Savanna glade hotspots: Plant community development and synergy with large herbivores

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ABSTRACT

In African savannas, abandonment of traditional livestock corrals (bomas) creates long-term mosaics of nutrient hotspots embedded in a lower-nutrient matrix. It is unclear how plant communities develop over time on these sites in clay-rich "black cotton" soils or how herbivores attracted to these sites affect vegetation development. I first examined whether treeless "glades", derived from abandoned bomas, function as nutrient and herbivore hotspots. Soil, vegetation, and herbivore data were collected on glades of varying ages. The results indicated that glades persist as long-term ($\geq$four decades) patches (0.25 —1.0 ha) of improved soil texture and increased nutrient levels, palatable grasses, and herbivore use. Glade vegetation also appears to undergo succession from Cynodon plectostachyus to Pennisetum stramineum dominance. Based on these patterns, exclusion cages were used to test herbivore effects on glade vegetation development. I found that large herbivores may retard succession by suppressing invasion of P. stramineum into C. plectostachyus-dominated areas. These results provide evidence that abundant anthropogenic glades function as long-term nutrient and wildlife hotspots in black cotton soils, distinct from similar hotspots in other soil types. The findings provide evidence that large herbivores can exert control over development and persistence of glades through their effects on plant community dynamics.

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1. Introduction

Landscape heterogeneity is an important and influential driver of ecological processes, particularly in savanna ecosystems (Adler et al., 2001; DuToit et al., 2003; Scholes and Walker, 2004). For millennia, pastoralists throughout eastern and southern African savannas have created large-scale landscape mosaics that persist many decades (Augustine, 2003; Muchiru et al., 2008) and even several centuries (Blackmore et al., 1990). Herded livestock forage over the landscape during the day and deposit dung in temporary thorn fence corrals (bomas) at night, concentrating large amounts of nutrients and organic matter (Reid and Ellis, 1995; Treydte et al., 2006). After abandonment, corral sites support distinctive, nutrient-rich plant communities and typically persist as long-term hotspots of highly fertilized soils (Stelfox, 1986; Blackmore et al., 1990; Reid and Ellis, 1995; Young et al., 1995; Augustine, 2003; Treydte et al., 2006). Individual hotspots occur at densities of ~2 km^{-2} (Young et al., 1995, K. Veblen unpublished results) and

collectively can cover up to 17% of some landscapes (Blackmore et al., 1990).

One of the most profound effects of these landscape features can be to attract (or repel) large ungulate herbivores. Soil nutrient levels (e.g., pools of nitrogen, phosphorus or potassium) in old boma sites can be more than twenty times levels in the rest of the landscape (Reid and Ellis, 1995; Augustine, 2003), and in savannas, nutrient-enriched areas often are foci of foraging activity where herbivores can satisfy critical nutrient requirements (McNaughton, 1988; Augustine, 2004; Grant and Scholes, 2006). Accordingly, several studies in eastern Africa have documented increased herbivore activity in former boma sites relative to surrounding lower-nutrient vegetation (Stelfox, 1986; Young et al., 1995; Muchiru et al., 2008; van der Waal et al., 2011).

Although some general patterns of nutrient enrichment and herbivore use associated with former boma sites have emerged, it is unclear how these patterns may differ under markedly different soil conditions. In particular, high-clay "black cotton" vertisol soils cover millions of hectares across East and Southern Africa, yet no studies have investigated the dynamics of former boma sites in these soils or how dynamics may differ from those in more moderately textured soils. Soil texture can have important consequences for soil nutrient profiles (e.g., drainage or nutrient retention over time) and

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may in turn have cascading effects on both plant and herbivore communities associated with former boma sites.

Although patterns of association between large herbivores and old boma sites have been relatively well documented, comparatively little information exists on how plant communities develop at these sites or on how large herbivores might influence that development. In southern Kenya, Muchiru et al. (2009) found that boma plant communities underwent a relatively straightforward successional process from bare ground to colonization by herbaceous species and eventually woody species. Although vegetation development is likely to differ among ecosystems (where factors such as rainfall or soil type differ), no other studies have examined boma vegetation development. Moreover, no studies have explicitly addressed or experimentally tested how large herbivores (which are often attracted to corral sites) influence the vegetation development and/or successional trajectory of boma plant communities.

Herbivores have the potential to influence vegetation development in corral hotspots in two major ways. First, herbivores can indirectly affect plants by influencing soil nutrient status. For example, herbivores may forage in nutrient-rich corral areas and excrete elsewhere (thereby exporting nutrients) or may excrete in nutrient-rich areas, thereby compensating, or overcompensating, for the nutrients that are removed via herbivory (McNaughton, 1984; Adler et al., 2001; Augustine et al., 2003).

Second, by affecting individual plant species differently, herbivores may have important effects on plant–plant interactions in old boma sites. In *Acacia drepanolobium* savannas in central Kenya, one of the dominant boma species, *Cynodon plectostachyus*, is a prostrate, stoloniferous grass, while the other dominant species, *Pennisetum stramineum*, is an ascending bunchgrass (hereafter referred to as *Cynodon* and *Pennisetum*). Grazing may favor shorter-statured plants such as *Cynodon* because they are better-adapted to escape and/or recover from grazing (Noy-Meir et al., 1989; Huntly, 1991). Taller grasses, such as *Pennisetum*, may in turn be better competitors, but also may be more susceptible to grazing damage and hence less competitive under grazed conditions (Mack and Thompson, 1982; Noy-Meir et al., 1989; Huntly, 1991). Herbivores can influence both the rate and direction of change in plant communities (Skarpe, 2001) and may play an important role in the development of the specialized *Cynodon–Pennisetum* plant communities associated with abandoned bomas.

Here, I focus on long-term nutrient hotspots derived from livestock corrals in a black cotton soil *A. drepanolobium* savanna. In these landscapes, temporary livestock bomas result in a mosaic of treeless glades that develop after boma abandonment. The objectives of this study were to 1) determine whether these black cotton glades are hotspots of elevated nutrients and increased use by large herbivores, 2) identify long-term vegetation development patterns in glade vegetation, and 3) perform an experimental test of how large herbivores may influence glade development by altering the rate or trajectory of succession in glade plant communities.

