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1 **Savanna glade hotspots: plant community development and synergy with large herbivores**

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1 **Abstract**

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

18

19 **Key words:** *Acacia drepanolobium*, cattle-wildlife interactions, grazing lawn, kraal, Laikipia,
20 landscape heterogeneity

21

1 **1. Introduction**

2 Landscape heterogeneity is an important and influential driver of ecological processes,
3 particularly in savanna ecosystems (Adler et al., 2001; DuToit et al., 2003; Scholes and Walker,
4 2004). For millennia, pastoralists throughout eastern and southern African savannas have created
5 large-scale landscape mosaics that persist many decades (Augustine, 2003; Muchiru et al., 2008)
6 and even several centuries (Blackmore et al., 1990). Herded livestock forage over the landscape
7 during the day and deposit dung in temporary thorn fence corrals (bomas) at night, concentrating
8 large amounts of nutrients and organic matter (Reid and Ellis, 1995; Treydte et al., 2006). After
9 abandonment, corral sites support distinctive, nutrient-rich plant communities and typically
10 persist as long-term hotspots of highly fertilized soils (Stelfox, 1986; Blackmore et al., 1990;
11 Reid and Ellis, 1995; Young et al., 1995; Augustine, 2003; Treydte et al., 2006). Individual
12 hotspots occur at densities of $\sim 2\text{km}^{-2}$ (Young et al. 1995, K.Veblen unpublished results), and
13 collectively can cover up to 17% of some landscapes (Blackmore et al., 1990).

14 One of the most profound effects of these landscape features can be to attract (or repel)
15 large ungulate herbivores. Soil nutrient levels (e.g., pools of nitrogen, phosphorus or potassium)
16 in old boma sites can be more than twenty times levels in the rest of the landscape (Reid and
17 Ellis, 1995; Augustine, 2003), and in savannas, nutrient-enriched areas often are foci of foraging
18 activity where herbivores can satisfy critical nutrient requirements (McNaughton, 1988;
19 Augustine, 2004; Grant and Scholes, 2006). Accordingly, several studies in eastern Africa have
20 documented increased herbivore activity in former boma sites relative to surrounding lower-
21 nutrient vegetation (Stelfox, 1986; Young et al., 1995; Muchiru et al., 2008; van der Waal et al.,
22 2011).

23 Although some general patterns of nutrient enrichment and herbivore use associated with

1 former boma sites have emerged, it is unclear how these patterns may differ under markedly
2 different soil conditions. In particular, high-clay “black cotton” vertisol soils cover millions of
3 hectares across East and Southern Africa, yet no studies have investigated the dynamics of
4 former boma sites in these soils or how dynamics may differ from those in more moderately
5 textured soils. Soil texture can have important consequences for soil nutrient profiles (e.g.,
6 drainage or nutrient retention over time) and may in turn have cascading effects on both plant
7 and herbivore communities associated with former boma sites.

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

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

1 Second, by affecting individual plant species differently, herbivores may have important
2 effects on plant-plant interactions in old boma sites. In *Acacia drepanolobium* savannas in
3 central Kenya, one of the dominant boma species, *Cynodon plectostachyus*, is a prostrate,
4 stoloniferous grass, while the other dominant species, *Pennisetum stramineum*, is an ascending
5 bunchgrass (hereafter referred to as *Cynodon* and *Pennisetum*). Grazing may favor shorter-
6 statured plants such as *Cynodon* because they are better-adapted to escape and/or recover from
7 grazing (Noy-Meir et al., 1989; Huntly, 1991). Taller grasses, such as *Pennisetum*, may in turn
8 be better competitors, but also may be more susceptible to grazing damage and hence less
9 competitive under grazed conditions (Mack and Thompson, 1982; Noy-Meir et al., 1989; Huntly,
10 1991). Herbivores can influence both the rate and direction of change in plant communities
11 (Skarpe, 2001) and may play an important role in the development of the specialized *Cynodon* -
12 *Pennisetum* plant communities associated with abandoned bomas.

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

20

21 **2. Materials and methods**

22 *2.1 Study site*

23 This research was conducted in *Acacia drepanolobium* savanna in the semi-arid Laikipia District

1 of central Kenya. The study area encompasses portions of the Mpala Conservancy and adjacent
2 Jessel Ranch (36°52'E, 0°17'N). Annual rainfall is variable, averaging 500 - 600 mm, with the
3 highest peak in mean rainfall occurring March-May (mean in April, 1998-2005: 115 mm) and
4 the longest and most pronounced dry season typically from December through March (mean in
5 February, 1998-2005: 9 mm). The area is underlain with "black cotton" soils, poorly drained
6 vertisols with high (>50%) clay content (Ahn and Geiger, 1987). Ninety-seven percent of the
7 tree canopy cover is *Acacia drepanolobium* Sjost., and 90% of herbaceous cover is comprised of
8 five grass species: *Pennisetum mezianum* Leeke *P. stramineum* Peter, *Themeda triandra* Forssk.,
9 *Lintonia nutans* Stapf., and *Brachiaria lachnantha* (Hochst.) Stapf. (Young et al., 1998).
10 Common resident large mammals include: elephant (*Loxodonta africana* Blumenbach), zebra
11 (*Equus burchelli* Gray), Grant's gazelle (*Gazella granti* Brooke), hartebeest (*Alcelaphus*
12 *buselaphus* Pallas), steinbuck (*Raphicerus campestris* Thunberg), eland (*Taurotragus oryx*
13 Pallas), oryx (*Oryx gazella beisa* L.), giraffe (*Giraffa camelopardalis* L.), spotted hyaena
14 (*Crocuta crocuta* Erxleben), and lion (*Panthera leo* L.).

