

Megaherbivores and cattle alter edge effects around ecosystem hotspots in an African savanna

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ABSTRACT

Wild mammalian herbivores and cattle are fundamental drivers of African savanna ecosystems and have strong impacts on woody vegetation. However, few experimental studies have investigated the separate and combined influences of different large herbivores on spatial vegetation patterning. In East Africa, temporary cattle corrals (bomas) develop after abandonment into productive, treeless 'glades' that attract both domestic and wild herbivores. Edges of glades exhibit unusually high densities of large trees. We used a long-term, broad-scale manipulative experiment to test whether megaherbivores (elephants and giraffes), wild meso-herbivores (15–1000 kg), or cattle caused shifts in woody plant abundances in glade edges. We also examined cascading effects of megaherbivore and cattle exclusion on symbiotic *Acacia* ants and wild meso-herbivores in glade edges. Megaherbivore exclusion resulted in increased densities of tall trees, reproductive trees, and non-aggressive *Acacia* ant species in glade edges. Cattle presence reduced meso-herbivore use inside and away from glades, but not in glade edges. Our results suggest that megaherbivores and cattle can dampen the magnitude of spatial patterns associated with glades and glade edges. These findings provide insight into the development and maintenance of spatial heterogeneity in savannas, and emphasize that land use change and mammalian extinctions have complex, cascading ecological consequences.

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1. Introduction

In patchy and fragmented landscapes, ecological edge effects can have major impacts on ecosystem structure and functioning, biotic interactions, and management (Fagan et al., 1999; Harper et al., 2005; Ries et al., 2004). Edge effects are interactions between two adjacent ecosystems or land cover types separated by an abrupt transition (Murcia, 1995). In savannas as in forests, edge effects are often associated with changes in the composition and structure of woody plant communities (Young et al., 1995; e.g., Brits et al., 2002; Lima-Ribeiro, 2008). In Brazilian cerrado fragments, for example, woody plants near fragment edges are shorter and thinner than plants in fragment interiors (Lima-Ribeiro, 2008). Edge-related changes in woody plant structure and composition

can have cascading effects on other species and processes (Fagan et al., 1999; Porensky, 2011).

Large mammalian herbivores shape African savanna ecosystems and have strong impacts on woody vegetation (e.g., Augustine and McNaughton, 2004; Goheen et al., 2010; Pellew, 1983; Porensky and Veblen, 2012). Thus, in these landscapes, large herbivores are likely to influence edge effect patterns associated with woody vegetation. However, few experimental studies have examined whether edge effects are altered by large herbivores (but see Allombert et al., 2005; Didham et al., 2009; Fox et al., 1997), and to our knowledge, none has done so in Africa where large herbivores are still abundant and diverse. Further, to our knowledge, the separate and combined impacts of different guilds of large herbivores on edge effects have not been experimentally tested (but see observational work by Brits et al., 2002; de Beer et al., 2006). With a better understanding of how large herbivores alter edge effects, ecologists will be able to better comprehend the maintenance of spatial heterogeneity in savannas, as well as the potential landscape-level consequences of mammalian extinctions.

We used a long-term, broad-scale manipulative experiment to determine how various large herbivores alter edge effects around

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anthropogenic nutrient hotspots. For centuries, pastoralists in sub-Saharan Africa have corralled their cattle in temporary thorn-fence ‘bomas’ at night for protection against predators and stock raiders (Blackmore et al., 1990; Western and Dunne, 1979). Bomas are typically 50–100 m in diameter and are used for months or years before being abandoned. After abandonment, dung-filled boma sites develop into distinctive ecosystem ‘hotspots’ that persist for decades to centuries (Augustine, 2003; Blackmore et al., 1990; Young et al., 1995). At our study site, abandoned bomas develop into treeless, productive ‘glades’ that harbor nutrient-rich plant species and are used preferentially by livestock and wild herbivores (Augustine, 2003, 2004; Porensky, 2011; Veblen, 2012; Veblen and Young, 2010; Young et al., 1995). Glades are common in this landscape (found at densities of about 2 glades per km², Veblen, 2012), and represent major sources of structural and functional heterogeneity.

Glades can have edge effects that extend at least 100 m into the surrounding savanna matrix (Porensky, 2011; Young et al., 1995). One striking pattern associated with glade edges is an unusually high density of large trees (Porensky, 2011), which might be related to high nutrient availability within glades (Veblen, 2012) or a competitive advantage gained by tree seedlings growing in heavily grazed areas (Riginos and Young, 2007). Large trees around glades might also reflect the legacy of an establishment phase that occurred during or soon after active boma use (Muchiru et al., 2009). In this study, we investigated impacts of different large herbivores on woody vegetation patterns in glade edges. Large herbivores are known to affect the long-term development of herbaceous communities in glades (Veblen, 2008; Veblen and Young, 2010), but their impacts on co-occurring woody plants remain unclear (but see Porensky and Veblen, 2012).

Ecological edges can have strong influences on the interactions among different associated species (Fagan et al., 1999). Our study system gave us the opportunity to experimentally investigate how large herbivores, by altering vegetation in glade edges, may have cascading impacts on other animal taxa. For example, by thinning tall trees around glades, elephants may decrease the use of glade edges by other herbivores that respond to the micro-climatic benefits and high-quality forage found beneath trees (Ludwig et al., 2008; Treydte et al., 2009). Conversely, reduced tree densities may afford increased visibility and enhanced predator detection, which might be attractive to mid-sized herbivores (Riginos and Grace, 2008). Further, large herbivores could affect invertebrate communities associated with glade edges. In particular, the presence or absence of megaherbivore browsers might alter the relative abundances of ant species that are symbiotic with the dominant *Acacia* tree species in our system (Young et al., 1997).

This study used a broad-scale manipulative experiment to test three hypotheses about large herbivores and glade edge effects.

- 1) Woody vegetation patterns in glade edges are significantly altered by large herbivores.
- 2) Different guilds of large herbivores (e.g., cattle vs. megaherbivores) have different impacts on woody vegetation patterns.
- 3) Impacts of large herbivores on woody vegetation have cascading consequences for mid-sized herbivores and symbiotic *Acacia* ants.

