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2013

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24 **ABSTRACT**

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

42 **Keywords:** spatial heterogeneity; *Acacia drepanolobium*; *Crematogaster* species;
43 *Tetraponera penzigi*; pastoral; livestock-wildlife interactions

44

45 **1. INTRODUCTION**

46 In patchy and fragmented landscapes, ecological edge effects can have major impacts on
47 ecosystem structure and functioning, biotic interactions, and management (Fagan et al., 1999;
48 Ries et al., 2004; Harper et al., 2005). Edge effects are interactions between two adjacent

49 ecosystems or land cover types separated by an abrupt transition (Murcia, 1995). In savannas
50 as in forests, edge effects are often associated with changes in the composition and structure
51 of woody plant communities (Young et al., 1995; e.g., Brits et al., 2002; Lima-Ribeiro,
52 2008). In Brazilian cerrado fragments, for example, woody plants near fragment edges are
53 shorter and thinner than plants in fragment interiors (Lima-Ribeiro, 2008). Edge-related
54 changes in woody plant structure and composition can have cascading effects on other
55 species and processes (Fagan et al., 1999; Porensky, 2011).

56 Large mammalian herbivores shape African savanna ecosystems and have strong impacts
57 on woody vegetation (e.g., Pellew, 1983; Augustine and McNaughton, 2004; Goheen et al.,
58 2010; Porensky and Veblen, 2012). Thus, in these landscapes, large herbivores are likely to
59 influence edge effect patterns associated with woody vegetation. However, few experimental
60 studies have examined whether edge effects are altered by large herbivores (but see Fox et
61 al., 1997; Allombert et al., 2005; Didham et al., 2009), and to our knowledge, none has done
62 so in Africa where large herbivores are still abundant and diverse. Further, to our knowledge,
63 the separate and combined impacts of different guilds of large herbivores on edge effects
64 have not been experimentally tested (but see observational work by Brits et al., 2002; de Beer
65 et al., 2006). With a better understanding of how large herbivores alter edge effects,
66 ecologists will be able to better comprehend the maintenance of spatial heterogeneity in
67 savannas, as well as the potential landscape-level consequences of mammalian extinctions.

68 We used a long-term, broad-scale manipulative experiment to determine how various
69 large herbivores alter edge effects around anthropogenic nutrient hotspots. For centuries,
70 pastoralists in sub-Saharan Africa have corralled their cattle in temporary thorn-fence
71 ‘bomas’ at night for protection against predators and stock raiders (Western and Dunne,
72 1979; Blackmore et al., 1990). Bomas are typically 50-100 m in diameter and are used for
73 months or years before being abandoned. After abandonment, dung-filled boma sites develop

74 into distinctive ecosystem ‘hotspots’ that persist for decades to centuries (Blackmore et al.,
75 1990; Young et al., 1995; Augustine, 2003). At our study site, abandoned bomas develop into
76 treeless, productive ‘glades’ that harbor nutrient-rich plant species and are used preferentially
77 by livestock and wild herbivores (Young et al., 1995; Augustine, 2003, 2004; Veblen and
78 Young, 2010; Porensky, 2011; Veblen, 2012). Glades are common in this landscape (found at
79 densities of about 2 glades per km², Veblen, 2012), and represent major sources of structural
80 and functional heterogeneity.

81 Glades can have edge effects that extend at least 100 m into the surrounding savanna
82 matrix (Young et al., 1995; Porensky, 2011). One striking pattern associated with glade edges
83 is an unusually high density of large trees (Porensky, 2011), which might be related to high
84 nutrient availability within glades (Veblen, 2012) or a competitive advantage gained by tree
85 seedlings growing in heavily grazed areas (Riginos and Young, 2007). Large trees around
86 glades might also reflect the legacy of an establishment phase that occurred during or soon
87 after active boma use (Muchiru et al., 2009). In this study, we investigated impacts of
88 different large herbivores on woody vegetation patterns in glade edges. Large herbivores are
89 known to affect the long-term development of herbaceous communities in glades (Veblen,
90 2008; Veblen and Young, 2010), but their impacts on co-occurring woody plants remain
91 unclear (but see Porensky and Veblen, 2012).

92 Ecological edges can have strong influences on the interactions among different
93 associated species (Fagan et al., 1999). Our study system gave us the opportunity to
94 experimentally investigate how large herbivores, by altering vegetation in glade edges, may
95 have cascading impacts on other animal taxa. For example, by thinning tall trees around
96 glades, elephants may decrease the use of glade edges by other herbivores that respond to the
97 micro-climatic benefits and high-quality forage found beneath trees (Ludwig et al., 2008;
98 Treydte et al., 2009). Conversely, reduced tree densities may afford increased visibility and

99 enhanced predator detection, which might be attractive to mid-sized herbivores (Riginos and
100 Grace, 2008). Further, large herbivores could affect invertebrate communities associated with
101 glade edges. In particular, the presence or absence of megaherbivore browsers might alter the
102 relative abundances of ant species that are symbiotic with the dominant *Acacia* tree species in
103 our system (Young et al., 1997).

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

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

112 **2. METHODS**

113 **2.1 Study area**

114 This study took place at the Mpala Research Centre in Laikipia County, Kenya (0°17'N,
115 36°52'E, 1800 m asl), where more than 2,000 Boran cattle (*Bos indicus*) coexist with
116 abundant wildlife on a 17,000 ha conservancy. The climate is semi-arid with a mean annual
117 rainfall of 500-600 mm (Young et al., 1998).

118 The study site is located on “black cotton” vertisol soil that supports some of the most
119 productive rangelands in Africa (Young et al., 1998). Large mammalian herbivores are
120 abundant; species include the endangered Grevy’s zebra (*Equus grevyi*), the more common
121 Burchell’s zebra (*Equus quagga burchelli*), eland (*Taurotragus oryx*), oryx (*Oryx beisa*),
122 hartebeest (*Alcelaphus buselaphus*), steinbuck (*Raphicerus campestris*), Grant’s gazelle
123 (*Nanger [Gazella] granti*), warthog (*Phacochoerus africanus*), and occasionally bush duiker

124 (*Sylvicapra grimmia*) or impala (*Aepyceros melampus*). These species are categorized as
125 meso-herbivores hereafter. The study site also supports low densities of African buffalo
126 (*Syncerus caffer*), which are not included in meso-herbivore analyses since their dung piles
127 are indistinguishable from those of cattle. In addition, two megaherbivore species, giraffe
128 (*Giraffa camelopardis reticulata*) and African elephant (*Loxodonta africana*), are present.

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

134 In our study system, *A. drepanolobium* trees are typically inhabited by one of four species
135 of ants: *Tetraponera penzigi*, *Crematogaster mimosae*, *C. nigriceps*, or *C. sjostedti* (Young et
136 al., 1997; Stanton et al., 2002). These ants exist within a competitive hierarchy associated
137 with differently-sized trees. *Tetraponera penzigi* and *C. nigriceps* are competitively
138 subordinate and tend to be found on smaller trees, while *C. mimosae* and *C. sjostedti* are
139 competitively dominant and often found on larger trees (Young et al., 1997; Stanton et al.,
140 2002; Palmer et al., 2010). The four species also differ in their ability to defend trees against
141 megaherbivore browsing: *Tetraponera penzigi* and *C. sjostedti* ants are less aggressive, while
142 *C. mimosae* and *C. nigriceps* are more aggressive towards browsers (Young et al., 1997;
143 Stanton et al., 2002; Young et al., 2003; Palmer et al., 2010). Hereafter, we refer to ants based
144 on these two aggressiveness classes.

