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Grasses and browsers reinforce landscape heterogeneity

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by excluding trees from ecosystem hotspots

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15 **ABSTRACT**

16 Spatial heterogeneity in woody cover affects biodiversity and ecosystem function, and may be
17 particularly influential in savanna ecosystems. Browsing and interactions with herbaceous plants
18 can create and maintain heterogeneity in woody cover, but the relative importance of these
19 drivers remains unclear, especially when considered across multiple edaphic contexts. In African
20 savannas, abandoned temporary livestock corrals develop into long-term, nutrient-rich ecosystem
21 hotspots with unique vegetation. In central Kenya, abandoned corral sites persist for decades as
22 treeless ‘glades’ in a wooded matrix. Though glades are treeless, areas between adjacent glades
23 have higher tree densities than the background savanna or areas near isolated glades. The
24 mechanisms maintaining these distinctive woody cover patterns remain unclear. We asked
25 whether browsing or interactions with herbaceous plants help to maintain landscape
26 heterogeneity by differentially impacting young trees in different locations. We planted the
27 mono-dominant tree species (*Acacia drepanolobium*) in four locations: inside glades, far from
28 glades, at edges of isolated glades and at edges between adjacent glades. Within each location we
29 assessed the separate and combined effects of herbivore exclusion (caging) and herbaceous plant
30 removal (clearing) on tree survival and growth. Both caging and clearing improved tree survival
31 and growth inside glades. When herbaceous plants were removed, trees inside glades grew more
32 than trees in other locations, suggesting that glade soils were favorable for tree growth. Different
33 types of glade edges (isolated vs. non-isolated) did not have significantly different impacts on
34 tree performance. This represents one of the first field-based experiments testing the separate and
35 interactive effects of browsing, grass competition and edaphic context on savanna tree
36 performance. Our findings suggest that by excluding trees from otherwise favorable sites, both
37 herbaceous plants and herbivores help to maintain functionally important landscape

38 heterogeneity in African savannas.

39 **KEYWORDS:** boma; grazing lawn; tree-grass interactions; spatial heterogeneity; edge
40 interactions

41 **INTRODUCTION**

42 Understanding heterogeneity in vegetation structure has been a central goal of ecology,
43 particularly in savanna ecosystems where mechanisms of tree-grass coexistence have long been
44 debated (Walter 1971; Walker et al. 1981; Scholes and Archer 1997; Jeltsch et al. 2000;
45 Sankaran et al. 2004). Patterns of woody cover in savannas can be driven by a multitude of
46 factors including rainfall, nutrients, herbivory, fire, interactions with grasses or other woody
47 plants, and interactions among these factors (Dublin et al. 1990; Scholes and Archer 1997;
48 Jeltsch et al. 2000; van Langevelde et al. 2003; Sankaran et al. 2005; Riginos and Grace 2008;
49 van der Waal et al. 2011). Heterogeneity in woody cover is important because it alters and
50 possibly enhances biodiversity and ecosystem function (Young et al. 1995; Rietkerk et al. 2004;
51 Riginos and Grace 2008; Lundholm 2009; Gregory et al. 2010).

52 In African savannas, heterogeneity in woody cover often is associated with heterogeneity in
53 soil quality. Woody cover can be affected by regional-scale nutrient gradients as well as nutrient-
54 rich micro-sites (e.g., termite mounds) (Sankaran et al. 2005; Fox-Dobbs et al. 2010; Levick et
55 al. 2010). Intermediate in scale are nutrient-rich sites derived from traditional livestock corrals
56 (Western and Dunne 1979; Blackmore et al. 1990; Lamprey and Reid 2004). Throughout African
57 savannas, former corral sites develop into long-term, nutrient-rich patches with unique
58 vegetation (Blackmore et al. 1990; Reid and Ellis 1995; Young et al. 1995; Augustine 2003;
59 Muchiru et al. 2009; van der Waal et al. 2011), distinctive plant community dynamics (Veblen
60 2008; Veblen and Young 2010; Veblen in revision) and broad-ranging ecological impacts

61 (Augustine 2004; Gregory et al. 2010).

62 In wooded savannas, corral sites can persist as grass-dominated ‘glades,’ easily recognizable
63 for decades to centuries as large treeless patches (50-100 m in diameter) embedded in a wooded
64 matrix (Young et al. 1995; Muchiru et al. 2009; Veblen and Young 2010). Though glade
65 interiors are treeless, areas between nearby glades (<150 m apart) have higher densities of trees
66 than either the background savanna or areas near isolated glades (Porensky 2011). It is not clear
67 how these distinctive patterns of woody cover associated with glade interiors (no trees) and
68 adjacent glade edges (many trees) are maintained over the long-term. Inside nutrient-rich glades,
69 at glade edges, and in the background savanna, we assessed the relative importance of two
70 mechanisms that may drive heterogeneity in woody cover: herbivory and interactions with
71 herbaceous plants.

72 Herbivory has major impacts on woody cover in savanna ecosystems (Pellew 1983;
73 Augustine and McNaughton 2004; Goheen et al. 2010) and could play a particularly important
74 role in determining woody cover patterns associated with glades, where use by mid-sized,
75 mixed-feeder herbivores is elevated (Young et al. 1995; van der Waal et al. 2011). Herbivore
76 preference may lead to elevated browsing pressure and reduced tree survival or growth within
77 glades, particularly for young trees (seedlings and saplings) (Goheen et al. 2004; Midgley et al.
78 2010). Thus, initial anthropogenic disturbance may generate herbivore-mediated feedbacks that
79 help maintain glades in a treeless state over the long term.