2. Methods

2.1. Study area

This study took place at the Mpala Research Centre in Laikipia County, Kenya (0°17'N, 36°52'E, 1800 m a.s.l.), where more than

2000 Boran cattle (*Bos indicus*) coexist with abundant wildlife on a 17,000 ha conservancy. The climate is semi-arid with a mean annual rainfall of 500–600 mm (Young et al., 1998).

The study site is located on “black cotton” vertisol soil that supports some of the most productive rangelands in Africa (Young et al., 1998). Large mammalian herbivores are abundant; species include the endangered Grevy’s zebra (*Equus grevyi*), the more common Burchell’s zebra (*Equus quagga burchelli*), eland (*Taurotragus oryx*), oryx (*Oryx beisa*), hartebeest (*Alcelaphus buselaphus*), steinbuck (*Raphicerus campestris*), Grant’s gazelle (*Nanger [Gazella] granti*), warthog (*Phacochoerus africanus*), and occasionally bush duiker (*Sylvicapra grimmia*) or impala (*Aepyceros melampus*). These species are categorized as meso-herbivores hereafter. The study site also supports low densities of African buffalo (*Syncerus caffer*), which are not included in meso-herbivore analyses since their dung piles are indistinguishable from those of cattle. In addition, two megaherbivore species, giraffe (*Giraffa camelopardis reticulata*) and African elephant (*Loxodonta africana*), are present.

The dominant woody species in this system is *Acacia drepanolobium*. This small tree grows up to 6 m tall and accounts for 97% of total woody cover at our study site (Riginos and Grace, 2008; Young et al., 1998). Individuals produce hollow swollen spines that are inhabited by symbiotic ants, which defend the tree against herbivory (Palmer et al., 2010; Young and Okello, 1998; Young et al., 1997).

In our study system, *A. drepanolobium* trees are typically inhabited by one of four species of ants: *Tetraponera penzigi*, *Crematogaster mimosae*, *Crematogaster nigriceps*, or *Crematogaster sjostedti* (Stanton et al., 2002; Young et al., 1997). These ants exist within a competitive hierarchy associated with differently-sized trees. *T. penzigi* and *C. nigriceps* are competitively subordinate and tend to be found on smaller trees, while *C. mimosae* and *C. sjostedti* are competitively dominant and often found on larger trees (Palmer et al., 2010; Stanton et al., 2002; Young et al., 1997). The four species also differ in their ability to defend trees against megaherbivore browsing: *T. penzigi* and *C. sjostedti* ants are less aggressive, while *C. mimosae* and *C. nigriceps* are more aggressive toward browsers (Palmer et al., 2010; Stanton et al., 2002; Young et al., 1997, 2003). Hereafter, we refer to ants based on these two aggressiveness classes.

Our work took place within the Kenya Long-term Exclusion Experiment (KLEE), which has been assessing the separate and combined impacts of different herbivores on this savanna ecosystem since 1995 using a broad-scale approach (Young et al., 1998). The experiment consists of three replicate blocks, each with six 200 × 200 m treatment plots (Fig. 1). Different barriers exclude different guilds of herbivores (see also Appendix): 1) Visual markers serve to keep individually-herded cattle (C) in designated plots. 2) A two-strand electric line 2 m off the ground excludes only megaherbivores (elephants and giraffes; M). 3) A nine-strand electric game fence excludes all meso-herbivores 15–1000 kg (W) as well as megaherbivores. There are gates in the game fence to allow entry by herded cattle. In addition to total exclusion plots (O), treatment combinations include C, W, WC, MW and MWC, where letters indicate the types of animals allowed into the plots (e.g., WC plots allow meso-herbivores and cattle). Smaller herbivores (steinbuck, hares, rodents, and invertebrates) have access to all plots. Individually-herded groups of cattle were run in each C, WC or MWC plot for 2 h 6–8 times per year, producing impacts similar to the overall ranch stocking density (see Odadi et al., 2007) while limiting human and livestock presence to a few hours per year.

The KLEE study design includes six glades (abandoned boma sites), which were divided in 1995 by the herbivore exclusion fences to create 18 glade portions (Fig. 1a, Young et al., 1998). These include several glade portions adjacent to the KLEE plots that are

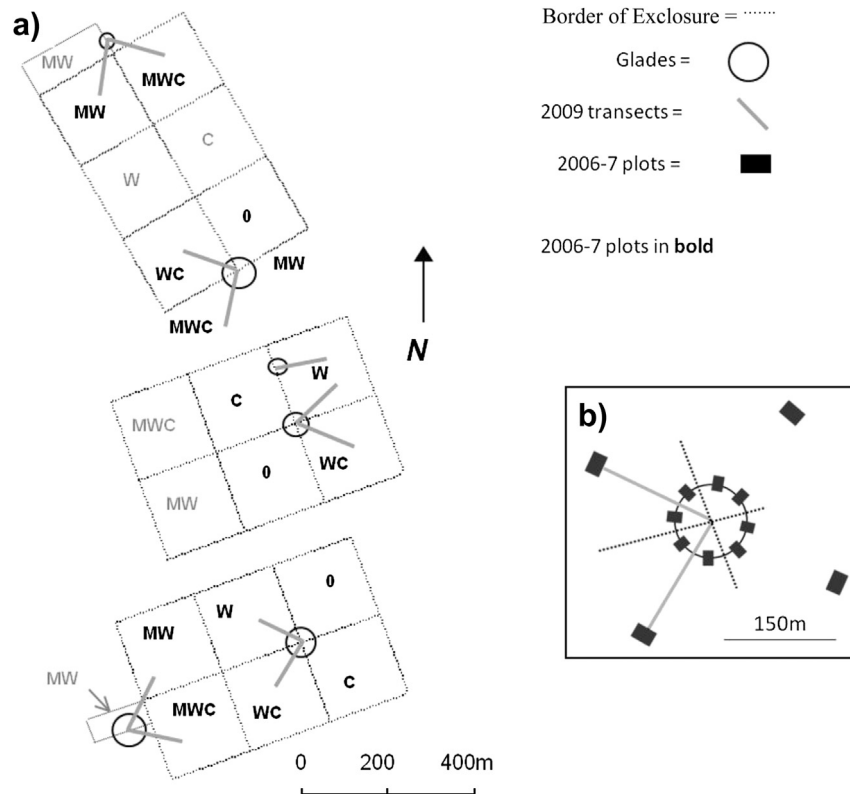


Fig. 1. a) Diagram of the Kenya Long-term Exclosure Experiment, including herbivore treatment labels, locations of glade portions and 2009 sampling transect locations. See Table 1 for explanations of treatment abbreviations. Glade portions occurring in treatment plots labeled in bold were sampled in 2006–2007, and b) provides a detailed view of 2006–2007 sample plot locations.

