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Impacts of traditional livestock corrals on woody plant communities in an East African savanna

Kari E. Veblen, *Utah State University*

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Running title: Livestock corral effects on savanna trees

Kari E. Veblen

Utah State University, Department of Wildland Resources, 5230 Old Main Hill, Logan, UT 84322-5230, USA. Email: kari.veblen@usu.edu

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In African savannas, harvesting of trees and shrubs for construction of traditional livestock corrals has the potential to significantly alter the appearance of the landscape. Tree and shrub communities surrounding traditional corrals of different ages were assessed. Even at the oldest sites, densities of very tall trees and woody species diversity were higher at corral edges. These results illustrate that effects of livestock activity persist for at least forty years, particularly in high use areas.

Abstract. In African savannas, humans and their livestock leave long-term legacies on the landscape in the form of abandoned livestock bomas (corrals). Once abandoned, bomas develop into nutrient-rich herbivore hotspots characterized by distinctive plant communities. Impacts of bomas, however, extend beyond the boundaries of the boma site itself. This is especially true for woody species which are intensively harvested for boma fencing material and fuel wood. Following boma abandonment, it is not clear how quickly or to what extent woody plant communities may change and develop over time. A chronosequence approach was used to investigate the effects of traditional livestock bomas on woody plant communities over time in an *Acacia drepanolobium* Sjost. savanna in central Kenya. Densities of woody species associated with boma sites that had been abandoned <4, 7-42, and >42 years before were measured. Reductions in densities of the dominant tree, *Acacia drepanolobium*, were still detectable after more than forty-two years, especially in the highest impact zones at boma edges (up to 60 m from the boma). Despite these overall reductions, the edge zones of old boma sites had unusually high densities of very large *A. drepanolobium* trees. Shortly after boma abandonment, woody species richness increased at edges of newly abandoned bomas, as did densities of the uncommon shrub, *Lycium europaeum* L., and these changes persisted for several decades. These patterns likely result from interactions among species within the woody plant community, as well as interactions with herbivores and edaphic factors.

Additional keywords: black cotton soil, glade, kraal, livestock-wildlife interactions, pastoralism

Introduction

Globally, humans and their livestock leave enduring ecological legacies (e.g., Blackmore *et al.* 1990; Knapp 1996; Reitalu *et al.* 2010). In East African savannas, the presence of humans and their livestock is ancient and pervasive and can exert major controls over the long-term distribution of plants and nutrients (Augustine 2003; Muchiru *et al.* 2009). Periodic abandonment of traditional thorn-fence livestock bomas (corrals) creates mosaics of long-term (decades to centuries) nutrient hotspots where nutrient levels can be more than twenty times higher than levels in the rest of the savanna landscape (Augustine 2003; Reid and Ellis 1995). These sites typically host distinctive plant communities and function as foci of activity of wild herbivores (Stelfox 1986; Reid and Ellis 1995; Young *et al.* 1995; Treydte *et al.* 2006; Muchiru *et al.* 2008; Veblen 2012).

Spatially, the effects of bomas are not limited to the boma area itself (approx. 0.25 - 1.0 ha), but rather extend into the surrounding landscape. This should be especially true for woody species, which are harvested locally for fence-building and maintenance material for bomas, and to a lesser extent housing beams and firewood (Western and Dunne 1979). Reductions in densities of woody species surrounding bomas likely stimulate shifts in woody plant community composition over time. In a study of the effects of bomas in a bushed grassland area of southern Kenya, Muchiru *et al*. (2009) found evidence for species-specific responses by woody plants over time.

Similar boma-driven shifts in woody plant communities likely occur in *Acacia drepanolobium* savannas, an ecosystem type that covers millions of hectares across East and Southern Africa. A recent study in central Kenya found evidence for distinctive woody communities associated with edges of old bomas in *A. drepanolobium* savanna (Porensky 2011).

How these patterns develop over time, however, is not clear. The long-term successional development of herbaceous vegetation in boma interiors ("glades") has been described for this ecosystem (Veblen 2012), but development of woody plant communities around former boma sites has not yet been investigated. Here, how traditional livestock corrals influence woody plant communities over time in an *Acacia drepanolobium* savanna is investigated.