2. Materials and methods

2.1. Study site

This research was conducted in *A. drepanolobium* savanna in the semi-arid Laikipia District of central Kenya. The study area (36°52′E, 0°17′N) encompasses portions of the Mpala Conservancy and adjacent Jessel Ranch. Annual rainfall is variable, averaging 500–600 mm, with the highest peak in mean rainfall occurring March–May (mean in April, 1998–2005: 115 mm) and the longest and most pronounced dry season typically from December through March (mean in February, 1998–2005: 9 mm). The area is underlain with "black cotton" soils, poorly drained vertisols with high (>50%)

clay content (Ahn and Geiger, 1987). Ninety-seven percent of the tree canopy cover is *A. 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). Common resident large mammals include: elephant (*Loxodonta africana* Blumenbach), zebra (*Equus burchelli* Gray), Grant's gazelle (*Gazella granti* Brooke), hartebeest (*Alcelaphus buselaphus* Pallas), steinbuck (*Raphicerus campestris* Thunberg), eland (*Taurotragus oryx* Pallas), oryx (*Oryx gazella beisa* L.), giraffe (*Giraffa camelopardalis* L.), spotted hyaena (*Crocuta crocuta* Erxleben), and lion (*Panthera leo* L.).

Historic (centuries-long) cattle management has created a landscape mosaic of treeless glades (approx. 2 km^{-2}) derived from abandoned livestock bomas embedded in a wooded savanna matrix. Current land managers employ local herders who, practicing traditional livestock husbandry, use thorn fencing to build 0.25–1.0 ha bomas to corral livestock nightly for months to years at a time. Trees are cleared inside the boma and are used, in addition to trees harvested from the surrounding area, to build and maintain the thorn fence. Once abandoned, the original boma area remains treeless long after the thorn fence and cattle dung (up to 0.5 m deep) have disappeared.

In the herbaceous plant community, the highly palatable mat-forming grass, *C. plectostachyus* K. Schum, colonizes the dung layer within months of abandonment, covering the entire boma area in as few as two to three years (K. Veblen, unpublished results). Glade herbaceous vegetation is comprised of dense stands of *Cynodon* and another perennial grass species, the palatable bunchgrass *P. stramineum*. Immediately outside the glade boundary, the *Cynodon–Pennisetum* community abruptly gives way to a vegetation composition and density resembling background non-glade vegetation, including less-palatable grasses and virtually no *Cynodon*.

2.2. Glade chronosequence survey

To determine changes in glades over time, I measured herbaceous vegetation, soil characteristics, and large herbivore use associated with glades in two age classes. I located glades in my study area by using a 2003 8 km × 8 km Quickbird satellite image (DigitalGlobe, 2003). Ground truthing confirmed that these features were indeed glades. These glades were cross-referenced with 1961 aerial photos to determine which glades existed prior to 1961. I used five randomly selected post-1961 ("young") glades, and five randomly selected pre-1961 ("old") glades for the chronosequence sampling described below. During selection, one glade was rejected because trees had not been cleared, and others were rejected when they were directly adjacent to an already-selected glade. I confirmed date of last use by visiting each glade with two independent groups of herders who had resided in the area for the past fifty to eighty years.

2.3. Vegetation sampling

In August 2003, for each of the young and old glades, herbaceous vegetation was sampled along a transect that began at glade center and ended 60 m outside the glade (Fig. 1a). Each transect was oriented in a randomly selected cardinal direction that avoided major landscape features such as roads and other glades. Tree presence around the glade perimeter demarcated glade edge (and distance of zero). For a given glade, the center occurred at a point between −40 m and −15 m, depending on glade size (Fig. 1a). I sampled every 5 m between glade center and +15 m, and at +30 m and +60 m, for a total of 123 sample locations (mean of 12.3 per glade). At each sampling location, a ten-point pin frame was used to
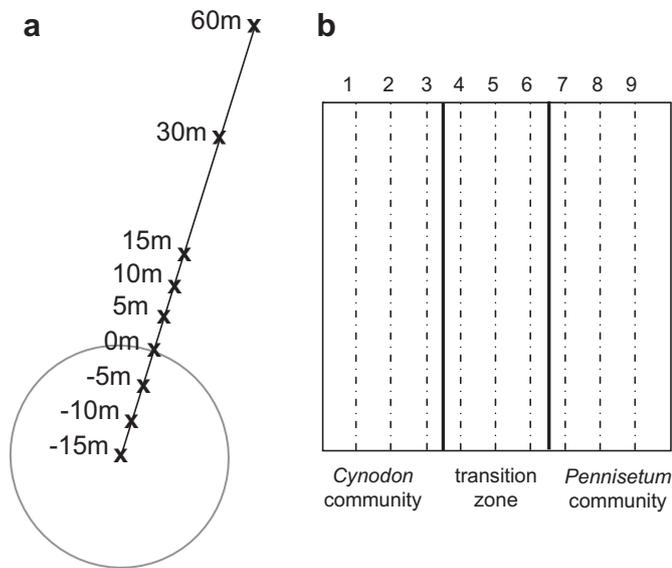
Fig. 1. Glade sampling (a) occurred along transects extending from glade center to 60 m beyond glade edge (x's indicate sampled distances). Experimental 1 m × 1 m plots (b) were divided into three zones (*Cynodon* community, transition zone, and *Pennisetum* community), and nine pin frames (dashed lines) were placed 10 cm apart across the plot.

quantify aerial plant cover, counting the first hit of every species on each pin, for a maximum of ten hits/species/pin frame (with total aerial cover summed across all species typically far exceeding ten hits or 100%). At each sampling location, I also recorded presence of each species rooted within a 1 m² quadrat. For statistical analysis, at each glade, samples along the transect were averaged into three distance categories: 1) inside (between glade center and −10 m), 2) glade edge (between −5 m and +10 m) and 3) outside, but near the glade (between +15 and +60 m).

2.4. Soil sampling

Soil samples from 0 to 10 cm depth were collected at vegetation sample points (described above) in August 2003. This depth is within the primary rooting zone of herbaceous vegetation and the depth at which boma activity significantly affects soils (Augustine, 2003; Treydte et al., 2006). If a sample point fell under the canopy of a tree or where termite diggings were present, the collection point was shifted 1–2 m to avoid these features. Soils were dried and shipped to the United States for analyses by A&L Western Laboratories, Inc. in Modesto, CA; samples were analyzed using the methodology outlined in Gavlak et al. (1994). Samples were tested for pools of potassium (K), sodium (Na), calcium (Ca), and magnesium (Mg). Also measured were pH, organic matter (OM) content, soil texture (percent sand, silt and clay), and cation exchange capacity (CEC). Additional soil samples were collected in August 2008 and analyzed for total nitrogen (N) and phosphorus (P) using the Kjeldahl acid digestion procedure. For N and P sampling, in each of the ten previously sampled (young and old) glades and five new (randomly located) non-glade areas, I combined soil from four random locations within a 10 m × 10 m area and collected a sub-sample of that mixture for analysis at the International Centre for Research in Agroforestry (ICRAF) Soil and Plant Laboratory in Nairobi Kenya.