80 Very high densities of trees between nearby glades also may be caused by a combination of
81 anthropogenic legacies and herbivore-mediated feedbacks. During active corral use, intensive
82 livestock activity and human presence between nearby corrals may initiate a burst of tree
83 establishment by reducing grass cover, deterring browsers and increasing nutrient levels,

84 especially if low grass cover causes reduced fire intensity or frequency (e.g., Tobler et al. 2003;
85 van Langevelde et al. 2003; Augustine and McNaughton 2004; Muchiru et al. 2009; Davies et al.
86 2010; Goheen et al. 2010). Over the long-term, herbivore behaviors may reinforce high tree
87 densities between glades. The mid-sized wildlife species most likely to browse on tree seedlings
88 tend to avoid heavily-treed areas (Riginos and Grace 2008). Reduced browsing pressure in
89 heavily-treed areas between nearby glades could further increase tree density.

90 Herbaceous plants (hereafter ‘grasses’) can also exert controls over young trees (Riginos and
91 Young 2007). Grasses often compete intensely with young trees (e.g., van der Waal et al. 2009;
92 Cramer et al. 2010). Glades in our study site typically have very high grass cover (Veblen 2008;
93 Porensky 2011), creating an environment in which grass competition may be severe enough to
94 kill young trees (e.g., van der Waal et al. 2011). Areas between nearby glades have unusually
95 low cover of dense glade grasses, which may release young trees from competition and help
96 explain increased tree densities between nearby glades (Porensky 2011). At low-moderate
97 densities (e.g., between nearby glades), grasses may even facilitate young trees by concealing
98 them from herbivores (Western and Maitumo 2004; Riginos and Young 2007). Differences in
99 grass cover can also impact tree density via interactions with fire (van Langevelde et al. 2003;
100 Davies et al. 2010), although fire has been suppressed at our study site for decades.

101 This work goes beyond previous studies by experimentally testing the separate and combined
102 effects of both herbivory and grasses on the survival and growth of young trees planted in the
103 field in different edaphic contexts. Specifically, we determined the relative importance of
104 herbivores and grasses as drivers of 1) extremely low densities of trees inside glades and 2) high
105 densities of trees between nearby glades.

106 **METHODS**

107 **Study site** - This research took place in central Kenya on Mpala Conservancy (36°52'E, 0°17'N)
108 and neighboring Jessel Ranch. These properties are managed for livestock production as well as
109 biodiversity conservation, and host a full complement of wildlife species including native
110 ungulates and their predators (see Young et al. 1998). Soils are 'black cotton' vertisols
111 characterized by high clay content and poor drainage (Deckers et al. 2001). Mean annual rainfall
112 is 500-600 mm. Topography is relatively uniform, and vegetation is dominated by a single tree
113 species (*Acacia drepanolobium*, comprising 97% of total woody cover) and five grass species
114 (Young et al. 1998). The study area includes dozens of glades that are irregularly distributed
115 throughout the landscape, creating variability in inter-glade distance (Fig. 1). Fire has not been
116 an active part of this ecosystem since the 1960s, although small portions of the study site have
117 been experimentally burned in recent years (RL Sensenig, personal communication).

118 **Seed collection and germination** - Between September 2008 and January 2009, we collected
119 seeds from 33 adult *A. drepanolobium* trees located throughout the study site. Source trees were
120 all greater than 3 m tall and occupied by the same symbiotic *Acacia* ant species (*Crematogaster*
121 *mimosae*). Source trees were separated from each other by at least 60 m. In total, we collected
122 1518 seeds, or 46 ± 3 (1 SE) seeds per source tree. We randomly assigned half of the seeds from
123 each source tree to a 'sapling' treatment and the other half to a 'seedling' treatment.

124 Germination and initial tree growth took place in a tree nursery operated by Kiwi Consultants
125 Ltd. in Nanyuki, Kenya, 40 km from the study site. Seeds assigned to the sapling treatment were
126 germinated in February 2009, and seeds assigned to the seedling treatment were germinated in
127 June 2009. All trees were grown in potting soil and fertilized once during initial growth. Trees
128 were kept outdoors under shade cloth for the first 2-3 months of growth and then moved into full
129 sun. On 15-Aug-2009 we clipped the top 3 cm of each sapling to simulate natural browsing and

130 induce allocation to defense structures (c.f. Young et al. 2003). In October 2009, we retrieved
131 484 saplings and 245 seedlings from the nursery. Most saplings had well-developed woody stem
132 tissue, while seedlings were just beginning to form woody tissue. Trees were individually tagged.
133 For each tree, we measured stem length (length of the longest stem, measured while
134 straightening the stem as much as possible), diameter at 3 cm height (hereafter ‘basal diameter’),
135 and number of branches.

136 ***Experimental design and data collection*** - We split the study area into 5 blocks based on
137 property ownership and geographic position (Fig. 1). Within each block we randomly chose a
138 relatively isolated glade (>250 m from any other glade), a non-isolated glade (<150 m from a
139 second glade), and a ‘no glade’ area (>300 m from any glade). We planted trees in four 11x11 m
140 plots in each block: within the isolated glade, 25 m outside the edge of the isolated glade, 25 m
141 outside the edge of the non-isolated glade, and at a random location within the ‘no-glade’ area
142 (Fig. 1). The 25 m edge distance was chosen to match the observed location of peak tree
143 densities between nearby glades (Porensky 2011). Glade edges were defined as in previous work
144 (Porensky 2011). We used aerial photographs from 1961 to ensure that all glades were >45 years
145 old. Plots inside glades were all located in areas dominated by the grass *Pennisetum stramineum*
146 to reduce variability caused by differences in glade vegetation (Veblen 2008).