Methods

This research was conducted in the semi-arid Laikipia District of central Kenya. The study area encompasses portions of the Mpala Conservancy and adjacent Jessel Ranch (36° 52' E, 0° 17' N). Annual rainfall is variable, averaging 400 - 600 mm, and the area is underlain with "black cotton" soils, poorly drained vertisols with high (>50 %) clay content (Ahn and Geiger 1987). Ninety-seven per cent of the tree canopy cover is *Acacia drepanolobium* Sjost., and 90 % of herbaceous cover is comprised of five grass species: *Pennisetum mezianum* Leeke, *P. stramineum* Peter, *Themeda triandra* Forssk*., Lintonia nutans* Stapf*.,* and *Brachiaria lachnantha* (Hochst.) Stapf. (Young *et al.* 1998). The area hosts a full complement of native wildlife species (Veblen 2012).

In this ecosystem, abandoned traditional thorn-fence bomas develop into long-term, nutrient-rich treeless "glades" embedded in a wooded savanna matrix at densities of ~2 km^{-2} (Veblen 2012). Land managers employ local herders who use thorn fencing to build 0.25 - 1.0 ha bomas to corral livestock nightly for months to years at a time. Trees are harvested from inside the boma and then the surrounding area to maintain fences throughout the lifetime of the boma. Trees inside the boma are entirely eliminated, whereas trees surrounding the boma are thinned, but not entirely eliminated. The most intensively used areas occur within 10 – 20 m of the boma

(K. Veblen pers. obs), and the woody plant community associated with fully developed glades begins to resemble background conditions within 100 m (Porensky 2011). Once abandoned, the original boma area remains completely treeless long after the fence and cattle dung have disappeared. Tree recruitment is virtually non-existent in glades for at least 100 years (K. Veblen unpublished data).

To assess changes in woody plant communities over time, I sampled along a chronosequence of glades in 2003. All recently abandoned bomas (<4 yrs; "new glades") in this area were then identified by local ranch managers, herders and field guides. I used aerial photos from 1961 and satellite imagery from 2003 to identify all "intermediate" (7 - 42 yrs) and "old" (>42 yrs) glades in an 8 km x 8 km area of my study site (see Veblen 2012).

I assessed densities of the dominant tree, *Acacia drepanolobium*, in a random selection of six new (<4 yrs), four intermediate (7 - 42 yrs old), and five old glades (>42 yrs old). In each glade I sampled plots at three locations: Edge, Outside and Background. "Edge" plots were 20 m x 30 m, with the long edge extending from approximately 10 m inside to 20 m outside the boma/glade. "Outside" plots were 20 m x 20 m plots placed 40 m - 60 m from glade edge, outside of the heaviest-use zone, but within the tree-harvesting zone. "Background" plots were 20 m x 30m, with the long edge placed 170 m – 200 m away from the edge, well outside the heaviest use zone. In each plot, I counted all *A. drepanolobium* trees that were greater than 1 m tall. Trees were assigned to one of three size classes: short (1-2 m tall), tall (> 2 m tall, dbh < 10 cm), or large (> 2 m tall, dbh > 10 cm). Edge and Outside plots associated with intermediate and old glades were sampled in 2003, and the remaining plots (Edge/Outside/Background of the six new glades and Background of the intermediate and old glades) were sampled in 2007. All ages (e.g., <4 yrs) refer to age at time of first sampling.

I then assessed densities of all non-*A. drepanolobium* woody species at the same glade

sites, plus an additional three randomly-selected intermediate glades in 2006-2007 (to achieve

sufficient sample size). Plots were again placed at Edge, Outside, and Background locations, but

were increased to 2500 m^2 to increase sample sizes of non-*A. drepanolobium* woody species that

make up only 3% of woody cover (Young *et al*. 1998). At each glade, I placed four 25 m x 25 m

Edge sub-plots in a row along the glade edge, so that each sub-plot bisected the glade edge (total

= 2500 m^2). Outside and Background plots were each 50 m x 50 m, placed 60 m – 110 m (within

the tree-harvesting zone; farther away from the glade than *Acacia* plots because edge depth is

expected to be greater for less common non-*Acacia* species, sensu Young *et al.* 1995), and 150 m

- 200 m (well outside the heaviest zone; overlapping with *Acacia* plots) away, respectively.

