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Tree resprout dynamics following fire depend on herbivory by wild ungulate herbivores

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Abstract

1. Savanna tree cover is dynamic due to disturbances such as fire and herbivory. Frequent fires can limit a key demographic transition from sapling to adult height classes in savanna trees. Saplings may be caught in a 'fire trap', wherein individuals repeatedly resprout following fire top-kill events. Saplings only rarely escape the cycle by attaining a fire-resistant height (e.g. taller than the minimum scorch height) during fire-free intervals.

2. Large mammalian herbivores also may trap trees in shorter size classes. Browsing herbivores directly limit sapling height, while grazing herbivores such as cattle facilitate sapling growth indirectly via grass removal. Experimental studies investigating how meso-wildlife, megaherbivores and domestic livestock affect height of resprouts following fire are rare, but necessary for fully understanding how herbivory may reinforce (or counteract) the fire trap. In our study system, interactive fire–herbivore effects on transitions from sapling (<1 m) to adult tree (>1 m) height classes may be further influenced by plant defences, such as symbiotic ants.

3. We used the Kenya Long-term Exclosure Experiment (KLEE) to investigate how post-fire resprout size of a widespread monodominant East African tree, *Acacia drepanolobium* was influenced by (a) herbivory by different combinations of cattle, meso-wildlife (15–1,000 kg) and megaherbivores (>1,000 kg) and (b) the presence of acacia–ant mutualists that confer tree defences. We sampled height, stem length and ant occupancy of resprouts exposed to different herbivore combinations before and after controlled burns.

4. Resprout height of saplings that were short prior to fire (<1 m) was reduced primarily by meso-wildlife. Negative effects of elephants on post-fire resprout height increased with pre-fire tree size, suggesting that resprouts of the tallest trees (with the greatest potential to escape the fire trap cycle) were preferentially browsed and reduced in height by elephants. There were no significant cattle effects.

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5. *Synthesis*. We provide experimental evidence for two potential pathways through which large herbivores exert control over sapling escape from the fire trap: (a) post-fire meso-wildlife browsing of short (<1 m) resprouts and (b) elephant browsing of the largest size class of resprouts, which would otherwise be most likely to escape the fire trap.

KEYWORDS

browse trap, bush encroachment, coppice, *Crematogaster*, recruitment limitation, sapling, storage effect, tree–grass co-existence

1 | INTRODUCTION

Tree cover and density are fundamental properties of savannas that affect many ecosystem processes and services, and understanding which factors influence savanna tree cover has long been a focus of ecology (Bond, 2008; House, Archer, Breshears, & Scholes, 2003; Lehmann et al., 2014; Sankaran, Ratnam, & Hanan, 2004; Scholes & Archer, 1997). In these systems, fire has been identified as a key determinant of tree cover, primarily via its influence on demographic transitions between tree life stages (Grady & Hoffmann, 2012; Higgins, Bond, & Trollope, 2000; Staver, Bond, Stock, van Rensburg, & Waldram, 2009; van Langevelde et al., 2003; Wakeling, Staver, & Bond, 2011). Frequent fires prolong the critical transition from sapling to adult size classes via a 'fire trap' cycle, whereby individuals that resprout after fire fail to reach a fire-resistant height (generally, taller than the flame scorch height) before being top-killed by a subsequent fire (Gignoux, Clobert, & Menaut, 1997; Higgins et al., 2000; Hoffmann et al., 2009; Mondal & Sukumar, 2015; Staver et al., 2009; VanderWeide & Hartnett, 2011; Werner & Prior, 2013). Here, we use 'sapling recruitment' to mean the transition from sapling (<1 m) to a tree (>1 m) height class (i.e. taller than the grass layer). The term 're-sprout' is used to describe trees in all pre-fire size classes that were top-killed and thereby retrogressed back to the sapling stage (<1 m). Escape from the fire trap is influenced by factors such as fire behaviour (Werner & Prior, 2013), edaphic conditions (Bond & Midgley, 2001; Grady & Hoffmann, 2012; Schafer & Just, 2014) and tree species traits (Bond, Cook, & Williams, 2012; de Dantas & Pausas, 2013). Recently, several authors have suggested that large browsing herbivores also play an important role in delaying or preventing tree escape from the fire trap by consuming plant tissues that would otherwise attain a fire-resistant height (Sankaran, Augustine, & Ratnam, 2013; Staver & Bond, 2014). However, there has been little experimental investigation of how different types of herbivores influence escape from the fire trap (but see Staver et al., 2009).

Negative effects of elephants on tree cover may be amplified by fire (Okello, Young, Riginos, Kelly, & O'Connor, 2008; Pellegrini, Pringle, Govender, & Hedin, 2017). For example, elephant damage prior to fire reduces post-fire tree survival and recovery (Shannon et al., 2011; Vanak et al., 2012), and large trees weakened by fire damage experience increased rates of elephant toppling (Asner & Levick, 2012; Levick, Baldeck, & Asner, 2015; Pringle et al., 2015).

