Generation of Ecosystem Hotspots Using Short-Term Cattle Corrals in an African Savanna ☆, ☆☆, ★

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Generation of Ecosystem Hotspots Using Short-Term Cattle Corrals in an African Savanna ☆,☆☆,★

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A B S T R A C T

Worldwide, many rangelands are managed for multiple uses, and it is increasingly important to identify livestock management practices that maximize rangeland productivity, biodiversity, and wildlife conservation. In sub-Saharan Africa, pastoralists and ranchers use temporary thorn-fence corrals ("bomas") to protect livestock at night. Traditional boma sites (used for months or years, then abandoned) develop into productive ecosystem hotspots ("glades") that attract diverse wildlife and persist for decades or even centuries. In central Kenya, livestock managers have recently begun using metal-fenced "mobile bomas," which are moved after only days or weeks. Although the assumption is that mobile boma sites will also develop into glades, whether or not this is true remains unclear. We used a broad-scale manipulative experiment to evaluate the ecosystem-level effects of mobile bomas used for 1 month. We also investigated impacts of initial boma density on glade development. We randomly assigned 12 plots to one of three density treatments: one boma, two bomas 200 m apart, or two bomas 100 m apart. Before the experiment and at 1, 6, 12, 18, and 32 months after boma abandonment, we sampled soil nutrients, foliar nutrients, plant communities, and wildlife use (via dung counts) within abandoned boma sites (experimental glades) and at paired reference sites (200 m away). After 18 months, surface soil nutrient concentrations in experimental glades were similar to those in traditionally formed glades. Experimental glade plant communities became dominated by a palatable, rhizomatous grass species, *Cynodon plectostachyus*. After 32 months, wildlife use by browsing and mixed feeding ungulates was 9 times higher in experimental glades than at paired reference sites. Boma density had few impacts on within-glade development patterns. These results demonstrate that by concentrating livestock in short-term corrals, managers can create ecosystem hotspots that increase functional heterogeneity, attract wildlife, and provide palatable forage for livestock.

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Introduction

Rangelands worldwide are increasingly being managed for multiple ecosystem services, often including both livestock production and wildlife conservation. Management of the livestock that dominate many of these systems can have long-term impacts, including shifting ecosystems across thresholds into alternative ecological states. A common example is bush encroachment, wherein heavy or prolonged livestock grazing can lead to increases in woody plant cover (Scholes and Archer, 1997; Coetzee et al., 2008). Recently, however, some attention has focused on how livestock can be used as a tool to achieve restoration and conservation objectives; for example, by rejuvenating sagebrush for sage-grouse habitat improvement (Dziba et al., 2007; Petersen et al., 2014); increasing plant diversity in ephemeral wetlands (Marty, 2005); or reducing undesirable invasive annual grass cover and associated fire risk (Diamond et al., 2009; Workgroup, 2010). In sub-Saharan Africa, centuries-long traditional livestock husbandry practices lead to the creation of ecological hotspots with high nutrient availability, high productivity, unique plant communities, and preferential use by wildlife (Blackmore et al., 1990; Reid and Ellis, 1995; Young et al., 1995; Augustine et al., 2003; Treydte et al., 2006b; Muchiru et al., 2009; Söderström and Reid, 2010; van der Waal et al., 2011; Veblen, 2012; Donihue et al., 2013). Here we investigate the conditions necessary to create

these hotspots and follow their initial development over 2.5 years in order to learn how livestock can be used as a tool for increasing long-term rangeland productivity and biodiversity.

Across eastern and southern Africa, livestock are traditionally kept in thorn-fence corrals, or "bomas," at night for protection against predation and theft (Western and Dunne, 1979; Blackmore et al., 1990). Traditional bomas range from 10 to more than 100 m in diameter and are used for months or years before being abandoned (Blackmore et al., 1990; Augustine, 2003; Muchiru et al., 2009; Söderström and Reid, 2010; van der Waal et al., 2011; Veblen, 2012). The accumulated

dung layer (which can be more than 50 centimeters deep: Augustine, 2003; Muchiru et al., 2009; Veblen, 2012) results in large amounts of nitrogen, phosphorus, organic carbon, and other nutrients being concentrated at abandoned sites (Reid and Ellis, 1995; Augustine, 2003; Augustine et al., 2011; van der Waal et al., 2011; Veblen, 2012). Livestock disturbance and associated dung deposition have lasting effects on the vegetation that establishes at these sites (e.g., Stelfox, 1986; Reid and Ellis, 1995; Young et al., 1995; Muchiru et al., 2009; van der Waal et al., 2011; Veblen, 2012; Vuorio et al., 2014). Similar patterns have been observed in North America, where temporary sheep
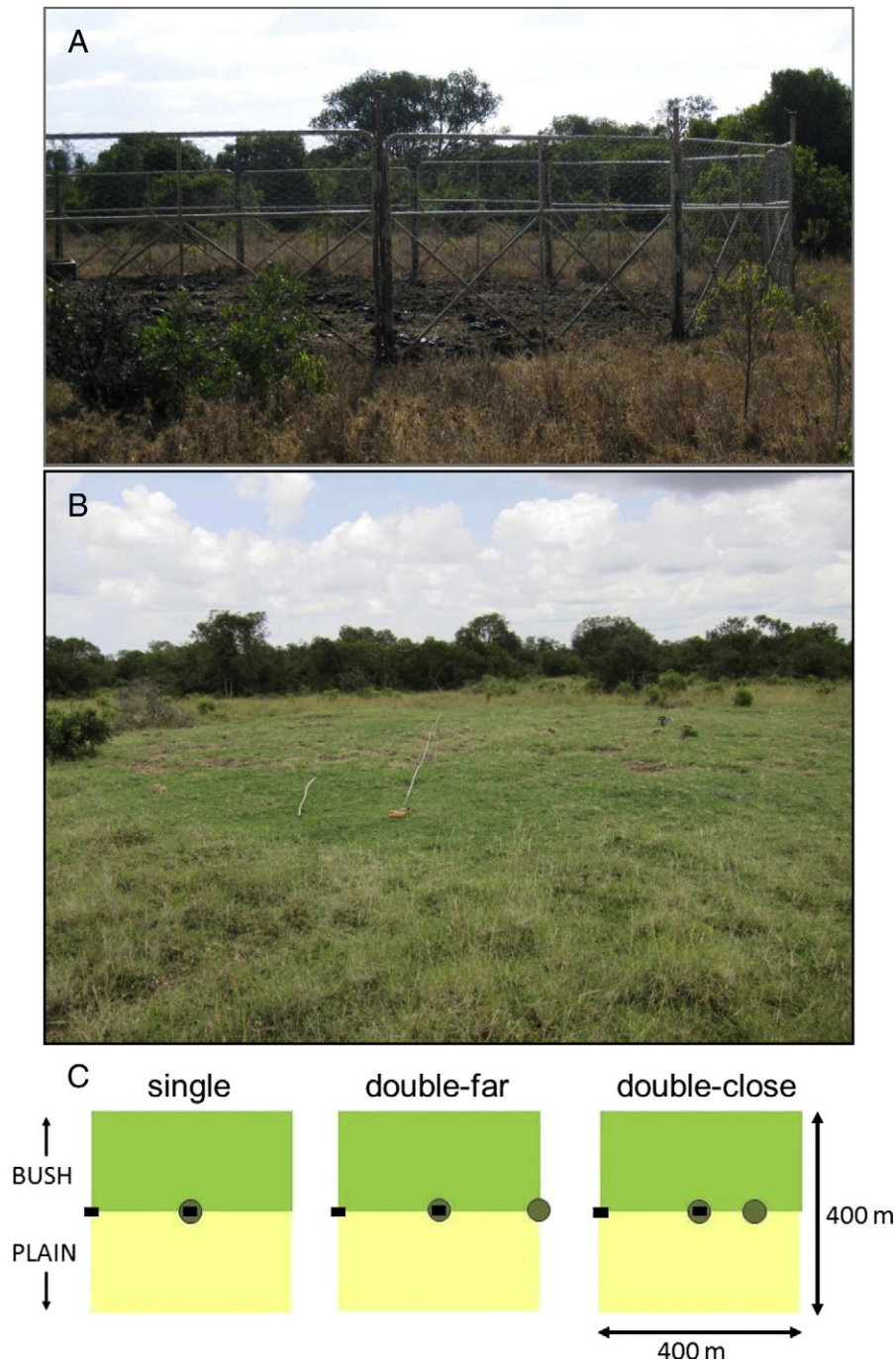