15 Historic (centuries-long) cattle management has created a landscape mosaic of treeless
16 glades (approx. 2 km²) derived from abandoned livestock bomas embedded in a wooded
17 savanna matrix. Current land managers employ local herders who, practicing traditional
18 livestock husbandry, use thorn fencing to build 0.25 - 1.0 ha bomas to corral livestock nightly for
19 months to years at a time. Trees are cleared inside the boma and are used, in addition to trees
20 harvested from the surrounding area, to build and maintain the thorn fence. Once abandoned, the
21 original boma area remains treeless long after the thorn fence and cattle dung (up to 0.5 m deep)
22 have disappeared.

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

9

10 *2.2 Glade chronosequence survey*

11 To determine changes in glades over time, I measured herbaceous vegetation, soil characteristics,
12 and large herbivore use associated with glades in two age classes. I located glades in my study
13 area by using a 2003 8 km x 8 km Quickbird satellite image (DigitalGlobe, 2003). Ground
14 truthing confirmed that these features were indeed glades. I cross-referenced these glades with
15 1961 aerial photos to determine which glades existed prior to 1961. I used five randomly
16 selected post-1961 (“young”) glades, and five randomly selected pre-1961 (“old”) glades for the
17 chronosequence sampling described below. During selection, one glade was rejected because
18 trees had not been cleared, and others were rejected when they were directly adjacent to an
19 already-selected glade. I confirmed date of last use by visiting each glade with two independent
20 groups of herders who had resided in the area for the past fifty to eighty years.

21

22 *2.3 Vegetation sampling*

1 In August 2003, for each of the young and old glades, herbaceous vegetation was sampled along
2 a transect that began at glade center and ended 60 m outside the glade (Fig. 1a). Each transect
3 was oriented in a randomly selected cardinal direction that avoided major landscape features
4 such as roads and other glades. Tree presence around the glade perimeter demarcated glade edge
5 (and distance of zero). For a given glade, the center occurred at a point between -40 m and -15
6 m, depending on glade size (Fig. 1a). I sampled every 5 m between glade center and +15 m, and
7 at +30 m and +60 m, for a total of 123 sample locations (mean of 12.3 per glade). At each
8 sampling location, a ten-point pin frame was used to quantify aerial plant cover, counting the
9 first hit of every species on each pin, for a maximum of ten hits/species/pin frame (with total
10 aerial cover summed across all species typically far exceeding ten hits, or 100%). At each
11 sampling location, I also recorded presence of each species rooted within a 1 m² quadrat. For
12 statistical analysis, at each glade, samples along the transect were averaged into three distance
13 categories: 1) inside (between glade center and -10 m), 2) glade edge (between -5 m and +10 m)
14 and 3) outside, but near the glade (between +15 and +60 m).

15

16 *2.4 Soil sampling*

17 Soil samples from 0-10 cm depth were collected at vegetation sample points (described above) in
18 August 2003. This depth is within the primary rooting zone of herbaceous vegetation and the
19 depth at which boma activity significantly affects soils (Augustine, 2003; Treydte et al., 2006). If
20 a sample point fell under the canopy of a tree or where termite diggings were present, the
21 collection point was shifted 1-2 m to avoid these features. Soils were dried and shipped to the
22 United States for analyses by A&L Western Laboratories, Inc. in Modesto, CA; samples were
23 analyzed using the methodology outlined in Gavlak et al. (1994). Samples were tested for pools

1 of potassium (K), sodium (Na), calcium (Ca), and magnesium (Mg). Also measured were pH,
2 organic matter (OM) content, soil texture (percent sand, silt and clay), and cation exchange
3 capacity (CEC). Additional soil samples were collected in August 2008 and analyzed for total
4 nitrogen (N) and phosphorus (P) using the Kjeldahl acid digestion procedure. For N and P
5 sampling, in each of the ten previously sampled (young and old) glades and five new (randomly
6 located) non-glade areas, I combined soil from four random locations within a 10 m x 10 m area
7 and collected a sub-sample of that mixture for analysis at the International Centre for Research in
8 Agroforestry (ICRAF) Soil and Plant Laboratory in Nairobi Kenya.

9

10 *2.5 Dung counts*

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

22 Herbivore dung counts were not converted into absolute densities because direct
23 translations can be problematic (e.g., Fuller, 1991). Instead, dung counts were used to provide

1 estimates of relative use (i.e., glade vs. non-glade areas) for each species during a given time
2 period. When used to estimate relative habitat use, dung counts are at least as reliable as aerial or
3 ground counts(see review by Barnes, 2001 and references contained in Young et al., 2005)(see
4 review by Barnes, 2001 and references contained in Young et al., 2005)(see review by Barnes,
5 2001 and references contained in Young et al., 2005)(see review by Barnes, 2001 and references
6 contained in Young et al., 2005)(see review by Barnes, 2001 and references contained in Young
7 et al., 2005)(see review by Barnes, 2001 and references contained in Young et al., 2005)(see
8 review by Barnes, 2001 and references contained in Young et al., 2005) . Relative differences in
9 herbivore dung densities were assumed to indicate differences in herbivore use.

10

11 *2.6 Herbivore exclusion experiment*

12 I used 1 m x 1 m x 1 m herbivore exclusion cages to assess how herbivory influences vegetation
13 change in glades, specifically *Pennisetum* invasion into *Cynodon*-dominated areas. Most
14 intermediate-aged and older glades contain large patches of *Cynodon*-dominated areas
15 surrounded by a *Pennisetum*-dominated invasion front. In five of these glades one grazed and
16 one ungrazed (caged) plot were randomly located along the *Cynodon-Pennisetum* boundary. All
17 plots were located to include three zones: *Cynodon*-dominated community, *Pennisetum*-
18 dominated community, and the transition zone between the two communities (Fig. 1b).
19 Throughout the experiment a 10-cm vegetation-free buffer was maintained around each plot (by
20 removing above-ground vegetation) to prevent encroachment from outside. The five grazed plots
21 were left open to grazing, and five ungrazed plots were caged with chicken wire mesh (4 cm
22 diameter holes) to exclude larger vertebrate herbivores. The lower third of the cage was covered
23 with 30 cm tall hardware cloth (0.5 cm mesh) to also exclude the dominant rodent, *Saccostomus*

1 *mearnsi*. This species strongly prefers foraging on forbs over grasses (Metz and Keesing, 2001).
2 However, it also can clip grasses and create tunnels through vegetation, particularly in enclosure
3 cages where dense stands of grass provide cover from predators (personal observation).