Elephants also can limit sapling recruitment by trampling (Cumming & Cumming, 2003) and/or directly consuming tissues <1 m (Lagendijk, Mackey, Page, & Slotow, 2011), effects that could be magnified in burned areas (Dublin, 1986) but remain untested.

The impacts of meso-wildlife (15–1,000 kg) on tree cover, too, may be amplified following fire. Many wildlife species preferentially forage in burned sites (Sensenig, Demment, & Laca, 2010), and post-fire wildlife browsing can reduce tree and shrub cover (Andruk, Schwope, & Fowler, 2014; Rhodes, Anderson, & St Clair, 2017; Silva, Catry, Moreira, & Bugalho, 2015). Meso-herbivore browsers directly suppress tree height and biomass (Augustine & McNaughton, 2004; Sankaran et al., 2013; Staver & Bond, 2014) and decrease height : stem diameter ratios (Moncrieff, Chamaille-Jammes, Higgins, O'Hara, & Bond, 2011), which could delay demographic transitions out of the short, multi-stemmed and fire-vulnerable 'sapling' size class, into single-stem, high canopy and fire-resistant heights (Okello, O'Connor, & Young, 2001). Grazing herbivores—either wild or domestic—on the other hand, can indirectly facilitate woody sapling growth by reducing grass competition and increasing available resources (Palmer & Brody, 2013; Riginos & Young, 2007; Scholes & Archer, 1997).

Theoretical models have examined how different types of herbivores (e.g. grazing vs. browsing) could interact with fire to produce long-term changes in tree cover (Baxter & Getz, 2005; De Michele, Accatino, Vezzoli, & Scholes, 2011; Higgins et al., 2000; Holdo, 2006; Holdo, Holt, & Fryxell, 2009, 2013; van Langevelde et al., 2003). However, absent from these models are the processes by which different types of herbivores influence the development of fire resistance traits such as 'escape' height (Osborne et al., 2018). To our knowledge, there are no experimental studies quantifying the potentially interactive effects of megaherbivores, meso-wildlife and cattle on post-fire resprout height or potential for escape from the fire trap.

An added layer of complexity in understanding post-fire tree responses to herbivory is the potential for plant defences to influence herbivory. Investments in plant defence have been shown to decrease in some acacia species when resprouting after fire (Vadigi & Ward, 2012). In our study system the dominant tree, *Acacia drepanolobium*, has evolved an ant mutualism to defend against browsing ungulates (Palmer & Brody, 2013). Because *A. drepanolobium* ant occupancy is closely correlated with growth and browse damage for individual saplings (Riginos & Young, 2007), the post-fire resprouting

phase, when ant colonies are reduced or absent, may render trees even more vulnerable to browsing. We hypothesized that since fire reduces ant mutualism defence in *A. drepanolobium* (Kimuyu, Sensenig, Riginos, Veblen, & Young, 2014; Sensenig et al., 2017), it should, therefore, increase vulnerability of resprouts to browsing and ultimately delay the transition to fire-resistant height classes.

Here, we used the Kenya Long-term Exclosure Experiment (KLEE) (Young, Okello, Kinyua, & Palmer, 1997) to investigate how fire, herbivory regime and ant defences affect post-fire resprout size of a widespread monodominant East African tree, *A. drepanolobium*. We predicted that (a) post-fire resprout height would be increased by cattle and reduced by meso-wildlife and megaherbivores, and (b) the presence of ant mutualists would increase height (and therefore fire resistance) of resprouting trees.

2 | MATERIALS AND METHODS

2.1 | Study site

This research was carried out at the Mpala Ranch and Conservancy (0°17′N, 36°52′E; 1,800 m a.s.l.) in an *A. drepanolobium* ('whistling thorn') wooded savanna in the Laikipia District, Kenya. Mean annual rainfall is 580 mm/year and occurs in a weakly tri-modal pattern with major peaks in April–May and November, and minor peak in July. The study site is situated on a flat plateau underlain with deep clay-rich vertisol ('black cotton') soils. *Acacia drepanolobium* occurs as a monodominant shrub or dwarf tree on vertisol sites throughout East Africa (Deckers, Spaargaren, & Nachtergaele, 2001; Ross, 1979). This species is highly adapted to fire with a relatively thick bark (Midgley, Sawe, Abanyam, Hintsa, & Gacheru, 2016) and strong post-fire resprouting (Okello et al., 2008). It is the most widespread myrmecophyte tree in East Africa (Ross, 1979), producing domatia (swollen thorns) and extrafloral nectaries that provide food rewards to ants (Young, Stubblefield, & Isbell, 1997). These ant species include *Crematogaster mimosae* (Cm), *Crematogaster nigriceps* (Cn), *Crematogaster sjostedti* (Cs) and *Tetraponera penzigi* (Tp), which provide varying levels of protection against browsing insects and mammalian herbivores including elephants (Palmer et al., 2010; Young, Stubblefield, et al., 1997).