maintained in herbivore treatments (Fig. 1a, Young et al., 1998) which results in comparable environmental conditions within each portion. Historical aerial photographs indicate that all of these glades have been present for more than 40 years.

2.2. Data collection

Over 2006–2007, we determined whether woody communities in glade edges differed from background conditions across herbivore treatments. For all glade portions in KLEE (Fig. 1a), we sampled woody species in large plots at the glade edge and at 150 m away from the glade. At 150 m outside the perimeter of each of the 18 glade portions, we placed the closest, long edge of a 40 × 30 m plot (Fig. 1b). At glade edge, we split sampling into two 20 × 30 m plots to increase the amount of curvilinear glade perimeter captured by our plots. Each 20 × 30 m plot was placed at glade edge, spanning 10 m inside to 20 m outside the glade perimeter (Fig. 1b). We counted all *A. drepanolobium* trees rooted in each sample plot and categorized them into three height classes: <1 m, 1–3 m, and >3 m tall. We also recorded all occurrences of non-*A. drepanolobium* woody species (excluding seedlings).

In 2009 (a drought year), we looked more closely at *A. drepanolobium*, collected edge data with higher spatial resolution, and investigated meso-herbivore use of glades and glade edges. The 2006–2007 data suggested that meso-herbivores had no consistent effects on woody vegetation patterns around glades (see Results). Therefore, in 2009 we concentrated on the effects of cattle and megaherbivores. We used four of the six KLEE treatments (W, WC, MW, and MWC) to investigate a full factorial of megaherbivore and cattle effects. The 2006–2007 data revealed a strong pattern in the largest size class of *A. drepanolobium* trees

(>3 m). In 2009, we further subdivided this large size class into 3–4 m and >4 m size classes to improve the resolution of our data. For all size classes we also included metrics of *A. drepanolobium* reproduction and symbiotic ant occupancy. Finally, we used dung counts to investigate interactions within the herbivore community.

For all 2009 surveys, we set up 150 m-long transects at each glade inside or adjacent to KLEE treatment plots. Each transect started in the center of a glade and extended away from the glade and into one of the treatment plots (Fig. 1a). Along each transect, we recorded the following response variables:

- (1) For each *A. drepanolobium* tree within 4 m of the transect line, we recorded its distance along the transect, its height, and its reproductive status (flowering or fruiting vs. non-reproductive). Trees were classified into four height categories: <1 m, 1–3 m, 3–4 m, and >4 m. We also recorded the species identity of any symbiotic ant species present on each tree.
- (2) For each dung pile within 4 m of the transect line, we recorded its distance along the transect and the animal species that produced it. Previous work suggests that dung counts are a reliable method to determine relative animal use (Augustine, 2003; Young et al., 1995, 2005). Buffalo and cattle dung piles were indistinguishable, and therefore these two species were lumped as 'cattle + buffalo'. However, cattle are >10 times more abundant than buffalo at the study site. Other species were classified as 'grazers' (zebra, hartebeest and warthog), 'mixed feeders/browsers' (eland, oryx, steinbuck, Grant's gazelle, bush duiker and impala), or 'megaherbivores' (elephant and giraffe).

For each of these response variables, data were binned into 5 m distance intervals along each transect.

2.3. Statistical analyses

2.3.1. 2006–2007 surveys

We used split-plot designs to test treatment effects on woody vegetation. For woody (non-*A. drepanolobium*) species densities and the three *A. drepanolobium* size class densities, each model included the following fixed effects: main plot effect of herbivore treatment (O, C, W, WC, MW, MWC), subplot effect of distance (inside, edge, outside of glade), and the herbivore*distance interaction. Block, glade nested within block, and the block*glade interaction were included as random effects. For all statistical analyses, we used generalized linear mixed models (GLMMs), maximum-likelihood methodology and Satterthwaite's approximation of degrees of freedom (PROC MIXED, version 9.1, SAS Institute Inc, 2008). Variance-weighting was used when variances were not homogenous, and values were log-transformed when necessary. We used Tukey's HSD analyses for post-hoc comparisons, and we report means ± 1 SE throughout the results.

2.3.2. 2009 surveys: standardizing the glade edge

One of the most defining structural characteristics of glades is their persistent lack of trees, so tree density was used to standardize the location of the glade edge across transects. Although this 'glade edge' location is not necessarily intended to reflect a functional edge, our observations suggest it is largely coincident with the location of the original boma fence. The glade edge was defined as the first 5 m interval in which we found ≥ 4 *A. drepanolobium* trees/40 m². For each transect, this glade edge distance was defined at 0 m, so that areas inside and outside the glade had negative and positive distance values, respectively.