145 Our work took place within the Kenya Long-term Exclosure Experiment (KLEE), which
146 has been assessing the separate and combined impacts of different herbivores on this savanna
147 ecosystem since 1995 using an exceptionally broad-scale approach (Young et al., 1998). The
148 experiment consists of three replicate blocks, each with six 200 x 200 m treatment plots (Fig.

149 1). Different barriers exclude different guilds of herbivores (see also Appendix): 1) Visual
150 markers serve to keep individually-herded cattle (C) in designated plots. 2) A two-strand
151 electric line 2 m off the ground excludes only megaherbivores (elephants and giraffes; M). 3)
152 A nine-strand electric game fence excludes all meso-herbivores 15-1000kg (W) as well as
153 megaherbivores. There are gates in the game fence to allow entry by herded cattle. In
154 addition to total exclusion plots (O), treatment combinations include C, W, WC, MW and
155 MWC, where letters indicate the types of animals allowed into the plots (e.g., WC plots allow
156 wildlife and cattle). Smaller herbivores (steinbuck, hares, rodents, and invertebrates) have
157 access to all plots. Individually-herded groups of cattle were run in each C, WC or MWC plot
158 for 2 hours 6-8 times per year, producing impacts similar to the overall ranch stocking density
159 (see Odadi et al., 2007) while limiting human and livestock presence to a few hours per year.

160 The KLEE study design includes six glades (abandoned boma sites), which were divided
161 in 1995 by the herbivore exclusion fences to create 18 glade portions (Fig. 1a, Young et al.,
162 1998). These include several glade portions adjacent to the KLEE plots that are maintained in
163 herbivore treatments (Fig. 1a, Young et al., 1998) which results in comparable environmental
164 conditions within each portion. Historical aerial photographs indicate that all of these glades
165 have been present for more than 40 years.

166 **2.2 Data collection**

167 Over 2006-2007, we determined whether woody communities in glade edges differed from
168 background conditions across herbivore treatments. For all glade portions in KLEE (Fig. 1a),
169 we sampled woody species in large plots at the glade edge and at 150 m away from the glade.
170 At 150 m outside the perimeter of each of the 18 glade portions, we placed the closest, long
171 edge of a 40 x 30 m plot (Fig. 1b). At glade edge, we split sampling into two 20 x 30 m plots
172 to increase the amount of curvilinear glade perimeter captured by our plots. Each 20 x 30 m
173 plot was placed at glade edge, spanning 10 m inside to 20 m outside the glade perimeter (Fig.

174 1b). We counted all *A. drepanolobium* trees rooted in each sample plot and categorized them
175 into three height classes: <1 m, 1-3 m, and >3 m tall. We also recorded all occurrences of
176 non-*A. drepanolobium* woody species (excluding seedlings).

177 In 2009 (a drought year), we looked more closely at *A. drepanolobium*, collected edge
178 data with higher spatial resolution, and investigated meso-herbivore use of glades and glade
179 edges. The 2006-2007 data suggested that meso-herbivores had no consistent effects on
180 woody vegetation patterns around glades (see Results). Therefore, in 2009 we concentrated
181 on the effects of cattle and megaherbivores. We used four of the six KLEE treatments (W,
182 WC, MW, and MWC) to investigate a full factorial of megaherbivore and cattle effects. The
183 2006-2007 data also revealed a strong pattern in the largest size class of *A. drepanolobium*
184 trees (>3 m). In 2009, we further subdivided this large size class into 3-4 m and >4 m size
185 classes to improve the resolution of our data. For all size classes we also included metrics of
186 *A. drepanolobium* reproduction and symbiotic ant occupancy. Finally, we used dung counts
187 to investigate interactions within the herbivore community.

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

192 (1) For each *A. drepanolobium* tree within 4 m of the transect line, we recorded its
193 distance along the transect, its height, and its reproductive status (flowering or fruiting
194 vs. non-reproductive). Trees were classified into four height categories: <1 m, 1-3 m,
195 3-4 m, and >4 m. We also recorded the species identity of any symbiotic ant species
196 present on each tree.

197 (2) For each dung pile within 4 m of the transect line, we recorded its distance along the
198 transect and the animal species that produced it. Previous work suggests that dung

199 counts are a reliable method to determine relative animal use (Augustine 2003, Young
200 et al. 1995, 2005). Buffalo and cattle dung piles were indistinguishable, and therefore
201 these two species were lumped as ‘cattle+buffalo’. However, cattle are >10 times
202 more abundant than buffalo at the study site. Other wildlife were classified as
203 ‘grazers’ (zebra, hartebeest and warthog), ‘mixed feeders/browsers’ (eland, oryx,
204 steinbuck, Grant’s gazelle, bush duiker and impala), or ‘megaherbivores’ (elephant
205 and giraffe).

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

208 **2.3 Statistical analyses**

209 *2.3.1 2006-2007 surveys*

210 We used split-plot designs to test treatment effects on woody vegetation. For woody (non-*A.*
211 *drepanolobium*) species densities and the three *A. drepanolobium* size class densities, each
212 model included the following fixed effects: main plot effect of herbivore treatment (O, C, W,
213 WC, MW, MWC), subplot effect of distance (inside, edge, outside of glade), and the
214 herbivore*distance interaction. Block, glade nested within block, and the block*glade
215 interaction were included as random effects. For all statistical analyses, we used generalized
216 linear mixed models (GLMMs), maximum-likelihood methodology and Satterthwaite’s
217 approximation of degrees of freedom (PROC MIXED, version 9.1, SAS Institute 2002).
218 Variance-weighting was used when variances were not homogenous, and values were log-
219 transformed when necessary. We used Tukey’s HSD analyses for post-hoc comparisons, and
220 we report means \pm 1 SE throughout the results.

221 *2.3.2 2009 surveys: standardizing the glade edge*

222 One of the most defining structural characteristics of glades is their persistent lack of trees, so
223 tree density was used to standardize the location of the glade edge across transects. Although

224 this 'glade edge' location is not necessarily intended to reflect a functional edge, our
225 observations suggest it is largely coincident with the location of the original boma fence. The
226 glade edge was defined as the first 5 m interval in which we found ≥ 4 *A. drepanolobium*
227 trees/40 m². For each transect, this glade edge distance was defined at 0 m, so that areas
228 inside and outside the glade had negative and positive distance values, respectively.

229 2.3.3 2009 surveys: spatially coarse-scale analysis

230 For each response variable along each transect, we averaged binned values for two
231 standardized distance intervals: -25 to 0 m (inside glade), and 0 to 25 m (glade edge). For
232 each distance interval, we compared among treatments using GLMMs with the following
233 predictors and their interactions: block (a random factor), cattle exclusion, and
234 megaherbivore exclusion. The cattle*megaherbivore interaction term was removed from
235 models in which it was non-significant ($p > 0.10$). Response variables included overall tree
236 density, tree density separated by size class, overall density of meso-herbivore dung piles,
237 meso-herbivore dung density separated by feeding guild, overall density of trees occupied by
238 *Acacia* ants, and ant occupancy separated by species aggressiveness. For analyses involving
239 multiple herbivore guilds, tree size classes or ant species, MANOVAs were used initially to
240 establish overall significance. For all other analyses, we used GLMMs with maximum-
241 likelihood methodology and Satterthwaite's approximation of degrees of freedom (PROC
242 MIXED, version 9.1, SAS Institute 2002). Response variables were log-transformed when
243 necessary to achieve normality. Due to the low replication of this broad-scale experiment, we
244 set α at 0.10. We also used a generalized linear mixed model (with predictors as described
245 above and log-transformed glade radius as the response variable) to confirm that cattle and
246 megaherbivore exclusion had no significant impacts on glade radius. We report means ± 1 SE
247 throughout the results.