For both data sets (*A. drepanolobium* by size class and non-*A. drepanolobium* woody

species), I performed a MANOVA before performing protected univariate ANOVA on

individual response variables. Species richness of woody plants was analyzed in a univariate

ANOVA. In all models, I used split-plot designs to test main plot effects of glade age class (new,

intermediate and old), sub-plot effects of location relative to glade (Edge, Out, Background) and

the interaction between age class and location. For all univariate analyses, I used general linear

mixed models (GLMMs), treating glade as a random effect, using variance-weighting when

variances were not homogenous. I used maximum-likelihood methodology, as well as

Satterthwaite's approximation of degrees of freedom (PROC MIXED, version 9.1, SAS Institute

2002). Tukey's HSD post-hoc analyses were used for all data.

Results

Responses of the three size classes of *A. drepanolobium* differed with respect to distance class

and glade age. The densities of short trees were statistically similar at all distances for all age classes (location: $F_{2,24}$=1.69, $P = 0.21$, age: $F_{2,24}$=1.13, $P = 0.36$, age x location: $F_{4,24}$=1.28, $P = 0.31$; Fig. 1c). However, reduced densities of 'tall' *Acacia drepanolobium* trees (the most common size class, 55 % of all trees) were associated with new glades; densities of 'tall' *A. drepanolobium* (>2 m tall, <10 cm dbh) on the landscape were significantly lower around new glades (<4 yrs old) than intermediate or old glades (age: $F_{2,24}$= 12.58, $P = 0.001$; Tukey P<0.05; Fig.1b). In this size class, densities of *A. drepanolobium* also differed significantly according to proximity to glades; densities were significantly lower in Edge and Out plots than Background plots, consistently across glades of all ages (location $F_{2,24}$=11.91, $P = 0.0003$; Tukey P<0.05; age x location $F_{4,24}$=0.26, $P = 0.50$).

Distinctive woody plant communities also developed at glade edges. One striking pattern was evident only in the oldest glades. Densities of 'large' *A. drepanolobium* trees (>2 m, >10 cm dbh), were 3.5 to 10 times higher around the edges of old glades than at any other sampling location (age x location: $F_{4,24}$=12.1, P<0.0001; Tukey P<0.05; Fig. 1a). Edge patterns of other woody species developed early (within 4 yrs of boma abandonment) and persisted over the long-term. In particular, densities of the shrub, *Lycium europaeum*, which is relatively uncommon in background vegetation, were significantly higher at edges of glades of all age classes than elsewhere on the landscape (location: $F_{2,30} = 3.76$, $P = 0.04$; Tukey P<0.05; Fig. 2a). Densities of *Acacia mellifera* Benth., a species strongly preferred for boma fence building, were significantly lower at glade edges (of all age classes) than elsewhere on the landscape (location: $F_{2,28.1} = 3.65$, $P = 0.04$; Tukey P<0.05; Fig. 2b). Finally, woody species richness was significantly higher at glade edges, though differences between values (s.e. of mean in brackets) were small [location: $F_{2,30.8}$= 3.34, $P = 0.049$; Tukey P<0.05; edge: 5.44 (0.49) spp. 2500 m^{-2}, out: 4.06 (0.43),

background: 4.39 (0.43)].

Glades occurred at an average density of ~2 km^{-2} and at an average size of 0.625 ha (Veblen 2012), thereby covering 1.25 % of the landscape. Glade effects on densities of *A. drepanolobium* occurred at 50 m ("Out" plots), thereby extending glade effects to 5.6 % of the landscape. Any effects observed in "Background" plots (at 185 m) would result in 33.2 % of the landscape being influence by glades.