2.3.3. 2009 surveys: spatially coarse-scale analysis

For each response variable along each transect, we averaged binned values for two standardized distance intervals: –25 to 0 m (inside glade), and 0–25 m (glade edge). For each distance interval, we compared among treatments using GLMMs with the following predictors and their interactions: block (a random factor), cattle exclusion, and megaherbivore exclusion. The cattle*megaherbivore interaction term was removed from models in which it was non-significant ($p > 0.10$). Response variables included overall tree density, tree density separated by size class, overall density of meso-herbivore dung piles, meso-herbivore dung density separated by feeding guild, overall density of trees occupied by *Acacia* ants, and ant occupancy separated by species aggressiveness. For analyses involving multiple herbivore guilds, tree size classes or ant species, MANOVAs were used initially to establish overall significance. For all other analyses, we used GLMMs with maximum-likelihood methodology and Satterthwaite's approximation of degrees of freedom (PROC MIXED, version 9.1, SAS Institute Inc, 2008). Response variables were log-transformed when necessary to achieve normality. Due to the low replication of this broad-scale experiment, we set α at 0.10. We also used a generalized linear mixed model (with predictors as described above and log-transformed glade radius as the response variable) to confirm that cattle and megaherbivore exclusion had no significant impacts on glade radius. We report means ± 1 SE throughout the results.

2.3.4. 2009 surveys: spatially fine-scale analysis

For response variables significantly affected by cattle or megaherbivore exclusion (based on the coarse-scale analysis above), we fit continuous nonlinear models to identify the distance ranges over which significant differences occurred. We used the following

model, which includes linear, sigmoid, and unimodal edge effect shape components:

$$y = a + bX + \frac{b_1}{1 + e^{(b_2 - X)^{b_3}}} + h * e^{\frac{-(X - x_0)^2}{2W^2}}$$

linear
sigmoid
unimodal

where X is distance from the edge and the other variables are fitted constants. For each response variable along each transect, we fitted the model using the nonlinear platform in JMP (version 8.0, SAS Institute, Inc., Cary, NC, USA) and an expectation maximization approach (for methodological details, see Porensky, 2011). We averaged fitted models within different treatments and then identified regions in which the 90% confidence intervals of the different average models were non-overlapping. In these regions, treatments were considered significantly different. To reduce the influence of outliers, we only compared standardized distance values at which at least four transects from each treatment had data. The model-fitting and subsequent model-averaging process should further reduce the influence of outliers.

3. Results

3.1. 2006–2007 surveys

Densities of the largest individuals (> 3 m tall) of the dominant tree, *A. drepanolobium*, were three times higher in glade edges than far from glades (Table 1, distance effect $F_{1,12.2} = 57.34$, $p < 0.0001$). However, this effect occurred only in plots without megaherbivores (edge > out, treatment*distance class interaction $F_{5,12.3} = 3.42$, $p = 0.04$, Tukey HSD $p < 0.05$ for W, WC, and C; for O $p = 0.19$). In MW and MWC plots, the two plot types that allow entry to megaherbivores, edges did not have significantly higher densities (Table 1). For 1–3 m tall *A. drepanolobium* trees there were no significant distance or treatment effects (Table 1). For small (< 1 m tall) trees, no significant distance effects could be found. The C plots (cattle only) had 39–60% fewer small *A. drepanolobium* individuals

Table 1

Mean (± 1 SE, in trees per hectare) densities of three size classes of *Acacia drepanolobium* trees in glade edges and 150 m outside of glades in six herbivore treatments. Herbivore treatments allow different combinations of the following: cattle ("C"), wild meso-herbivores > 15 kg ("W"), and wild megaherbivores (elephants and giraffes, "M"). No herbivores are allowed in "O" plots. Letters in the > 3 m tree category indicate significant differences across all 12 means (Tukey's HSD, $\alpha = 0.05$). Differences were not significant in the < 1 m and 1–3 m categories.

Tree size class	Herbivore treatment	Edge		150 m away	
		Mean (#/ha)	\pm SE	Mean (#/ha)	\pm SE
<1 m	C	128	53	314	23
	MW	304	21	521	229
	MWC	461	69	264	84
	O	367	121	389	161
	W	286	66	725	168
	WC	442	17	686	225
1–3 m	C	797	57	917	128
	MW	742	217	1433	608
	MWC	875	230	519	136
	O	1339	167	1136	363
	W	1003	61	1253	287
	WC	1222	242	1075	393
>3 m	C	^a 653	129	^b 286	85
	MW	^{ab} 329	71	^b 208	50
	MWC	^b 189	26	^b 131	31
	O	^{ab} 486	92	^b 225	97
	W	^a 864	220	^b 158	17
	WC	^a 664	266	^b 131	64

than the other treatments, but this was statistically significant only compared to WC (meso-herbivores + cattle, Table 1, treatment effect $F_{5,15.8} = 2.92$, $p = 0.05$). In other words, plots allowing only cattle had fewer small trees than plots allowing both meso-herbivores and cattle. However, small tree density did not differ significantly between total exclusion plots (O) and plots allowing meso-herbivores (W).

Densities of two common woody shrubs, *Lycium europaeum* L. and *Rhus natalensis* Krauss, were significantly higher in glade edges than outside glades (*L. europaeum*: $44.1 \pm 13.9 \text{ ha}^{-1}$ vs. 3.9 ± 3.0 , $F_{1,19.1} = 5.83$, $p = 0.03$; *R. natalensis*: 16.2 ± 4.1 vs. 5.4 ± 1.2 , $F_{1,14} = 7.95$, $p = 0.01$). Densities of the other most common shrub, *Cadaba farinosa* Forssk., did not differ significantly by distance (27.9 ± 4.1 vs. 20.1 ± 5.4 , $F_{1,11.2} = 1.98$, $p = 0.19$). None of these shrubs responded significantly to herbivore treatments.

3.2. 2009: transect-wide meso-herbivore results

Averaged across treatments (W, WC, MW and MWC) and distances from glades, meso-herbivore (excluding cattle and buffalo) dung comprised 63% zebra, 19% eland, 6% oryx, 5% hartebeest, 4% steinbuck, and 3% other species. In plots where cattle were allowed, cattle + buffalo dung and zebra dung each accounted for $37 \pm 6\%$ of total dung. In plots where cattle were excluded, cattle + buffalo dung accounted for $3 \pm 1\%$ and zebra dung accounted for $60 \pm 4\%$ of total dung. Zebra dung was 70% more abundant in plots where cattle were excluded (129 ± 16 vs. 222 ± 16 dung piles; $t = -4.11$, $p = 0.003$, $df = 8.8$).