147 Within each plot, we created two replicates of a 2x2 factorial design that included
148 mammalian herbivore exclusion (caging) and herbaceous vegetation removal (clearing). The four
149 treatments included caged, cleared, caged+cleared, and control (no caging or clearing). We
150 randomly assigned treatments to eight 1.5x1.5 m ‘sites’ within each 11x11 m plot (Fig. 1). Sites
151 were arranged in a grid and separated from one another by 1.5 m. Sites assigned to caged and
152 caged+cleared treatments were covered by a 1x1x1 m chicken-wire cage. To reduce rodent

153 incursions, we covered the bottom half-meter of each cage with ≤ 1.3 cm mesh. At sites assigned
154 to cleared and caged+cleared treatments, we clipped all non-woody plants (almost entirely
155 grasses) at ground level. At intervals throughout the experiment (0.5, 1.5, 3 and 6 months after
156 planting), grass regrowth was sprayed with herbicide. Although the goal of caging was to protect
157 trees from browsing, the cages also eliminated herbivory on herbaceous vegetation. In order to
158 separate the direct effects of reduced browsing (the factor of interest) from indirect effects of
159 reduced grazing inside cages (e.g., shading of trees by tall grasses), caged herbaceous plants
160 were occasionally clipped so that average vegetation height inside cages matched that of
161 surrounding, uncaged vegetation.

162 Within each 1.5x1.5 m site, we planted two randomly-chosen saplings and either one or two
163 randomly-chosen seedlings (for a total of 16 saplings and 12 seedlings per plot, Fig. 1). Due to
164 unexpectedly high mortality at the nursery, we were unable to plant two seedlings at every site,
165 but within each plot we planted three seedlings per treatment. For each plot, we randomly chose
166 which of the two sites assigned to a given treatment would receive 2 seedlings and which would
167 receive 1 seedling. The orientation of seedlings and saplings within each site was also assigned
168 randomly. Within each site, trees were planted ~ 70 cm apart (the maximum amount of separation
169 possible given the size of the cages). Trees were planted in mid-October 2009, just before a short
170 rainy season. At the time of planting, we watered each seedling or sapling with 1 L. We did not
171 add any more water after planting. In total, we planted 320 saplings and 240 seedlings.

172 Trees were monitored in late August 2010. For each individually-tagged tree, we recorded
173 survival, stem length, basal diameter and number of branches (measured as described above). Of
174 the 457 surviving trees, six were excluded from basal diameter analysis because the main stem
175 had died or been severely browsed or broken.

176 **Statistical Analysis** - The experiment had a blocked split-split-plot design with location as the
177 main plot effect, treatment (caging and/or clearing) as the subplot effect, and tree age class as the
178 sub-subplot effect. To evaluate factors responsible for reduced tree density inside glades, we
179 compared three locations: far from glade, isolated glade edge and inside glade. To evaluate
180 factors responsible for increased tree density between nearby glades, we compared isolated glade
181 edges to non-isolated glade edges.

182 We analyzed tree survival using a generalized linear mixed model with a binary conditional
183 probability distribution and residual pseudo-likelihood estimation. For trees that survived, we
184 analyzed three different growth responses (stem length growth, basal diameter growth and
185 branch production) using linear mixed models with restricted maximum-likelihood estimation.
186 We analyzed each growth response separately because we expected stem length, basal diameter
187 and branch production to be differently affected by our treatments. In all cases we used
188 Satterthwaite's approximation of degrees of freedom and a 'variance components' covariance
189 structure. For all models, fixed predictors included location, treatment, tree age class and all two-
190 way interactions. If interactions were significant, we analyzed simple effects (e.g., differences
191 among treatments within each location and differences among locations within each treatment).
192 Random factors included block, location*block and site nested within location*block. We used
193 transformations or variance-weighting when necessary in order to meet the assumptions of the
194 models. We used Tukey's HSD method ($\alpha = 0.05$) for post-hoc mean comparisons. All analyses
195 were conducted in SAS 9.2 (SAS Institute Inc., Cary, North Carolina USA).

196 **RESULTS**

197 **Baseline tree sizes** - For seedlings, baseline stem length (measured just prior to planting) was
198 15.6 ± 0.4 (1 SE) cm and baseline basal diameter was 2.2 ± 0.04 mm. For saplings, baseline stem

199 length was 25.0 ± 0.5 cm and baseline basal diameter was 3.4 ± 0.06 mm. For both size classes,
200 baseline branch number was 1.1 ± 0.02 branches.

201 **PART I: inside and outside of isolated glades**

202 **Survival** - Saplings had significantly higher survival than seedlings (85% vs. 77%, $F_{1,402}=3.55$,
203 $P=0.04$). Interactions involving age class were not significant, but the interaction between
204 location (far from glade, glade edge, or inside glade) and treatment (caging and/or clearing)
205 significantly affected survival ($F_{6,402}=3.06$, $P=0.006$).

206 Simple effects analysis revealed that caging and clearing did not significantly impact survival
207 far from glades ($F_{3,136}=2.55$, $P=0.06$) or at glade edges ($F_{3,38,9}=2.10$, $P=0.12$), but strongly
208 affected survival inside glades ($F_{3,136}=11.16$, $P<0.0001$). Inside glades, trees in the control
209 treatment had less than one third the survival of trees in any other treatment (Fig. 2a-c, Table 1).