The Mpala Ranch and Conservancy is managed for both wildlife conservation and livestock production. Cattle are stocked at low to moderate densities (0.10–0.15 cattle ha^{-1}), although they outnumber native ungulates (Veblen, Porensky, Riginos, & Young, 2016). The meso-wildlife community includes grazers (e.g. plains zebras *Equus burchelli*, Grevy's zebra *Equus grevyi*, hartebeest *Alcelaphus buselaphus*, Cape buffalo *Syncerus caffer* and oryx *Oryx gazella*), as well as browsers and mixed feeders (e.g. Grant's gazelles *Gazella granti* and eland *Taurotragus oryx*). The two megaherbivores in the system are browsing giraffes *Giraffa camelopardalis*, which do not feed on saplings, and mixed feeding elephants *Loxodonta africana*. For herbivore abundances in KLEE see Veblen et al. (2016). Prior to our (and other) experimental burn treatments (described below), fire had not been an active part of the study site since the 1970s (Sensenig et al., 2017).

2.2 | Experimental design

We monitored the size-dependent response of trees top-killed by prescribed fire and subsequently exposed to herbivory by different combinations of cattle, meso-wildlife (15–1,000 kg) and megaherbivores (elephants). We accounted for the natural presence (or absence) of ant mutualists to determine whether plant defences mediated the effects of specific herbivore groups on post-fire resprout height.

The Kenya Long-term Exclosure Experiment (KLEE) was established in 1995 (Young, Okello, et al., 1997). Semi-permeable fencing is used to control access by meso-wildlife (large mammals 15–1,000 kg, 'W') and megaherbivores (elephants and giraffes, 'M'), and herding is used to control access by livestock (cattle, 'C'). Each of three blocks (North, Central and South) contains six 200 × 200 m (4 ha) herbivory treatment plots (total of 18 plots). Naming conventions for the six plot types—MWC, MW, WC, W, C and O—denote which herbivores are present within a given treatment, for example, MWC = all large herbivore groups present and O = no large herbivores present (Supporting Information S1). Steenbok *Raphicerus campestris*, small (12 kg) ungulate browsers, are present within all plots, as are rodents, mostly *Saccostomus mearnsi* (Keesing, 1998). Cattle are herded into C, WC and MWC plots typically six to eight times per year to maintain a grass utilization rate comparable to the surrounding rangeland. The timing and number of grazing days largely depends on forage production (i.e. seasonal precipitation). The KLEE grazing regime is representative of stocking densities and grazing frequency used on large cattle ranches in Laikipia (Odadi, Young, & Okeyo-Owuor, 2007).

One 30 × 30 m (0.09 ha) subplot within each of the 18 KLEE plots was burned during a 3-day period in February 2013 (see Kimuyu et al., 2014 for details). Prior to burning each subplot, all *A. drepanolobium* trees were labelled with aluminium tags, and measurements of height, stem diameter and ant occupancy were recorded. After 18 months, we re-measured all trees that had been top-killed by the fire treatments and were resprouting from live below-ground tissues in three to six belt transects (30 × 5 m) per plot (*n* = 755 resprouting trees). We recorded ant species occupancy, tree resprout height (max height of live tissue) and total stem length (sum length of all live stems and branches; sensu Okello et al., 2001; Riginos & Young, 2007).