2.5. Dung counts

To estimate relative use, all herbivore dung piles (identified to species level) were counted in plots inside and outside of glades.

Cattle were included in these counts because although humans guide cattle movement across the landscape, dung counts nevertheless provide information about finer-scale movement patterns. Two 20 m × 20 m blocks (total = 800 m²) were searched inside each glade. In two cases where it was impossible to avoid curvilinear glade edges, a single 20 m × 20 m plot or two 20 m × 10 m plots were sampled. To quantify herbivore dung outside of each glade, I exhaustively sampled a 4 m × 100 m dung transect perpendicular to the vegetation transect at 200 m from glade edge. Because herbivores respond to both intra- and inter-annual rainfall, sampling occurred at the end of the wet season in June 2005 and 2006 and at the end of the dry season in March 2006 and 2007. Dung was crushed in situ three months prior to each sampling, allowing me to count only recent dung.

Herbivore dung counts were not converted into absolute densities because direct translations can be problematic (e.g., Fuller, 1991). Instead, dung counts were used to provide estimates of relative use (i.e., glade vs. non-glade areas) for each species during a given time period. When used to estimate relative habitat use, dung counts are at least as reliable as aerial or ground counts (see review by Barnes, 2001 and references contained in Young et al., 2005). Relative differences in herbivore dung densities were assumed to indicate differences in herbivore use.

2.6. Herbivore exclusion experiment

I used 1 m × 1 m × 1 m herbivore exclusion cages to assess how herbivory influences vegetation change in glades, specifically *Pennisetum* invasion into *Cynodon*-dominated areas. Most intermediate-aged and older glades contain large patches of *Cynodon*-dominated areas surrounded by a *Pennisetum*-dominated invasion front. In five of these glades one grazed and one ungrazed (caged) plot were randomly located along the *Cynodon*−*Pennisetum* boundary. All plots were located to include three zones: *Cynodon*-dominated community, *Pennisetum*-dominated community, and the transition zone between the two communities (Fig. 1b). Throughout the experiment a 10-cm vegetation-free buffer was maintained around each plot (by removing above-ground vegetation) to prevent encroachment from outside. The five grazed plots were left open to grazing, and five ungrazed plots were caged with chicken wire mesh (4 cm diameter holes) to exclude larger vertebrate herbivores. The lower third of the cage was covered with 30 cm tall hardware cloth (0.5 cm mesh) to also exclude the dominant rodent, *Saccostomus mearnsi*. This species strongly prefers foraging on forbs over grasses (Metz and Keesing, 2001). However, it also can clip grasses and create tunnels through vegetation, particularly in exclosure cages where dense stands of grass provide cover from predators (personal observation).

At the beginning of the experiment, in July/August 2004 (rainfall April–June 2004 = 282 mm), and three years later in July 2007 (rainfall April–June 2007 = 273 mm), I assessed aerial vegetation cover in each plot. Nine ten-point pin frames were evenly placed parallel to the invasion front, and number of first pins hit on each species were counted (maximum of 10 hits per species). Changes in plant cover were calculated as (final pin hits minus initial pin hits)/(initial pin hits). I also measured height of the highest hit of each species at each pin location after three years of herbivore exclusion.

2.7. Statistical analyses

The following vegetation and soil chronosequence MANOVA and ANOVA analyses were treated as split-plot designs, testing main plot effects of glade age class (young, old) and subplot effects of distance from glade (in, edge, out). Grass cover values (*Cynodon* and *Pennisetum*) were response variables in a MANOVA, and

following significant MANOVA results, *Cynodon* and *Pennisetum* were analyzed separately in protected univariate ANOVAs. This procedure of MANOVA, followed by protected univariate ANOVAs was repeated for species richness (grass and forbs), texture (sand, silt, and clay), and soil properties (all other soil properties in Table 1 except N and P). The 2008 N and P soil data were not treated as a split-plot design, but were analyzed in a one-way ANOVA of glade age (3 levels: young, old, non-glade) effects on total N and P.

Chronosequence dung data were analyzed in the same split-plot design described above, except sampling period (June 05, March 06, June 06, March 07) was added as a repeated factor, and "edge" was omitted from the distance category (since dung was not counted at that distance). Total wildlife dung (i.e., all species pooled) and individual ungulate herbivore species were analyzed in separate ANOVAs. Oryx and hartebeest were pooled into one category because their sample numbers were low and their body size and feeding habits are similar (Estes, 1992).

The herbivore exclusion experiment was analyzed as a split-plot MANOVA followed by protected univariate ANCOVA tests (treating initial cover as covariate). Grazing was the main treatment effect, and vegetation zone within the plot (*Cynodon* community, transition, or *Pennisetum* community) was treated as a subplot effect. Response variables were changes in *Cynodon* and *Pennisetum* cover. For each species, baseline cover (pin hits) was treated as a covariate. Height was not included in a MANOVA, but was analyzed in a univariate model testing the effects of grazing on the difference in height between *Pennisetum* and *Cynodon*.

For all of the above analyses I used general linear mixed models (GLMMs), treating glade as a random effect, and I used variance-weighting when variances were not homogenous. Maximum-likelihood methodology, as well as Satterthwaite's approximation of degrees of freedom were used (PROC MIXED, version 9.1, SAS Institute 2002). Tukey's HSD post-hoc analyses were used for all data except the 2008 soil data for which I instead used planned linear contrasts to test the effects of glade age on soil properties: a) young vs. old glade and b) glade vs. non-glade.