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

11

12 2.7 Statistical analyses

13 The following vegetation and soil chronosequence MANOVA and ANOVA analyses were
14 treated as split-plot designs, testing main plot effects of glade age class (young, old) and subplot
15 effects of distance from glade (in, edge, out). Grass cover values (*Cynodon* and *Pennisetum*)
16 were response variables in a MANOVA, and following significant MANOVA results, *Cynodon*
17 and *Pennisetum* were analyzed separately in protected univariate ANOVAs. This procedure of
18 MANOVA, followed by protected univariate ANOVAs was repeated for species richness (grass
19 and forbs), texture (sand, silt, and clay), and soil properties (all other soil properties in Table 1).
20 The 2008 N and P soil data were not treated as a split-plot design, but were analyzed in a one-
21 way ANOVA of glade age (3 levels: young, old, non-glade) effects on total N and P.

22 Chronosequence dung data were analyzed in the same split-plot design described above,
23 except sampling period (June 05, March 06, June 06, March 07) was added as a repeated factor,

1 and “edge” was omitted from the distance category (since dung was not counted at that distance).
2 Total wildlife dung (i.e., all species pooled) and individual ungulate herbivore species were
3 analyzed in separate ANOVAs. Oryx and hartebeest were pooled into one category because their
4 sample numbers were low and their body size and feeding habits are similar (Estes, 1992).

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

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

19

20 **3. Results**

21 *3.1 Chronosequence: vegetation*

22 Herbaceous vegetation cover varied with respect to glade age and proximity to glade (age:
23 Wilk’s $\lambda = 0.28$, $F_{2,7} = 9.15$, $p = 0.011$; location: Wilk’s $\lambda = 0.23$, $F_{4,30} = 8.21$, $p = 0.0001$;

1 age*distance: Wilk's $\lambda = 0.34$, $F_{4,30} = 5.34$, $p = 0.0023$). Herbaceous vegetation inside young
2 glades was dominated by the stoloniferous perennial grass, *Cynodon plectostachyus* (Fig. 2a),
3 whereas old glade vegetation was dominated by the perennial bunchgrass, *Pennisetum*
4 *stramineum* (Fig. 2b). Although *Cynodon* cover was higher inside glades of both ages, its cover
5 was three times greater in young than old glades (age*distance: $F_{2,14.3} = 5.16$, $p = 0.02$). *Cynodon*
6 was rare outside glades (15 - 60 m away: mean 4.3 ± 3.3 % cover, Fig. 2a) and absent from
7 background vegetation. *Pennisetum* cover was two to three times higher inside old glades than
8 outside (age*distance: $F_{2,24} = 8.35$, $p = 0.0018$). Cover values of all other species were too low
9 for statistical analyses.

10 In glades, mean grass species richness per m² was 3.1 ± 0.5 , and forb species richness
11 was 3.7 ± 0.8 . These values were significantly lower than outside (15 - 60m) of glades (grass:
12 6.7 ± 0.4 and forb 9.5 ± 0.9), and edges showed intermediate values (MANOVA distance effect
13 Wilk's $\lambda = 0.18$, $F_{4,30} = 10.37$, $p < 0.0001$; univariate distance effect for grass $F_{2,16} = 21.52$, $p <$
14 0.0001 ; forbs $F_{2,16} = 22.2$, $p < 0.0001$). Glades hosted at least seven specialist plant species. One
15 forb, *Tribulus terrestris*, and one grass, *Dactyloctenium aegypticum*, occurred only in glades,
16 regardless of age. Two forbs, *Medicago laciniata* and *Plectranthus* sp., and one grass species,
17 *Sporobolus pyramidalis*, occurred only in old glade quadrats, while introduced jimson weed,
18 *Datura stramonium*, occurred only in young glade quadrats. The forb *Hibiscus flavifolius*
19 occurred only in quadrats associated with old glades (inside, edge and outside).

20 The common grasses in background vegetation (other than *Pennisetum stramineum*) were
21 depressed or entirely absent inside glades; *Brachiaria* and *Lintonia* were never found inside
22 glades, and *Themeda* was found in only two of ten glades. *Pennisetum mezianum* occurred in all
23 outside plots, but occurred in only one young glade and two old glades. "Outside" plots were

1 dominated by the same five grass species that comprise 90% of the herbaceous cover in this
2 landscape (Young et al., 1998).

3

4 *3.2 Chronosequence: soil properties*

5 MANOVA results indicate that soil nutrient properties were significantly different inside glades
6 than elsewhere (Table 1; distance: Wilk's $\lambda = 0.06$, $F_{14,20}=4.42$, $p = 0.001$). Relative to outside,
7 soils inside glades were two times higher in organic matter ($F_{2,16.5} = 14.23$, $p = 0.0003$), and 1.5
8 times higher in potassium ($F_{2,9.94} = 12.73$, $p = 0.0018$). Soils inside glades were 3.5 times higher
9 in total % nitrogen (Table 1; $F_{1,12} = 12.62$, $p = 0.004$) and 6 times higher in total % phosphorus
10 (Table 1; $F_{1,12} = 47.63$, $p < 0.0001$). None of these soil properties differed significantly between
11 young and old glade soils (i.e., age effect $p < 0.05$). Although it was not higher inside glades,
12 cation exchange capacity (CEC) was 24% higher in young than old glades (age*distance: $F_{2,16} =$
13 4.38 , $p = 0.03$).