2.3 | Data analysis

For tree resprout height and total stem length, we tested factorial combinations of cattle (two levels: present 'C' vs. absent 'O') and wildlife (three levels: all wildlife absent 'O', only meso-wildlife present 'W' or both meso-wildlife and megaherbivores present 'MW'), as well as effects of pre-fire tree height and post-fire ant species occupancy (four levels: none, Cn, Cm, Cs). We excluded from analysis data for resprouts occupied post-fire by the ant mutualist *Tetraponera penzigi* due to low abundance following the fire: Tp occupied only 17 of 755 top-killed trees (2.3%). This low post-fire
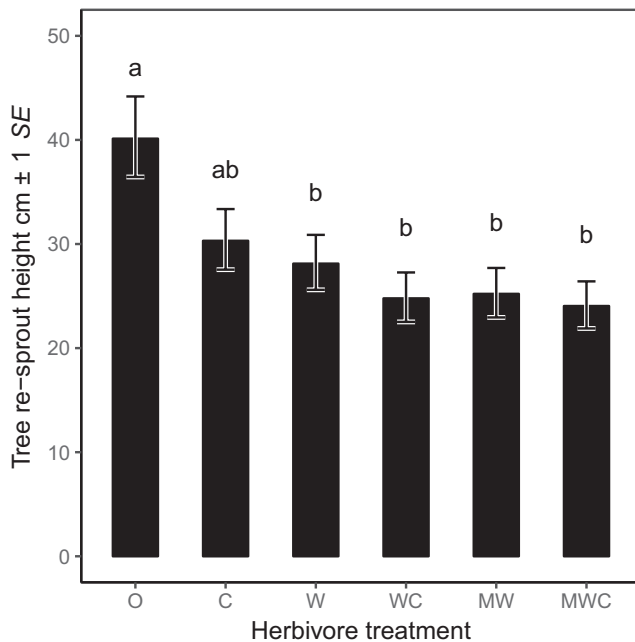
FIGURE 1 Post-fire resprout height of trees in different herbivory treatments. Estimated means at pre-fire height = 100 cm are averaged across levels of post-fire ant occupancy. C = cattle allowed, W = meso-wildlife allowed, M = megaherbivores allowed and O = all large herbivores excluded. Bars not sharing letters indicate significant differences in Tukey HSD comparisons ($p < 0.05$ with Kenward–Roger *df*). Values are back transformed to the original height scale

abundance is consistent with previous reports of *Tetraponera* mortality during fire (Kimuyu et al., 2014) and low post-fire *Tetraponera* recruitment (Sensenig et al., 2017).

Data were analysed in a blocked split–split plot design with herbivore treatment plots as the whole plot units nested within blocks. The six herbivore treatments comprised fixed effects factors which were randomly assigned to whole plots. Trees within a plot were clustered as 'tree-sets', such that each tree-set was associated with one level of ant occupancy (none, Cs, Cn or Cm). These tree-sets served as the split plot units; ant occupancy was the split plot fixed effects factor assigned to these tree-sets. Individual trees within sets were the split–split units, with pre-fire tree size measured on each tree as a fixed effects continuous covariate.

We used generalized linear mixed models to do separate analyses of resprout height and total stem length response. For each model, fixed factors included wildlife (O, W, MW), cattle (O, C), ant occupancy (none, Cs, Cn, Cm) and pre-fire tree size. Because fire resistance in *A. drepanolobium* is primarily a function of height (Okello et al., 2008), we used pre-fire height (which was highly correlated with pre-fire stem diameter, $r = 0.8$) as a covariate to account for size-dependent response. The random effects structure included intercepts for block, plot (nested in block) and tree-set (nested in block and plot). For each response variable, we fit three candidate models to test hypothesized interactions among wildlife, cattle, ant and pre-fire tree height. These included a global model examining all possible interactions

(four-way interaction), a reduced three-way interaction model including wildlife × ant × pre-fire height, and our a priori hypothesis model including two-way interactions among cattle × wildlife, ant × wildlife, ant × pre-fire height and wildlife × pre-fire height. We retained cattle × wildlife and ant × wildlife interaction terms in all models to test *a priori* hypotheses. We fit candidate models using maximum likelihood (ML) estimation and used the small sample size-corrected version of Akaike Information Criterion (AIC_c) to select among the candidate models (Arnold, 2010). The selected models were fit using Restricted Maximum Likelihood (REML) estimation and type III *F* tests using the Kenward–Roger method to obtain approximate denominator *df*.

Pairwise mean comparisons of resprout height or total stem length among combinations of cattle, wildlife and ant levels were evaluated as needed using the Tukey method to control family-wise Type I error rate. We evaluated the estimated marginal means (i.e. *ls means*) of resprout height and stem length at the pre-fire tree height of 1 m. For visualization of interactions involving trees over a range of pre-fire heights, we estimated marginal means at several values of pre-fire height (20, 100, 200, 300 and 400 cm). For the resprout height model, we constructed post hoc pairwise tests to compare the effect of pre-fire height among the three wildlife treatment levels. We considered differences among factors to be significant at the $p < 0.05$ level. In all analyses, we log transformed post-fire height and post-fire stem length to better meet normality, homogeneity of variance and linearity assumptions. The pre-fire height covariate was log transformed and centred on its overall mean value to improve interpretability of the main effects.

In order to qualitatively compare herbivory effects on growth of burned versus unburned trees, we conducted similar analyses on unburned trees (Supporting Information S2).

3 | RESULTS

3.1 | Post-fire tree height

We monitored the response of 738 top-killed trees whose pre-fire heights ranged from 4 to 512 cm (mean = 81 cm, median = 50 cm). Live resprouting stem tissues originated from the base of charred tree skeletons/stumps near the soil surface (we found no epicormic resprouting). The height of the resprouts 18 months post-fire ranged from 4 to 103 cm (mean = 26 cm, median = 24 cm).