3. Results

3.1. Chronosequence: vegetation

Herbaceous vegetation cover varied with respect to glade age and proximity to glade (age: Wilk's $\lambda = 0.28$, $F_{2,7} = 9.15$, $p = 0.011$; location: Wilk's $\lambda = 0.23$, $F_{4,30} = 8.21$, $p = 0.0001$; age*distance: Wilk's $\lambda = 0.34$, $F_{4,30} = 5.34$, $p = 0.0023$). Herbaceous vegetation inside young glades was dominated by the stoloniferous perennial

grass, *C. plectostachyus* (Fig. 2a), whereas old glade vegetation was dominated by the perennial bunchgrass, *P. stramineum* (Fig. 2b). Although *Cynodon* cover was higher inside glades of both ages, its cover was three times greater in young than old glades (age*-distance: $F_{2,14.3} = 5.16$, $p = 0.02$). *Cynodon* was rare outside glades (15–60 m away: mean $4.3 \pm 3.3\%$ cover, Fig. 2a) and absent from background vegetation. *Pennisetum* cover was two to three times higher inside old glades than outside (age*distance: $F_{2,24} = 8.35$, $p = 0.0018$). Cover values of all other species were too low for statistical analyses.

In glades, mean grass species richness per m^2 was 3.1 ± 0.5, and forb species richness was 3.7 ± 0.8. These values were significantly lower than outside (15–60 m) of glades (grass: 6.7 ± 0.4 and forb 9.5 ± 0.9), and edges showed intermediate values (MANOVA distance effect Wilk's $\lambda = 0.18$, $F_{4,30} = 10.37$, $p < 0.0001$; univariate distance effect for grass $F_{2,16} = 21.52$, $p < 0.0001$; forbs $F_{2,16} = 22.2$, $p < 0.0001$). Glades hosted at least seven specialist plant species. One forb, *Tribulus terrestris*, and one grass, *Dactyloctenium aegypticum,* occurred only in glades, regardless of age. Two forbs, *Medicago laciniata* and *Plectranthus* sp., and one grass species, *Sporobolus pyramidalis*, occurred only in old glade quadrats, while introduced jimson weed, *Datura stramonium*, occurred only in young glade quadrats. The forb *Hibiscus flavifolius* occurred only in quadrats associated with old glades (inside, edge and outside).

The common grasses in background vegetation (other than *P. stramineum*) were depressed or entirely absent inside glades; *Brachiaria* and *Lintonia* were never found inside glades, and *Themeda* was found in only two of ten glades. *P. mezianum* occurred in all outside plots, but occurred in only one young glade and two old glades. "Outside" plots were dominated by the same five grass species that comprise 90% of the herbaceous cover in this landscape (Young et al., 1998).

3.2. Chronosequence: soil properties

MANOVA results indicate that soil nutrient properties were significantly different inside glades than elsewhere (Table 1; distance: Wilk's $\lambda = 0.06$, $F_{14,20} = 4.42$, $p = 0.001$). Relative to outside, soils inside glades were two times higher in organic matter ($F_{2,16.5} = 14.23$, $p = 0.0003$) and 1.5 times higher in potassium ($F_{2,9.94} = 12.73$, $p = 0.0018$). Soils inside glades were 3.5 times higher in total % nitrogen (Table 1; $F_{1,12} = 12.62$, $p = 0.004$) and 6 times higher in total % phosphorus (Table 1; $F_{1,12} = 47.63$, $p < 0.0001$). None of these soil properties differed significantly between young and old glade soils (i.e., age effect $p < 0.05$). Although it was not higher inside glades, cation exchange capacity

Table 1
Mean (± 1SE) values of soil properties associated with young ($n = 5$) and old ($n = 5$) glades derived from abandoned cattle corrals. Soil N and P were measured inside each glade, and in non-glade areas ($n = 5$). All other soil properties were measured at three distances (inside, edge, outside of glades) associated with each glade. SE = standard error of the mean.

	Young glades (post-1961)			Old glades (pre-1961)		
	Inside	Edge	Outside	Inside	Edge	Outside
N (%)	0.51 ± 0.14	–	0.16 ± 0.0067	0.61 ± 0.18	–	0.16 ± 0.0067
P (%)	0.10 ± 0.017	–	0.019 ± 0.0013	0.13 ± 0.019	–	0.019 ± 0.0013
OM (%)	13.87 ± 2.08	8.12 ± 1.56	5.03 ± 0.29	7.41 ± 0.65	7.3 ± 0.79	5.24 ± 0.37
K (ppm)	1321.17 ± 258.68	1162.68 ± 142.65	808.6 ± 26.73	1230.51 ± 36.41	1173.43 ± 70.15	854.03 ± 37.37
Mg (ppm)	535.55 ± 73.7	638.68 ± 66.49	724.15 ± 22.47	498.28 ± 34.85	559.48 ± 49.78	699.75 ± 76.52
Ca (ppm)	1905.12 ± 192.69	2217.68 ± 215.63	2470.38 ± 189.17	1866.71 ± 83.27	2522.7 ± 263.52	2756.6 ± 238.35
Na (ppm)	25.25 ± 7.51	69.8 ± 12.92	170.33 ± 20.49	14.27 ± 1.45	34.55 ± 13.76	139.17 ± 28.83
CEC (meq/100 g)	24.55 ± 0.78	24.54 ± 1.68	24.47 ± 0.78	19.8 ± 0.41	24.47 ± 1.24	25.69 ± 2.06
pH	6.34 ± 0.19	6.49 ± 0.11	6.59 ± 0.03	6.63 ± 0.03	6.52 ± 0.05	6.58 ± 0.03
Sand (%)	47.94 ± 6.34	35.04 ± 2.98	28.81 ± 2.27	39.92 ± 2.15	33.94 ± 1.08	29.04 ± 2.83
Silt (%)	21.48 ± 1.72	22.27 ± 2.07	18.43 ± 1.3	29.91 ± 1.07	25.48 ± 0.89	23.55 ± 2.64
Clay (%)	30.57 ± 5.1	42.69 ± 4.85	52.76 ± 3.1	30.17 ± 1.85	40.59 ± 1.82	47.41 ± 5.35
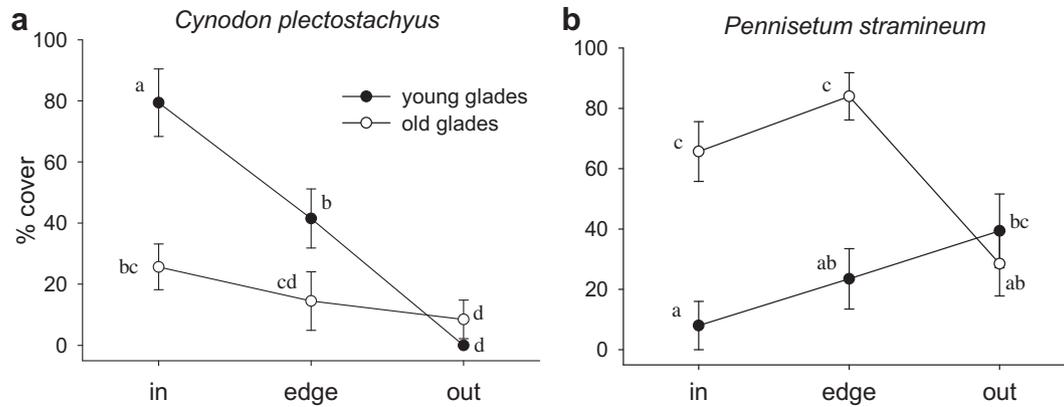
Fig. 2. Mean (±1 SE) aerial cover of *Cynodon plectostachyus* (a) and *Pennisetum stramineum* (b) in five young glades and five old glades at three distances (inside, edge and outside of glades). For each species, shared letters indicate no significant differences at the $p = 0.05$ level, according to Tukey's HSD.