14 In comparison to outside glades, glade soils were 28% lower in Mg ($F_{2,16} = 7.47$, $p =$
15 0.005), 28% lower in Ca ($F_{2,16} = 12.35$, $p = 0.0006$) and 89% lower in Na ($F_{2,16} = 40.13$, $p <$
16 0.0001). In new glades, pH was non-significantly lower than outside (age*distance: $F_{2,11.5} = 3.04$,
17 $p = 0.09$). MANOVA results indicate soil texture was significantly different inside glades and
18 varied strongly with distance from glades (distance: Wilk's $\lambda = 0.32$, $F_{6,28} = 3.52$, $p = 0.01$;
19 age*distance: Wilk's $\lambda = 0.68$, $F_{6,28} = 0.99$, $p = 0.45$). Most notable was the moderate clay
20 content found inside glades (30% clay) relative to the extremely high (50% clay) levels found in
21 outside plots ($F_{2,16} = 14.57$, $p = 0.0002$).

22

23 *3.3 Herbivore response to glades*

1 Dung count results (summed across species) suggest that herbivores prefer glade habitat (total
2 herbivore dung density inside: 79.7 ± 7.9 , outside: 37.6 ± 3.8 ; $F_{1,20.6} = 19.12$, $p = 0.0003$), and this
3 effect was most pronounced in young glades during dry times (distance*age*sampling period:
4 $F_{3,49.7} = 5.76$, $p = 0.0018$). During the dry season (March), total wildlife herbivore dung was
5 higher in young glades relative to outside transects, but only significantly (12 times higher)
6 during the second sampling year. This seasonal pattern was strongest for Grant's gazelles and
7 zebras (distance*age*sampling period: Grant's gazelle $F_{3,47.6} = 3.88$, $p = .014$, zebra $F_{3,44.5} = 3.37$,
8 $p = 0.027$; Tukey HSD $p < 0.05$; Fig. 3). Elephants also were associated with young glades for all
9 sampling periods (distance*age $F_{1,8.13} = 5.94$, $p = 0.04$, Tukey HSD $p < 0.05$, Fig. 3). Oryx and
10 hartebeest favored glades over non-glades (distance $F_{1,15.2} = 4.57$, $p = 0.049$), preferring young
11 glades during the second year (age*sampling period $F_{3,24.9} = 3.38$, $p = 0.034$, Tukey HSD $p <$
12 0.05 , Table 2). Cattle also were associated with young glades (age*distance $F_{1,6.37} = 11.51$, $p =$
13 0.013 , Tukey HSD $p < 0.05$, Fig. 3), but preferred glades of all ages during wet times
14 (distance*sampling period $F_{3,15.1} = 4.25$, $p = 0.023$). The second sampling year (2006-2007) was
15 unusually wet; the six months preceding the March 2007 dry season received more than double
16 the rainfall of the six months preceding March 2006 (T.P. Young, unpublished results).

17

18 3.4 *Effects of herbivore exclusion on vegetation*

19 The 1 m x 1 m plots set up to investigate large herbivore effects on succession revealed
20 significant herbivore effects, which varied according to community zone within the plot (i.e.,
21 *Cynodon* community, *Pennisetum*-dominated community or transition zone) (grazing: Wilk's $\lambda =$
22 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,
23 large herbivores had little influence on *Cynodon* cover. *Cynodon* consistently decreased in cover

1 (i.e., cover change < 0) over the 3-year course of the experiment, regardless of herbivore
2 exclusion treatment (Fig. 4a). One exception was in the *Pennisetum* zone where grazing
3 sometimes increased *Cynodon* cover. Herbivore exclusion decreased *Cynodon* growth by 156 %
4 ($F_{1,7.38} = 10.66$, $p = 0.01$) and increased *Pennisetum* growth by 343% ($F_{1,19} = 35.63$, $p < 0.0001$,
5 Fig. 4). The difference in crown height between *Pennisetum* and *Cynodon* (and potential for
6 shading) was greater when grazers were excluded (5.0 ± 3.5 cm grazed, 14.0 ± 4.2 cm ungrazed,
7 $F_{1,16.7} = 4.04$, $p = 0.06$). Grazing removal also promoted *Pennisetum* invasion into *Cynodon*
8 zones; when grazers were excluded, *Pennisetum* invaded and its cover increased threefold in the
9 *Cynodon* zone (grazing*zone: $F_{2,18.9} = 23.71$, $p < 0.0001$, Fig. 4b). In contrast, grazing decreased
10 *Pennisetum* growth in the *Cynodon* zone (significant grazing*zone, Tukey HSD grazed vs.
11 ungrazed, $p < 0.05$). Mean differences in the transition zone, though non-significant, also
12 suggest that *Pennisetum* growth increased under grazing exclusion (Fig. 4b).

13

14 **4. Discussion**

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

1 successional stage that is highly palatable to grazers.

2

3 *4.1 Glades as long-term nutrient hotspots*

4 Historic aerial photos indicate that treeless glades in the Laikipia black cotton ecosystem persist

5 for at least four decades, their distinctive vegetation communities initially dominated by

6 *Cynodon plectostachyus* and gradually replaced by *Pennisetum stramineum*. The herbaceous

7 plant species composition only sixty meters outside of glades was qualitatively similar to

8 composition in non-glade (>150 m away) background vegetation sampled six months later (T. P.

9 Young, unpublished results), consistent with the results of Porensky (2011). The only exception

10 was the low presence of *Cynodon*, which was virtually absent in background vegetation.