Discussion

The paucity of 'tall' trees 40 - 60 m from edges reveals that the tree-harvesting effects of bomas extend far beyond the boundaries of the original corral. Although the actual boma sites only cover 1.25 % of the landscape, reductions in tree density extend to 5.6 % of the landscape. Additionally, increases in background tree densities with increasing glade age (Fig. 1b) suggest that harvesting effects may extend even farther into background plots. This potentially influences 33.2 % of the landscape, similar to what Young *et al*. (1995) found for tree-glade relationships in a nearby ecosystem.

In areas closest to glades, where harvesting during active boma use would have been most intense, reduced densities of the dominant tree, *Acacia drepanolobium*, were apparent immediately following abandonment of bomas. This result is consistent with a more general pattern of high harvesting impacts near settlements and attenuating effects with increasing distance or intensity of use (Luoga *et al.* 2002; Pote *et al.* 2006; Morris *et al.* 2009). Relative densities of 'tall' *A. drepanolobium* and another less common but highly desired species for boma construction, *Acacia mellifera*, were lowest at glade edges, for even the oldest glades. This suggests that recovery of edge communities to background densities may take longer than the

42+ years since abandonment of "old" glades. Rate and extent of recovery likely are a function of disturbance intensity (Western and Dunne 1979). In this system, length of boma occupation and, hence, disturbance intensity, may be declining in recent years with increasing availability of mechanized transport to aid boma construction and increasing densities of woody vegetation across the landscape (which result in shorter harvesting distances for boma construction).

These results revealed two changes in woody plant communities that were evident soon after abandonment of bomas and persisted over several decades. First, species richness was highest at edges of glades of all ages. This result is consistent with work in other ecosystems (Muchiru *et al.* 2009; Young *et al.* 1995), though this study system is relatively species-poor (perhaps due to harsh conditions associated with high soil clay content), and absolute differences in species richness were small. Second, glade edges hosted higher densities of the shrub, *Lycium europaeum*, results that are consistent with Porensky *et al*. (*in press*). My results are the first to demonstrate that *L. europeaum* colonizes early in boma development in this system. In southern Kenya, Muchiru *et al.* (2009) found initial increases in the density of *L. europaeum* were followed by rapid declines over time. My results are suggestive of similar, but slower (non-significant) declines.

My results indicate that edges of the oldest glades are characterized by high densities of large (>10 cm dbh) trees, consistent with Porensky (2011). These results further reveal that new and intermediate-aged glades do not exhibit the same patterns of large trees at glade edges. This suggests that the pattern of larger trees at glade edges develops slowly (>40 yrs). Alternatively, changing pastoral practices in the area (discussed above) may explain the distinctive edge pattern associated with old glades. In particular, nutrient enrichment may have been greater under historic, more intensive, use and contributed to early vigorous growth of large trees at glade

edges. Either way, the clustering of large trees around glades may be important functionally for multiple taxa. Tall trees create shade in a landscape otherwise lacking shade trees. Herbivores then cluster under shade trees and can fertilize the understories with their droppings (Treydte *et al.* 2010), potentially helping perpetuate long-term feedbacks between herbivores and glade use (sensu Veblen 2012). Birds also respond favourably to glades (Gregory *et al.* 2010), possibly due to a combination of short grass inside glades and tall trees at their edges. Finally, geckos and arthropod densities also are associated with nutrient enrichment and taller trees at glade edges (Donihue *et al. in press*). Overall, my results highlight clear edge effects, which contribute to distinctive glade edge communities (Porensky 2011).