3.3. 2009: coarse-scale analysis

Cattle and megaherbivore exclusion had no significant impacts on glade radius (W = 35 ± 9 m, WC = 28 ± 3 m, MW = 28 ± 3 m, MWC = 27 ± 4 m; all p -values >0.10). In glade edges, herbivore treatments significantly affected tree size structure (tree size class MANOVA: cattle effect *Wilk's* $\lambda = 0.04$, $p = 0.02$; megaherbivore effect *Wilk's* $\lambda = 0.05$, $p = 0.03$). In particular, the density of large trees (>4 m tall) in glade edges was more than three times higher when megaherbivores were excluded (Fig. 2; 2.0 ± 0.2 vs. 0.6 ± 0.2 trees/40 m²; megaherbivore $F_{1,5.29} = 50.44$, $p = 0.0007$). Cattle exclusion did not significantly affect large tree density in glade edges ($F_{1,3.74} = 1.43$, $p = 0.3$). In glade edges, neither cattle nor megaherbivore exclusion significantly affected the density of trees in other size classes (Fig. 2) or overall tree density (all p -values >0.10).

Cattle exclusion and megaherbivore exclusion both led to higher densities of reproductively active trees in glade edges. When cattle were excluded, the density of reproductively active trees was 80% higher (3.2 ± 0.6 vs. 1.8 ± 0.3 flowering or fruiting trees/40 m²; $F_{1,8} = 9.42$, $p = 0.02$). Similarly, the density of reproductively active trees was over twice as high when megaherbivores were excluded (Fig. 2; 3.2 ± 0.6 vs. 1.5 ± 0.2 flowering or fruiting trees/40 m²; $F_{1,8} = 13.25$, $p = 0.007$).

Cattle and megaherbivore exclusion affected the densities of trees occupied by different types of ants in glade edges (cattle*megaherbivore effect *Wilk's* $\lambda = 0.27$, $p = 0.07$). Megaherbivore exclusion resulted in higher densities of non-aggressive ants (*T. penzigi* and *C. sjostedti*), especially when cattle were also excluded (Fig. 3; cattle $F_{1,7} = 4.93$, $p = 0.06$; megaherbivore $F_{1,7} = 11.89$, $p = 0.01$; cattle*megaherbivore $F_{1,7} = 4.43$, $p = 0.07$). Neither cattle nor megaherbivore exclusion significantly affected the density of trees occupied by more aggressive ants (*C. nigriceps* and *C. mimosae*; p -values >0.10). Similarly, the overall density of ant-occupied trees in glade edges was not significantly affected by either cattle or megaherbivore exclusion (p -values >0.10).

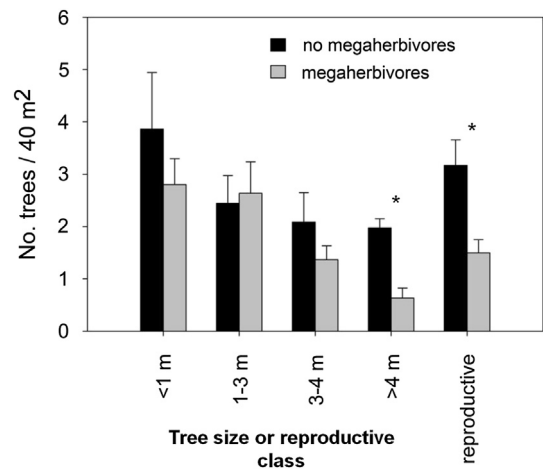


Fig. 2. Mean density (± 1 SE; in trees per 40 m²) of *A. drepanolobium* trees of different sizes and reproductive states in glade edges (0–25 m distance class), in plots to which megaherbivores did or did not have access. Asterisks indicate significant differences between herbivore treatments at the $p < 0.05$ level.

Inside glades, cattle exclusion significantly affected the density of wildlife dung piles (wildlife MANOVA: cattle effect *Wilk's* $\lambda = 0.32$, $p = 0.06$; megaherbivore effect *Wilk's* $\lambda = 0.64$, $p = 0.3$). For grazers (zebra, hartebeest and warthog), the density of dung piles inside glades was more than twice as high when cattle were excluded (10.8 ± 1.3 vs. 4.7 ± 1.0 grazer dung piles per 40 m²; cattle effect $F_{1,8} = 19.45$, $p = 0.002$). Dung densities for browsers and mixed feeders (eland, oryx, steinbuck, Grant's gazelle, bush duiker and impala) inside glades were also more than twice as high when cattle were excluded (3.8 ± 0.6 vs. 1.7 ± 0.5 browser/mixed feeder dung piles per 40 m²; cattle effect $F_{1,8} = 6.45$, $p = 0.03$).

Megaherbivore exclusion did not significantly affect the density of wildlife dung piles inside glades (grazers: $F_{1,8} = 2.97$, $p = 0.12$; browsers/mixed feeders: $F_{1,8} = 0.08$, $p = 0.8$). Moreover, neither cattle nor megaherbivore exclusion significantly impacted the density of wildlife dung piles in glade edges (MANOVA p -values >0.10). Inside glades, neither cattle nor megaherbivore exclusion significantly affected overall tree density, the density of reproductively active trees, or the density of ant-occupied trees (all p -values >0.10). Separating trees by size class and separating ants by

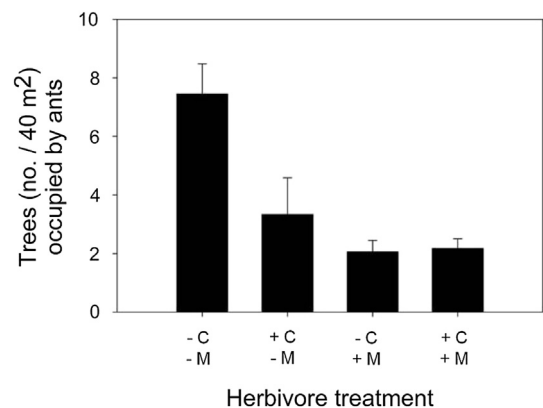


Fig. 3. Mean densities (± 1 SE; in trees per 40 m²) of trees hosting non-aggressive ant species (*C. sjostedti* and *T. penzigi*) in different large herbivore treatments. +M = plots allowing megaherbivores; -M = plots excluding megaherbivores; +C = plots allowing cattle; -C = plots excluding cattle. The interaction between cattle and megaherbivore presence was significant at the $p < 0.10$ level (cattle $F_{1,7} = 4.93$, $p = 0.06$; megaherbivore $F_{1,7} = 11.89$, $p = 0.01$; cattle*megaherbivore $F_{1,7} = 4.43$, $p = 0.07$).

aggressiveness did not reveal any additional patterns inside glades (MANOVA p -values >0.10).