11 Dominance by *Cynodon* species appears to be characteristic of treeless glades across a

12 diversity of ecosystems in eastern Africa, including nearby areas of similar rainfall but different

13 soil types (Stelfox, 1986; Young et al., 1995), and dryer and wetter areas of different soil types

14 elsewhere in East Africa (Treydte et al., 2006; Muchiru et al., 2009). Although plant species

15 richness is lower inside than outside glades, glades increase species richness at the landscape

16 level by supporting *Cynodon* and other species that are otherwise rare or absent in the

17 background landscape. Glades also demarcate original corral sites. In southern Africa, distinctive

18 vegetation communities identify former corral sites for hundreds of years post-abandonment

19 (Blackmore et al., 1990), and interviews with local inhabitants in my study system suggest that

20 boma sites are recognizable more than a century after abandonment (K. Veblen, unpublished

21 results).

22 Nitrogen, phosphorus and potassium levels remained elevated in glade soils over the >40-

23 year time-span identified in this study. Elevated nutrient levels, attributable largely to intense

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

18 Patterns of calcium, magnesium and sodium contrasted strongly with those observed in
19 other ecosystems. Whereas other studies have found Ca, Mg and Na levels in former boma sites
20 to be equal to or greater than non-boma sites (Blackmore et al., 1990; Augustine, 2003; Muchiru
21 et al., 2009), levels of these nutrients to be lower in black cotton boma sites. Even more
22 strikingly, this is the first report of a difference in texture (decreased clay) in old boma sites
23 (Augustine, 2003; Scholes and Walker, 2004; van der Waal et al., 2011). This result is surprising

1 because soil texture is considered a relatively static property and should not be affected by
2 livestock or wildlife activity (Brye, 2003 and references therein). Significant soil textural
3 changes would be expected to have important long-term consequences (in contrast to changes in
4 nutrient levels which could return to baseline levels over time). One potential explanation for
5 altered soil texture may be that densities of termite mounds, which cover ~20% of the landscape
6 (Fox-Dobbs et al., 2010), are twice as high in glades (K.Veblen, unpublished results). Termites
7 alter soil texture, often concentrating clay particles in sandy soils (Konate et al., 1999; e.g.,
8 Grube, 2001). In this clay-rich black cotton study system, termites reduce clay content, possibly
9 by importing sand particles (Fox-Dobbs et al., 2010). Termites also reduce Mg, Ca and Na (T.M.
10 Palmer, unpublished results). Lowered clay content decreases surface area for cation adhesion,
11 and increased sand content and bioperturbation may enhance soil drainage and leaching of
12 cations such as Ca, Mg, and Na. Further work is needed to elucidate any spatial and/or
13 developmental relationships between glades and termites.

14

15 *4.2 Glades as herbivore hotspots*

16 Abandoned livestock corrals were hotspots for large herbivores in this ecosystem, a pattern of
17 habitat use observed elsewhere in eastern and southern Africa (Young et al., 1995; Augustine,
18 2004; Scholes and Walker, 2004; Muchiru et al., 2008; van der Waal et al., 2011). Nutrient
19 enrichment is known to attract grazers to non-boma-derived hotspots (McNaughton, 1988;
20 McNaughton et al., 1997; Anderson et al., 2010; Stock et al., 2010), suggesting that elevated soil
21 N, P and K levels may be at least partially responsible for the hotspot effect of glades in this
22 system. At a nearby sandy loam site in central Kenya, glade vegetation appears to provide a
23 critical source of phosphorus, a nutrient that occurs at much lower levels in the background

1 vegetation (Augustine, 2003; Augustine, 2004).

2 Herbivore preference for glade habitat may be further reinforced by the maintenance of
3 vegetation in a more nutritious state. Just as herbivory maintains grazing lawns across sub-
4 Saharan Africa (McNaughton, 1984; Verweij et al., 2006; Waldram et al., 2008), it appears to
5 maintain young glades in my study system in a short-grass state. *Cynodon plectostachyus*, which
6 dominates young glades but is rare elsewhere, is a preferred forage species (Pratt and Gwynne,
7 1977) and is well-adapted to grazing by way of its prostrate growth form and tolerance to
8 trampling (McNaughton, 1984; Georgiadis and McNaughton, 1988). Grazing stimulates new
9 shoot growth and likely results in higher foliar nutrient (Coetsee et al., 2011 and references
10 therein).

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

19 Although glade habitat in general was preferred by wild herbivores, the effect appeared to
20 be most pronounced during the dry season. It should be noted, however, that the weaker pattern
21 during the wet season may be a result of more rapid dung decomposition during wet times.
22 Nonetheless, the comparison of inside versus outside indicates clear herbivore preference for
23 glades during the dry season. This pattern has been observed in other African savannas (Scholes

1 and Walker, 2004, but see Augustine 2004; Muchiru et al., 2008) and may be attributable to
2 glade vegetation characteristics during the dry season. In Tanzania, Treydte et al. (2006) found
3 that dry season crude protein levels were higher in herbaceous glade vegetation than in
4 surrounding vegetation, and in southern Africa (Grant and Scholes, 2006) found that foliar
5 phosphorus associated with termite mound hotspots remained elevated throughout the dry
6 season. Similarly, in my study system, glade vegetation stays green longer into the dry period
7 than surrounding vegetation and becomes lush and green more quickly at the onset of rainy
8 periods (K. Veblen, personal observation). Together, these lines of evidence suggest that former
9 boma sites may provide important 'dry season refuges' (sensu Ilius and O'Connor, 2000), where
10 large herbivores can obtain nutritious forage during dry periods.