210 Tree survival did not differ significantly across locations within the cleared ($F_{2,7,18}=0.84$,
211 $P=0.5$) or caged+cleared ($F_{2,36,26}=1.06$, $P=0.4$) treatments. However, survival did differ by
212 location within the caged ($F_{2,27,11}=4.65$, $P=0.02$) and control ($F_{2,6,61}=9.17$, $P=0.01$) treatments.
213 Survival far from glades was 55% higher than survival inside glades for the cage treatment and
214 over 300% higher for the control treatment (Fig. 2a-c, Table 1).

215 **Stem length growth** - Seedling stem lengths grew significantly more than those of saplings (8.6
216 ± 0.8 vs. 3.4 ± 0.6 cm; $F_{1,272}=31.95$, $P<0.0001$). Interactions involving age class were not
217 significant. The interaction between location and treatment significantly affected stem length
218 growth ($F_{6,104}=3.28$, $P=0.005$).

219 Treatment significantly affected stem length growth at all three locations (far from glades
220 $F_{3,120}=10.73$, $P<0.0001$; glade edge $F_{3,31,3}=9.18$, $P=0.0002$; inside glades $F_{3,24,5}=7.51$, $P=0.001$).
221 Far from glades and at glade edges, caged+cleared trees grew about 8 cm more than cleared

222 trees, while caged and control trees had intermediate growth (Fig. 2d-f, Table 1). Inside glades,
223 growth of caged+cleared trees was over three times that of trees in other treatments (Fig. 2d-f,
224 Table 1).

225 Stem length growth did not differ significantly across locations within any treatments (cage
226 $F_{2,82.9}=0.33$, $P=0.7$; caged+cleared $F_{2,7.16}=4.07$, $P=0.07$; clear $F_{2,7.39}=1.49$, $P=0.3$; control
227 $F_{2,5.86}=0.01$, $P=0.99$; Fig. 2d-f, Table 1).

228 **Basal diameter growth** - Seedling basal diameters increased significantly more than those of
229 saplings (0.8 ± 0.1 vs. 0.2 ± 0.1 mm; $F_{1,269}=46.15$, $P<0.0001$). Interactions involving age class
230 were not significant, but growth was significantly affected by the interaction between location
231 and treatment ($F_{6,116}=6.56$, $P<0.0001$).

232 Treatment significantly affected basal diameter growth far from glades ($F_{3,119}=4.04$,
233 $P=0.009$) and inside glades ($F_{3,28.5}=6.61$, $P=0.002$). Far from glades, growth of caged+cleared
234 trees was over 4.5 times that of trees in other treatments (Fig. 2g-i, Table 1). Inside glades,
235 cleared and caged+cleared trees grew significantly more than caged trees, while control trees had
236 intermediate growth (Fig. 2g-i, Table 1). Treatment did not significantly affect basal diameter
237 growth at glade edges ($F_{3,118}=1.87$, $P=0.1$).

238 Within the cage treatment, basal diameter growth differed significantly among locations
239 ($F_{2,84.5}=3.45$, $P=0.04$). Caged trees inside glades grew significantly less than caged trees in glade
240 edges, while caged trees far from glades had intermediate growth (Fig. 2g-i, Table 1). Locations
241 also differed significantly within the cleared treatment ($F_{2,9.65}=4.01$, $P=0.05$). Cleared trees
242 inside glades grew over 10 times as much as cleared trees far from glades, while cleared trees at
243 glade edges had intermediate growth (Fig. 2g-i, Table 1). Basal diameter growth did not differ
244 significantly across locations within the caged+cleared ($F_{2,7.16}=3.97$, $P=0.07$) or control

245 ($F_{2,9.66}=0.02$, $P=0.98$) treatments.

246 **Branch production** - Saplings produced significantly more new branches than seedlings ($2.9 \pm$
247 0.2 vs. 2.3 ± 0.2 new branches; $F_{1,257}=13.14$, $P=0.0003$). Interactions involving age class were
248 not significant. Branch production was significantly affected by the interaction between location
249 and treatment ($F_{6,86.4}=3.29$, $P=0.006$).

250 Treatment significantly affected branch production in all locations (far from glades
251 $F_{3,120}=9.02$, $P<0.0001$; glade edges $F_{3,31}=7.04$, $P=0.001$; inside glades $F_{3,26.9}=14.58$, $P<0.0001$).
252 Far from glades and at glade edges, caged+cleared trees produced over twice as many branches
253 as caged trees, while cleared and control trees produced an intermediate number of branches
254 (Fig. 2j-1, Table 1). Inside glades, cleared and caged+cleared trees produced more than three
255 times as many branches as caged and control trees (Fig. 2j-1, Table 1).

256 Branch production was not significantly affected by location in the cage ($F_{2,24.9}=0.40$,
257 $P=0.7$), caged+cleared ($F_{2,11.7}=1.82$, $P=0.2$) or control ($F_{2,7.62}=1.47$, $P=0.3$) treatments. In the
258 cleared treatment, location had significant effects on branch production ($F_{2,8.36}=6.62$, $P=0.02$).
259 Cleared trees inside glades produced almost three times as many branches as cleared trees at
260 glade edges, and cleared trees far from glades produced an intermediate number of branches
261 (Fig. 2j-1, Table 1).

262 **PART II: isolated vs. non-isolated glade edges**

263 **Survival** - When we compared isolated and non-isolated edges, tree survival was only affected
264 by treatment ($F_{3,85.28}=5.68$, $P=0.001$). Caged and caged+cleared trees had about 30% higher
265 survival than control trees, and cleared trees had intermediate survival (Fig. 3a). Edge type, tree
266 age class, and interactions had no significant impact on survival.