Fig. 1. A, Metal-fenced bomas protect livestock from predators and are easy to move. B, Experimental boma site 32 months after abandonment. C, Sampling design. Circles represent experimental boma sites (17.4 ± 0.7 m in diameter), and small rectangles represent 8 × 14 m sampling subplots.

bedding sites develop into sites with more available nutrients and distinctive plant communities (Leytem and Seefeldt, 2008; Seefeldt and Leytem, 2011).

In central Kenya, abandoned boma sites develop into treeless, lawn-grass-dominated, highly productive and nutrient-rich "glades" that persist for at least 50 years (Augustine, 2003; Augustine et al., 2003, 2011; Veblen, 2012) through a combination of legacy effects and animal-mediated feedbacks (e.g., Augustine et al., 2003; Veblen and Young, 2010; Porensky and Veblen, 2012; Veblen, 2012). In this region, novel livestock management practices have prompted increased interest in the process of glade development. Livestock managers have recently developed metal-fenced bomas (Fig. 1A and B) designed to better protect livestock against lion predation. These metal-fenced bomas have the added advantage of being highly portable. The so-called "mobile bomas" (or "predator-proof bomas") are now moved after only days or weeks (rather than months or years) so that livestock can access new forage. It is unclear whether managers can successfully use mobile bomas (which are occupied for 1 month or less) to create glades similar to those formed by traditional boma management. Augustine (2003) calculated that more than a year of nightly cattle dung deposition would be necessary to generate nitrogen concentrations comparable with those observed in the surface soils of recently abandoned bomas, and even more time would be required to concentrate the requisite amount of phosphorus. However, local knowledge (collected via structured interviews) suggests that some traditional bomas, which subsequently converted to glades, were used for less than a year (KEV, unpublished data). At sites used for relatively short amounts of time, wildlife may facilitate glade conversion by continuing to deposit nutrients on abandoned boma sites (Augustine et al., 2003; van der Waal et al., 2011; Veblen, 2012).

Because of strong edge effects around abandoned boma sites, boma density may affect glade development. Glades that developed from traditional bomas have edge effects that can extend at least 100 m into the surrounding savanna landscape (Young et al., 1995; Muchiru et al., 2009; Söderström and Reid, 2010; Porensky, 2011; Veblen, 2013; Vuorio et al., 2014; but see Reid and Ellis, 1995), and previous work suggests that these edge effects are influenced by the presence of other, nearby glades (Porensky, 2011; Donihue et al., 2013). In particular, areas between glades that are 150 to 200 m apart (center-to-center) tend to have higher densities of small trees, less cover of glade-specialist grass, and less animal use (Porensky, 2011; Donihue et al., 2013). However, it remains unclear whether these patterns are driven by the density of glades or by some other correlated factor (e.g., herders selectively placing more bomas in sites with more small trees). In addition to influencing ecological patterns between glades (e.g., via increased animal traffic between sites), glade density may influence patterns within glades (e.g., by concentrating higher animal use on the nutrient-rich glade site itself). Therefore, we expected the development of abandoned mobile boma sites to be altered by the presence and proximity of other nearby bomas.

The experiment addressed two specific research hypotheses. First, we hypothesized that short-term mobile boma sites would develop into glades (nutrient-enriched hotspots with unique plant communities that are attractive to wildlife). Second, we hypothesized that bomas separated by a small distance (e.g., 100 m) would develop stronger glade-like characteristics (i.e., higher nutrients, wildlife use, glade-specialist plant cover) than bomas separated by a larger distance.

Methods

Study Site

The study took place at Ol Pejeta Conservancy (36.87°E, 0.04°N), a 36 500 ha property managed both for cattle production and wildlife conservation. The Conservancy, located at the southern edge of Kenya's Laikipia plateau (~1800 m asl), experiences a semiarid to mesic climate with an average annual rainfall of 700 to 900 mm (Wahungu et al., 2011). In addition to ~6 000 Boran cattle, the Conservancy hosts a wide variety of native herbivore species, including zebra *(Equus burchelli),* hare *(Lepus capensis),* impala *(Aepyceros melampus),* giraffe *(Giraffa camelopardalis reticulata),* elephant *(Loxodonta africana),* African buffalo *(Syncerus caffer),* Grant's gazelle *(Nanger [Gazella] granti),* eland *(Taurotragus oryx),* hartebeest *(Alcelaphus buselaphus),* warthog *(Phacochoerus africanus),* Thompson's gazelle *(Eudorcas [Gazella] thomsonii),* common duiker *(Sylvicapra grimmia),* and waterbuck *(Kobus ellipsiprymnus).* The Conservancy is also home to healthy predator populations (including lion, hyena, cheetah, and leopard) and several rare or endangered herbivores, including black rhinoceros *(Diceros bicornis),* Grevy's zebra *(Equus grevyi),* and white rhinoceros *(Ceratotherium simum;* olpejetaconservancy.org).

Dominant plant communities at Ol Pejeta Conservancy include treeless plains (on sandier soils), open savannas dominated by the tree *Acacia drepanolobium* Harms ex Sjöstedt (on intermediate soils), and dense bushlands co-dominated by the shrub species *Euclea divinorum* Hiern, *Scutia myrtina* (Burm. f.) Kurz, and *Rhamnus staddo* A. Rich. (on clay-rich soils). Within this mosaic, plains serve as important foraging areas for domestic and wild herbivores and are dominated by five grass species: *Themeda triandra* Forssk., *Pennisetum stramineum* A. Peter, *Pennisetum mezianum* Leeke, *Cynodon plectostachyus* (K. Schum.) Pilg., and *Sporobolus nervosus* Hochst. It is unclear whether plains remain treeless because of soil properties, land use history (e.g., very old boma sites), heavy use by herbivores, or some combination of these and other factors. In savannas and bushlands, conservancy managers are interested in protecting and encouraging *A. drepanolobium,* which provides palatable forage for black rhinoceros (Wahungu et al., 2011). Seedling survival and recruitment of this species are currently very low due to heavy browsing (Wahungu et al., 2011). In contrast, managers are interested in limiting the spread of several undesirable shrubs (e.g., *E. divinorum).* This study therefore assessed the long-term impacts of bomas on *A. drepanolobium* trees and shrubs.

Experimental Design

Within a 10×15 km study region we chose twelve 400×400 m plots. Plots were randomly located along preexisting boundaries separating bushland or savanna areas (>10% canopy cover) from large, open plains (<10% canopy cover; Fig. 1). Plots were separated by at least 600 m center to center. Each plot was located > 500 m from existing bomas or glades to avoid any potential interference from preexisting features (Porensky, 2011). Plots were randomly assigned to and equally distributed among three density treatments: one mobile boma ("single" treatment), two mobile bomas 200 m apart center to center ("double-far" treatment), or two mobile bomas 100 m apart center to center ("double-close" treatment; Fig. 1C).