Height of resprouts 18 months post-fire was negatively affected by all combinations of herbivore treatments that included wildlife ('W', 'WC', 'MW', 'MWC') relative to the no-herbivore ('O') treatment (Figure 1, Table 1). Height reductions in the cattle only treatment ('C') were not significantly different from the no-herbivore or any treatment that included wildlife (Figure 1), but cattle effects were significant overall (Table 1). At a pre-fire height of 100 cm (the height at which we chose to make mean comparisons), the addition of megaherbivores did not appear to reduce resprout height more than the effects of wildlife alone. However, when evaluated across all pre-fire tree heights, resprout height was positively related to pre-fire height (Figure 2)—a relationship that differed significantly among

TABLE 1 Type III ANOVA table for the resprout height model

	F	df	df_{K-R}	p
(Intercept)	2,315.3	1	2.2	<0.001
Wildlife	6.8	2	13.8	0.009
Cattle	6.9	1	9.9	0.025
Ant	24.1	3	58.2	<0.001
Log(pre-fire height)	45.9	1	689.2	<0.001
Wildlife : cattle	1.4	2	9.8	0.287
Ant : log(pre-fire height)	1.5	3	685.0	0.222
Wildlife : log(pre-fire height)	5.5	2	712.2	0.004
Wildlife : ant	1.6	6	48.0	0.166

wildlife treatment levels (log(pre-fire height) × wildlife interaction; $F_{2,712.2}$ = 5.53 p = 0.004; Figure 2, Table 1). In particular, mega-herbivore presence diminished the positive effect of pre-fire size compared to no-wildlife and meso-wildlife treatments (O vs. MW slope contrast; p = 0.001, and W vs. MW slope contrast; p = 0.008, Figure 2). The negative effects of megaherbivores (i.e. the difference between MW and O) became more pronounced as pre-fire tree size increased. Although we did not perform a true statistical test of the fire × wildlife interaction a supplemental analysis of unburned trees suggests effects of wildlife browsing were less pronounced in the absence of fire (Supporting Information S2).
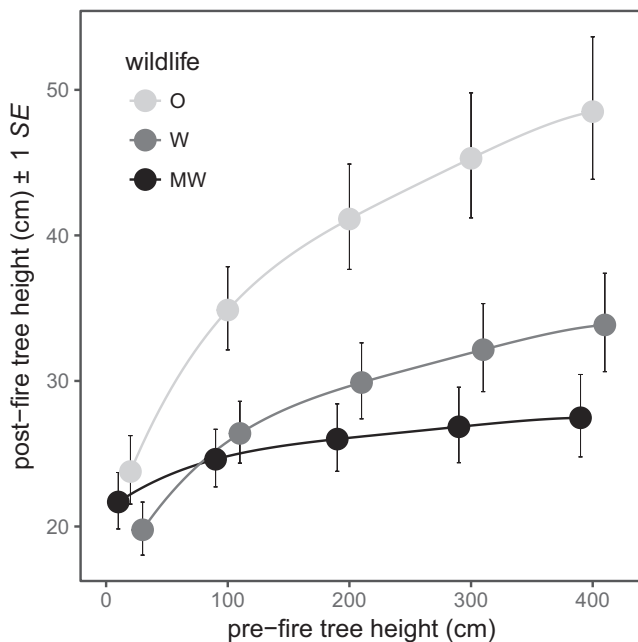

FIGURE 2 Fitted model height of trees exposed to three levels of wildlife herbivory: O = all wild herbivores excluded; W = meso-wildlife allowed; MW = meso-wildlife and megaherbivores (i.e. elephants) allowed. The log(pre-fire height) × wildlife slope coefficients were 0.17, 0.16 and 0.09, respectively, for O, W and MW treatments. Standard error bars displayed at pre-fire height = 20, 100, 200, 300 and 400 cm. Values back transformed to the original scale. Symbols are jittered along the horizontal axis to eliminate overlap

Resprout height 18 months post-fire was positively associated with the presence of defensive ants, regardless of ant species. After controlling for other variables, the estimated marginal means for ant-occupied trees were 6–9 cm (24%–37%) taller than unoccupied trees at pre-fire height = 100 cm (Figure 3). Ant occupancy status and relative proportion of trees in each ant level changed between pre- and post-fire sampling periods (Table 2). The proportion of unoccupied trees increased (+24%) as did the proportion of trees occupied by the ant Cm (+42%). The proportion of trees occupied by the remaining ant species decreased after fire: Tetraponera (−86%), Cs (−20%) and Cn (−10%) (Table 2).