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

18

19 *4.3 Feedbacks between glades and large herbivores*

20 These results from black cotton soils provide experimental evidence that large herbivores may
21 influence succession and vegetation development associated with abandoned livestock bomas.
22 Although progression from *Cynodon* to *Pennisetum* dominance always occurred eventually
23 (regardless of herbivory), grazing slowed that process (i.e., grazing removal accelerated

1 *Pennisetum* invasion). Given the long-term patterns of *Pennisetum* invasion (Fig. 2), it is
2 unlikely that grazing changes the overall trajectory of vegetation development in glades.
3 However, the presence of grazers may reduce the rate of *Pennisetum* invasion and lengthen the
4 time period that vegetation is maintained in a desirable *Cynodon* state, further attracting grazers.

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

11 Evidence from a variety of ecosystems suggests two primary pathways for herbivores to
12 affect plant community dynamics: plant tolerance to herbivory and herbivore selectivity
13 (Augustine and McNaughton, 1998). First, plant species vary in their tolerances to herbivory
14 (Hawkes and Sullivan, 2001), and my results suggest that grazing of less tolerant *Pennisetum* at
15 least partially suppressed its ability to competitively displace more tolerant *Cynodon*. As
16 discussed above, *Cynodon* is grazing-tolerant and maintained in short-statured monocultures by
17 heavy grazing. *Pennisetum stramineum*, on the other hand is a superior competitor (Veblen,
18 2008), but appears to be less grazing-tolerant. Second, herbivores can benefit one plant species
19 by preferentially foraging on its competitor(s) (e.g., Veblen and Young, 2010). Zebra, the
20 dominant wildlife grazers in this system, show preference for *Pennisetum* (Young et al., 1995)
21 and may therefore play an important role in suppressing the rate of *Pennisetum* displacement of
22 *Cynodon* and contribute to the longer-term persistence of *Cynodon* in glades.

23 Herbivores also may indirectly influence glade plant succession through soil feedbacks

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

10

11 *4.4 Conclusion*

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

18 Nutrient hotspots play a potentially important role in wildlife conservation (Grant and
19 Scholes, 2006). However, cattle-derived nutrient hotspots in particular may be especially
20 important because they constitute a largely positive example of a system in which livestock and
21 wildlife can synergistically share the landscape. Arguably, multi-use rangelands, shared by
22 livestock and wildlife, are at the heart of future successes in savanna conservation. My results
23 also suggest that large herbivores, and their management, have the potential to exert control over

1 the long-term persistence of the glade mosaic. Thus, if glade-like landscape features are found to
2 be of local conservation value, active management of livestock or livestock-to-wildlife ratios
3 could potentially be used as a tool for maintaining glade habitat for wildlife species. Thus,
4 further investigation into the effects of livestock and large herbivore wildlife on glade
5 development is warranted.

6

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1 **Table 1.** Mean (\pm 1SE) values of soil properties associated with young (n=5) and old (n=5) glades derived from abandoned cattle
2 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
3 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 \pm 0.14	-	0.16 \pm 0.0067	0.61 \pm 0.18	-	0.16 \pm 0.0067
P (%)	0.10 \pm 0.017	-	0.019 \pm 0.0013	0.13 \pm 0.019	-	0.019 \pm 0.0013
OM (%)	13.87 \pm 2.08	8.12 \pm 1.56	5.03 \pm 0.29	7.41 \pm 0.65	7.3 \pm 0.79	5.24 \pm 0.37
K (ppm)	1321.17 \pm 258.68	1162.68 \pm 142.65	808.6 \pm 26.73	1230.51 \pm 36.41	1173.43 \pm 70.15	854.03 \pm 37.37
Mg (ppm)	535.55 \pm 73.7	638.68 \pm 66.49	724.15 \pm 22.47	498.28 \pm 34.85	559.48 \pm 49.78	699.75 \pm 76.52
Ca (ppm)	1905.12 \pm 192.69	2217.68 \pm 215.63	2470.38 \pm 189.17	1866.71 \pm 83.27	2522.7 \pm 263.52	2756.6 \pm 238.35
Na (ppm)	25.25 \pm 7.51	69.8 \pm 12.92	170.33 \pm 20.49	14.27 \pm 1.45	34.55 \pm 13.76	139.17 \pm 28.83
CEC (meq/100g)	24.55 \pm 0.78	24.54 \pm 1.68	24.47 \pm 0.78	19.8 \pm 0.41	24.47 \pm 1.24	25.69 \pm 2.06
pH	6.34 \pm 0.19	6.49 \pm 0.11	6.59 \pm 0.03	6.63 \pm 0.03	6.52 \pm 0.05	6.58 \pm 0.03
Sand (%)	47.94 \pm 6.34	35.04 \pm 2.98	28.81 \pm 2.27	39.92 \pm 2.15	33.94 \pm 1.08	29.04 \pm 2.83
Silt (%)	21.48 \pm 1.72	22.27 \pm 2.07	18.43 \pm 1.3	29.91 \pm 1.07	25.48 \pm 0.89	23.55 \pm 2.64
Clay (%)	30.57 \pm 5.1	42.69 \pm 4.85	52.76 \pm 3.1	30.17 \pm 1.85	40.59 \pm 1.82	47.41 \pm 5.35

4

1 **Figure captions**

2 **Figure 1.**

3 Glade sampling (a) occurred along transects extending from glade center to 60 m beyond glade
4 edge (x's indicate sampled distances). Experimental 1 m x 1m plots (b) were divided into three
5 zones (*Cynodon* community, transition zone, and *Pennisetum* community), and nine pin frames
6 (dashed lines) were placed 10 cm apart across the plot.

7

8 **Figure 2.**

9 Mean (± 1 SE) aerial cover of *Cynodon plectostachyus* (a) and *Pennisetum stramineum* (b) in
10 five young glades and five old glades at three distances (inside, edge and outside of glades). For
11 each species, shared letters indicate no significant differences at the $p = 0.05$ level, according to
12 Tukey's HSD.