248 2.3.4 2009 surveys: spatially fine-scale analysis

249 For response variables significantly affected by cattle or megaherbivore exclusion (based on
 250 the coarse-scale analysis above), we fit continuous nonlinear models to identify the distance
 251 ranges over which significant differences occurred. We used the following model, which
 252 includes linear, sigmoid, and unimodal edge effect shape components:

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

linear
sigmoid
unimodal

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

265 3. RESULTS

266 3.1 2006-2007 surveys

267 Densities of the largest individuals (>3 m tall) of the dominant tree, *Acacia drepanolobium*,
 268 were three times higher in glade edges than far from glades (Table 1, distance effect $F_{1,12,2} =$
 269 57.34, $p < 0.0001$). However, this effect occurred only in plots without megaherbivores
 270 (edge>out, treatment*distance class interaction $F_{5,12,3} = 3.42$, $p = 0.04$, Tukey HSD $p < 0.05$ for
 271 W, WC, and C; for O $p = 0.19$). In MW and MWC plots, the two plot types that allow entry to
 272 megaherbivores, edges did not have significantly higher densities (Table 1). For 1-3 m tall A.

273 *drepanolobium* trees there were no significant distance or treatment effects (Table 1). For
274 small (<1 m tall) trees, no significant distance effects could be found. The C plots (cattle
275 only) had 39-60% fewer small *A. drepanolobium* individuals than the other treatments, but
276 this was statistically significant only compared to WC (meso-herbivores + cattle, Table 1,
277 treatment effect $F_{5, 15.8} = 2.92, p = 0.05$). In other words, plots allowing only cattle had fewer
278 small trees than plots allowing both meso-herbivores and cattle. However, small tree density
279 did not differ significantly between total exclusion plots (O) and plots allowing meso-
280 herbivores (W).

281 Densities of two common woody shrubs, *Lycium europaeum* L. and *Rhus natalensis*
282 Krauss, were significantly higher in glade edges than outside glades (*L. europaeum*: $44.1 \pm$
283 13.9 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 , $F_{1,14} =$
284 $7.95, p = 0.01$). Densities of the other most common shrub, *Cadaba farinosa* Forssk., did not
285 differ significantly by distance (27.9 ± 4.1 vs. 20.1 ± 5.4 , $F_{1,11.2} = 1.98, p = 0.19$). None of
286 these shrubs responded significantly to herbivore treatments.

287 **3.2 2009: Transect-wide meso-herbivore results**

288 Averaged across treatments (W, WC, MW and MWC) and distances from glades, meso-
289 herbivore (excluding cattle and buffalo) dung comprised 63% zebra, 19% eland, 6% oryx, 5%
290 hartebeest, 4% steinbuck, and 3% other species. In plots where cattle were allowed, cattle+
291 buffalo dung and zebra dung each accounted for $37 \pm 6\%$ of total dung. In plots where cattle
292 were excluded, cattle+buffalo dung accounted for $3 \pm 1\%$ and zebra dung accounted for $60 \pm$
293 4% of total dung. Zebra dung was 70% more abundant in plots where cattle were excluded
294 (129 ± 16 vs. 222 ± 16 dung piles; $t = -4.11, p = 0.003, df = 8.8$).

295 **3.3 2009: Coarse-scale analysis**

296 Cattle and megaherbivore exclusion had no significant impacts on glade radius (W= 35 ± 9
297 m, WC= 28 ± 3 m, MW= 28 ± 3 m, MWC= 27 ± 4 m; all p -values > 0.10). In glade edges,

298 herbivore treatments significantly affected tree size structure (tree size class MANOVA:
299 cattle effect *Wilk's* $\lambda = 0.04$, $p = 0.02$; megaherbivore effect *Wilk's* $\lambda = 0.05$, $p = 0.03$). In
300 particular, the density of large trees (>4 m tall) in glade edges was more than three times
301 higher when megaherbivores were excluded (Fig. 2; 2.0 ± 0.2 vs. 0.6 ± 0.2 trees/ 40 m²;
302 megaherbivore $F_{1,5,29} = 50.44$, $p = 0.0007$). Cattle exclusion did not significantly affect large
303 tree density in glade edges ($F_{1,3,74} = 1.43$, $p = 0.3$). In glade edges, neither cattle nor
304 megaherbivore exclusion significantly affected the density of trees in other size classes (Fig.
305 2) or overall tree density (all p -values >0.10).

306 Cattle exclusion and megaherbivore exclusion both led to higher densities of
307 reproductively active trees in glade edges. When cattle were excluded, the density of
308 reproductively active trees was 80% higher (3.2 ± 0.6 vs. 1.8 ± 0.3 flowering or fruiting trees/
309 40 m²; $F_{1,8} = 9.42$, $p = 0.02$). Similarly, the density of reproductively active trees was over
310 twice as high when megaherbivores were excluded (Fig. 2; 3.2 ± 0.6 vs. 1.5 ± 0.2 flowering
311 or fruiting trees/ 40 m²; $F_{1,8} = 13.25$, $p = 0.007$).

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

321 Inside glades, cattle exclusion significantly affected the density of wildlife dung piles
322 (wildlife MANOVA: cattle effect *Wilk's* $\lambda = 0.32$, $p = 0.06$; megaherbivore effect *Wilk's* $\lambda =$

323 0.64, $p= 0.3$). For grazers (zebra, hartebeest and warthog), the density of dung piles inside
324 glades was more than twice as high when cattle were excluded (10.8 ± 1.3 vs. 4.7 ± 1.0
325 grazer dung piles per 40 m^2 ; cattle effect $F_{1,8}= 19.45$, $p= 0.002$). Dung densities for browsers
326 and mixed feeders (eland, oryx, steinbuck, Grant's gazelle, bush duiker and impala) inside
327 glades were also more than twice as high when cattle were excluded (3.8 ± 0.6 vs. 1.7 ± 0.5
328 browser/mixed feeder dung piles per 40 m^2 ; cattle effect $F_{1,8}= 6.45$, $p= 0.03$).

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

337 **3.4 2009: Fine-scale analysis**

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

348 For densities of large trees (>4 m tall), reproductively active trees and trees occupied by
349 non-aggressive ants, we compared fitted models from transects in plots with or without
350 megaherbivores. When megaherbivores were excluded, large tree densities were significantly
351 higher at distances between -10 and 10 m, 15-35 m, and 65-80 m outside glade edge (Fig.
352 4c). Transects without megaherbivores also had significantly more reproductively active trees
353 between 20 and 35 m (Fig. 4d). These results indicate that megaherbivore exclusion led wider
354 peaks for large and reproductively active tree densities in glade edges (Fig. 4c,d).
355 Megaherbivore exclusion did not significantly affect non-aggressive ant occupancy at any
356 distance, likely because of the interaction between cattle and megaherbivore effects (see
357 above, Figs. 3 and 4e).

