassland plant communities in North America and South Africa. Ecology.
- 430 Leonard, S. W. J., J. B. Kirkpatrick, and J. B. Marsden-Smedley. 2010. Variation in the effects of
- 431 vertebrate grazing on fire potential between grassland structural types. Journal of Applied
- 432 Ecology 47:876-883.
- 433 Levick, S. R., G. P. Asner, T. Kennedy-Bowdoin, and D. E. Knapp. 2009. The relative influence
 434 of fire and herbivory on savanna three-dimensional vegetation structure. Biological
- 435 Conservation 142:1693–1700.

100

TZ 1

- 436 Maclean, J. E., J. R. Goheen, D. F. Doak, T. M. Palmer and T. P. Young. 2012. Cryptic
- 437 herbivores mediate the strength and form of ungulate impacts on a long-lived savanna tree.
 438 Ecology 92:1626–1636.
- Madden, D. and T. P. Young. 1992. Symbiotic ants as an alternative defense against giraffe
 herbivory in spinescent *Acacia drepanolobium*. Oecologia 91:235-238.
- 441 Mapiye, C., M. Mwale, N. Chikumba and M. Chimonyo. 2008. Fire as a rangeland management
- tool in the savannas of southern Africa: A review. Tropical and Subtropical Agroecosystems
 8:115-124.
- 444 Martins, D. J. 2010. Not all ants are equal: obligate acacia ants provide different levels of
- 445 protection against mega-herbivores. African Journal of Ecology 48:1115–1122.

- 446 Moncrieff, G. R., L. M. Kruger, J. J. Midgley, and S. J. McNaughton. 2008. Stem mortality of
- 447 *Acacia nigrescens* induced by the synergistic effects of elephants and fire in Kruger National
- 448 Park, South Africa. Journal of Tropical Ecology 24:655–662.
- 449 Moore, M. M., W.W. Covington, and P. Z. Fule 1999. Reference conditions and ecological
- 450 restoration: A southwestern ponderosa pine perspective. Ecological Applications 9:1266–
- **451** 1277.
- McNaughton, S. J., R. W. Ruess, and S. W. Seagle. 1988. Large mammals and process
 dynamics in African ecosystems. <u>Bioscience</u> 38:794-800.
- 454 Okello, B. D., T. P. Young, C. Riginos, D. Kelly and T. O'Connor. 2008. Short-term survival and
- 455 long-term mortality of *Acacia drepanolobium* after a controlled burn in Laikipia, Kenya.
- 456 African Journal of Ecology 46:395-401.
- Palmer, T. M., and A. K. Brody. 2007. Mutualism as reciprocal exploitation: ant guards defend
 foliar but not reproductive structures of an African ant-plant. Ecology 88:3004–301.
- Palmer, T. M., and A. K. Brody. 2013. Enough is enough: the effects of symbiotic ant abundance
 on herbivory, growth, and reproduction in an African acacia. Ecology 94:683–691.
- 461 Palmer, T. M., M. L. Stanton, T. P. Young, J. R. Goheen, R. M Pringle and R. Karban. 2008a.
- 462 Breakdown of an ant-plant mutualism following the loss of large herbivores from an African463 savanna. Science 319:192-195.
- 464 Palmer, T. M., M. L. Stanton, T. P. Young, J. R. Goheen, R. M Pringle and R. Karban. 2008b.
- 465 Putting ant-acacia mutualisms to the fire: Response. Science 319:1760-1761.
- 466 Palmer, T. M., M. L. Stanton, T. P. Young, J. S. Lemboi, J. R. Goheen and R. M. Pringle. 2013.
- 467 A role for indirect facilitation in maintaining diversity in a guild of African acacia ants.
- 468 Ecology 94:1531-1539.

469	Pringle, R. M., T. M. Palmer, J. R. Goheen, D. J. McCauley, and F. Keesing. 2011. Ecological
470	importance of large herbivores in the Ewaso ecosystem. Smithsonian Contributions to
471	Zoology 632:43-53.

472 Riginos, C. and J. B. Grace. 2008. Tree density affects wild ungulate habitat use and herbaceous

473 community characteristics in a Kenyan savanna. Ecology 89:2228-2238.