3.4. 2009: fine-scale analysis

To examine herbivore effects at a finer spatial scale, we compared average fitted models obtained from transects in different treatments. Average models were considered significantly different wherever their 90% confidence intervals did not overlap. For grazer use, browser use, reproductively active trees and trees occupied by non-aggressive ants, we compared fitted models from transects in plots with or without cattle. At distances < -20 m, between -20 and 0 m, and between 50 and 90 m outside glade edge, grazer use was significantly higher in transects without cattle (Fig. 4a). At distances between -15 and 5 m, browser use was also significantly higher in transects without cattle (Fig. 4b). Transects without cattle had significantly more reproductively active trees between 5 and 15 m outside glade edge, and significantly more non-aggressive ants between 40 and 50 m outside glade edge.

For densities of large trees (>4 m tall), reproductively active trees and trees occupied by non-aggressive ants, we compared fitted models from transects in plots with or without megaherbivores. When megaherbivores were excluded, large tree densities were significantly higher at distances between -10 and 10 m, 15 – 35 m, and 65 – 80 m outside glade edge (Fig. 4c). Transects without megaherbivores also had significantly more reproductively active trees between 20 and 35 m (Fig. 4d). These results indicate that megaherbivore exclusion led to wider peaks for large and reproductively active tree densities in glade edges (Fig. 4c and d). Megaherbivore exclusion did not significantly affect non-aggressive ant occupancy at any distance, likely because of the interaction between cattle and megaherbivore effects (see above, Figs. 3 and 4e).

4. Discussion

Megaherbivores and cattle both significantly altered glade edge effects in this savanna landscape mosaic. Megaherbivores reduced the spatial heterogeneity created by glades, not by reducing

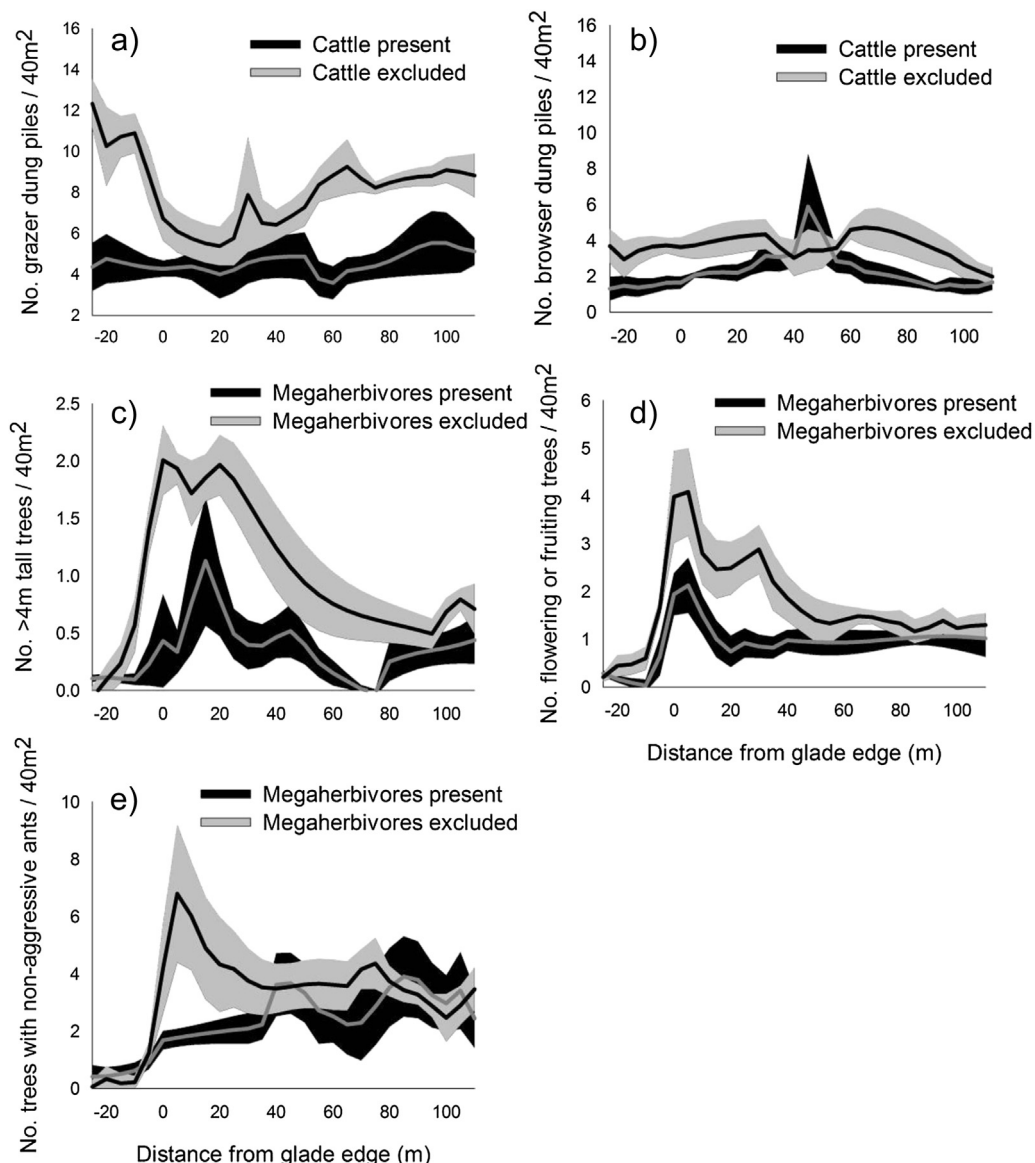


Fig. 4. Average fitted models (± 1 SE) for densities of a) grazer dung piles, b) browser dung piles, c) large trees (>4 m tall), d) reproductively active trees, and e) non-aggressive ants.

differences between glades and the background savanna, but by reducing unique traits associated with glade edges: high densities of large trees, reproductively active trees and non-aggressive *Acacia* ants. Cattle also reduced the densities of reproductively active trees and non-aggressive *Acacia* ants in glade edges. Cattle further dampened spatial heterogeneity by weakening meso-herbivore preference for glade interiors. These results suggest a combination of direct and indirect effects (Fig. 5), and further research is needed to clarify some of the relevant mechanisms.