267 **Stem length growth** - Stem growth was not significantly affected by edge type, but was affected

268 by the interaction between treatment and tree age class ($F_{3,182}=2.72$, $P=0.046$). Treatments had
269 significant effects on stem length growth for both saplings ($F_{3,55.3}=16.54$, $P<0.0001$) and
270 seedlings ($F_{3,57.3}=6.94$, $P=0.0005$). Saplings that were caged or caged+cleared grew significantly
271 more than control or cleared trees (Fig. 3b). Seedling results were similar except that growth in
272 the control treatment was intermediate between the cleared treatment and the other treatments
273 (Fig. 3b). In three out of four treatments, seedlings grew significantly more than saplings (caged:
274 8.5 ± 1.0 vs. 4.9 ± 1.1 cm, $F_{1,55.1}=5.64$, $P=0.02$; cleared: 1.3 ± 1.2 vs. -2.9 ± 1.2 cm, $F_{1,51}=6.91$,
275 $P=0.01$; control: 5.5 ± 1.5 vs. -0.8 ± 1.5 cm, $F_{1,35.4}=9.88$, $P=0.003$). In the caged+cleared
276 treatment, stem length growth did not differ significantly between tree age classes (6.7 ± 1.2 cm
277 for seedlings vs. 7.1 ± 1.1 cm for saplings, $F_{1,49.1}=0.04$, $P=0.8$).

278 **Basal diameter growth** - Across edge types, basal diameters of seedlings grew significantly more
279 than those of saplings (0.4 ± 0.05 vs. -0.1 ± 0.05 mm; $F_{1,217}=49.61$, $P<0.0001$). Edge type,
280 treatment and all interactions had no significant impact on growth, though we observed a trend
281 towards more growth in isolated than non-isolated edges ($F_{1,8.37}=4.35$, $P=0.07$; Fig. 3c).

282 **Branch production** - Branch production in glade edges was affected by tree age class and
283 treatment. Saplings produced about 30% more branches than seedlings (2.2 ± 0.1 vs. 1.6 ± 0.2
284 new branches, $F_{1,179}=13.57$, $P=0.0003$). Caged+cleared trees produced significantly more
285 branches than caged and control trees, and cleared trees produced significantly more branches
286 than control trees ($F_{3,63.5}=8.11$, $P<0.0001$, Fig. 3d). Edge type and all interactions did not
287 significantly affect branch production.

288 **DISCUSSION**

289 Previous studies have identified herbivores, grass competition and soil nutrients – along with
290 other factors such as fire and rainfall regime – as important drivers of woody vegetation cover

291 and density in savanna landscapes (Knoop and Walker 1985; Augustine and McNaughton 2004;
292 Sankaran et al. 2005; Goheen et al. 2007; Bond 2008; Riginos 2009; Cramer et al. 2010; Goheen
293 et al. 2010; van der Waal et al. 2011). To our knowledge, our study is the first to experimentally
294 test the separate and combined impacts of browsing, competition with herbaceous plants, and
295 edaphic context on tree survival and growth in a field setting. We examined these factors in the
296 absence of fire, which is not a major factor at our study site, although fire is a critical driver of
297 tree cover in many savannas (Sankaran et al. 2005; Bond 2008). The lack of fire in our system
298 provides an opportunity to distinguish direct impacts of grasses and browsing from more
299 indirect, fire-mediated impacts on tree cover (e.g., Roques et al. 2001; van Langevelde et al.
300 2003; Staver et al. 2009).

301 ***Impacts of grasses and browsing*** - Our results provide field-based evidence that the influence of
302 grass and browsers on woody cover depends strongly on edaphic context. Both browsing and
303 grass competition reduced *A. drepanolobium* survival, but only inside nutrient-rich glades. Grass
304 removal improved survival inside glades more than herbivore exclusion, and the combination of
305 grass removal and herbivore exclusion led to the highest survival rates. Outside glades, however,
306 browsing and grasses had no significant impacts on survival. These results differ from those of
307 van der Waal et al. (2011), who planted young trees in field plots in South Africa and found that
308 fertilization, but neither herbivory nor the interaction of fertilizer and herbivory, reduced tree
309 survival.

310 Grass competition emerged as the major factor limiting basal diameter growth and branch
311 production inside glades, and to a lesser degree it also limited growth outside glades. These
312 results support previous studies in our system (Riginos and Young 2007; Riginos 2009) and
313 other savannas (Knoop and Walker 1985; van der Waal et al. 2009; Cramer et al. 2010; Ward

314 and Esler 2011) which found that grass competition can significantly restrict tree growth and
315 recruitment. In a pot experiment, van der Waal et al. (2011) went a step further by showing that
316 competition between grasses and trees was more intense when plants were grown in glade-
317 derived, nutrient-rich soil. Our results support these findings, in that growth reductions due to
318 grass competition were greater inside than outside glades.

319 In contrast to basal diameter and branch production results, which suggested that grass
320 removal overwhelmingly benefits trees, stem length growth results revealed a tradeoff between
321 the benefits (release from competition) and costs (e.g., increased visibility to herbivores, Riginos
322 and Young 2007) of grass removal. Inside glades, cleared and control trees had similar stem
323 length growth, and this growth was significantly less than that of caged+cleared trees. This result
324 suggests that the benefits of grass removal were offset by negative impacts of increased
325 visibility. Outside glades, the negative impacts of grass removal were even more prominent.
326 Caged and cleared+caged trees had significantly higher stem length growth than cleared trees,
327 while control trees had intermediate growth. Thus, outside glades the negative impacts of
328 increased apparency seemed to significantly outweigh any benefits of release from competition.
329 By continually reducing tree height, browsers can have large impacts on three dimensional
330 landscape structure in this ecosystem (see also Levick et al. 2009). Continual browsing is also
331 likely to keep small trees in the grass layer, making them more susceptible to damage and
332 mortality during fire (Okello et al. 2008; Staver et al. 2009; Midgley et al. 2010).

