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

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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

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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 km^2, 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.

2. METHODS

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.

7

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 ± 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

9

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 m^2. 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:

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

$$\underbrace{}_{\textbf{linear}} \quad \underbrace{}_{\textbf{sigmoid}} \quad \underbrace{}_{\textbf{unimodal}}$$

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.

3. RESULTS

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 ±

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 ± 6% of total dung. In plots where cattle

292   were excluded, cattle+buffalo dung accounted for 3 ± 1% and zebra dung accounted for 60 ±

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 λ*= 0.04, *p*= 0.02; megaherbivore effect *Wilk's λ*= 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 m^2;

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 m^2; $F_{1,8}$= 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 m^2; $F_{1,8}$= 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 λ*= 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 λ*= 0.32, *p*= 0.06; megaherbivore effect *Wilk's λ*=

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 km^2 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 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. *Cremmatogaster 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.

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604

605

7. TABLES

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)	± SE	mean (#/ha)	± 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

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 m^2) 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 m^2) 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

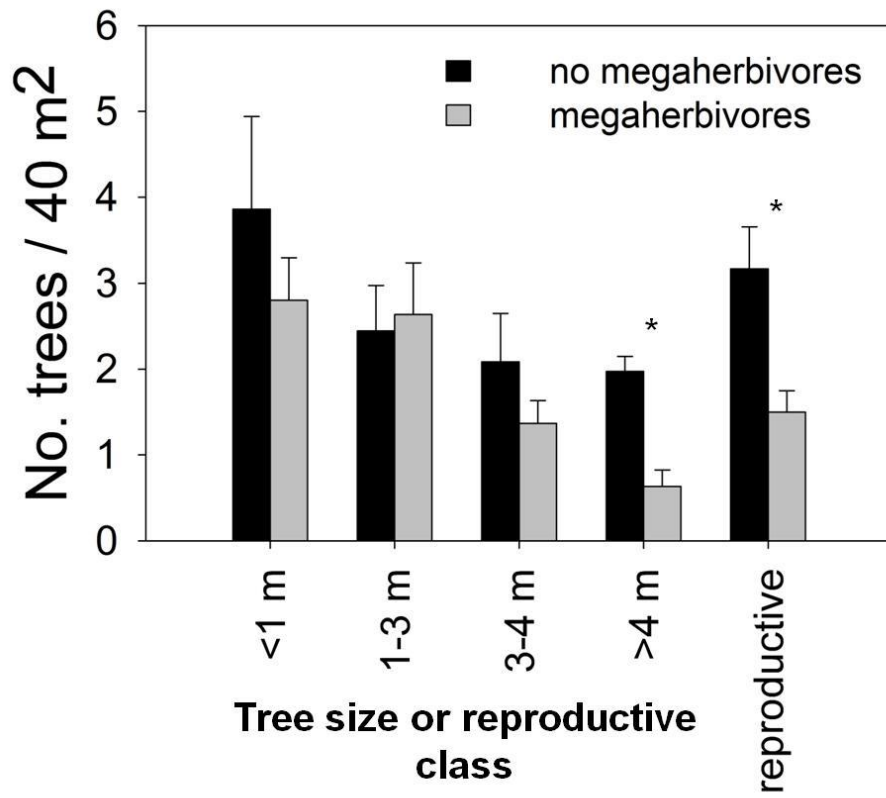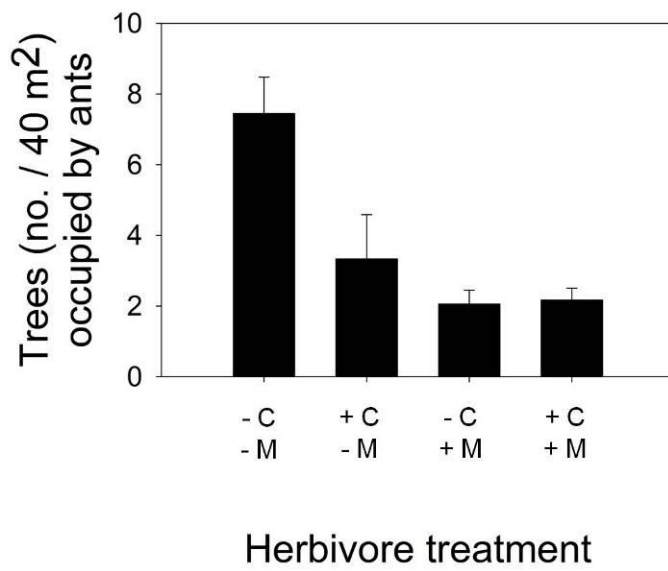638 arrows and gray ovals indicate currently untested mechanisms.
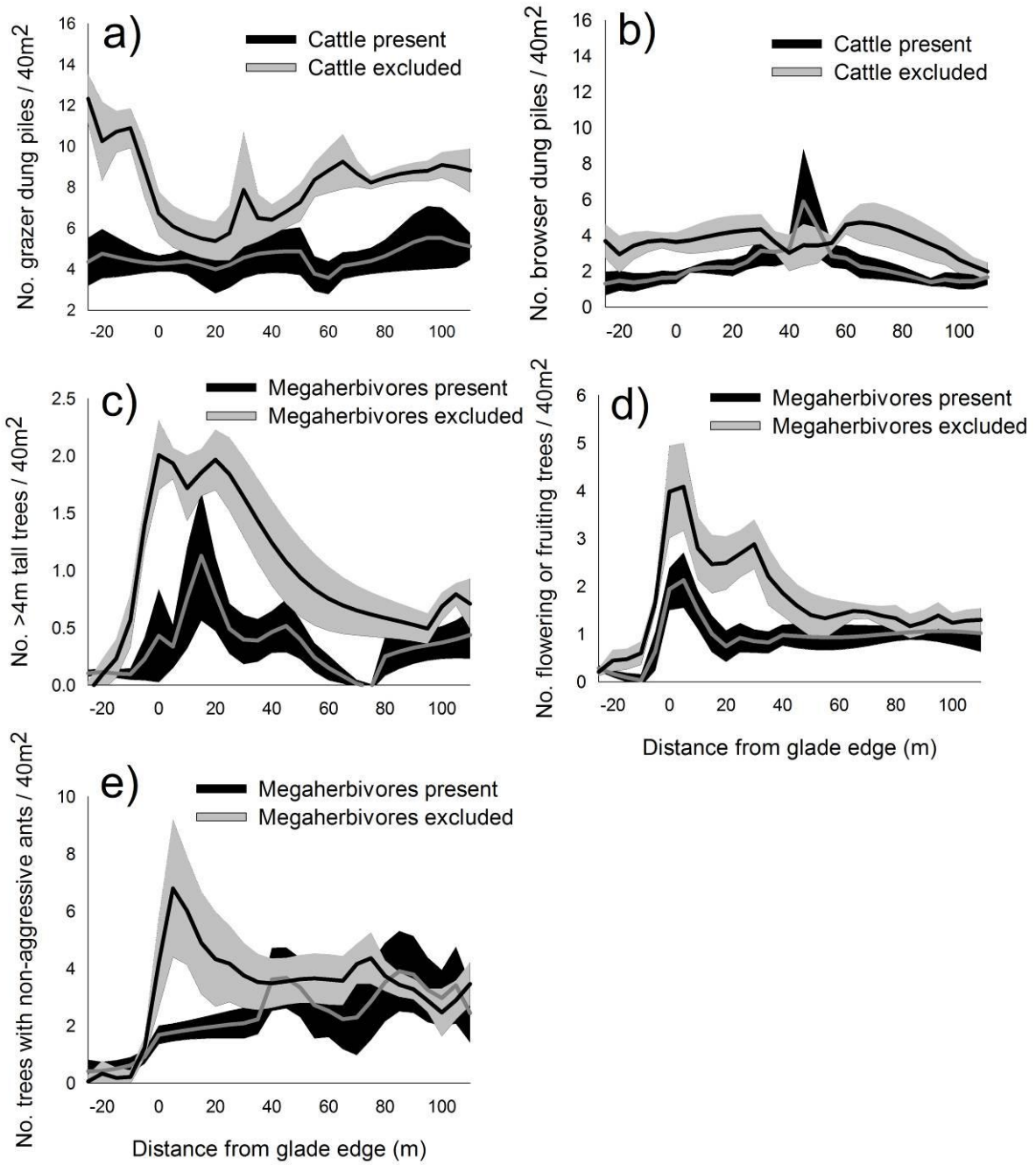
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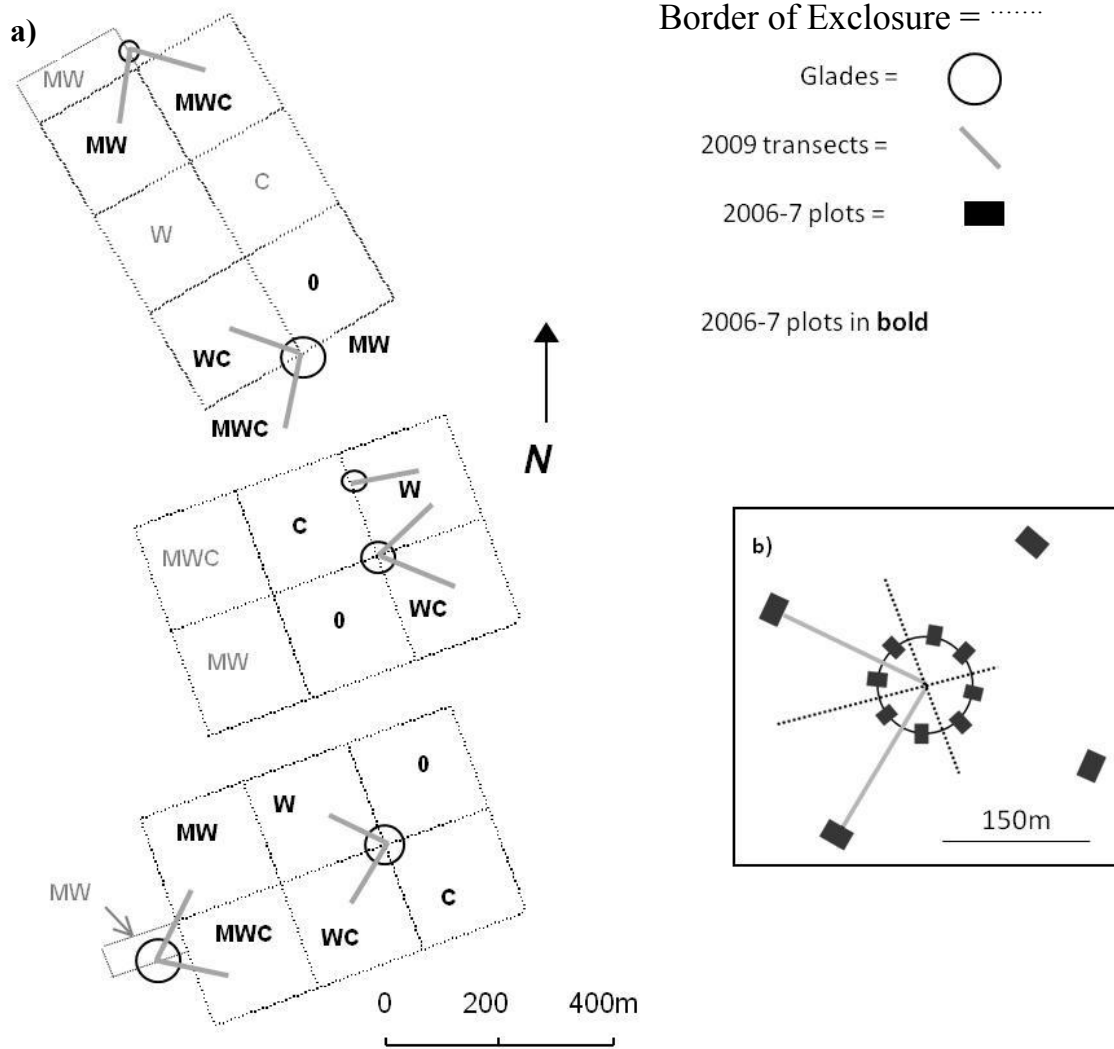
Figure 1