13

14 **Figure 3.**

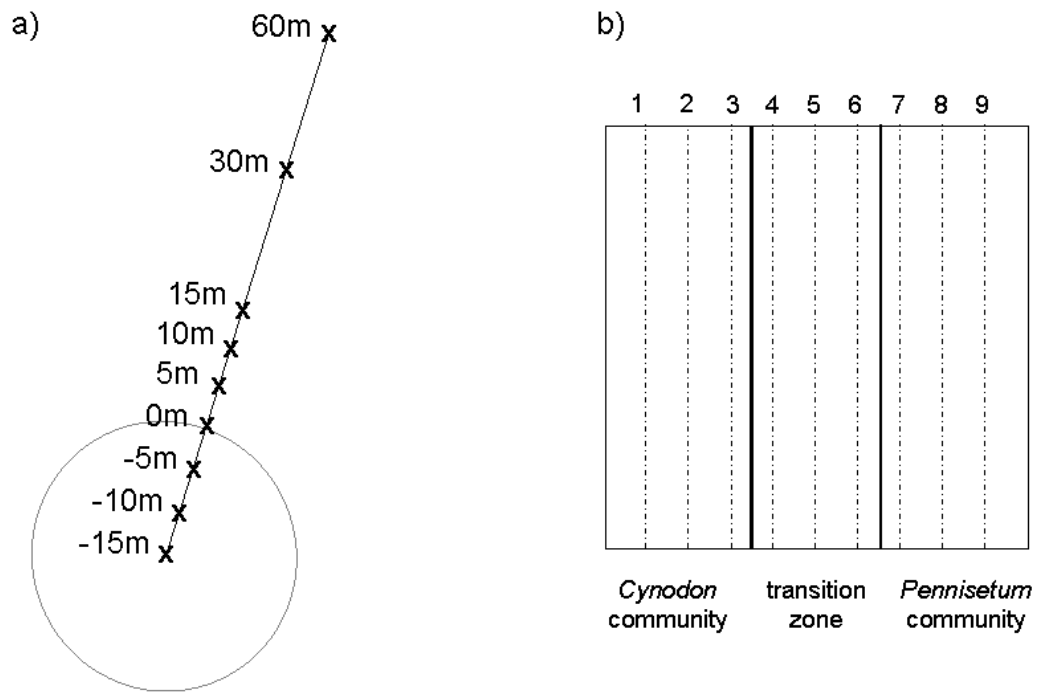
15 Herbivore dung densities (± 1 SE) at two distances (inside and 200m outside) from young glades
16 ($n=5$) and old glades ($n=5$) in two wet seasons (June 2005 & 2006) and two dry seasons (March
17 2006 & 2007). Asterisks indicate significant Tukey HSD ($p < 0.05$) comparisons of in/out when
18 there was a significant distance*age*sampling period effect for an herbivore species. Note
19 different scales across species.

20

21 **Figure 4.**

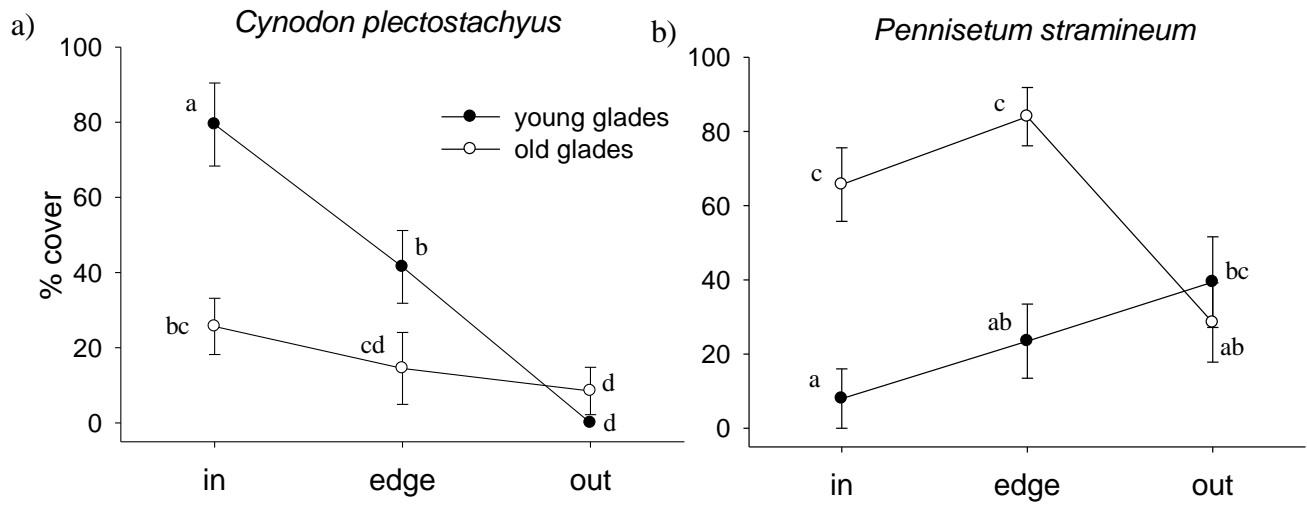
22 Mean (± 1 SE) changes (calculated as [final pin hits minus initial pin hits] / [initial pin hits]) in
23 *Cynodon plectostachyus* and *Pennisetum stramineum* cover in five glades, after three years, in

- 1 response to two factors: 1) grazing (presence/absence) and 2) location within a 1x1 m plot
- 2 (*Cynodon* community/transition zone/*Pennisetum* community).
- 3