- 474 Riginos, C., Grace, J.B., D.J. Augustine & T.P. Young. 2009. Local versus landscape-scale
 475 effects of savanna trees on grasses. Journal of Ecology 97:1337-1345.
- 476 Sankaran, M., N. P. Hanan, R. J. Scholes, J. Ratnam, D. J. Augustine, B. S. Cade, J. Gignoux, S.
- 477 I. Higgins, X. Le Roux, F. Ludwig, J. Ardo, F. Banyikwa, A. Bronn, G. Bucini, K. K. Caylor,
- 478 M. B. Coughenour, A. Diouf, W. Ekaya, C. J. Feral, E. C. February, P. G. H. Frost, P.
- 479 Hiernaux, H. Hrabar, K. L. Metzger, H. H. T. Prins, S. Ringrose, W. Sea, J. Tews, J. Worden,
- and N. Zambatis. 2005. Determinants of woody cover in African savannas. Nature 438:846-849.
- 482 Sankaran, M., J. Ratnam, and N. Hanan. 2004. Tree-grass coexistence in savannas revisited -
- 483 insights from an examination of assumptions and mechanisms invoked in existing models.
 484 Ecology Letters 7:480–490.
- Sankaran, M., J. Ratnam, and N. Hanan. 2008. Woody cover in African savannas: the role of
 resources, fire and herbivory. Global Ecology and Biogeography 17:236-245.
- 487 Savadogo, P., D. Zida, L. Sawadogo, D. Tiveau, M. Tigabu, and P. C. Oden. 2007. Fuel and fire
- 488 characteristics in savanna-woodland of West Africa in relation to grazing and dominant grass
- 489 type. International Journal of Wildland Fire 16:531-539.
- 490 Savage, M. and J. N. Mast. 2005. How resilient are southwestern ponderosa pine forests after
- 491 crown fires? Canadian Journal of Forest Research 35:967-977.

- 492 Scholes, R. J. and Archer, S. R. 1997. Tree-grass interactions in savannas. Annual Review of
 493 Ecology and Systematics 28:517–554.
- 494 Sensenig, R. L. 2008. Fire Ecology in Laikipia, Kenya. Booklet distributed to Laikipia
- 495 landowners, managers, and stakeholders. 79pp
- Sensenig, R. L., M. Demment, and E. A. Laca. 2010. Allometric scaling predicts preferences for
 burned patches in a guild of East African grazers. Ecology 91:2898-2907.
- 498 Stanton, M. L. and T. M. Palmer. 2011. The high cost of mutualism: effects of four species of
- East African ant symbionts on their myrmecophyte host tree. Ecology 92:1073–1082.
- 500 Staver, A. Carla; W. J. Bond, W. D. Stock, S. J. van Rensburg, and M. S. Waldram. 2009.
- 501 Browsing and fire interact to suppress tree density in an African savanna. Ecological502 Applications 19:1909-1919.
- 503 Winston S. W. and W. S. W. Trollope. 2011. Personal perspectives on commercial versus
- 504 communal African fire paradigms when using fire to manage rangelands for domestic
- 505 livestock and wildlife in southern and East African ecosystems. Fire Ecology 7:57-72.
- 506 van Auken, O.W. 2000. Shrub invasions of North American semiarid grasslands. Annual Review
- 507 of Ecology and Systematics 31:197–215.
- Van Dyke, F. and J. A. Darragh. 2006. Short- and longer-term effects of fire and herbivory on
 sagebrush communities in south-central Montana. Environmental Management 38: 365–376.
- 510 Van Langevelde, F., C. A. D. M. Van de Vijver, L. Kumar, J. Van de Koppel, N. De Ridder, J.
- 511 Van Andel, A.K. Skidmore, J. W. Hearne, L. Stroosnijder, W. J. Bond, H. H. T. Prins, and M.
- 512 Rietkerk. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. Ecology
- **513** 84:337–350.