Meso-herbivore exclusion did not have strong impacts on *A. drepanolobium* density or size structure in glade edges. Cattle probably have stronger impacts than wild meso-herbivores because of their higher biomass density (cattle have 5–10 times higher biomass per km² than wild ungulates). Differences between meso-herbivores and cattle might also be related to differences in the timing of grazing (continuous vs. discontinuous), evolutionary history in the system (long vs. short), or diet (though dietary overlap between cattle and the dominant meso-herbivore, zebra, is probably large) (Odadi et al., 2007, 2011).

4.1. *A. drepanolobium*

One of the most striking edge effects in our study system is the high density of large trees in glade edges. Although it is not clear what causes rings of tall, dense trees to form at glade edges, we found that megaherbivore exclusion clearly enhanced this effect. The abundance of large trees in glade edges was significantly higher in plots where megaherbivores were excluded (Table 1; Figs. 2, 4 and 5). This suggests that megaherbivores preferentially feed on large trees in glade edges, perhaps because higher tree densities and taller trees in glade edges represent attractive forage patches. Elephants often seem to browse preferentially on larger trees, especially in high tree density areas (Augustine and McNaughton, 2004; Pellew, 1983). Trees next to glades may also contain more nutrients than trees in the background savanna, and this enhanced nutrient content may attract elephant and giraffe browsing.

Elephant foraging typically leads to killing, coppicing or reduction of tree size (Augustine and McNaughton, 2004; Goheen et al., 2007; Van de Vijver et al., 1999) while giraffe browsing tends to be focused on taller trees and can severely slow tree growth (Pellew, 1983).

Whereas only megaherbivores had a negative effect on tree density in glade edges, both megaherbivores and cattle reduced fruiting and flowering of *A. drepanolobium* (Fig. 5). These results may be driven by changes in browsing pressure. Megaherbivore exclusion reduces browsing directly, and cattle exclusion may also reduce browsing pressure by increasing understory forb biomass (Odadi et al., 2013). In cattle exclusion plots, wild ungulates may be able to meet nutritional needs by eating forbs, and therefore may be less likely to browse on trees. Reduced browsing can increase reproduction by increasing tree size, since larger trees are more likely to reproduce (Goheen et al., 2007; Palmer et al., 2010). Reduced browsing can also cause reduced investment in defense (Palmer et al., 2008; Young et al., 2003), which may lead to increased investment in reproduction (Goheen et al., 2007). Finally, increased reproduction in the absence of megaherbivores and cattle could be an indirect consequence of increased densities of non-aggressive ants. *C. sjostedti* occupation is associated with increased fruiting in *A. drepanolobium*, and *T. penzigi* is also associated with higher fruiting probabilities than either *C. mimosae* or *C. nigricipes* (Palmer et al., 2010).

If increased flowering and fruiting near glades leads to higher seedling recruitment inside glades, herbivore exclusion might reduce the persistence of glades as treeless areas (by promoting tree reproduction). Alternatively, higher seed availability in the absence of large herbivores might enhance granivorous insect and rodent populations, which in turn could suppress seedling establishment and keep glades treeless (Palmer and Brody, 2007; Walters et al., 2005). Moreover, relationships between the presence of reproductive structures and actual seed production or seedling recruitment are probably highly variable (Goheen et al., 2007, 2010). In light of these complications, impacts of different

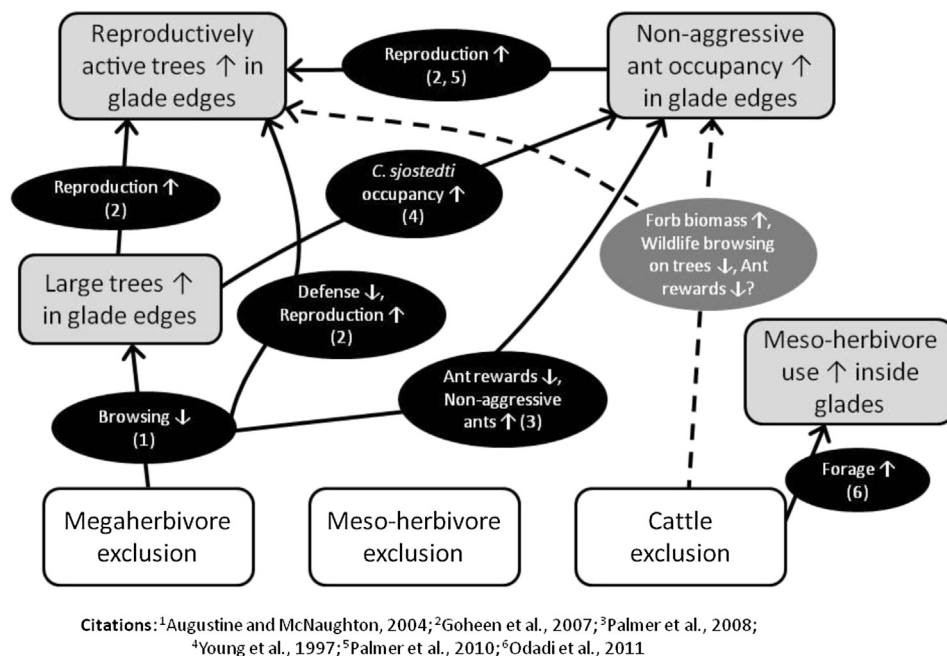


Fig. 5. Conceptual diagram illustrating direct and indirect effects of herbivore treatments on meso-herbivore use and *A. drepanolobium* density, reproductive status and ant occupancy. White boxes indicate herbivore treatments and gray boxes indicate results from this study. Solid arrows and black ovals indicate mechanisms supported by published research. Dotted arrows and the gray oval indicate currently untested mechanisms.

herbivores on tree recruitment inside and near glades warrant further study.