333 As mentioned previously, glades are only one of several major sources of edaphic variation
334 in savanna ecosystems. Our work and that of van der Waal et al. (2011) suggest that at
335 intermediate spatial scales, edaphic context can modify the importance of grass competition and
336 browsing as drivers of tree survival and growth. Findings from both studies support the

337 hypothesis that tree establishment is more limited by grass competition in nutrient-rich patches.
338 The two studies differ in their conclusions about role of browsing and its interactions with
339 nutrient context. These findings add to the existing body of work on how edaphic context
340 influences savanna tree cover (e.g., Eckhardt et al. 2000; Dickie et al. 2007; Levick et al. 2010),
341 and suggest that future research is necessary in other landscapes and at multiple scales.

342 ***Tree age*** - We found significant and consistent differences in survival and growth between
343 seedlings and saplings. Saplings had higher survival and branch production, but seedlings had
344 higher stem length growth and basal diameter growth. These results parallel those of previous
345 studies on other plant species (Horvitz and Schemske 2002; Hodar et al. 2008). Although some
346 studies (e.g., Hodar et al. 2008) identified interactions between age and experimental treatments,
347 we found that seedlings and saplings generally displayed similar responses across herbivore,
348 grass competition, and planting location treatments.

349 To establish inside glades, trees must disperse into glades as seeds, avoid seed death (via
350 predation, pathogens, or desiccation), germinate, emerge, and survive seedling and sapling
351 growth stages. In this study, we focused on the latter two stages, but processes during other life
352 stages may also limit tree establishment inside glades. Predation by rodents may be important for
353 seeds and young seedlings (Goheen et al. 2004; Walters et al. 2005; Goheen et al. 2010),
354 especially given high rodent densities inside glades (Veblen, unpublished data). In this study,
355 rodents likely contributed to seedling mortality in uncaged treatments, especially in the control
356 treatment where grasses provided protective cover from predation (Peles and Barrett 1996).
357 Rodents are unlikely to have caused mortality of saplings, and this may have contributed to the
358 higher survival rates of saplings compared to seedlings.

359 ***Isolated vs. non-isolated glade edges*** - Tree survival and growth did not differ significantly

360 between isolated and non-isolated glade edges, suggesting that high densities of trees between
361 nearby glades are not maintained via reduced impacts of grass or herbivores on trees at the
362 seedling or sapling stages. However, reduced grass competition and herbivory may help maintain
363 high tree densities between glades by impacting other tree life stages. For example, reduced
364 wildlife use of areas between nearby glades (Porensky 2011) may cause increased *A.*
365 *drepanolobium* seed production (Goheen et al. 2007), which may then result in higher tree
366 recruitment. Alternatively, high tree densities may be a legacy of past events. Livestock and
367 human impacts create a region of intensive use (i.e., low grass cover, high livestock use and low
368 wildlife use) around active corrals, and impacts are especially pronounced between active corrals
369 and nearby glades (unpublished data, see also Muchiru et al. 2009). The combination of low
370 browser density, low grass cover and ample fertilization in areas between active corrals and
371 nearby glades may initiate a burst of tree establishment, especially if low grass cover causes
372 reduced fire intensity or frequency (e.g., Tobler et al. 2003; van Langevelde et al. 2003;
373 Augustine and McNaughton 2004; Goheen et al. 2007; Goheen et al. 2010). Increased tree
374 establishment during boma use could have long-term consequences for local tree densities.

375 ***Landscape heterogeneity*** - At our study site, grasses and browsers may be able to maintain the
376 conversion of wooded savanna to treeless grassland even in the absence of fire, but only in
377 edaphically distinct landscape patches. Grasses and browsing, separately and especially in
378 combination, reduced the survival and growth of *A. drepanolobium* seedlings and saplings inside
379 glades, but not outside glades. When grasses were removed (in cleared and caged+cleared
380 treatments), survival rates inside glades were high and statistically indistinguishable from
381 survival rates outside glades. Moreover, when grasses were removed, trees inside glades had
382 higher basal diameter growth and produced more branches than trees planted in other locations.

383 Thus, in the absence of grass competition, *A. drepanolobium* actually grows better in glade-like
384 conditions. Herbivores consume trees (a top-down mechanism), while grasses reduce the
385 availability of resources required by trees (a bottom-up mechanism). In our system, both
386 mechanisms appear to increase landscape heterogeneity by helping to maintain glades in a
387 treeless state.