Mechanisms

Competitive and edaphic conditions likely contribute to the development of specialized woody communities at glade edges (Porensky and Veblen 2012; van der Waal *et al.* 2011). The legacy of lower densities of mid-sized (<10 cm dbh) *A. drepanolobium* at glade edges would reduce intra-specific competition, allowing some of the remaining trees to rapidly grow larger (>10 cm dbh) and also releasing other species, such as *L. europaeum*, from inter-specific competition. Similarly, lower cover of grasses associated with livestock grazing during and immediately following occupation of a boma could release woody species from competition (Porensky and Veblen 2012; Riginos and Young 2007). High nutrient conditions at glade edges also may promote growth of larger *A. drepanolobium* or shift the competitive environment in favour of other species such as *L. europaeum*. In particular, newer glades soils are characterized by high organic matter, nitrogen, phosphorus and potassium contents (Veblen 2012). Older glades are characterized by soils with a high phosphorus content (Augustine 2003, Veblen 2012) and,

unique to this glade system, a high nitrogen content (Veblen 2012). This system also is characterized by exceptionally high clay content; high shrink-swell capacity likely contributes to limited establishment of woody species outside of glades (Porensky and Veblen 2012).

Glade edge communities also may be shaped in part by herbivory. During occupation of bomas, focused livestock activity may lead to trampling or browsing of some woody plants. After abandonment, wild grazing and browsing herbivores are attracted to developing glades (Veblen 2012). Elevated grazing may limit seedling recruitment and establishment of *Acacia* spp. (c.f.Riginos and Young 2007; Goheen *et al.* 2010; Porensky and Veblen 2012), and elevated browse pressure may limit larger size classes of trees (Kuijper *et al.* 2010) around glade edges. Increased herbivory could help explain why densities of mid-sized *A. drepanolobium* were still depressed even around the oldest glades or why densities of small (1-2 m) trees showed no clear patterns. Trees in this smallest size class are not necessarily very young trees. Rather, they may be older trees suppressed by browsing of coppices and shoots, and/or they may formerly have been taller trees prior to having their tops broken off by elephants. Elephants (and other herbivores) show preference for glade habitat (Veblen 2012) and are known to have major effects on tree densities in this ecosystem (Goheen *et al.* 2007), particularly at glade edges (Porensky *et al. in press*).

Conclusions

In this savanna ecosystem, traditional livestock bomas have pronounced long-term effects on the surrounding woody plant communities, including reductions in densities of the dominant woody species, *Acacia drepanolobium*, and increased densities of large trees and less common shrub species. Aside from the obvious effects of intense tree harvesting, herbivores also likely

contribute to these patterns. Herbivores have been shown to directly suppress tree reproduction, establishment and survival in this system (Goheen *et al.* 2010; Porensky and Veblen 2012). Although both wild and domestic herbivores, including their interactions clearly can influence plant-plant interactions associated with the herbaceous glade community (Veblen 2008; Veblen and Young 2010), the nature of inter- and intra-specific interactions within the woody community warrants further investigation.

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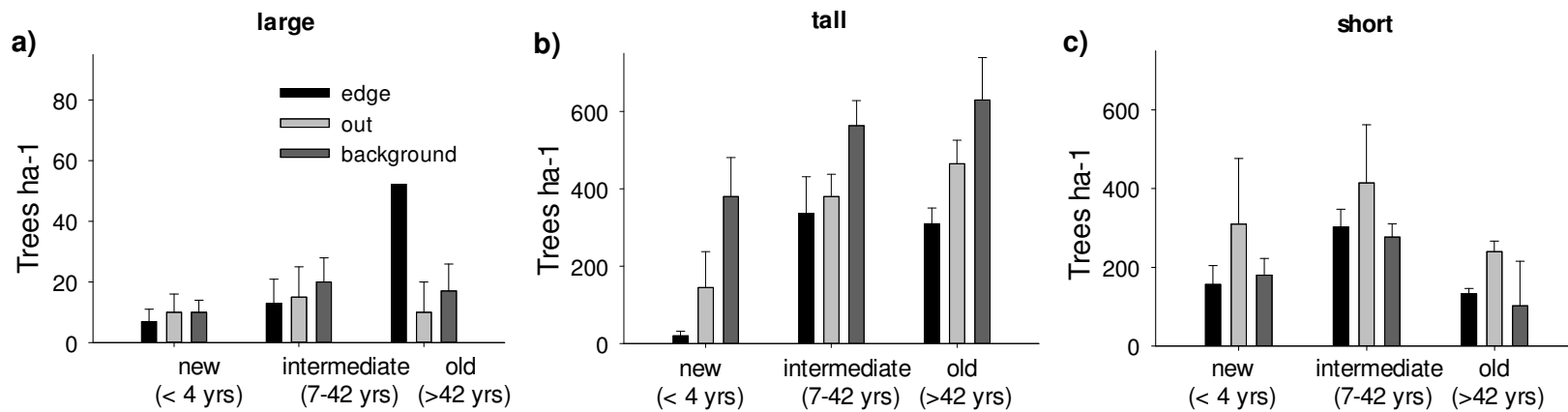
Fig. 1. Densities of a) large (>2 m, >10 cm dbh), b) tall (>2 m), and c) short (1-2 m) *Acacia drepanolobium* trees associated with