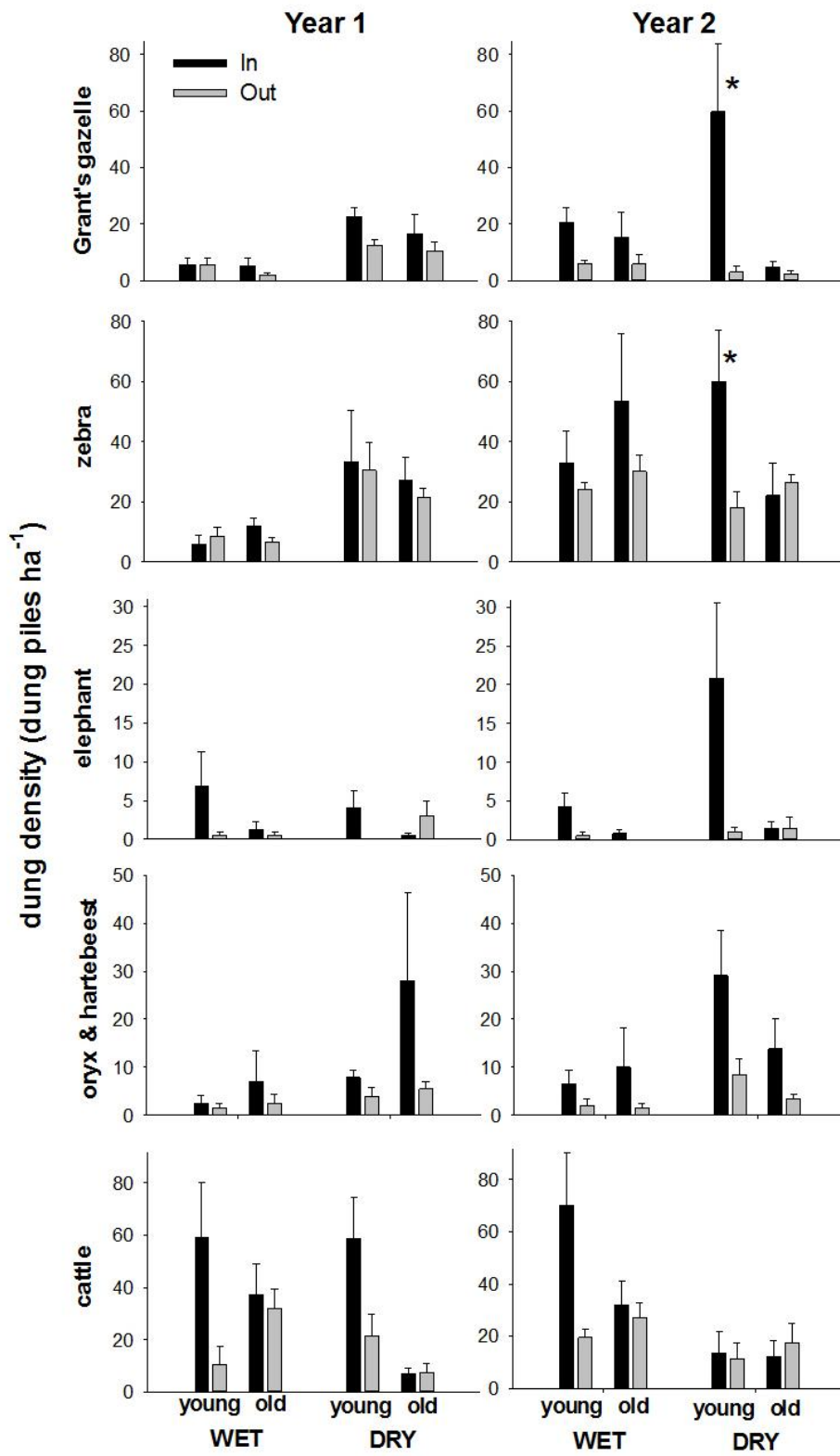
1
2 **Figure 1.**

3



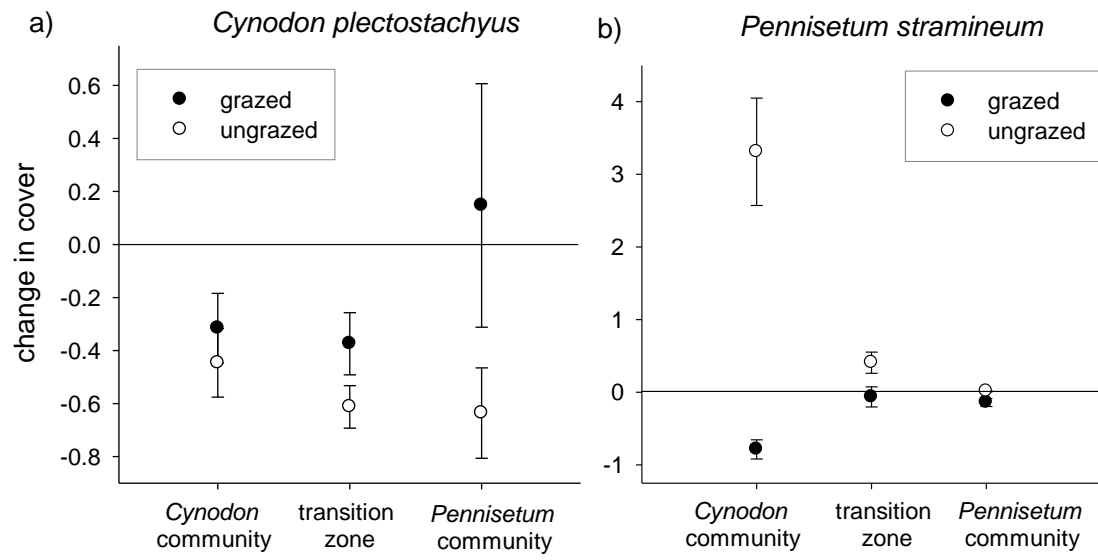
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Figure 2.



1

2 **Figure 3.**



1

2 **Figure 4.**

3