(CEC) was 24% higher in young than old glades (age*distance: $F_{2,16} = 4.38$, $p = 0.03$).

In comparison to outside glades, glade soils were 28% lower in Mg ($F_{2,16} = 7.47$, $p = 0.005$), 28% lower in Ca ($F_{2,16} = 12.35$, $p = 0.0006$) and 89% lower in Na ($F_{2,16} = 40.13$, $p < 0.0001$). In new glades, pH was non-significantly lower than outside (age*distance: $F_{2,11.5} = 3.04$, $p = 0.09$). MANOVA results indicate soil texture was significantly different inside glades and varied strongly with distance from glades (distance: Wilk's $\lambda = 0.32$, $F_{6,28} = 3.52$, $p = 0.01$; age*distance: Wilk's $\lambda = 0.68$, $F_{6,28} = 0.99$, $p = 0.45$). Most notable was the moderate clay content found inside glades (30% clay) relative to the extremely high (50% clay) levels found in outside plots ($F_{2,16} = 14.57$, $p = 0.0002$).

3.3. Herbivore response to glades

Dung count results (summed across species) suggest that herbivores prefer glade habitat (total herbivore dung density inside: 79.7 ± 7.9, outside: 37.6 ± 3.8; $F_{1,20.6} = 19.12$, $p = 0.0003$), and this effect was most pronounced in young glades during dry times (distance*age*sampling period: $F_{3,49.7} = 5.76$, $p = 0.0018$). During the dry season (March), total wildlife herbivore dung was higher in young glades relative to outside transects, but only significantly (12 times higher) during the second sampling year. This seasonal pattern was strongest for Grant's gazelles and zebras (distance*age*sampling period: Grant's gazelle $F_{3,47.6} = 3.88$, $p = 0.014$, zebra $F_{3,44.5} = 3.37$, $p = 0.027$; Tukey HSD $p < 0.05$; Fig. 3). Elephants also were associated with young glades for all sampling periods (distance*age $F_{1,8.13} = 5.94$, $p = 0.04$, Tukey HSD $p < 0.05$, Fig. 3). Oryx and hartebeest favored glades over non-glades (distance $F_{1,15.2} = 4.57$, $p = 0.049$), preferring young glades during the second year (age*sampling period $F_{3,24.9} = 3.38$, $p = 0.034$, Tukey HSD $p < 0.05$, Fig. 3). Cattle also were associated with young glades (age*distance $F_{1,6.37} = 11.51$, $p = 0.013$, Tukey HSD $p < 0.05$, Fig. 3), but preferred glades of all ages during wet times (distance*sampling period $F_{3,15.1} = 4.25$, $p = 0.023$). The second sampling year (2006–2007) was unusually wet; the six months preceding the March 2007 dry season received more than double the rainfall of the six months preceding March 2006 (T.P. Young, unpublished results).

3.4. Effects of herbivore exclusion on vegetation

The 1 m × 1 m plots set up to investigate large herbivore effects on succession revealed significant herbivore effects, which varied according to community zone within the plot (i.e., *Cynodon* community, *Pennisetum*-dominated community or transition zone) (grazing: Wilk's $\lambda = 0.11$, $F_{2,3} = 11.85$, $p = 0.038$; grazing*zone: Wilk's $\lambda = 0.19$, $F_{4,24} = 7.93$, $p = 0.0003$). In general, large herbivores had little influence on *Cynodon* cover. *Cynodon* consistently decreased in cover (i.e., cover change < 0) over the 3-year course of the experiment, regardless of herbivore exclusion treatment (Fig. 4a). One exception was in the *Pennisetum* zone where grazing sometimes increased *Cynodon* cover. Herbivore exclusion decreased *Cynodon* growth by 156% ($F_{1,7.38} = 10.66$, $p = 0.01$) and increased *Pennisetum* growth by 343% ($F_{1,19} = 35.63$, $p < 0.0001$, Fig. 4). The difference in crown height between *Pennisetum* and *Cynodon* (and potential for shading) was greater when grazers were excluded (5.0 ± 3.5 cm grazed, 14.0 ± 4.2 cm ungrazed, $F_{1,16.7} = 4.04$, $p = 0.06$). Grazing removal also promoted *Pennisetum* invasion into *Cynodon* zones; when grazers were excluded, *Pennisetum* invaded and its cover increased threefold in the *Cynodon* zone (grazing*zone: $F_{2,18.9} = 23.71$, $p < 0.0001$, Fig. 4b). In contrast, grazing decreased *Pennisetum* growth in the *Cynodon* zone (significant grazing*zone, Tukey HSD grazed vs. ungrazed, $p < 0.05$). Mean differences in the transition zone, though non-significant, also suggest that *Pennisetum* growth increased under grazing exclusion (Fig. 4b).

4. Discussion

In other pastoral landscapes throughout eastern and southern Africa, abandoned boma sites serve as long-term hotspots of high nutrient levels, palatable grasses and herbivore use. Here, I evaluated the degree to which glades function as hotspots in an *A. drepanolobium* savanna landscape underlain by high-clay "black cotton" soils. Glade soil N and P levels were 3.5 and 6 times higher, respectively, than outside glades, and overall herbivore use was twice as high as elsewhere on the landscape. The consequences of glade-related nutrient heterogeneity for herbivore diversity may be especially important in black cotton landscapes where soils and vegetation are relatively homogenous. I also present experimental evidence that large herbivores, through their effects on dominant plant species, may contribute to maintenance of glades in a successional stage that is highly palatable to grazers.