glades of three ages. At each glade, trees were counted in plots at three locations: edge, out (50 m away), and background (185 m

away). MANOVA results indicated significant age, location and age x location effects (age: Wilk's $\lambda = 0.28$, $F_{6,20} = 3.01$, $P = 0.03$;

location: Wilk's $\lambda = 0.27$, $F_{6,44} = 6.87$, $P < .0001$, age x location: Wilk's $\lambda = 0.25$, $F_{12,58.5} = 3.36$, $P = 0.0009$). Significant univariate test

results for 'large' (age x location) and 'tall' (age, location) trees are included in the text. Tukey HSD tests ($\alpha=0.05$) indicated that

'large' tree densities were significantly greater in edges of old glades than in any other treatment combination. Similarly, 'tall' tree

densities were significantly lower in new than intermediate or old glades, and greater in background densities relative to edge and

outside. Note different scale on y axis for 'large' trees.
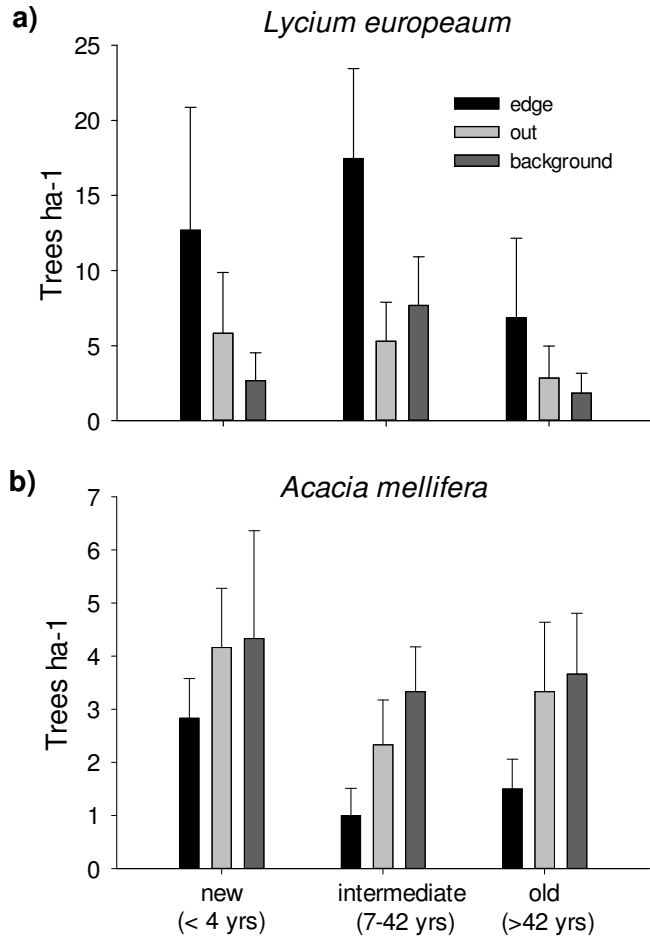
Fig. 2. Densities (mean ± s. e. of mean) of two woody species, a) *Lycium europaeum* and b)

Acacia mellifera, associated with glades of three ages. At each glade, trees were counted in plots

at three locations: edge, out (85 m away), and background (175 m away). MANOVA results

indicated significant location effects (Wilk's λ=0.61, $F_{6,56}$= 2.66, P = 0.025). Note different

scales on y axes.