From February to March 2009 (at the end of the dry season), each boma (mean diameter = 17.4 m) within each plot was used by approximately 200 cows for 1 month and then abandoned. During the month of use, herders slept in portable houses adjacent to each boma. During daylight hours, herders directed cattle to grazing areas within a half-day's walk of the boma(s). At double-close and double-far plots, the two herds of 200 head were managed as separate units but often grazed in the same general area. Salt was the only dietary supplement provided. All experimental plots were less than 2 km from water. One month of occupancy was chosen as a compromise between traditional management, in which each boma is occupied for months to years, and modern management, in which each

boma is occupied for days to weeks. Hereafter, abandoned experimental boma sites are called "experimental glades" to distinguish them from the glades (well-established ecosystem hotspots) described in previous observational studies (e.g., Veblen, 2012). For the duration of the study (32 months), livestock managers did not create any additional bomas within 600 m of the center of any plot, with one exception: we discontinued monitoring at one of the "single" plots after 12 months due to the placement of a new boma inside the plot. All plots were grazed periodically (at similar intensities) by cattle.

Data Collection

We measured vegetation and herbivore use (via dung counts) before initiating the experiment (Jan–Feb 2009 = "baseline" or 0 months), soon after abandonment (cattle dung and understory plants only, Feb–Mar 2009 = 1 month), and at 6 months (Aug–Sep 2009), 12 months (Feb–Mar 2010), 18 months (Aug–Sep 2010), and 32 months (Oct–Nov 2011) after abandonment. At 0 and 18 months, we also collected soil and plant samples. We collected data and samples at two 8×14 m subplots within each plot (Fig. 1C). One subplot was inside the experimental glade. The second subplot was 200 m away from the experimental glade, and we used this subplot as a plot-specific control, or "reference." In double-boma plots, the reference subplot was located in the direction opposite the second boma (Fig. 1C). Previous studies suggest glade edge effects rarely extend as far as 200 m (Reid and Ellis, 1995; Young et al., 1995; Muchiru et al., 2009; Porensky, 2011; Vuorio et al., 2014). Thus, we expect that our experimental bomas had minimal impacts on the ecology of reference subplots.

Within each subplot, we recorded the number of herbivore dung piles and the species of animal that produced each pile. During each survey, piles were crushed in place to prevent re-counting. We used dung counts to assay relative animal use. Across multiple studies and systems (Young et al., 1995; Barnes, 2001; Young et al., 2005), this approach has been shown to be effective in measuring spatial variation in animal distributions for a given site within a sampling period. Although cattle are far more abundant than buffalo at the study site, buffalo and cattle dung piles were indistinguishable. These two species were therefore lumped as "cattle + buffalo." Other wildlife species were classified as either "grazers" (zebra, hare, hartebeest, warthog, waterbuck, and white rhino) or "mixed feeders/browsers" (black rhino, duiker, elephant, eland, giraffe, Grant's gazelle, impala, oryx, steinbuck, and Thompson's gazelle).

In a 1×1 m quadrat placed at the center of each subplot, we visually estimated aerial percent cover by species for all vegetation present < 0.5 m above ground level (species were identified using Agnew and Agnew, 1994; Agnew, 2006). Percent cover and percent bare ground + litter totaled 100%. We counted all woody plant individuals (including *A. drepanolobium* and all other woody plants, the latter hereafter called "shrubs") rooted within each 8×14 m subplot. For each shrub individual, we recorded species identity.

We calculated species richness (number of species observed) and Shannon-Wiener species diversity (Shannon, 1948) for three communities present at each subplot: shrubs (calculated at the scale of 112 m^2 subplots), wild herbivores (calculated at the scale of 112 m^2 subplots), and understory plants (calculated at the scale of 1×1 m quadrats).

We collected four 10-cm-deep by 8-cm-diameter soil cores within each subplot. Each core was taken 2 m from the center of the subplot (N, E, S, and W directions were used for the baseline survey, while NE, NW, SE, and SW directions were used for the 18-month survey). During the 18-month survey, we observed that dung had been incorporated into boma surface soil and was no longer visible as a distinct

layer. Despite this evidence of mixing, our 18-month boma soil samples probably included a combination of partially decomposed manure and soil. Within each subplot, soil from the four cores was mixed together, and a subsample of the homogenized material was extracted for analysis. Samples were dried in a solar-powered oven at approximately 80–90°C. Roots > 1 mm in diameter were removed before analysis.

To sample plant nutrient quality at each subplot, we harvested material (>10 g dried) from each grass species with > 5% aerial cover in the 1×1 m quadrat located at the subplot center. Grass blades were harvested within 10 m of the center of the subplot but not from within the 1×1 m quadrat. For the baseline survey, which took place during a dry season, we were only able to collect brown grass leaves. For the 18-month survey, we collected only green grass leaves. Samples were dried in a solar-powered oven at approximately 80–90°C.

Soil and foliar nutrient analyses were conducted at Crop Nutrition Laboratory Services in Nairobi, Kenya. For baseline samples only, soil particle size was assessed using a hydrometer method (Table S1). All soil samples were analyzed for exchangeable K, Ca, Mg, and Na (ppm) using a Mehlich-3 extractant and atomic emission spectrometry (ICP). Available inorganic phosphorus (ppm) was measured using a modified Olsen method and colorimetric determination (described in Table S1). Soils were also analyzed for pH and CEC (meq/100g, potentiometric method in water); % total nitrogen (Kjeldahl digestion, colorimetric determination); and % total organic carbon (Walkley-Black procedure). Plant samples were analyzed for total % N (Kjeldahl digestion, titrimetric determination), % P, and % K (Dry Ashing and ICP). See Table S1 (available online at http://dx.doi.org/10.1016/j.rama.2015.01.002) for more information on soil and plant analysis methods. For each subplot, we ran a separate nutrient analysis for each grass species with > 5% cover. We then calculated a weighted average "nutrient quality index" based on relative species abundance at each subplot.

Statistical Analysis

We analyzed vegetation and dung data using generalized linear mixed models (GLMMs) (Pinheiro et al., 2013). Random factors included plot and subplot nested within plot, and we used an autoregressive AR(1) covariance structure to address the nonindependence of repeated surveys within the same subplot. Fixed effects included density treatment (single, double-close or double-far), distance from experimental glade (0 or 200 m), month (since abandonment), month^2 (to account for potential nonlinear effects over time), and all two- and three-way interactions. Interactions were removed from models in which they were not significant ($P > 0.05$). Month^2 terms were only included in models that also contained month terms. We did not consider higher order polynomials due to the relatively low temporal resolution of our dataset. For soil and forage quality data, we used a similar analysis approach, but because subplots were only resurveyed once (at 18 months) we removed the month^2 terms and associated interactions. Response values were transformed or variance weighted when necessary to meet model assumptions. Analyses were run in R 2.12.2 (package nlme, Pinheiro et al., 2013). Results are reported as untransformed means $\pm$ 1 SE.

Results

Boma Characteristics

Averaged across all 12 plots, experimental bomas were 17.4 ± 0.7 m in diameter and were used for 30.6 ± 0.6 days. Just after abandonment, dung depth inside experimental bomas was 11.6 ± 0.8 cm.

Table 1

Soil nutrient properties inside (0 m) and outside (200 m) of experimental bomas before use (0 months) and 18 months after abandonment at Ol Pejeta Conservancy in central Kenya (means $\pm$ 1 SE) and results of statistical tests for divergence between bomas and reference sites.