388 **Implications for management** - In general, spatial heterogeneity tends to be good for
389 biodiversity (e.g., Lundholm 2009; Tamme et al. 2010), and heterogeneity created via glades is
390 no exception (e.g., Young et al. 1995; Augustine 2004; Gregory et al. 2010; van der Waal et al.
391 2011). Glade treelessness is initiated by anthropogenic activities and attracts herbivores
392 (especially mid-sized species such as Grant's gazelles and oryx), probably by allowing for
393 improved predator detection (Riginos and Grace 2008). Grazers attracted to glades could
394 potentially promote tree establishment by reducing grass competition and fire frequency or
395 intensity (Roques et al. 2001; van Langevelde et al. 2003; Riginos and Young 2007). However,
396 the mixed-feeder herbivores most attracted to glades probably contribute to the maintenance of
397 these treeless sites both directly – by browsing on *A. drepanolobium* seedlings – and indirectly –
398 by increasing grass productivity through fertilization (Odadi 2010; Augustine et al. 2011; van der
399 Waal et al. 2011). Thus, our results suggest that loss of either livestock (which initiate glade
400 formation) or wildlife (which help to maintain glades) from this savanna ecosystem could lead to
401 homogenization of the landscape, with negative consequences for biodiversity. Many livestock-
402 wildlife interactions have negative impacts on human livelihoods or conservation objectives
403 (Young et al. 2005; Laporte et al. 2010). When managed sustainably, glades appear to represent
404 an example of positive synergy between livestock production and biodiversity conservation.

405

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560

561

TABLES

562 **Table 1.** Survival and growth of *A. drepanolobium* trees planted far from glades, at isolated
 563 glade edges and inside glades. For growth responses, means \pm SE were calculated across blocks
 564 (N = 5) after averaging over all seven trees present within each block*location*treatment
 565 combination. Within each combination of treatment and response variable, locations with shared
 566 letters are not significantly different (Tukey’s HSD method, $\alpha = 0.05$).

Treatment	Location	Survival	Stem length growth (cm)	Basal diameter growth (mm)	No. of new branches
cage	far from glade	100	7.6 \pm 0.9	0.7 \pm 0.3	3.2 \pm 0.6
+ clear	glade edge	97	7.1 \pm 1.9	0.3 \pm 0.1	3.0 \pm 0.5
	inside glade	91	15.7 \pm 4.0	1.6 \pm 0.6	4.7 \pm 1.1
cage	far from glade	97 a	6.8 \pm 1.2	0.1 \pm 0.1 ab	1.1 \pm 0.3
	glade edge	94 ab	6.0 \pm 0.9	0.2 \pm 0.1 a	1.4 \pm 0.2
	inside glade	63 b	4.0 \pm 1.7	-0.2 \pm 0.1 b	1.1 \pm 0.3
clear	far from glade	80	-0.2 \pm 1.0	0.1 \pm 0.2 b	2.6 \pm 0.3 ab
	glade edge	91	-1.2 \pm 2.1	0.4 \pm 0.2 ab	2.1 \pm 0.4 b
	inside glade	80	4.4 \pm 4.9	1.5 \pm 0.6 a	6.0 \pm 1.6 a
control	far from glade	86 a	3.1 \pm 1.0	0.1 \pm 0.1	2.2 \pm 0.4
	glade edge	77 a	2.1 \pm 2.8	0.1 \pm 0.2	1.1 \pm 0.4
	inside glade	20 b	1.6 \pm 2.6	0.04 \pm 0.04	1.3 \pm 0.3

567

568 **FIGURE LEGENDS**

569 **Fig. 1.** Map and diagram of experimental design. a) The study area was divided into five blocks.
570 Glades are visible as large red spots in this Quickbird image (DigitalGlobe 2003). b) Each block
571 contained four locations: far from glade, inside glade, isolated glade edge and non-isolated glade
572 edge. c) Within each location, two replicates of four treatments were randomly assigned to eight
573 sites. Treatments included control (0), caging (cg), clearing (cl), and both caging and clearing
574 (cg,cl). d) Saplings and seedlings were randomly assigned to each site.

575 **Fig. 2.** Survival (a-c) and growth (d-l) of trees planted a,d,g,j) far from glades, b,e,h,k) at glade
576 edges, and c,f,i,l) inside glades. For growth responses, bars are mean \pm SE calculated across
577 blocks (N = 5) after averaging over all seven trees present within each block*location*treatment
578 combination. Within each panel, bars with shared letters are not significantly different (Tukey's
579 HSD method, $\alpha = 0.05$).

580 **Fig. 3.** Survival (a) and growth (b-d) of trees planted in isolated and non-isolated glade edges.
581 For growth responses, bars are mean \pm SE calculated across blocks (N = 5) after averaging over
582 all seven trees present within each block*location*treatment combination. Within each panel,
583 across both edge types, treatments with shared letters are not significantly different (Tukey's
584 HSD method, $\alpha = 0.05$). For stem length growth, letters a and b indicate significance groups for
585 saplings, and letters c and d indicate significance groups for seedlings (tree age*treatment
586 $F_{3,182}=2.72, P=0.046$).