3.2 | Post-fire stem length

Resprout stem length was positively associated with pre-fire tree height and ant occupancy (Table 3, Figure 4), although there were no significant differences in predicted stem length among ant species (means and standard errors estimated at pre-fire tree height = 100 cm and back transformed: none = 213 cm [+14, −14], Cs = 377 cm [+34, −31], Cn = 351 cm [+39, −34] and Cm = 343 cm [+25, −23]). We did not find evidence that herbivore treatment significantly affected post-fire stem length (Table 3).

4 | DISCUSSION

Several authors have suggested that, together, fire and herbivory decrease sapling recruitment rates, thereby decreasing savanna tree cover and density (Dublin, Sinclair, & McGlade, 1990; Morrison, Holdo, & Anderson, 2016; Scholes & Archer, 1997; Staver et al., 2009). Using experimental fires within a long-term herbivore exclusion experiment, we performed the first empirical test of how factorial combinations of cattle, meso-wildlife and megaherbivores affect resprout size following fire. We found clear evidence that a wide range of tree height classes resprout after being top-killed by fire and are subsequently kept short primarily by large mammalian herbivores. We also found evidence that, by suppressing the height of the largest resprouts, elephants prolong susceptibility to future fire top-kill events, which could prevent saplings from escaping from the 'fire trap'. An important element of our experimental design is that trees were subject to a given herbivore treatment both before (i.e. KLEE herbivory treatments initiated 18 years prior to burn treatments, see Methods2) and after fire. As such, rather than isolate post-fire effects of any given herbivore type, our study provides important information on how long-term herbivore regimes influence resprout responses following fire (and indicates that herbivore effects on growth differ between burned and unburned trees; see Supporting Information S2).

4.1 | Herbivory effects on post-fire resprout height

We found that meso-wildlife, regardless of the presence of mega-herbivores, showed the strongest negative effects on saplings that were small (1 m) before top-kill. This is likely because resprouting
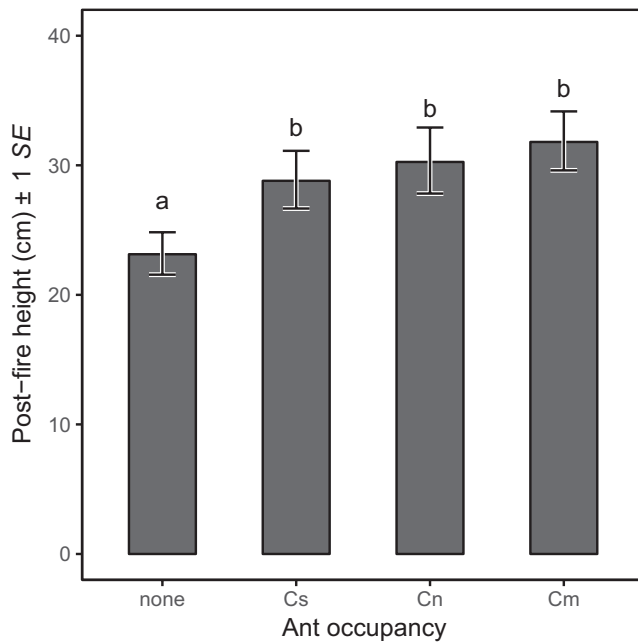
FIGURE 3 Post-fire resprout height among trees with different post-fire ant occupancy in order of increasing level of plant defence (0 = no ants, Cs = *Crematogaster sjostedti*, Cn = *Crematogaster nigriceps*, Cm = *Crematogaster mimosa*). Estimated means at pre-fire height = 100 cm and averaged across levels of cattle and wildlife. Bars not sharing letters indicate significant differences in Tukey HSD comparisons ($p < 0.05$ with Kenward–Roger *df*). Values are back transformed to the original height scale

tissues are most accessible to meso-herbivores. Meso-wildlife driven reductions in sapling height are consistent with previous work demonstrating that meso-wildlife browsers limit tree height both in the absence of fire (Augustine & McNaughton, 2004; Moncrieff, Chamaillé-Jammes, & Bond, 2014; Moncrieff et al., 2014; Sankaran et al., 2013) and during resprouting following fire (Andruk et al., 2014; Rhodes et al., 2017; Silva et al., 2015). We found the effects of meso-herbivores were greater in magnitude on burned than unburned trees (Supporting Information S2).