	0 months ($n = 12$)		18 months ($n = 11$)		GLMM effect tests
	Glade (0 m)	Reference (200 m)	Glade (0 m)	Reference (200 m)	(dist·month except where specified)
pH	6.48 ± 0.05	6.54 ± 0.1	6.91 ± 0.14	6.43 ± 0.06	$F_{1,20} = 12.2, P = 0.002$
Ca (ppm)	2605 ± 217	2877 ± 318	4698 ± 359	2888 ± 142	$F_{1,20} = 45.0, P < 0.0001$
K (ppm)	548 ± 57	531 ± 28	4667 ± 504	986 ± 45	$F_{1,20} = 96.7, P < 0.0001$
Mg (ppm)	493 ± 42	632 ± 66	1247 ± 158	538 ± 48	$F_{1,20} = 67.0, P < 0.0001$
P (ppm)	9.59 ± 3.16	5.74 ± 1.42	78.27 ± 7.3	7.18 ± 2.2	$F_{1,20} = 32.6, P < 0.0001$
N (%)	0.25 ± 0.02	0.24 ± 0.02	0.59 ± 0.07	0.19 ± 0.01	$F_{1,20} = 113, P < 0.0001$
OC (%)	2.15 ± 0.1	2.03 ± 0.14	5.42 ± 0.14	3.24 ± 0.2	$F_{1,20} = 148, P < 0.0001$
CEC (me per 100g)	–	–	50.9 ± 4.3	25.2 ± 1.2	Dist $F_{1,10} = 76.1, P < 0.0001$
Na (ppm)	–	–	307.6 ± 84.6	78.9 ± 8.8	Dist $F_{1,10} = 65.2, P < 0.0001$
Clay (%)	32 ± 1.8	35 ± 1.6	–	–	–
Sand (%)	35 ± 1.0	33 ± 1.2	–	–	–

Average dung deposition per boma (area·depth) was $27.6 \pm 2.4 \text{ m}^3$. Boma size, duration of use, and dung deposition did not differ significantly among the three density treatments (Table S2; available online at http://dx.doi.org/10.1016/j.rama.2015.01.002).

Soil Properties

Concentrations of soil nutrients increased dramatically inside experimental glades while generally remaining stable or declining at reference sites (Table 1). After 18 months, compared with reference soils, experimental glade surface soils had 3.1 times as much total nitrogen, more than 10 times as much inorganic phosphorus, 70% more organic carbon, 60% more exchangeable calcium, 2.3 times as much exchangeable magnesium, and 4.7 times as much exchangeable potassium (Table 1). Experimental glade soils also developed higher pH than non-glade soils (Table 1). For exchangeable sodium and CEC, we lacked baseline data and therefore could not evaluate divergence between experimental glade and reference soils over time. Nevertheless, at 18 months, experimental glade soils had 3.9 times as much exchangeable sodium and two times the CEC values as reference soils (Table 1).

Boma density treatments had no significant effects on soil nutrients or CEC (all P values > 0.3). We did observe a main effect of boma density on pH, with the highest values in the single treatment and the lowest values in the double-close treatment (single: 6.78 ± 0.11 [$n = 14$]; double-far: 6.60 ± 0.07 [$n = 16$]; double-close

6.41 ± 0.08 [$n = 16$]; $F_{2,9} = 4.75, P = 0.04$). The lack of a significant density·month interaction suggests that this difference was present at the start of the experiment.

Plant Nutrient Content

All of the foliar nutrient index values increased substantially between 0 and 18 months (Table 2), likely because of the methodological switch from brown leaf collection to green leaf collection. Of greater interest, foliar nutrients increased more inside experimental glades than at reference sites (Fig. 2; Table 2; distance·month for nitrogen index: $F_{1,17} = 230, P < 0.0001$; phosphorus index: $F_{1,19} = 27.6$, $P < 0.0001$; potassium index: $F_{1,17} = 7.46, P = 0.01$). After 18 months, foliar nitrogen, phosphorus, and potassium index values inside experimental glades were 2.5, 1.7, and 3.6 times as high as values at reference sites (Fig. 2). Indices were affected by changes in species composition, as well as within-species changes in nutrient concentrations (Table 2).

Foliar nutrient concentrations were also affected by boma density treatments. Nitrogen increased more over time in the double-close and single-density treatments than in the double-far treatment (Fig. 2A; density·month for $F_{2,17} = 8.55, P = 0.003$). Conversely, potassium increased more in the double-far and single treatments than in the double-close treatment (Fig. 2C; density·month $F_{2,17} = 7.39$, $P = 0.005$). Foliar phosphorus concentrations were not significantly affected by boma density treatments (Fig. 2B; $F_{2,9} = 0.3, P = 0.8$).

Table 2

Percent cover (absolute) and foliar nutrient concentrations for the four most common grass species at Ol Pejeta Conservancy in central Kenya. Data were collected inside (0 m) and outside (200 m) of experimental boma sites before use (0 months) and 18 months after abandonment (means $\pm$ 1 SE).

|		0 months ($n = 12$)		18 months ($n = 11$)	
Species	Property	Glade (0 m)	Reference (200 m)	Glade (0 m)	Reference (200 m)
Themeda triandra	Cover (%)	39.8 ± 6.1	28.0 ± 6.6	0 ± 0	35.6 ± 7.6
	N (%)	0.88 ± 0.06	0.99 ± 0.06	–	1.96 ± 0.28
	P (%)	0.09 ± 0.01	0.07 ± 0.01	–	0.19 ± 0.02
	K (%)	0.50 ± 0.05	0.50 ± 0.05	–	1.32 ± 0.11
Pennisetum stramineum	Cover (%)	3.8 ± 2.2	10.9 ± 3.8	0 ± 0	9.7 ± 4.5
	N (%)	1.08 ± 0.13	0.86 ± 0.06	–	2.07 ± 0.18
	P (%)	0.11 ± 0	0.08 ± 0.01	–	0.29 ± 0.07
	K (%)	0.49 ± 0.08	0.43 ± 0.05	–	2.42 ± 0.21
Pennisetum mezianum	Cover (%)	5.8 ± 2.9	3.4 ± 2.1	0 ± 0	5.3 ± 2.8
	N (%)	1.00 ± 0.14	1.03 ± 0.04	–	1.72 ± 0.28
	P (%)	0.11 ± 0.04	0.08 ± 0.04	–	0.28 ± 0.08
	K (%)	0.54 ± 0.19	0.50 ± 0.07	–	2.71 ± 0.27
Cynodon plectostachyus	Cover (%)	3.7 ± 1.6	4.5 ± 2.3	27.8 ± 8.2	5.2 ± 2.6
	N (%)	1.21 ± 0.20	1.09 ± 0.18	4.84 ± 0.15	2.11 ± 0.02
	P (%)	0.13 ± 0.02	0.13 ± 0.02	0.39 ± 0.02	0.21 ± 0.05
	K (%)	0.79 ± 0.09	0.69 ± 0.14	2.18 ± 0.09	1.74 ± 0.18
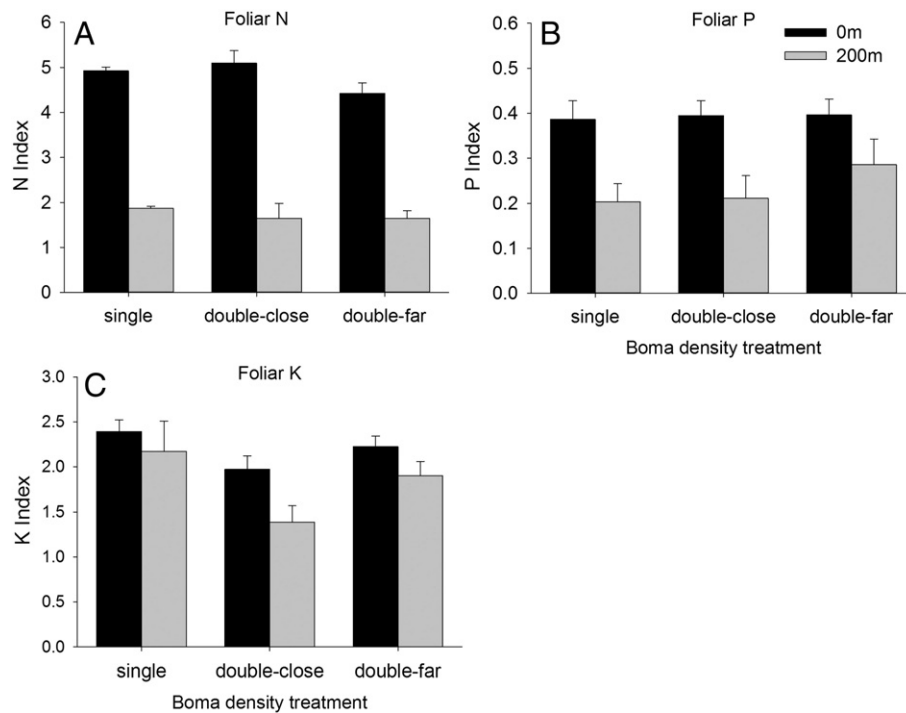
Fig. 2. Foliar nutrient indices (% nutrient values weighted based on the relative abundance of different grass species) inside experimental glades (0 m) vs. reference sites (200 m away) in different boma density treatments at 18 months after boma abandonment. A, Nitrogen. B, Phosphorus. C, Potassium. Means ± 1 SE.