### 4.1. Glades as long-term nutrient hotspots

Historic aerial photos indicate that treeless glades in the Laikipia black cotton ecosystem persist for at least four decades, their distinctive vegetation communities initially dominated by *C. plectostachyus* and gradually replaced by *P. stramineum*. The herbaceous plant species composition only 60 m outside of glades was
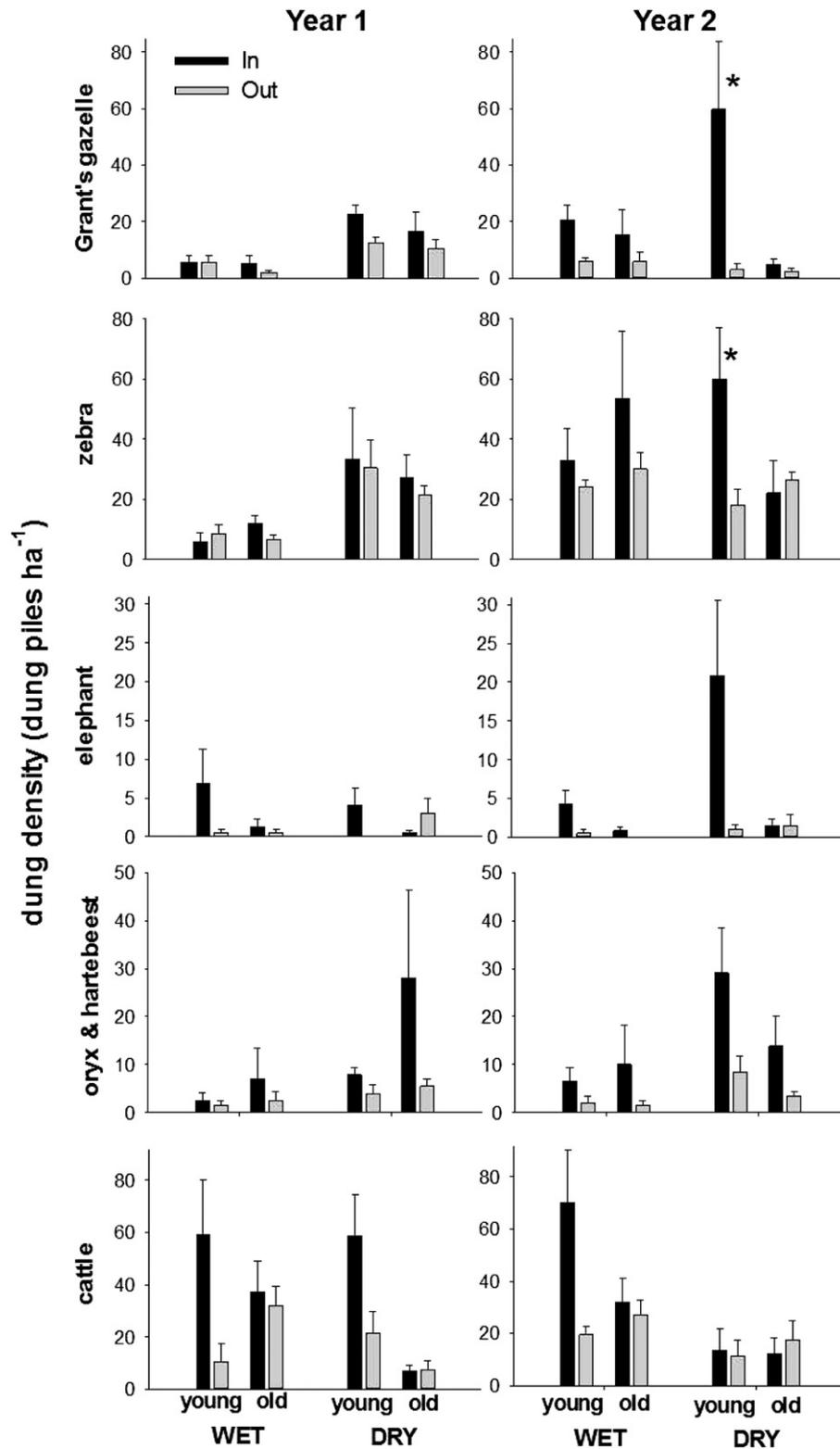
Fig. 3. Herbivore dung densities ($\pm$1 SE) at two distances (inside and 200 m outside) from young glades ($n = 5$) and old glades ($n = 5$) in two wet seasons (June 2005 & 2006) and two dry seasons (March 2006 & 2007). Asterisks indicate significant Tukey HSD ($p < 0.05$) comparisons of in/out when there was a significant distance*age*sampling period effect for an herbivore species. Note different scales across species.

qualitatively similar to composition in non-glade (>150 m away) background vegetation sampled six months later (T.P. Young, unpublished results), consistent with the results of Porensky (2011). The only exception was that *Cynodon* was present in glades, but virtually absent in background vegetation.