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644 **Figure 2**

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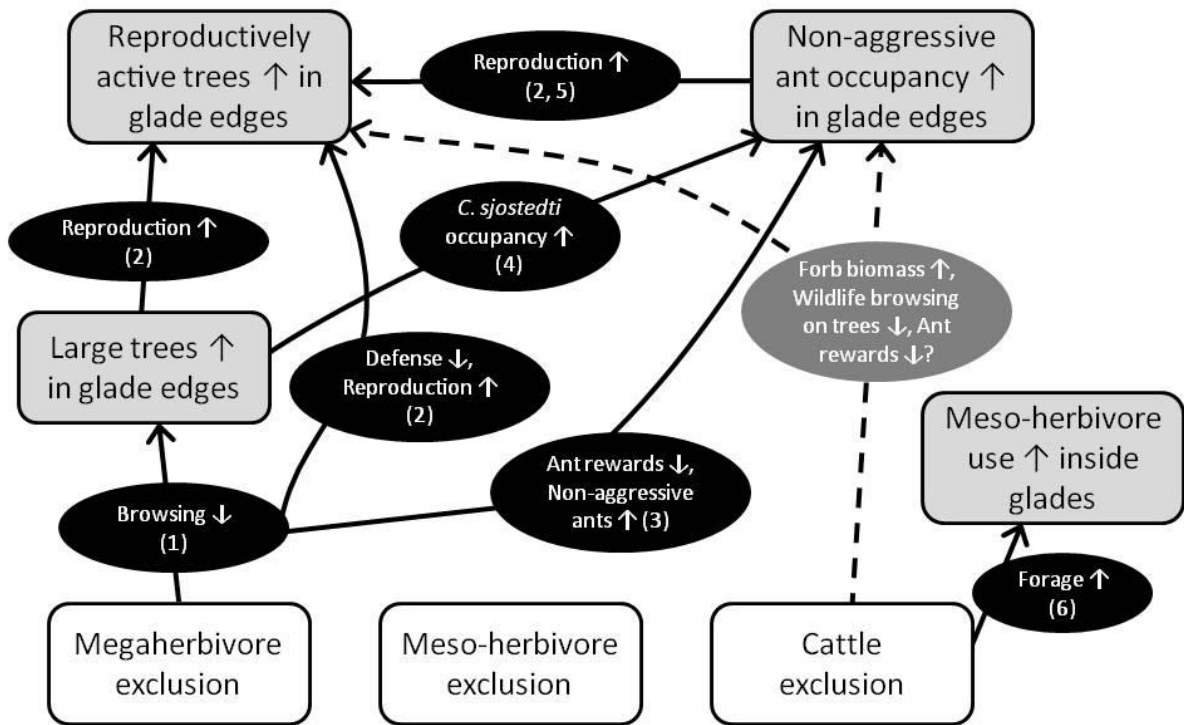
646   **Figure 3**

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Figure 4

Figure 5

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

653

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 were 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.

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.