Understory Plant Community

Inside experimental glades, total aerial cover of understory vegetation declined during boma use (replaced by a thick layer of dung) and then began to recover after boma abandonment, but this quadratic trend was not present at reference sites (Fig. 3A; distance·month $F_{1,112} = 6.19$, $P = 0.01$; distance·month^2 $F_{1,112} = 13.1$, $P = 0.0004$). Similar trends were apparent for understory Shannon-Wiener diversity (Fig. 3B; distance·month $F_{1,112} = 118$, $P < 0.0001$; distance·month^2 $F_{1,112} = 73.6$, $P < 0.0001$) and understory species richness (Fig. 3C; distance·month $F_{1,112} = 30.2$, $P < 0.0001$; distance·month^2 $F_{1,112} = 14.1$, $P = 0.0003$). After 32 months, total cover, species diversity, and species richness all remained higher at reference sites than inside experimental glades (2.1 times as high for total cover, 26.5 times as high for diversity, and 10 times as high for species richness). At the same time, several species were observed inside experimental glades but were rare or absent in other locations. These included *Solanum nigrum* L. and species in the genera *Amaranthus, Malva,* and *Cucumis.* Understory community response patterns did not differ significantly among boma density treatments (all P values > 0.1).

Separating plants by functional group indicated that community-level changes were driven by a glade-specialist grass, *C. plectostachyus,* which was one of only a few species able to colonize abandoned boma sites. Relative cover of *C. plectostachyus* increased to almost 100% inside experimental glades but remained below 10% at reference sites (Fig. 3D; distance·month $F_{1,80} = 107$, $P < 0.0001$; distance·month^2 $F_{1,80} = 41.9$, $P < 0.0001$). After 32 months, relative cover of *C. plectostachyus* was 6.5 times as high inside experimental glades as at reference sites (Fig. 3D). Cover of other grasses (Fig. 3E; dist·month $F_{1,80} = 166$, $P < 0.0001$; distance·month^2 $F_{1,80} = 63.4$, $P < 0.0001$) and forbs (Fig. 3F; distance·month $F_{1,80} = 6.38$, $P = 0.01$; distance·month^2 $F_{1,80} = 7.55$, $P = 0.007$) decreased during boma use and did not recover after abandonment. Changes in relative cover were paralleled by changes in the absolute cover of

C. plectostachyus, which increased linearly over time inside experimental glades but remained low at reference sites (distance·month $F_{1,113} = 21.3$, $P < 0.0001$). After 32 months, absolute cover of *C. plectostachyus* was 5.6 times as high at the center of experimental glades (36 ± 12% cover) as at reference sites (6.5 ± 2.9% cover). Absolute cover of *C. plectostachyus,* relative cover of *C. plectostachyus,* and relative cover of forbs and other grasses did not differ significantly among boma density treatments (all P values > 0.2).

Woody Plant Community

Inside experimental glades, *Acacia drepanolobium* tree densities declined dramatically between the baseline and 6-month surveys and then remained stable or recovered slightly over time. Outside experimental glades, tree densities declined slightly and slowly over the course of the study and did not recover (Fig. 4A; month $F_{1,88} = 8.09$, $P = 0.006$; distance·month^2 $F_{1,88} = 6.91$, $P = 0.01$). Before boma use, there were 4.2 times as many trees in the double-far as the double-close density treatment, while the single treatment had intermediate densities, and these differences persisted throughout the duration of the study (density treatment $F_{2,9} = 4.55$, $P = 0.04$).

Like tree density, shrub density inside experimental glades declined and then remained relatively stable over the course of the experiment (Fig. 4B; distance·month $F_{1,88} = 7.75$, $P = 0.007$; distance·month^2 $F_{1,88} = 5.78$, $P = 0.02$). Before boma use, double-far plots had more than 4 times as many shrubs as double-close plots, with single plots intermediate, and these patterns persisted throughout the study (density treatment $F_{2,9} = 4.14$, $P = 0.053$).

Shrub diversity (Shannon-Weiner index) was 3.4 times as high at reference sites as inside experimental glades (Fig. 4C; $F_{1,7} = 12.0$, $P = 0.01$) but did not differ significantly over time or among density treatments (P values > 0.1). Shrub species richness declined inside experimental glades and increased slightly outside experimental glades (Fig. 4D; distance·month $F_{1,88} = 4.81$, $P = 0.03$). Throughout the study, there were more shrub species in double-far plots than in
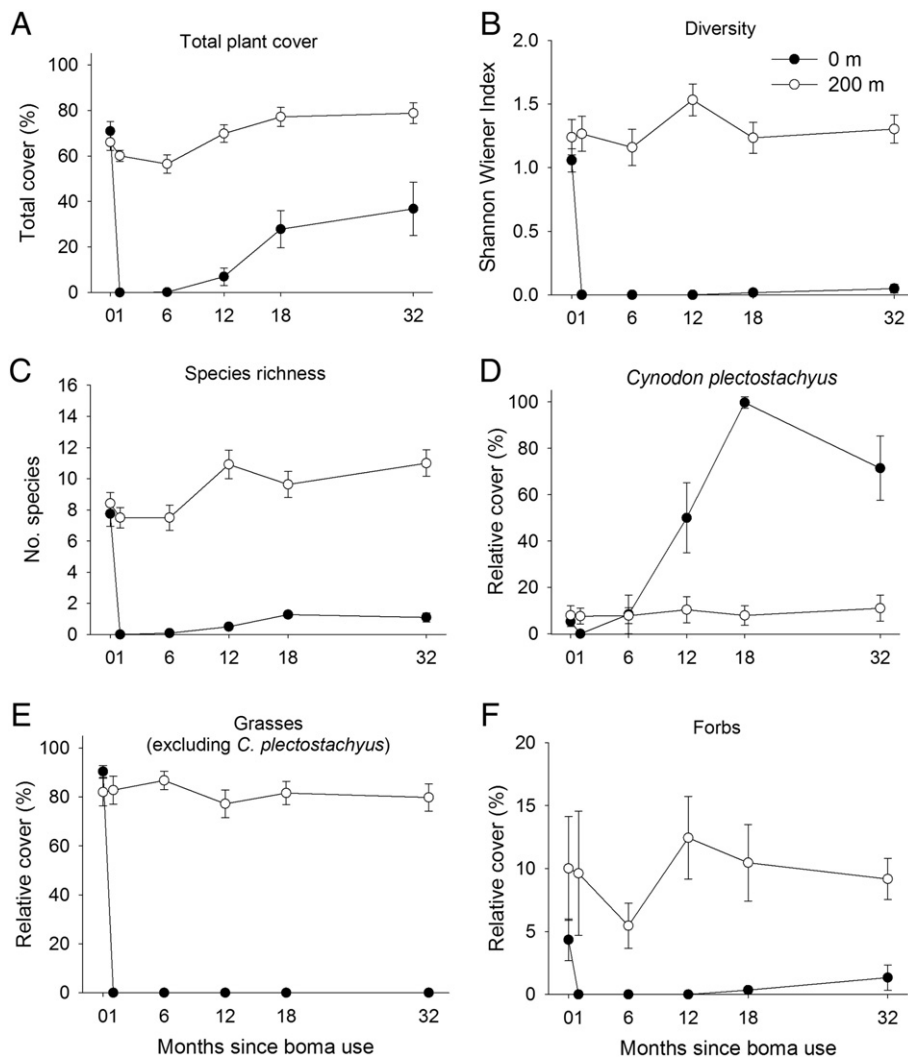
Fig. 3. Herbaceous plant community properties (per 1 m^2) inside experimental glades (0 m) vs. reference sites (200 m away) before boma use (0 months) and at 1, 6, 12, 18, and 32 months after abandonment. A, Total plant cover. B, Species diversity. C, Species richness. D, Relative cover of the grass, *Cynodon plectostachyus*. E, Relative cover of other grasses. F, Relative cover of forbs (note different scale). Means ± 1 SE.