358 **4. DISCUSSION**

359 Megaherbivores and cattle both significantly altered glade edge effects in this savanna
360 landscape mosaic. Megaherbivores reduced the spatial heterogeneity created by glades, not
361 by reducing differences between glades and the background savanna, but by reducing unique
362 traits associated with glade edges: high densities of large trees, reproductively active trees
363 and non-aggressive *Acacia* ants. Cattle also reduced the densities of reproductively active
364 trees and non-aggressive *Acacia* ants in glade edges. Cattle further dampened spatial
365 heterogeneity by weakening meso-herbivore preference for glade interiors. These results
366 reflect a combination of direct and indirect effects (Fig. 5), and further research is needed to
367 clarify some of the relevant mechanisms.

368 Meso-herbivore exclusion did not have strong impacts on *A. drepanolobium* density or
369 size structure in glade edges. Cattle probably have stronger impacts than wild meso-
370 herbivores because of their higher biomass density (cattle have 5–10 times higher biomass
371 per km² than wild ungulates). Differences between meso-herbivores and cattle might also be
372 related to differences in the timing of grazing (continuous vs. discontinuous), evolutionary

373 history in the system (long vs. short), or diet (though dietary overlap between cattle and the
374 dominant meso-herbivore, zebra, is probably large) (Odadi et al., 2007; Odadi et al., 2011).

375 **4.1 Acacia drepanolobium**

376 One of the most striking edge effects in our study system is the high density of large trees in
377 glade edges. Although it is not clear what causes rings of tall, dense trees to form at glade
378 edges, we found that megaherbivore exclusion clearly enhanced this effect. The abundance of
379 large trees in glade edges was significantly higher in plots where megaherbivores were
380 excluded (Table 1; Figs. 2, 4 and 5). This suggests that megaherbivores preferentially feed on
381 large trees in glade edges, perhaps because higher tree densities and taller trees in glade edges
382 represent attractive forage patches. Elephants often seem to browse preferentially on larger
383 trees, especially in high tree density areas (Pellew, 1983; Augustine and McNaughton, 2004).
384 Trees next to glades may also contain more nutrients than trees in the background savanna,
385 and this enhanced nutrient content may attract elephant and giraffe browsing. Elephant
386 foraging typically leads to killing, coppicing or reduction of tree size (Van de Vijver et al.,
387 1999; Augustine and McNaughton, 2004; Goheen et al., 2007) while giraffe browsing tends
388 to be focused on taller trees and can severely slow tree growth (Pellew, 1983).

389 Whereas only megaherbivores had a negative effect on tree density in glade edges, both
390 megaherbivores and cattle reduced fruiting and flowering of *A. drepanolobium* (Fig. 5).
391 These results may be driven by changes in browsing pressure. Megaherbivore exclusion
392 reduces browsing directly, and cattle exclusion may also reduce browsing pressure by
393 increasing understory forb biomass (Odadi et al., 2013). In cattle exclusion plots, wild
394 ungulates may be able to meet nutritional needs by eating forbs, and therefore may be less likely
395 to browse on trees. Reduced browsing can increase reproduction by increasing tree size, since
396 larger trees are more likely to reproduce (Goheen et al., 2007; Palmer et al., 2010). Reduced
397 browsing can also cause reduced investment in defense (Young et al., 2003; Palmer et al.,

398 2008), which may lead to increased investment in reproduction (Goheen et al., 2007). Finally,
399 increased reproduction in the absence of megaherbivores and cattle could be an indirect
400 consequence of increased densities of non-aggressive ants. *Crematogaster sjostedti*
401 occupation is associated with increased fruiting in *A. drepanolobium*, and *T. penzigi* is also
402 associated with higher fruiting probabilities than either *C. mimosae* or *C. nigriceps* (Palmer et
403 al., 2010).

404 If increased flowering and fruiting near glades leads to higher seedling recruitment inside
405 glades, herbivore exclusion might reduce the persistence of glades as treeless areas (by
406 promoting tree reproduction). Alternatively, higher seed availability in the absence of large
407 herbivores might enhance granivorous insect and rodent populations, which in turn could
408 suppress seedling establishment and keep glades treeless (Walters et al., 2005; Palmer and
409 Brody, 2007). Moreover, relationships between the presence of reproductive structures and
410 actual seed production or seedling recruitment are probably highly variable (Goheen et al.,
411 2007; Goheen et al., 2010). In light of these complications, impacts of different herbivores on
412 tree recruitment inside and near glades warrant further study.

413 **4.2 Symbiotic Acacia ants**

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

421 Megaherbivore and cattle exclusion may further affect changes in ant occupancy by
422 reducing browsing pressure (see section 4.1). Trees under lower herbivory pressure can

423 reduce production of ‘ant rewards’ in the form of nectaries and swollen spines (Huntzinger et
424 al., 2004; Palmer et al., 2008), causing ant species more dependent on rewards (e.g., *C.*
425 *mimosae*) to be replaced by ant species less dependent on rewards (e.g., *C. sjostedti*; Palmer
426 et al., 2008). Our results are similar to those of Palmer et al. (2008), who observed a
427 replacement of *C. mimosae* (aggressive) by *C. sjostedti* (non-aggressive) under herbivore
428 exclusion.

429 Changes in ant community composition can have major impacts on *A. drepanolobium*
430 survival, growth, architecture, parasitism and reproduction (Stanton et al., 1999; Palmer et al.,
431 2002; Riginos and Young, 2007; Palmer et al., 2008; Palmer et al., 2010). Our study shows
432 that these changes could have spatially explicit ecosystem effects, particularly in areas where
433 *A. drepanolobium* is dominant (Young et al. 1998).

434 **4.3 Mammal use**

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

440 Our data, collected during a drought, suggested that cattle reduced meso-herbivore
441 preference for glades (Fig. 4). Given that cattle spend only 12-16 hours per year inside each
442 glade portion, our results probably were not driven by direct interference between cattle and
443 wildlife. Though cattle had no significant effects on tree densities or size structure (Table 1),
444 cattle were associated with fewer reproductive trees and higher aggressive ant occupancy
445 (Fig. 3). By increasing aggressive ant occupancy, cattle could have made *A. drepanolobium*
446 trees less attractive to meso-herbivore browsers. However, our data suggest that cattle had
447 similar effects on meso-herbivore grazers and browsers. Thus, we hypothesize that the effects

448 of cattle on wildlife were driven mostly by indirect competition for herbaceous forage (Fig. 5;
449 Odadi et al., 2011).

450 In the presence of cattle, meso-herbivore dung levels were constant across the landscape,
451 suggesting a weak response of wildlife to glades. However, in the absence of cattle, meso-
452 herbivore preference for glade interiors was pronounced. Preference of wildlife for glade
453 interiors has also been found in other landscapes in eastern Africa (Young et al., 1995;
454 Augustine, 2004; Treydte et al., 2006b) and has been attributed to factors such as high forage
455 quality (Augustine, 2003; Treydte et al., 2006a) or better visibility within glades (Young et
456 al., 1995; Riginos and Grace, 2008). In the absence of cattle, high meso-herbivore dung
457 densities inside glades were offset by relatively low dung densities in glade edges. This edge
458 pattern may reflect foraging decisions made by meso-herbivores approaching glades which,
459 in the absence of cattle, are full of palatable forage.