Dominance by species in the *Cynodon* genus appears to be characteristic of treeless glades across a diversity of ecosystems in eastern Africa, including nearby areas of similar rainfall but different soil types (Stelfox, 1986; Young et al., 1995), and dryer and wetter areas of different soil types elsewhere in East Africa (Treydte
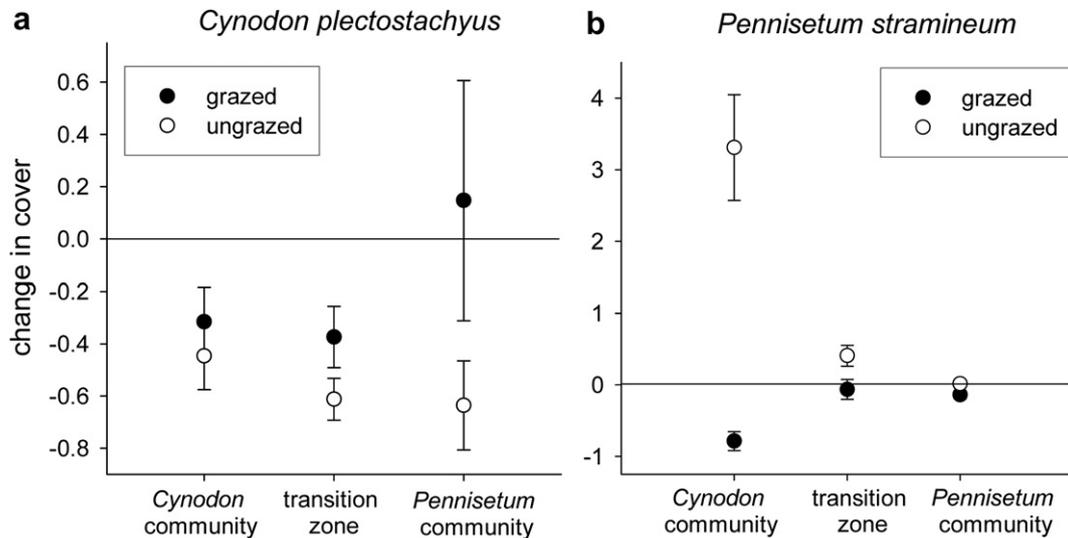
Fig. 4. Mean (±1 SE) changes (calculated as [final pin hits minus initial pin hits]/[initial pin hits]) in *Cynodon plectostachyus* and *Pennisetum stramineum* cover in five glades, after three years, in response to two factors: 1) grazing (presence/absence) and 2) location within a 1 × 1 m plot (*Cynodon* community/transition zone/*Pennisetum* community).

et al., 2006; Muchiru et al., 2009). Although plant species richness is lower inside than outside glades, glades increase species richness at the landscape level by supporting *Cynodon* and other species that are otherwise rare or absent in the background landscape. Glades also demarcate original corral sites. In southern Africa, distinctive vegetation communities identify former corral sites for hundreds of years post-abandonment (Blackmore et al., 1990), and interviews with local inhabitants in my study system suggest that boma sites are recognizable more than a century after abandonment (K. Veblen, unpublished results).

Nitrogen, phosphorus and potassium levels remained elevated in glade soils over the >40-year time-span identified in this study. Elevated nutrient levels, attributable largely to intense dung deposition by livestock during boma occupation, are typical of old boma sites across eastern and southern Africa (Blackmore et al., 1990; Reid and Ellis, 1995; Augustine, 2003; Treydte et al., 2006; Muchiru et al., 2009; van der Waal et al., 2011). Two of these studies (Augustine, 2003; Muchiru et al., 2009) assessed temporal changes and found that nitrogen levels declined over time. In contrast, my results indicate that nitrogen levels in black cotton glades did not appear to significantly decline over time. Moreover, nitrogen levels in the oldest black cotton glades were 3.8 times higher than background, whereas Augustine (2003) found glade nitrogen levels to be 1.9 times background in similarly-aged red sandy loam glades. The persistence of high nitrogen levels in black cotton glades may be a key factor explaining invasion of glades by *P. stramineum*, a species that may gain a competitive advantage in higher nitrogen sites (Riginos and Grace, 2008). My results also indicate that phosphorus and potassium levels in the oldest black cotton glades are 6.8 and 1.5 times higher (respectively) than background levels, similar to glades of the same age in neighboring red sandy loam soils (7.4 times and 2 times, respectively, Augustine, 2003). Phosphorus in particular appears to be an important component of former boma sites across multiple ecosystems presumably because, unlike nitrogen, phosphorus is not lost to volatilization and formation of mineral complexes minimize leaching (Schlesinger, 1997).

Patterns of calcium, magnesium and sodium contrasted strongly with those observed in other ecosystems. Whereas other studies have found Ca, Mg and Na levels in former boma sites to be equal to or greater than non-boma sites (Blackmore et al., 1990; Augustine,

2003; Muchiru et al., 2009), levels of these nutrients appear to be lower in black cotton boma sites. Even more strikingly, this is the first report of a difference in texture (decreased clay) in old boma sites (Augustine, 2003; Scholes and Walker, 2004; van der Waal et al., 2011). This result is surprising because soil texture is considered a relatively static property and should not be affected by livestock or wildlife activity (Brye, 2003 and references therein). Significant soil textural changes would be expected to have important long-term consequences (in contrast to changes in nutrient levels which could return to baseline levels over time). One potential explanation for altered soil texture may be that densities of termite mounds, which cover ∼20% of the landscape (Fox-Dobbs et al., 2010), are twice as high in glades (K. Veblen, unpublished results). Termites alter soil texture, often concentrating clay particles in sandy soils (Konate et al., 1999; e.g., Grube, 2001). In this clay-rich black cotton study system, termites reduce clay content, possibly by importing sand particles (Fox-Dobbs et al., 2010). Termites also reduce Mg, Ca and Na (T.M. Palmer, unpublished results). Lowered clay content decreases surface area for cation adhesion, and increased sand content and bioperturbation may enhance soil drainage and leaching of cations such as Ca, Mg, and Na. Further work is needed to elucidate any spatial and/or developmental relationships between glades and termites.

4.2. Glades as herbivore hotspots

Abandoned livestock corrals were hotspots for large herbivores in this ecosystem, a pattern of habitat use observed elsewhere in eastern and southern Africa (Young et al., 1995; Augustine, 2004; Scholes and Walker, 2004; Muchiru et al., 2008; van der Waal et al., 2011). Nutrient enrichment is known to attract grazers to non-boma-derived hotspots (McNaughton, 1988; McNaughton et al., 1997; Anderson et al., 2010; Stock et al., 2010), suggesting that elevated soil N, P and K levels may be at least partially responsible for the hotspot effect of glades in this system. At a nearby sandy loam site in central Kenya, glade vegetation appears to provide a critical source of phosphorus, a nutrient that occurs at much lower levels in the background vegetation (Augustine, 2003; Augustine, 2004).

Herbivore preference for glade habitat may be further reinforced by the maintenance of vegetation in a more nutritious state.

Just as herbivory maintains grazing lawns across sub-Saharan Africa (McNaughton, 1984; Verweij et al., 2006; Waldram et al., 2008), it appears to maintain young glades in my study system in a short-grass state. *C. plectostachyus*, which dominates young glades but is rare elsewhere, is a preferred forage species (Pratt and Gwynne, 1977) and is well-adapted to grazing by way of its prostrate growth form and tolerance to trampling (McNaughton, 1984; Georgiadis and McNaughton, 1988). Grazing stimulates new shoot growth and likely results in higher foliar nutrient (Coetsee et al., 2011 and references therein).