double-close plots, with the single treatment intermediate (double-far: 5.6 ± 0.8, single: 4.0 ± 0.7, double-close: 1.1 ± 0.2; $F_{2,9} = 4.08$, $P = 0.055$).

Large Herbivore Community

Across time periods, wild herbivore dung piles were more abundant inside experimental glades than at reference sites (Fig. 5A; distance $F_{1,11} = 28.6$, $P = 0.0002$). Although temporal trends in dung data should be interpreted cautiously, we do note that densities of dung piles declined and then recovered over time (month^2 $F_{1,90} = 4.59$, $P = 0.03$). Wild herbivore use did not differ significantly among boma density treatments ($F_{2,9} = 0.7$, $P = 0.5$).

Wild herbivore results were driven largely by browsing and mixed feeding herbivores. Of browser and mixed-feeder dung piles, 88% came from four species (38.5% impala, 19.9% Grant's gazelle, 15.7% giraffe, and 13.9% elephant). For browsers and mixed feeders, differences between experimental glades and reference sites became larger over time (Fig. 5B; distance·month $F_{1,88} = 11.8$, $P = 0.0009$, distance·month^2 $F_{1,88} = 5.91$, $P = 0.02$). After 32 months, browser and mixed feeder use was 10 times as high inside glades

as at reference sites. Wild grazer use did not differ significantly between experimental glades and reference sites (Fig. 5C; $F_{1,11} = 0.0002$, $P = 0.99$) or among different density treatments ($F_{2,9} = 0.8$, $P = 0.5$). In all locations, wild grazer use tended to decline after boma abandonment and then recover (month^2 $F_{1,90} = 13.6$, $P = 0.0004$). Cattle (and buffalo) data showed an intermediate pattern; dung pile densities declined and then recovered inside glades, but recovery was less apparent outside of glades (Fig. 5D; month^2 $F_{1,89} = 26.4$, $P < 0.0001$, distance·month $F_{1,89} = 4.10$, $P = 0.046$).

For wildlife species richness and Shannon-Wiener diversity, differences between experimental glades and reference sites grew over time (Fig. 5E-F; richness: distance·month $F_{1,89} = 22.2$, $P < 0.0001$; S-W diversity: distance·month $F_{1,89} = 19.4$, $P < 0.0001$).

Discussion

Nutrient-rich landscape patches are important in many arid and semi-arid rangelands (e.g., Abrahams et al., 1995; Derner and Briske, 2001; Maestre et al., 2001; Verweij et al., 2006; Perakis and Kellogg, 2007; Arnold et al., 2014), including much of sub-Saharan Africa where nutrient hotspots can be derived from traditional cattle corrals, or "bomas" (e.g., Blackmore et al., 1990; Reid and Ellis, 1995;
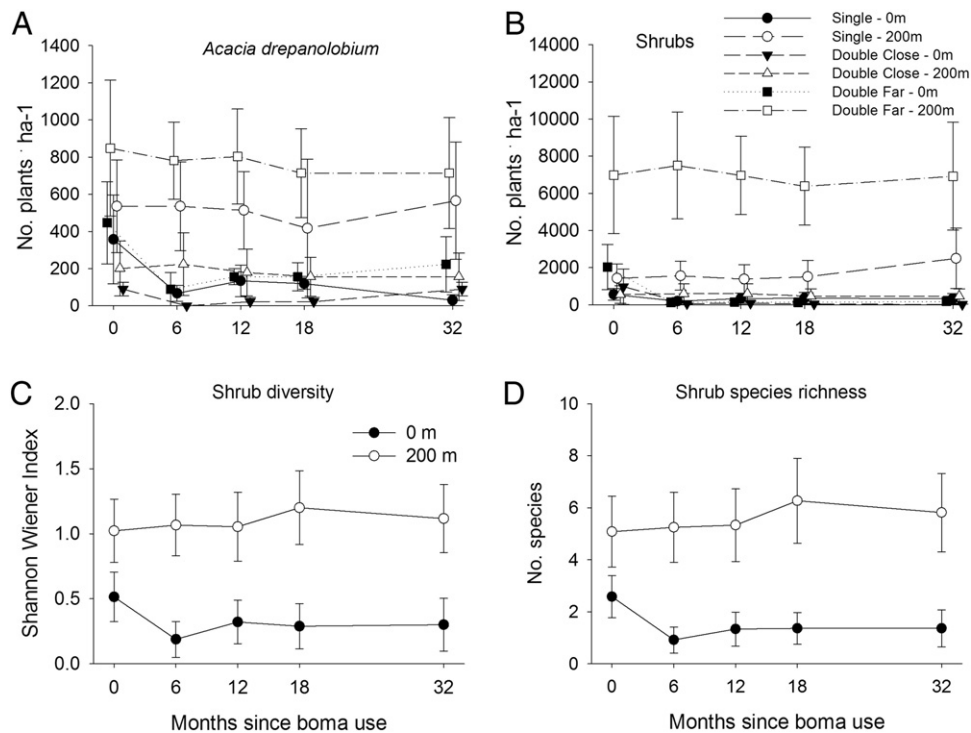
Fig. 4. Woody plant community properties (per 112 m^2) inside experimental glades (0 m) vs. reference sites (200 m away) in different boma density treatments before use (0 months) and at 6, 12, 18, and 32 months after abandonment. A, *Acacia drepanolobium* tree density (points jittered). B, Shrub density (points jittered). C, Shrub species diversity. D, Shrub species richness. Means ± 1 SE.

Treydte et al., 2006b; van der Waal et al., 2011). In East Africa, traditional bomas are used for many months before abandonment, and it was not known whether shorter-term "mobile" bomas could also develop into nutrient-rich hotspots. We found that metal-fenced bomas used by cattle for a single month initiated major shifts in soil and foliar nutrient concentrations, understory plant composition, woody plant abundance, and wildlife composition and abundance. All of these changes are consistent with patterns observed at traditionally formed hotspots in eastern and southern Africa (e.g., Young et al., 1995; Augustine, 2003; Muchiru et al., 2009; Söderström and Reid, 2010; van der Waal et al., 2011; Veblen, 2012).