460 Previous research has shown that grazing by wild meso-herbivores helps maintain glades
461 in a successional stage dominated by a highly palatable short-grass (Veblen and Young,
462 2010). This in turn further attracts wild herbivore grazing and may help maintain high glade
463 nutrient levels over the long-term by offsetting nutrient export via herbivory with nutrient
464 import via dung deposition. When cattle are present, these feedbacks may be weakened.

465 ***4.4 Conclusions***

466 Our findings demonstrate that large mammalian herbivores can have profound impacts on
467 landscape heterogeneity in an African savanna. Cattle and megaherbivores dampened the
468 ecosystem heterogeneity created by treeless glades embedded within a savanna matrix.

469 Although glade edges still retain high tree densities in the presence of megaherbivores, this
470 pattern would be even more striking if megaherbivores were excluded. Similarly, our results
471 suggest that wildlife preference for glade interiors would be even stronger in the absence of
472 cattle. Because glades are common features in livestock-dominated savanna landscapes, and

473 are now being actively managed for their ecosystem benefits (Porensky, Veblen, Riginos,
474 pers. observ.), our results can inform management decisions in areas where wildlife and
475 livestock share resources. More broadly, our results demonstrate that edge effects are
476 sensitive to the presence and activities of various types of large mammalian herbivores.
477 Future research could explore the nature and importance of this context-dependence in other
478 study systems, as well as its implications for biodiversity conservation in fragmented
479 landscapes.

480 **5. ACKNOWLEDGEMENTS**

481 The authors thank our Mpala Research Centre field team: F. Erii, M. Namoni and J.
482 Lochukuya. We also thank C. Riginos for valuable input and support. Funding was provided
483 by the Studienstiftung des Deutschen Volkes (to S.F.B.), NSF Graduate Research
484 Fellowships (to L.M.P. and K.E.V.), and an NSF Dissertation Improvement Grant (to
485 L.M.P.). The KLEE plots were built and maintained by grants from the Smithsonian
486 Institution (to A.P. Smith), The National Geographic Society (4691-91), NSF (LTREB BSR-
487 97-07477, 03-16402, and 08-16453) and the African Elephant Program of the U.S. Fish and
488 Wildlife Service (98210-0-G563) (to T.P.Y.).

489 **6. REFERENCES**

490 Allombert, S., Stockton, S., Martin, J.L., 2005. A natural experiment on the impact of
491 overabundant deer on forest invertebrates. *Conservation Biology* 19, 1917-1929.
492 Augustine, D.J., 2003. Long-term, livestock-mediated redistribution of nitrogen and
493 phosphorus in an East African savanna. *Journal of Applied Ecology* 40, 137-149.
494 Augustine, D.J., 2004. Influence of cattle management on habitat selection by impala on
495 central Kenyan rangeland. *Journal of Wildlife Management* 68, 916-923.
496 Augustine, D.J., McNaughton, S.J., 2004. Regulation of shrub dynamics by native browsing
497 ungulates on East African rangeland. *Journal of Applied Ecology* 41, 45-58.

498 Blackmore, A.C., Mentis, M.T., Scholes, R.J., 1990. The origin and extent of nutrient-
499 enriched patches within a nutrient-poor savanna in South-Africa. *Journal of Biogeography*
500 17, 463-470.

501 Brits, J., van Rooyen, M.W., van Rooyen, N., 2002. Ecological impact of large herbivores on
502 the woody vegetation at selected watering points on the eastern basaltic soils in the Kruger
503 National Park. *African Journal of Ecology* 40, 53-60.

504 de Beer, Y., Kilian, W., Versfeld, W., van Aarde, R.J., 2006. Elephants and low rainfall alter
505 woody vegetation in Etosha National Park, Namibia. *Journal of Arid Environments* 64, 412-
506 421.

507 Didham, R.K., Barker, G.M., Costall, J.A., Denmead, L.H., Floyd, C.G., Watts, C.H., 2009.
508 The interactive effects of livestock exclusion and mammalian pest control on the restoration
509 of invertebrate communities in small forest remnants. *New Zealand Journal of Zoology* 36,
510 135-163.

511 Fagan, W.F., Cantrell, R.S., Cosner, C., 1999. How habitat edges change species interactions.
512 *American Naturalist* 153, 165-182.

513 Fox, B.J., Taylor, J.E., Fox, M.D., Williams, C., 1997. Vegetation changes across edges of
514 rainforest remnants. *Biological Conservation* 82, 1-13.

515 Goheen, J.R., Palmer, T.M., Keesing, F., Riginos, C., Young, T.P., 2010. Large herbivores
516 facilitate savanna tree establishment via diverse and indirect pathways. *Journal of Animal*
517 *Ecology* 79, 372-382.

518 Goheen, J.R., Young, T.P., Keesing, F., Palmer, T.M., 2007. Consequences of herbivory by
519 native ungulates for the reproduction of a savanna tree. *Journal of Ecology* 95, 129-138.

520 Harper, K.A., Macdonald, S.E., Burton, P.J., Chen, J.Q., Brosnokske, K.D., Saunders, S.C.,
521 Euskirchen, E.S., Roberts, D., Jaiteh, M.S., Esseen, P.A., 2005. Edge influence on forest
522 structure and composition in fragmented landscapes. *Conservation Biology* 19, 768-782.

523 Huntzinger, M., Karban, R., Young, T.P., Palmer, T.M., 2004. Relaxation of induced indirect
524 defenses of acacias following exclusion of mammalian herbivores. *Ecology* 85, 609-614.

525 Lima-Ribeiro, M.D., 2008. Edge effects on vegetation and population structure in Cerradao
526 fragments of Southwest Goias, Brazil. *Acta Botanica Brasilica* 22, 535-545.

527 Ludwig, F., De Kroon, H., Prins, H.H.T., 2008. Impacts of savanna trees on forage quality for
528 a large African herbivore. *Oecologia* 155, 487-496.

529 Muchiru, A.N., Western, D., Reid, R.S., 2009. The impact of abandoned pastoral settlements
530 on plant and nutrient succession in an African savanna ecosystem. *Journal of Arid*
531 *Environments* 73, 322-331.

532 Murcia, C., 1995. Edge effects in fragmented forests: implications for conservation. *Trends in*
533 *Ecology & Evolution* 10, 58-62.

534 Odadi, W.O., Karachi, M.K., Abdulrazak, S.A., Young, T.P., 2011. African wild ungulates
535 compete with or facilitate cattle depending on season. *Science* 333, 1753-1755.

536 Odadi, W.O., Karachi, M.K., Abdulrazak, S.A., Young, T.P., 2013. Protein supplementation
537 reduces non-grass foraging by a primary grazer. *Ecological Applications* 23, 455-463.

538 Odadi, W.O., Young, T.P., Okeyo-Owuor, J.B., 2007. Effects of wildlife on cattle diets in
539 Laikipia rangeland, Kenya. *Rangeland Ecology & Management* 60, 179-185.

540 Palmer, T.M., Brody, A.K., 2007. Mutualism as reciprocal exploitation: African plant-ants
541 defend foliar but not reproductive structures. *Ecology* 88, 3004-3011.

542 Palmer, T.M., Doak, D.F., Stanton, M.L., Bronstein, J.L., Kiers, E.T., Young, T.P., Goheen,
543 J.R., Pringle, R.M., 2010. Synergy of multiple partners, including freeloaders, increases host
544 fitness in a multispecies mutualism. *Proceedings of the National Academy of Sciences of the*
545 *United States of America* 107, 17234-17239.