FIGURES

Figure 1

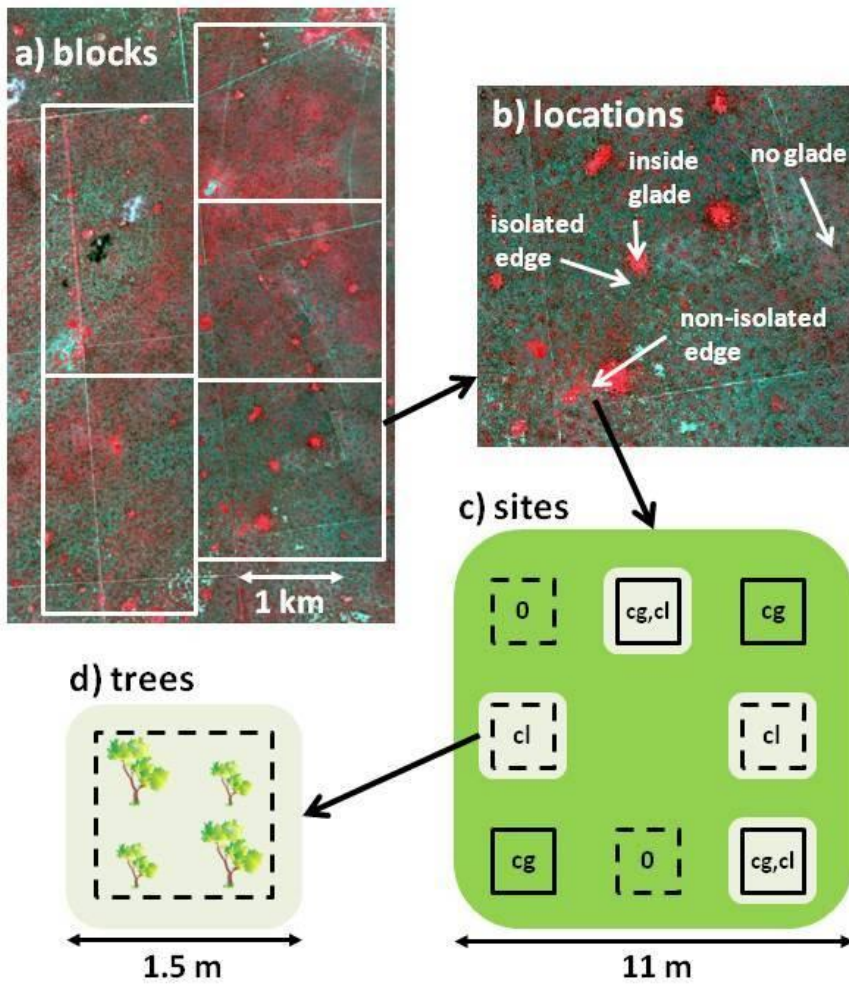


Figure 2

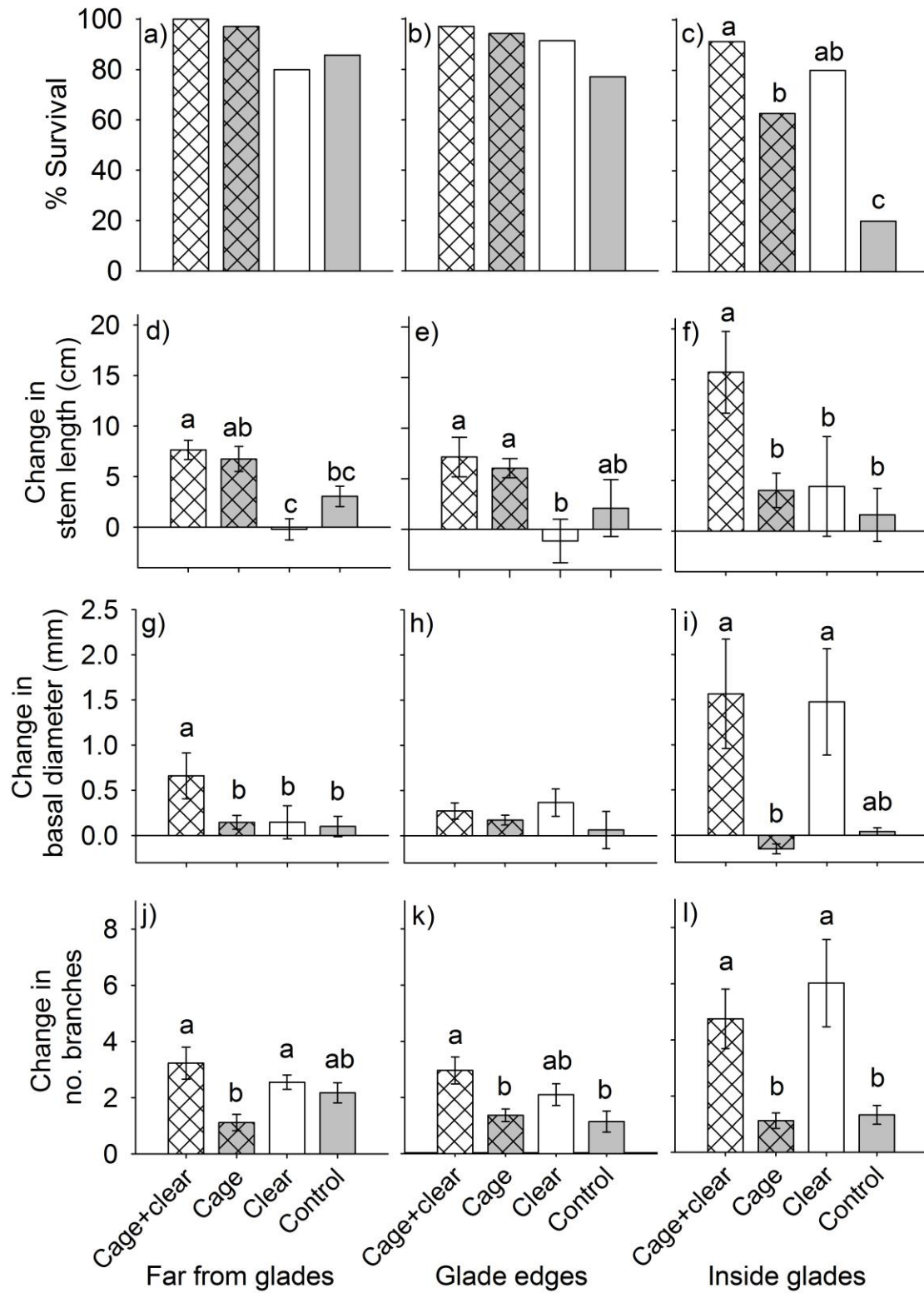


Figure 3