Eighteen months after boma abandonment, surface soil nutrient levels inside our experimental glades were similar to levels measured in long-term (>40 year-old) glades in eastern and southern Africa (Table 1; Blackmore et al., 1990; Young et al., 1995; Augustine, 2003; Muchiru et al., 2009; Augustine et al., 2011; van der Waal et al., 2011; Veblen, 2012). Previous work in our region (but on different soil/vegetation types) indicated that long-term glades had 1.9 to 3.8 times more total nitrogen than nonglade sites (Augustine et al., 2011; Veblen, 2012), and our experimental glades contained 2.1 times more total nitrogen than reference sites (Table 1). Similarly, long-term glade soils contained ~20 times background values of extractable inorganic phosphorus (Augustine et al., 2011); our experimental glade soils contained ~10 times reference values (Table 1). Levels of Mg and Ca in experimental glade soils were also comparable with levels observed in nearby traditionally formed glades (Augustine, 2003; but see Veblen, 2012). Soil nutrient enrichment has also been observed in association with sheep bedding sites in North America (Leytem and Seefeldt, 2008), historic agricultural settlements in South America (Glaser et al., 2001), and livestock watering points (i.e., "piospheres") globally (Tolsma et al., 1987; Andrew, 1988; Turner, 1998; Stumpp et al., 2005; Shahriary et al., 2012).

Increased soil nutrient concentrations in our experimental glades were paralleled by increased foliar nutrient content (Table 2; Fig. 2). High foliar nutrient levels reflected a shift in plant species composition toward a more palatable species *(C. plectostachyus)*, as well as increased nutrient concentrations within this species (Table 2). Similar patterns have been observed during traditional glade formation in other African systems (e.g., Young et al., 1995; Muchiru et al., 2009; van der Waal et al., 2011).

Changes in the understory plant community provide additional evidence that short-term boma sites received sufficient livestock use (dung deposition, urine, trampling, etc.) to develop into long-term glades. Experimental glades became dominated by *C. plectostachyus,* and *Cynodon* species are known to dominate traditionally formed glades in East Africa (e.g., Stelfox, 1986; Treydte et al., 2006a; Muchiru et al., 2009; Veblen, 2012; Vuorio et al., 2014). Moreover, like traditionally formed glades (e.g., Young et al., 1995; Muchiru et al., 2009; Veblen, 2012), our experimental glades had very low understory plant diversity (Fig. 3). Plant diversity losses were immediate (occurring during boma use), and diversity inside 32-month-old experimental glades was still less than 5% of diversity in reference sites. Other than *C. plectostachyus,* the plant species that managed to colonize experimental glades were mostly forbs. Several of these were rare or absent in the surrounding savanna and have been noted as glade specialists in other locations (e.g., *Malva* and *Cucumis* spp., KEV and LMP unpublished data; *Amaranthus* spp., Muchiru et al., 2009). Glade specialist plants are likely dispersed from glade to glade via ungulates and birds. Thus, our results provide experimental support for previous observational work (Young et al., 1995; Muchiru et al., 2009; Porensky, 2011; Veblen, 2012), suggesting that the unique plant communities found inside glades tend to increase plant diversity at a regional (1–100s of ha) but not local (<1 ha) scale (but see Vuorio et al., 2014).
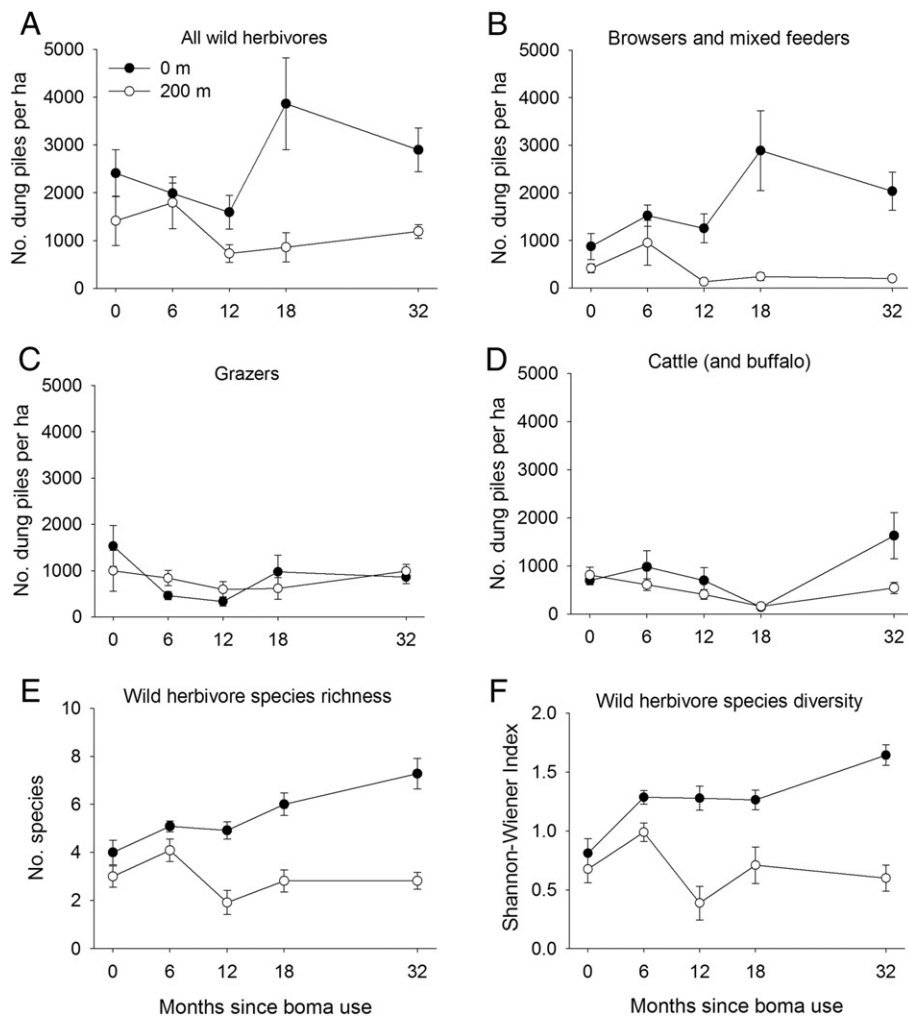
Fig. 5. Large herbivore use (measured using dung piles per 112 m²) inside experimental glades (0 m) vs. reference sites (200 m away) before boma use (0 months) and at 6, 12, 18, and 32 months after abandonment. A, All large herbivores (>15 kg). B, Browsers and mixed feeders. C, Grazers. D, Cattle (and buffalo). E, Species richness. F, Species diversity. Means ± 1 SE.

For tree and shrub densities, the effects of short-term bomas were moderate in comparison with the effects of traditional bomas. Woody plant densities declined dramatically inside experimental boma sites between the baseline and 6-month surveys, probably due to a combination of trampling, rubbing, and toxic nutrient addition. However, densities tended to remain stable or increase slightly between the 6-month and 32-month surveys (Fig. 4). We observed both resprouts and seedlings within experimental glades (LMP personal observation). By contrast, traditional glades in this region tend to remain virtually treeless for decades after abandonment (e.g., Porensky and Veblen, 2012; Veblen, 2012, 2013; Reid and Ellis, 1995 for abandoned bomas that become tree islands in northern Kenya). One month of boma use may not be enough to kill all the trees and shrubs inside boma sites and prevent the establishment of new individuals. Alternatively, it is possible that woody seedlings and resprouts inside developing glades will eventually be outcompeted by colonizing grasses or killed by browsers (e.g., Riginos and Young, 2007; van der Waal et al., 2009; Cramer et al., 2010; Porensky and Veblen, 2012). More moderate effects on trees might be attractive to land managers interested in conserving browse for wildlife but might also have negative consequences for grazing animals.