546 Palmer, T.M., Stanton, M.L., Young, T.P., Goheen, J.R., Pringle, R.M., Karban, R., 2008.
547 Breakdown of an ant-plant mutualism follows the loss of large herbivores from an African

548 savanna. *Science* 319, 192-195.

549 Palmer, T.M., Young, T.P., Stanton, M.L., 2002. Burning bridges: priority effects and the
550 persistence of a competitively subordinate acacia-ant in Laikipia, Kenya. *Oecologia* 133, 372-
551 379.

552 Pellew, R.A.P., 1983. The impacts of elephant, giraffe and fire upon the *Acacia tortilis*
553 woodlands of the Serengeti. *African Journal of Ecology* 21, 41-74.

554 Porensky, L.M., 2011. When edges meet: interacting edge effects in an African savanna.
555 *Journal of Ecology* 99, 923-934.

556 Porensky, L.M., Veblen, K.E., 2012. Grasses and browsers reinforce landscape heterogeneity
557 by excluding trees from ecosystem hotspots. *Oecologia* 168, 749-759.

558 Ries, L., Fletcher, R.J., Battin, J., Sisk, T.D., 2004. Ecological responses to habitat edges:
559 Mechanisms, models, and variability explained. *Annual Review of Ecology Evolution and*
560 *Systematics* 35, 491-522.

561 Riginos, C., Grace, J.B., 2008. *Acacia* tree density, wild ungulate habitat use, and the
562 herbaceous community in a Kenyan savanna: Bottom-up versus top-down effects. *Ecology*
563 89, 2228-2238.

564 Riginos, C., Young, T.P., 2007. Positive and negative effects of grass, cattle, and wild
565 herbivores on *Acacia* saplings in an East African savanna. *Oecologia* 153, 985-995.

566 Stanton, M.L., Palmer, T.M., Young, T.P., 2002. Competition-colonization trade-offs in a
567 guild of African *Acacia*-ants. *Ecological Monographs* 72, 347-363.

568 Stanton, M.L., Palmer, T.M., Young, T.P., Evans, A., Turner, M.L., 1999. Sterilization and
569 canopy modification of a swollen thorn acacia tree by a plant-ant. *Nature* 401, 578-581.

570 Treydte, A.C., Bernasconi, S.M., Kreuzer, M., Edwards, P.J., 2006a. Diet of the common
571 warthog (*Phacochoerus africanus*) on former cattle grounds in a Tanzanian savanna. *Journal*
572 *of Mammalogy* 87, 889-898.

573 Treydte, A.C., Grant, C.C., Jeltsch, F., 2009. Tree size and herbivory determine below-
574 canopy grass quality and species composition in savannahs. *Biodiversity and Conservation*
575 18, 3989-4002.

576 Treydte, A.C., Halsdorf, S.A., Weber, E., Edwards, P.J., 2006b. Habitat use of warthogs on a
577 former cattle ranch in Tanzania. *Journal of Wildlife Management* 70, 1285-1292.

578 Van de Vijver, C., Foley, C.A., Olf, H., 1999. Changes in the woody component of an East
579 African savanna during 25 years. *Journal of Tropical Ecology* 15, 545-564.

580 Veblen, K.E., 2008. Season- and herbivore-dependent competition and facilitation in a
581 semiarid savanna. *Ecology* 89, 1532-1540.

582 Veblen, K.E., 2012. Savanna glade hotspots: Plant community development and synergy with
583 large herbivores. *Journal of Arid Environments* 78, 119-127.

584 Veblen, K.E., Young, T.P., 2010. Contrasting effects of cattle and wildlife on the vegetation
585 development of a savanna landscape mosaic *Journal of Ecology* 98, 993-1001.

586 Walters, M., Milton, S.J., Somers, M.J., Midgley, J.J., 2005. Post-dispersal fate of *Acacia*
587 seeds in an African savanna. *South African Journal of Wildlife Research* 35, 191-199.

588 Western, D., Dunne, T., 1979. Environmental aspects of settlement site decisions among
589 pastoral Maasai. *Human Ecology* 7, 75-98.

590 Young, T.P., Okello, B.D., 1998. Relaxation of an induced defense after exclusion of
591 herbivores: spines on *Acacia drepanolobium*. *Oecologia* 115, 508-513.

592 Young, T.P., Okello, B.D., Kinyua, D., Palmer, T.M., 1998. KLEE: a longterm multi-species
593 herbivore exclusion experiment in Laikipia, Kenya. *African Journal of Range and Forage*
594 *Science* 14, 94-102.

595 Young, T.P., Palmer, T.A., Gadd, M.E., 2005. Competition and compensation among cattle,
596 zebras, and elephants in a semi-arid savanna in Laikipia, Kenya. *Biological Conservation*
597 122, 351-359.

598 Young, T.P., Patridge, N., Macrae, A., 1995. Long-term glades in *Acacia* bushland and their
599 edge effects in Laikipia, Kenya. *Ecological Applications* 5, 97-108.

600 Young, T.P., Stanton, M.L., Christian, C.E., 2003. Effects of natural and simulated herbivory
601 on spine lengths of *Acacia drepanolobium* in Kenya. *Oikos* 101, 171-179.

602 Young, T.P., Stubblefield, C.H., Isbell, L.A., 1997. Ants on swollen thorn acacias: Species
603 coexistence in a simple system. *Oecologia* 109, 98-107.

604

605

606 **7. TABLES**

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

614

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

615

616 **8. FIGURE LEGENDS**

617 **Fig. 1:** a) Diagram of the Kenya Long-term Exclosure Experiment, including herbivore
618 treatment labels, locations of glade portions and 2009 sampling transect locations. See Table
619 1 for explanations of treatment abbreviations. Glade portions occurring in treatment plots
620 labeled in bold were sampled in 2006-2007, and b) provides a detailed view of 2006-2007
621 sample plot locations.