An additional (but not mutually exclusive) explanation for herbivore glade preferences may be an attraction to treeless glade interiors. Areas of even moderately lower tree density in this *A. drepanolobium* ecosystem are preferred by herbivores, seemingly because openness provides better visibility and improved predator detection (Riginos and Grace, 2008). At a nearby site in central Kenya, impala (antelopes) showed clear preference for glades even when nutrient-rich vegetation was absent, suggesting they used glades for anti-predator defense (Augustine, 2004). Other work has found herbivore hotspot locations in the Serengeti to be a function of both nutrient enrichment and anti-predator behavior (Anderson et al., 2010).

Although glade habitat in general was preferred by wild herbivores, the effect appeared to be most pronounced during the dry season. It should be noted, however, that the weaker pattern during the wet season may be a result of more rapid dung decomposition during wet times. Nonetheless, the comparison of inside vs. outside indicates clear herbivore preference for glades during the dry season. This pattern has been observed in other African savannas (Scholes and Walker, 2004, but see Augustine, 2004; Muchiru et al., 2008) and may be attributable to glade vegetation characteristics during the dry season. In Tanzania, Treydte et al. (2006) found that dry season crude protein levels were higher in herbaceous glade vegetation than in surrounding vegetation, and in southern Africa Grant and Scholes, (2006) found that foliar phosphorus associated with termite mound hotspots remained elevated throughout the dry season. Similarly, in my study system, glade vegetation stays green longer into the dry period than surrounding vegetation and becomes lush and green more quickly at the onset of rainy periods (K. Veblen, personal observation). Together, these lines of evidence suggest that former boma sites may provide important 'dry season refuges' (sensu Ilius and O'Connor, 2000), where large herbivores can obtain nutritious forage during dry periods.

My results further suggest that the effectiveness of dry season refuges depends on rainfall levels preceding the dry season. Both wildlife and cattle used glades significantly more during the second year of the study, which was an unusually wet year. It has been suggested that wet season carrying capacity is tightly linked to the previous dry season's carrying capacity (Ilius and O'Connor, 2000), and effectiveness of dry season refuges also may be tightly linked to the previous wet season. Examination of herbivore use over future years will show whether this pattern persists over the long-term.

4.3. Feedbacks between glades and large herbivores

These results from black cotton soils provide experimental evidence that large herbivores may influence succession and vegetation development associated with abandoned livestock bomas. Although progression from *Cynodon* to *Pennisetum* dominance always occurred eventually (regardless of herbivory), grazing slowed that process (i.e., grazing removal accelerated *Pennisetum* invasion). Given the long-term patterns of *Pennisetum* invasion (Fig. 2), it is unlikely that grazing changes the overall trajectory of vegetation development in glades. However, the presence of grazers may reduce the rate of *Pennisetum* invasion and lengthen

the time period that vegetation is maintained in a desirable *Cynodon* state, further attracting grazers.

It should be noted that this study took place over a relatively short time period within the overall time-span of glade development and previous research indicates that short-term (<1 year) and long-term (8 years) glade vegetation patterns are sensitive to variations in both rainfall and herbivory (Veblen, 2008; Veblen and Young, 2010). Nonetheless, these results clearly illustrate significant effects of herbivore exclusion and plant community changes over this three year period.

Evidence from a variety of ecosystems suggests two primary pathways for herbivores to affect plant community dynamics: plant tolerance to herbivory and herbivore selectivity (Augustine and McNaughton, 1998). First, plant species vary in their tolerances to herbivory (Hawkes and Sullivan, 2001), and my results suggest that grazing of less tolerant *Pennisetum* at least partially suppressed its ability to competitively displace more tolerant *Cynodon*. As discussed above, *Cynodon* is grazing-tolerant and maintained in short-statured monocultures by heavy grazing. *P. stramineum,* on the other hand is a superior competitor (Veblen, 2008), but appears to be less grazing-tolerant. Second, herbivores can benefit one plant species by preferentially foraging on its competitor(s) (e.g., Veblen and Young, 2010). Zebra, the dominant wildlife grazers in this system, show preference for *Pennisetum* (Young et al., 1995) and may therefore play an important role in suppressing the rate of *Pennisetum* displacement of *Cynodon* and contribute to the longer-term persistence of *Cynodon* in glades.

Herbivores also may indirectly influence glade plant succession through soil feedbacks and nutrient cycling. My results indicate that soil nitrogen and phosphorus levels in glades remained high over time, presumably as a continued attractant to herbivores. Although soil nutrient levels were not measured in my small experimental exclosures, larger-scale experiments in a nearby study system suggest lower nutrient levels may have been lower in exclosures because herbivores help maintain high nutrient levels in glades (i.e., nutrient deposition by herbivores exceeds consumption) (Augustine et al., 2003). Additionally, herbivores can increase mineralization rates (McNaughton et al., 1997), and grazing in glades can increase production and net nitrogen availability (Augustine and McNaughton, 2006). Further investigation may reveal similar herbivore–nutrient relationships in the black cotton glade system.

4.4. Conclusion

Glades in black cotton soils show several similarities to boma-derived hotspots elsewhere in Africa, including nearby sandy loam soils. In particular, they function as nutrient-rich hotspots of palatable forage for cattle and wildlife. Black cotton glades differ, however, in that soil textural changes occur following boma abandonment, likely due to increased termite activity. Because black cotton soils are high in clay, the reduction in clay content associated with glades may have important functional consequences for plants and soil nutrients.

Nutrient hotspots play a potentially important role in wildlife conservation (Grant and Scholes, 2006). However, cattle-derived nutrient hotspots in particular may be especially important because they constitute a largely positive example of a system in which livestock and wildlife can synergistically share the landscape. Arguably, multi-use rangelands, shared by livestock and wildlife, are at the heart of future successes in savanna conservation. My results also suggest that large herbivores, and their management, have the potential to exert control over the long-term persistence of the glade mosaic. Thus, if glade-like landscape features are found to be of local conservation value, active

management of livestock or livestock-to-wildlife ratios could potentially be used as a tool for maintaining glade habitat for wildlife species. Thus, further investigation into the effects of livestock and large herbivore wildlife on glade development is warranted.

Acknowledgments

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