Our work goes a step further than previous work and provides quantitative evidence that, following fire, heights of the largest resprouting stems (>1 m pre-fire height) are reduced by elephants. We found that elephant presence diminished the positive effect of pre-fire tree height on post-fire resprout height (sensu Grady & Hoffmann, 2012; Schafer & Just, 2014), and the suppressive effects of elephant presence strengthened as pre-fire tree size increased. These results are consistent with evidence from our study system that elephant presence (Odadi et al., 2017) and density of elephant-damaged trees (Pringle et al., 2015) are greater in burned than unburned areas. Others have found that, elsewhere, elephant tree damage frequency increases with tree diameter (Holdo, 2006) and diverse herbivore assemblages that include megaherbivores such as elephants drive long-term declines in semi-arid savanna tree density (Pellegrini et al., 2017; Staver et al., 2009). Here, we have provided quantitative evidence that elephants limit the height of the largest (most capable of rapid growth following fire) resprouts, which are

those otherwise most likely to escape the fire trap cycle (Wakeling et al., 2011).

The presence of ant mutualists was associated with increased resprout height. Following fire, individuals that were occupied by ant mutualists of any species were taller than unoccupied resprouts, consistent with results of previous studies reporting ant presence confers defence against browsing (Palmer & Brody, 2007). An alternative interpretation of these latter results, however, is that ants preferentially colonized the tallest or healthiest resprouts post-fire (sensu Palmer, Young, Stanton, & Wenk, 2000) which offer greater nectar rewards and more domatia. Indeed, for a given pre-fire tree size, ant-occupied resprouts had higher post-fire stem length (biomass) than unoccupied resprouts, suggestive of greater 'health' (Figure 4). Only future studies of ant colonization dynamics can elucidate the level of herbivore defence conferred by ants following fire. The present study cannot rule out the possibility that other factors such as plot size or proximity to unburned ant colonies drove changes in ant occupancy.

Cattle presence did not increase resprout heights (e.g. via reduction of grass competition) as we had expected (Figure 1, Table 1). Reduced abundance of ant-occupied resprouts following fire (Table 2) as well as decreased worker ant density (Sensenig et al., 2017) may have left resprouting plant tissues vulnerable to consumption by cattle. Similarly, new resprouting tissues may have been more vulnerable to cattle due to the absence of physical defences (i.e. new unlignified spines), compounded by the low concentrations of polyphenolics and tannins in young *A. drepanolobium* leaves (Rubanza et al., 2005), though an extensive diet study (in unburned habitat) found no evidence that cattle consume *A. drepanolobium* (Odadi et al., 2007). We suggest several other potential reasons that cattle did not increase tree height as we had expected, and may instead have reduced it: (a) by reducing grass cover, cattle may have increased the apparency of resprouts to wild ungulate browsers (Riginos & Young, 2007), in particular steenbok, which are small browsers that have access to all KLEE plots; (b) grass reduction by cattle may have indirectly increased stress from the physical environment, for example, by increasing evaporative demand (Maestre, Bautista, & Cortina, 2003; Palmer et al., 2017); or (c) cattle may have trampled resprouting tree tissues (Cumming & Cumming, 2003).

4.2 | Herbivory effects on post-fire biomass

Resprout size often scales with pre-disturbance tree size (Grady & Hoffmann, 2012; Schafer & Just, 2014; Young & Francombe, 1991) due to factors such as root carbohydrate reserves (Schutz, Bond, & Cramer, 2009) or root depth and surface area (Nolan, Mitchell, Bradstock, & Lane, 2014). Accordingly, we found that total stem length of resprouts, a proxy for above-ground biomass, was strongly associated with pre-fire height. We expected to find negative effects of wildlife on total stem length due to post-fire browsing, but did not find significant differences in total stem length among herbivory treatments, perhaps because heavily browsed trees can exhibit compensatory growth (Fornara & du Toit, 2007; Gadd, Young,

TABLE 2 Total numbers and relative proportions of top-killed trees occupied by different symbiotic ant species pre-fire and 1.5 years post-fire, and percentage change pre- to post-fire, across all herbivore treatments combined. Total numbers of trees by herbivore treatments (right) where O = no herbivores, C = cattle only, W = meso-wildlife only, WC = meso-wildlife + cattle, MW = megaherbivores + meso-wildlife and MWC megaherbivores + meso-wildlife + cattle. Fire-resistant trees (i.e. those not top-killed by experimental fires) were excluded from the analysis