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

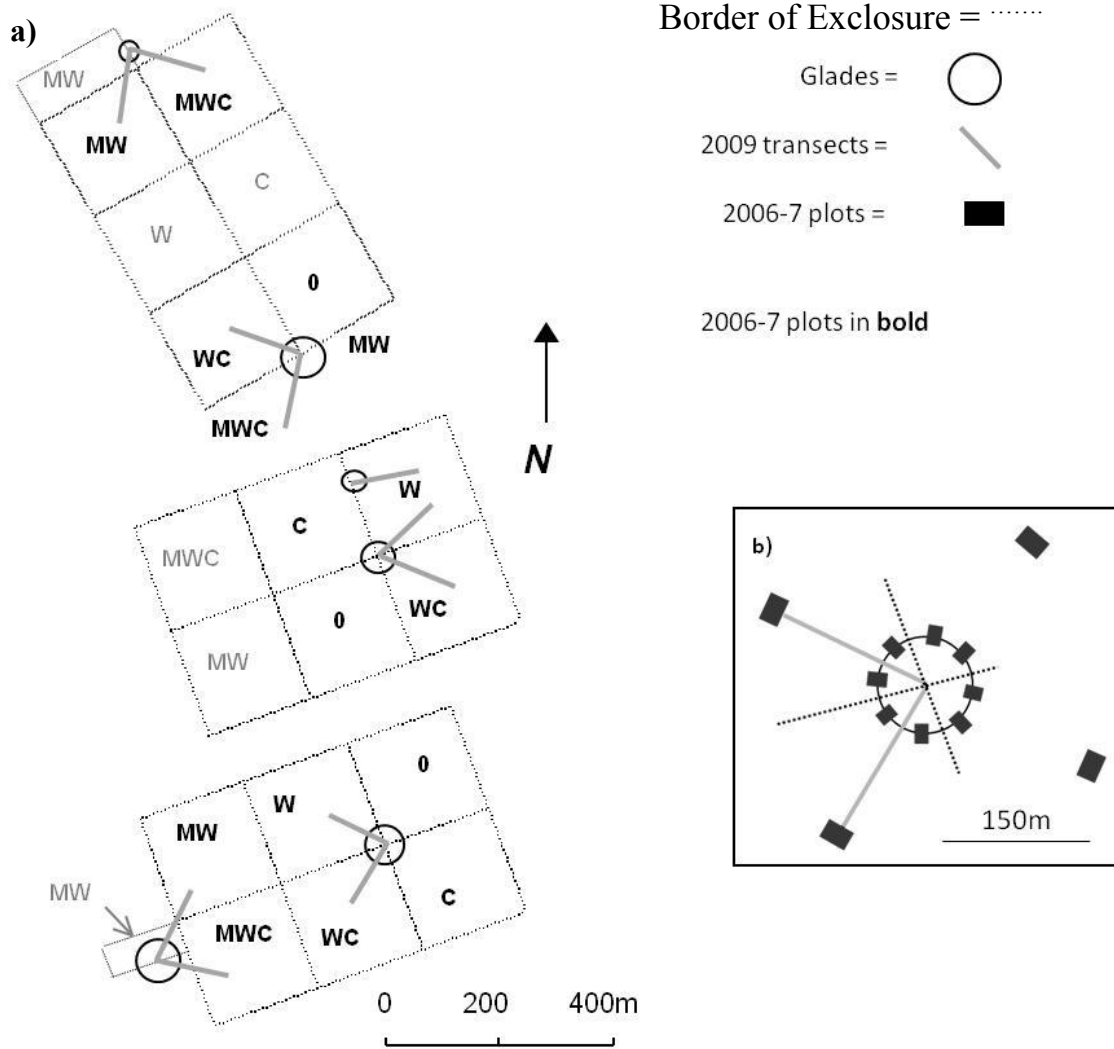
626 **Fig. 3:** Mean densities (± 1 SE, in trees per 40 m²) of trees hosting non-aggressive ant species
627 (*C. sjostedti* and *T. penzigi*) in different large herbivore treatments. + M = plots allowing
628 megaherbivores; - M = plots excluding megaherbivores; + C = plots allowing cattle; - C =
629 plots excluding cattle. The interaction between cattle and megaherbivore presence was
630 significant at the $p < 0.10$ level (cattle $F_{1,7} = 4.93$, $p = 0.06$; megaherbivore $F_{1,7} = 11.89$, $p =$
631 0.01 ; cattle*megaherbivore $F_{1,7} = 4.43$, $p = 0.07$).

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

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

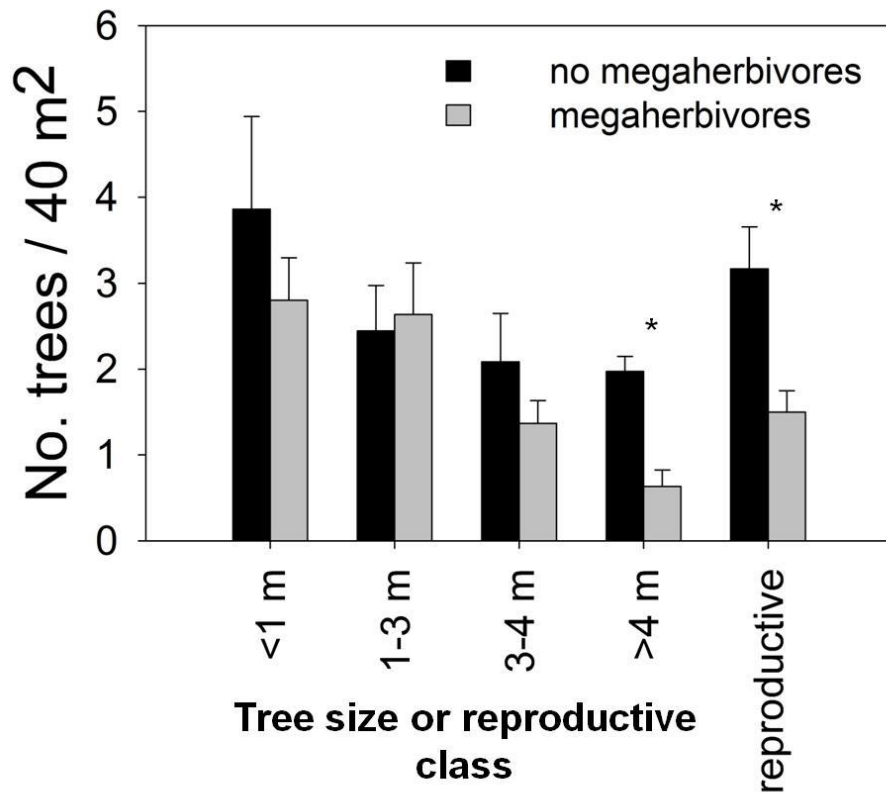
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640 **Figure 1**



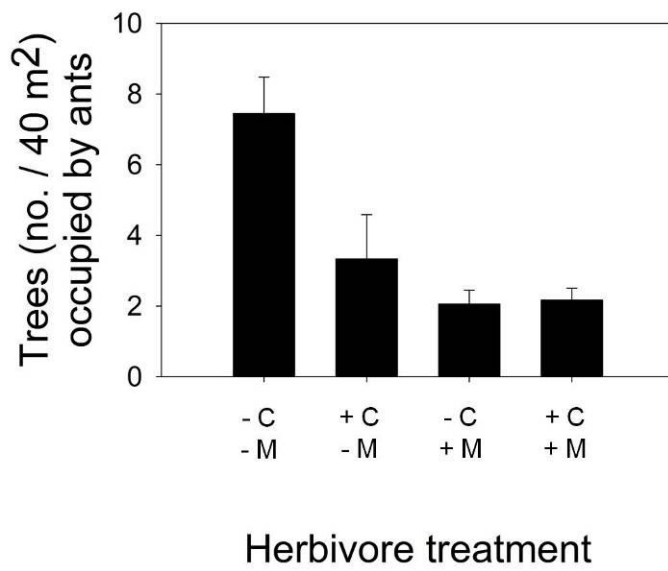
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644 **Figure 2**