After only 6 months, our experimental bomas were already beginning to function as wildlife hotspots (Fig. 5). Like traditional glades, our experimental glades were most attractive to mixed feeding herbivores such as impala and gazelles (Augustine et al., 2011; van der

Waal et al., 2011; Veblen, 2012). Experimental glades were also attractive to elephants, animals that primarily browse but also consume grass as part of their diets (Shannon et al., 2013). In other studies, glades attracted grazing herbivores such as zebra and warthogs (e.g., Young et al., 1995; Treydte et al., 2006b; Augustine et al., 2011; but see van der Waal et al., 2011), but we did not observe grazer attraction to our sites. Forage in experimental glades was relatively high quality but low quantity, and this combination may be less attractive to bulk-feeding grazers such as zebra. Despite the lack of grazer response, wildlife diversity differences between glades and reference sites became more pronounced throughout the experiment, suggesting that multiple different species were attracted to experimental glades. Cattle (and buffalo) use of experimental plots was low during the first 18 months of the experiment, but at 32 months, cattle and buffalo dung piles were more abundant in experimental glades than at reference sites. We believe this result reflects the return of cattle to our study region after moving to other parts of the Conservancy earlier in the experiment. Once cattle returned to the area, they used experimental glades more than paired reference sites.

Through repeated monitoring, we were able to examine the rate of change toward gladelike conditions (glade development) on experimental sites. Although wildlife were attracted to experimental glades after only 6 months, conversion of the understory plant community lagged behind the wildlife response. Our sites remained

virtually bare of vegetation for more than 12 months after boma abandonment (Fig. 3). Grass colonization was delayed partially because of drought during the first few months of the experiment (a weather station located 22 km north of our sites received less than 20% of average precipitation from February to September 2009). However, even after 32 months (including 19 months of average or above-average precipitation), plant cover at the center of the experimental glades was still less than 50% of reference levels (Fig. 3). On traditional glades, the grass colonization process often takes > 5 years, but resultant glades eventually have higher plant cover than the background savanna (e.g., Young et al., 1995; Muchiru et al., 2009; Porensky, 2011; Veblen, 2012). Given nutrient concentration levels observed in experimental glades (see earlier), we expect that the grass colonization process is still incomplete within our experimental glades, and they will become more densely vegetated over time. It remains to be tested whether boma sites used for less than 1 month (e.g., 1 or 2 weeks) are colonized more quickly. Seasonal shifts between sampling periods may have minor impacts on our interpretations of changes over time. However, because all plots and subplots were sampled at each time step, seasonal shifts should not have affected our conclusions about boma or boma density effects.

The degree to which our experimental bomas altered soil and foliar nutrient concentrations, plant communities, and wildlife use is intriguing because these bomas were occupied for only 1 month. Our results suggest that the amount of livestock use and dung deposition at traditional sites (where the dung layer is often twice as deep as the layer observed on our experimental bomas) far exceeds the amount needed to create a gladelike ecosystem hotspot. Although it is not certain how persistent our experimental glades will be, previous work suggests that once glades are formed, they are likely to persist because of elevated use by herbivores, which causes continued nutrient deposition, browsing, and selective grazing (Young et al., 1995; Augustine et al., 2003; Augustine, 2004; Veblen and Young, 2010; Augustine et al., 2011; Porensky, 2011; van der Waal et al., 2011; Porensky and Veblen, 2012; Veblen, 2012). The increased foliar nutrient levels observed in our experimental glades should help attract wildlife and initiate some of these herbivore-mediated feedbacks (sensu Augustine et al., 2003). Moreover, our herbivore use data support the idea that herbivore-mediated feedbacks may already be operating. To increase the utility of mobile bomas as a management tool, more work is needed to identify 1) the minimum amount of cattle use (and associated dung) needed to initiate a glade conversion and 2) the degree to which duration of boma use affects long-term glade persistence.

Boma density had few significant impacts on within-glade development. After 18 months, we did observe lower forage nitrogen levels in the double-far glades, compared with other density treatments. This pattern fits with previous observational work, suggesting that at intermediate densities (150–200 m center to center), glades are less attractive to wildlife (Porensky, 2011; Donihue et al., 2013). However, boma density did have any direct effects on wildlife use of experimental glades in this study. For the first 32 months after boma abandonment, the positive effects (e.g., nutrient enrichment, wildlife attraction) of short-term bomas do not appear to be compromised by the presence of additional boma sites nearby. It is possible that additional density effects could develop over time (e.g., as a result of differential wildlife use). Preliminary data suggest that boma density did affect the development of glade edge effects during the first 32 months of the study. More work is necessary to understand when, where, and why landscape context modulates ecological dynamics.

In addition to comparing mobile bomas with traditional bomas, our boma-making experiment solidifies the causal patterns inferred in previous work. Previous studies have assumed that before boma establishment, boma sites tend to be structurally and functionally similar to the background savanna landscape. However, most existing work has been observational (e.g., Young et al., 1995; Augustine, 2003; Muchiru et al., 2009; Porensky, 2011; van der Waal et al., 2011; Veblen, 2012), making it difficult to distinguish between boma effects and preexisting site variability. For example, if herders intentionally place bomas on sites with relatively high forage production, the high productivity observed inside glades could be at least partly derived from preexisting conditions. Findings from our experimental approach support the assumption that livestock bomas can create glade hotspots.

Implications

Our results indicate that short-term, metal-fenced bomas are a viable management tool for creating nutrient hotspots, that relatively short-term bomas can allow for the creation of far more ecosystem hotspots per unit time than previously under more traditional management, and that the positive effects of the resultant glades are not compromised by somewhat higher densities in the landscape. Boma-derived hotspots increase structural and functional heterogeneity, attract wildlife, and provide palatable forage for livestock. By breaking soil surface crusts while adding seeds and nutrients, bomas can also be used as a tool to revegetate bare patches (KEV and LMP, unpublished data). In the scientific literature, examples of livestock-derived ecosystem hotspots (sensu glades) are largely limited to Africa and a few other systems where livestock are herded (mostly sheep, e.g., Leytem and Seefeldt, 2008). In systems without herders, one promising mechanism for creating this type of long-term hotspot may be the use of portable attractants (e.g., supplements or water tanks, Bailey, 2004; Probo et al., 2013). In contrast, nonportable attractants can concentrate nutrients but also foster undesirable vegetation (e.g., Brooks et al., 2006) or become "sacrifice areas" (e.g., Brits et al., 2002).

The benefits of glades stem from their distinctiveness; by increasing heterogeneity, glades increase local productivity and regional biodiversity (see reviews by Lundholm, 2009; Tamme et al., 2010). Given that mobile bomas are quite portable and, according to our results, 1-month bomas can convert into glades, it may now be possible for managers to convert ever larger areas into glade vegetation. However, because livestock simply redistribute existing nutrients across the landscape (Augustine, 2003; Kizza et al., 2010), the productivity and palatability of glade grasses should decline as the proportion of boma-impacted area increases. Moreover, in a landscape dominated by glades, plant species that are currently common in nonglade areas could potentially become rare, leading to a decrease in regional plant (and forage) diversity. We caution that even in short-term scenarios, broad-scale nutrient redistribution can have long-term, ecosystem-wide consequences.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.rama.2015.01.002.

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