| Ant occupancy	ID	Pre-fire Total no. of trees	Pre-fire Relative proportion	Post-fire Total no. of trees	Post-fire Relative proportion	% change Relative change pre- to post-fire	O	C	W	WC	MW	MWC
No ants	O	328	0.43	406	0.54	0.24	62	55	96	43	90	60
Crematogaster sjostedti	Cs	106	0.14	85	0.11	−0.20	16	12	11	11	13	22
Crematogaster nigriceps	Cn	80	0.11	72	0.10	−0.10	5	10	23	12	14	8
Crematogaster mimosa	Cm	123	0.16	175	0.23	0.42	23	24	29	31	24	44
Tetraponera penzigi	Tp	118	0.16	17	0.02	−0.86	2	3	3	4	4	1
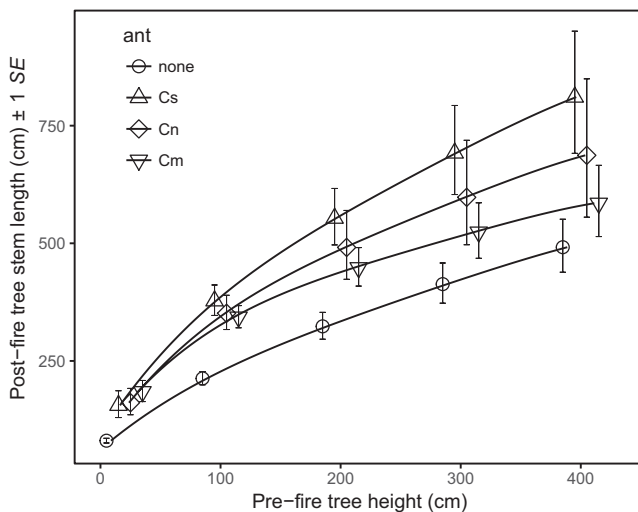
FIGURE 4 The effects of ant and pre-fire height on total stem length. Standard errors are estimated at pre-fire height = 20, 100, 200, 300 and 400 cm. Four levels of ant occupancy: none, *Crematogaster sjostedti* (Cs), *Crematogaster nigriceps* (Cn) and *Crematogaster mimosae* (Cm). Values back transformed to the original scale. Symbols are jittered along the horizontal axis to eliminate overlap

TABLE 3 Type III ANOVA table for the resprout stem length model

	F	df	df_{K-R}	p
(Intercept)	9,673.6	1	3.4	<0.001
Wildlife	0.3	2	15.7	0.779
Cattle	0.6	1	9.8	0.451
Ant	34.2	3	63.7	<0.001
Log(pre-fire height)	139.4	1	699.8	<0.001
Wildlife : cattle	0.5	2	9.7	0.615
Ant : log(pre-fire height)	2.4	3	691.5	0.066
Wildlife : log(pre-fire height)	0.7	2	715.0	0.501
Wildlife : ant	1.0	6	51.9	0.428

& Palmer, 2001; Riginos & Young, 2007). It is possible that 'legacy effects' of pre-fire herbivory (Johnstone et al., 2016) in KLEE plots have influenced our post-fire herbivory results; greater pre-fire browsing intensity may confer greater potential for compensatory growth following top-kill by fire (LaMalfa, unpub. data).

We also expected stem length and heights of resprouting trees to respond to herbivory in similar ways, but found two primary differences. First, post-fire browsing by wildlife decreased resprout height but had no significant effect on stem length. This could have occurred because the vertical height lost to browsing takes longer to replace due to delayed activation of a new apical meristem (Moncrieff et al., 2014), whereas unbrowsed lateral branches continue to elongate

horizontally. Second, cattle had no measurable effects on total stem length but appeared to decrease resprout height following fire. We had expected that, by removing grass, cattle would increase resource availability and thereby increase tree biomass. However, we did not find evidence that grass removal by cattle increased tree biomass or offset any negative effects of cattle on height.

5 | CONCLUSIONS

In the last century, changes in savanna vegetation structure and function have occurred as cattle have increasingly replaced native herbivores (du Toit & Cumming, 1999) and altered fire regimes (Roques, O'Connor, & Watkinson, 2001). Understanding how different types of large herbivores affect post-fire resprout size is important for predicting vegetation response to fire regimes across differing large herbivore assemblages (Bond, 2008; de Dantas & Pausas, 2013; Lehmann et al., 2014; Staver, Archibald, & Levin, 2011). Our results support the assertions of other authors that over long time-scales and many fire

cycles, the presence of wild browsing ungulates, both meso-wildlife and elephants, combined with fire creates a positive feedback that reduces or maintains low sapling recruitment (Dublin et al., 1990; Staver & Bond, 2014; Staver et al., 2009). Our study uniquely parsed out how different herbivore regimes affect post-fire resprout size. We also found evidence that reductions in post-fire ant–plant defence mediate browser-driven reductions in *A. drepanolobium* height, and we provide quantitative evidence that elephants exert important controls over tree demography by targeting the largest resprouts most likely to escape the fire trap.

AUTHORS' CONTRIBUTIONS

R.L.S., D.M.K., T.P.Y., C.R. and K.E.V. designed and implemented the KLEE experimental burns treatments. E.M.L., T.P.Y. and K.E.V. conceived the ideas and designed methodology; E.M.L. and D.M.K. collected the data; E.L. analysed the data and led the writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data and figures archived at Figshare: https://figshare.com/s/dc956 3e9a55fdb63900c (LaMalfa et al., 2019).

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SUPPORTING INFORMATION

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

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