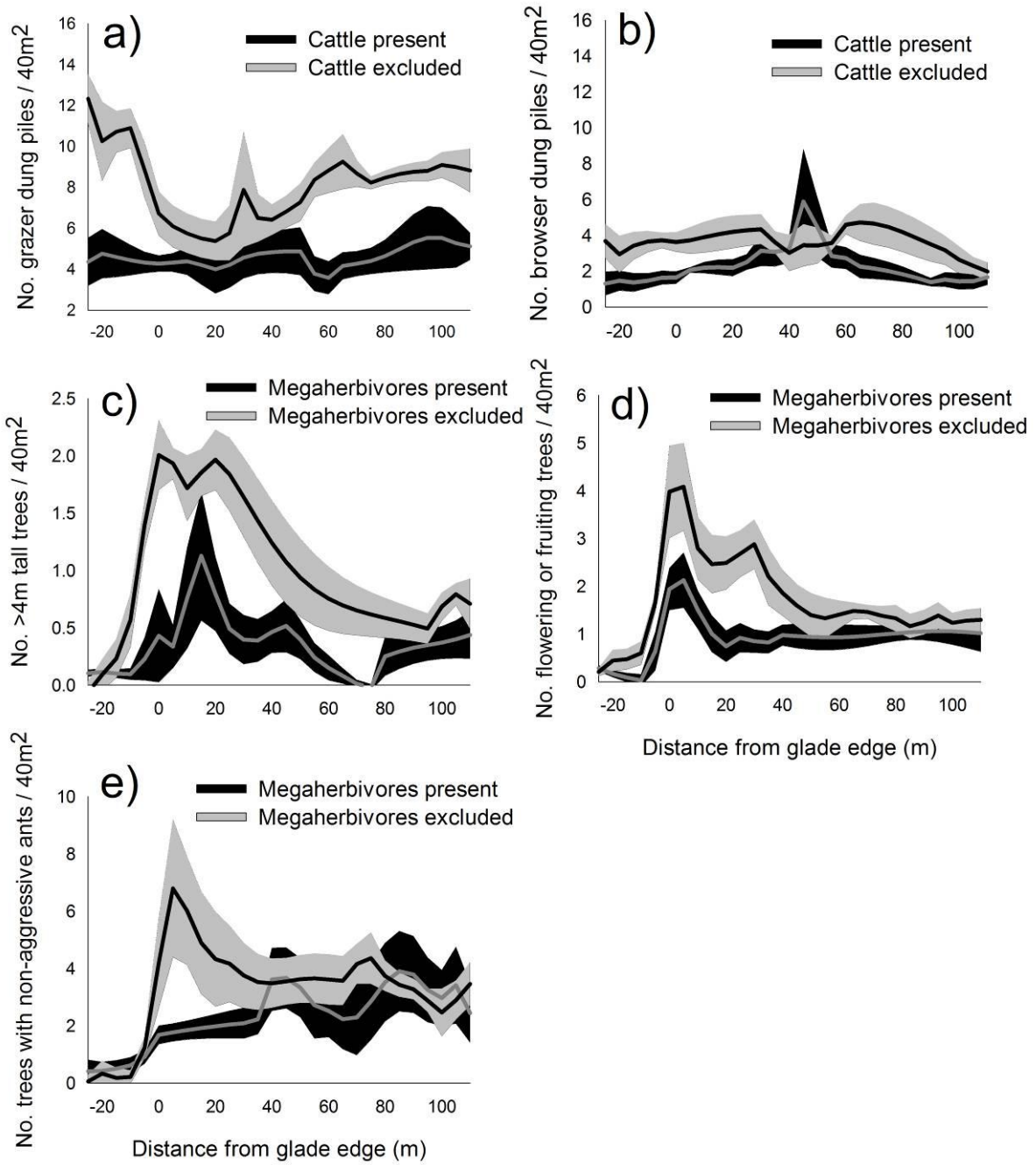
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646 **Figure 3**



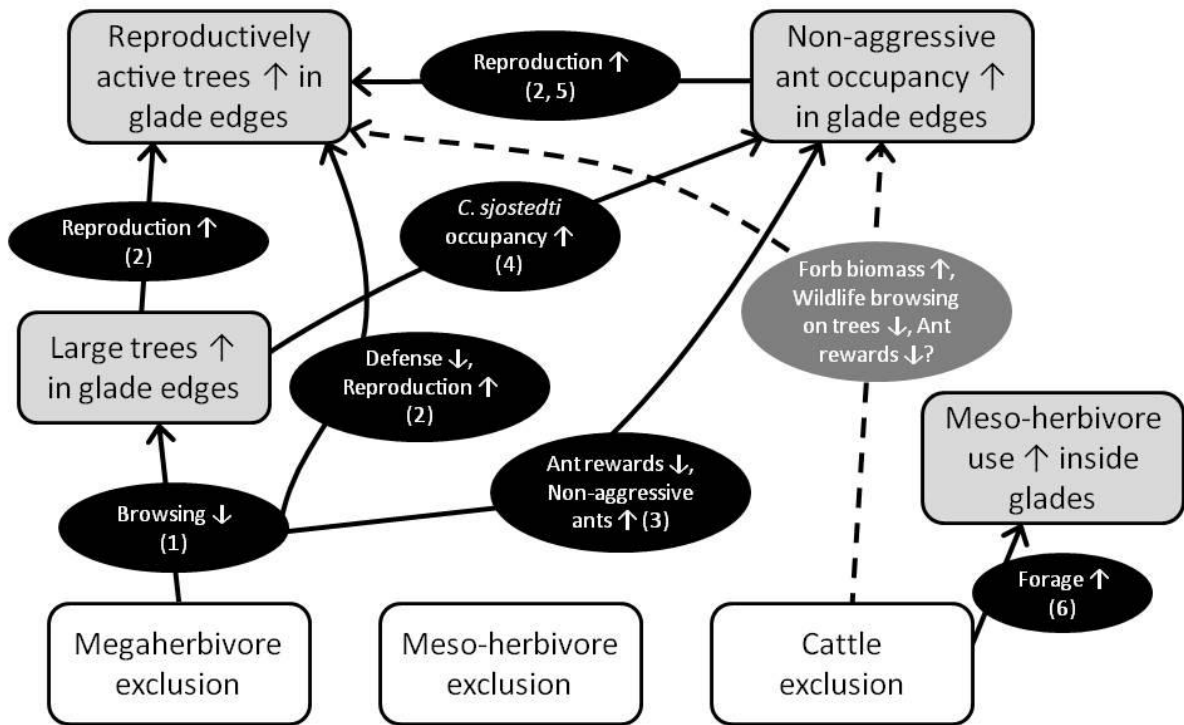
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Citations:¹Augustine and McNaughton, 2004; ²Goheen et al., 2007; ³Palmer et al., 2008; ⁴Young et al., 1997; ⁵Palmer et al., 2010; ⁶Odadi et al., 2011

654 *Appendix: Abundance of cattle and megaherbivore dung*

655 Dung measurements indicated that cattle and megaherbivore exclusion treatments were
656 effective. Inside glades, cattle + buffalo dung density was 10 times lower in plots where cattle
657 were excluded (5.7 ± 1.0 vs. 0.6 ± 0.2 dung piles/ 40 m^2). Similarly, in glade edges, cattle+
658 buffalo dung density was nearly 7 times lower in plots where cattle were excluded (6.2 ± 1.9
659 vs. 0.9 ± 0.4 dung piles/ 40 m^2). In plots where megaherbivores were excluded, no
660 megaherbivore dung piles were found either inside glades or in glade edges. In plots where
661 megaherbivores were allowed, average megaherbivore dung density was 0.9 ± 0.2 dung piles/
662 40 m^2 inside glades and 1.4 ± 0.2 dung piles/ 40 m^2 in glade edges.

*Highlights (for review)

Herbivores alter edge effects

Bucher et al.

Highlights

- In east Africa, temporary cattle corrals develop into productive, treeless glades.
- We investigated impacts of different large herbivores on glade edge effects.
- Megaherbivores reduced densities of tall and reproductive trees at glade edges.
- Cattle reduced meso-herbivore use of glade interiors, but not glade edges.
- Large herbivores dampened spatial patterns associated with glades and glade edges.