4.2. Symbiotic Acacia ants

Our study showed that the number of trees occupied by non-aggressive ants was higher when both megaherbivores and cattle were absent (Figs. 3 and 5). The dominant non-aggressive ant species (*C. sjostedti*) is more common in larger trees (Young et al., 1997), so increased densities of large trees certainly contributed to increased densities of non-aggressive ants. However, changes in large tree density are not sufficient to explain changes in ant occupancy (Fig. 4), and we found that megaherbivore and cattle exclusion did not significantly affect small- or medium-sized tree densities in glade edges.

Megaherbivore and cattle exclusion may further affect changes in ant occupancy by reducing browsing pressure (see Section 4.1). Trees under lower herbivory pressure can reduce production of 'ant rewards' in the form of nectaries and swollen spines (Huntzinger et al., 2004; Palmer et al., 2008), causing ant species more dependent on rewards (e.g., *C. mimosae*) to be replaced by ant species less dependent on rewards (e.g., *C. sjostedti*; Palmer et al., 2008). Our results are similar to those of Palmer et al. (2008), who observed a replacement of *C. mimosae* (aggressive) by *C. sjostedti* (non-aggressive) under herbivore exclusion.

Changes in ant community composition can have major impacts on *A. drepanolobium* survival, growth, architecture, parasitism and reproduction (Palmer et al., 2002, 2008, 2010; Riginos and Young, 2007; Stanton et al., 1999). Our study shows that these changes could have spatially explicit ecosystem effects, particularly in areas where *A. drepanolobium* is dominant (Young et al., 1998).

4.3. Mammal use

Cattle and zebra were the species whose dung was most frequently found at our study site; these two species dominate this savanna landscape (Young et al., 2005). The 70% increase in zebra dung in plots excluding cattle is consistent with previous studies demonstrating that cattle and zebra, both grazers, usually compete for their diet and prefer similar habitat, particularly during the dry season (Odadi et al., 2007, 2011; Young et al., 2005).

Our data, collected during a drought, suggested that cattle reduced meso-herbivore preference for glades (Fig. 4). Given that cattle spend fewer than 12–16 h per year inside each glade portion, our results probably were not driven by direct interference between cattle and wildlife. Though cattle had no significant effects on tree densities or size structure (Table 1), cattle were associated with fewer reproductive trees and higher aggressive ant occupancy (Fig. 3). By increasing aggressive ant occupancy, cattle could have made *A. drepanolobium* trees less attractive to meso-herbivore browsers. However, our data suggest that cattle had similar effects on meso-herbivore grazers and browsers. Thus, we hypothesize that the effects of cattle on wildlife were driven mostly by indirect competition for herbaceous forage (Fig. 5; Odadi et al., 2011).

In the presence of cattle, meso-herbivore dung levels were constant across the landscape, suggesting a weak response of wildlife to glades. However, in the absence of cattle, meso-herbivore preference for glade interiors was pronounced. Preference of wildlife for glade interiors has also been found in other landscapes in eastern Africa (Augustine, 2004; Treydte et al., 2006b; Young et al., 1995) and has been attributed to factors such as high forage quality (Augustine, 2003; Treydte et al., 2006a) or better visibility within glades (Riginos and Grace, 2008; Young

et al., 1995). In the absence of cattle, high meso-herbivore dung densities inside glades were offset by relatively low dung densities in glade edges. This edge pattern may reflect foraging decisions made by meso-herbivores approaching glades which, in the absence of cattle, are full of palatable forage.

Previous research has shown that grazing by wild meso-herbivores helps maintain glades in a successional stage dominated by a highly palatable short-grass (Veblen and Young, 2010). This in turn further attracts wild herbivore grazing and may help maintain high glade nutrient levels over the long-term by offsetting nutrient export via herbivory with nutrient import via dung deposition. When cattle are present, these feedbacks may be weakened.

4.4. Conclusions

Our findings demonstrate that large mammalian herbivores can have profound impacts on landscape heterogeneity in an African savanna. Cattle and megaherbivores dampened the ecosystem heterogeneity created by treeless glades embedded within a savanna matrix. Although glade edges still retain high tree densities in the presence of megaherbivores, this pattern would be even more striking if megaherbivores were excluded. Similarly, our results suggest that wildlife preference for glade interiors would be even stronger in the absence of cattle. Because glades are common features in livestock-dominated savanna landscapes, and are now being actively managed for their ecosystem benefits (Porensky, Veblen, Riginos, pers. observ.), our results can inform management decisions in areas where wildlife and livestock share resources. More broadly, our results demonstrate that edge effects are sensitive to the presence and activities of various types of large mammalian herbivores. Future research could explore the nature and importance of this context-dependence in other study systems, as well as its implications for biodiversity conservation in fragmented landscapes.

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Appendix. Abundance of cattle and megaherbivore dung

Dung measurements indicated that cattle and megaherbivore exclusion treatments were effective. Inside glades, cattle + buffalo dung density was 10 times lower in plots where cattle were excluded (5.7 ± 1.0 vs. 0.6 ± 0.2 dung piles/40 m²). Similarly, in glade edges, cattle + buffalo dung density was nearly 7 times lower in plots where cattle were excluded (6.2 ± 1.9 vs. 0.9 ± 0.4 dung piles/40 m²). In plots where megaherbivores were excluded, no megaherbivore dung piles were found either inside glades or in glade edges. In plots where megaherbivores were allowed, average megaherbivore dung density was 0.9 ± 0.2 dung piles/40 m² inside glades and 1.4 ± 0.2 dung piles/40 m² in glade edges.

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