514	Wahungu, G. M., L. K. Mureu and P. G. Macharial. 2009. Variability in survival and mortality
515	of Acacia drepanolobium Sjøstedt following prescribed burning at Olpejeta Conservancy,
516	Kenya. Afr. J. Ecol., 48, 744–750.
517	Waldram, M. S., W. J. Bond, and W. D. Stock. 2008. Ecological engineering by a mega-grazer:
518	White rhino impacts on a South African savanna. Ecosystems 11:101-112.
519	Young, T. P., C. H. Stubblefield and L. A. Isbell. 1997. Ants on swollen-thorn acacias: species
520	coexistence in a simple system. Oecologia 109:98-107.
521	Young, T. P., B. Okello, D. Kinyua, and T. M. Palmer. 1997. KLEE: the Kenya long-term
522	exclosure experiment. African Journal of Range and Forage Science 14:94-102.
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525	Ecological Archives
526	Appendix A: Ant survivorship (across all ant species) in different herbivore treatments
527 528	Appendix B: Air temperature, relative humidity, and wind speed with respect to time of day.
529	

Table 1. ANOVA for the effects of Cattle (C, O), Wildlife (MW, W, O) and block (N, C, S) on
the densities of trees >1m tall, mean herbaceous fuel loads, and mean minimum fire
temperatures, across all tile locations (heights). 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.

				Herbaceous fuel			
		Tree density		load		Minimum temp	
Source	d.f.	F	р	F	р	F	р
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						

Table 2. Ant survivorship on a per-tree basis. *The estimate for *C. mimosae* on taller trees include four trees whose surviving ants in treetops could not be reliably identified to species.

Tree height	N	Tetraponera	C. nigiceps	C. mimosae	C. sjostedti	Chi-square	Р
1-2m	132	5% (1/24)	91% (20/22)	70% (37/53)	37% (10/27)	44.52	< 0.0001
2-4m	372	13% (7/52)	82% (23/28)	75% (122/163)	52% (65/124)	69.98	< 0.0001
<u>≥</u> 4m	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		
р		0.34	0.63	0.64	0.31		

1 Figure captions

2	Figure 1. Schematic of the KLEE plots, and the burned subplots within each (solid squares).
3	The overgrazed subplots are hatched. The letters inside each plot indicate the large
4	herbivores allowed: C = cattle, M = mega-herbivores (elephants and giraffes), W = non-
5	mega-herbivore wildlife >15 kg, O = all large herbivores excluded.
6	Figure 2. a) Mean minimum fire temperature as a function of height above ground for tiles
7	placed at two heights in grassy areas away from trees, and for tiles placed beneath and at
8	different height in trees. Bars represent one standard error. b) Mean minimum fire
9	temperatures as a function of the pre-burn density of trees >1m tall. c) The abundance of fine
10	woody debris (<2cm diameter) as a function of the density of tree >1m tall along transects in
11	unburned areas.
12	Figure 3. Mean minimum fire temperatures as a function of herbivore treatment. Plots with
13	cattle burns cooler than plots without cattle and plots with more native herbivore guild
14	burned cooler than plots with fewer (MW, MWC < W, WC < O, C). Bars represent one
15	standard error.
16	Figure 4. Ant survivorship as a function of A. drepanolobium tree size, across all ant species.
17	Figure 5. Proportion of trees originally occupied by C. sjostedti that retained their ant colonies
18	after the burns, based on whether or not the tree had pre-burn evidence of damage by stem-
19	boring Cerambycid beetles. Beetle damage was rare in trees less the 250cm tall.
20	



24 Figure 1.





















45 Supplemental Materials

- 46
- 47

Appendix A

- 48 Ant survivorship (across all ant species) in different herbivore treatments
- 49

Treatment	W	0	MW	С	WC	MWC
Mean herbaceous	657	547	493	478	448	310
fuel load (gm/m ²)						
Mean minimum	143	152	118	128	115	110
temperature (°C)						
Ant survival, trees	27%	38%	52%	50%	80%	71%
1-2m tall						
Ant survival, trees	72%	69%	55%	61%	69%	70%
2-4m tall						

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Ant survivorship (across all ant species) in different herbivore treatments, here in order of
decreasing mean herbaceous fuel loads. Sample sizes for trees taller than 4m and shorter than
1m were insufficient for analysis. For 'Treatment', the letters represent the guilds of large
mammalian herbivores that were allowed access to the plots: M = megaherbivores (elephants
and giraffes); W = other large herbivores (>15kg); C = cattle. Plots excluding all three guilds
are designated O.

Appendix B

Air temperature, relative humidity, and wind speed with respect to time of day.

