

Development of edge effects around experimental ecosystem hotspots is affected by hotspot density and matrix type

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Abstract

Context Ecological edge effects are sensitive to landscape context, including matrix type and the presence of other nearby edges. In sub-Saharan Africa, temporary cattle corrals (bomas) develop into productive nutrient hotspots (glades) that attract diverse wildlife and persist for decades.

Objectives Building on previous descriptive work, we experimentally altered boma configurations in an African savanna and asked how boma density and matrix type (open plains vs. bushland) influence the development of edge effects around abandoned bomas.

Methods We randomly assigned eleven plots to three treatments: one boma, two bomas 200 m apart, or two bomas 100 m apart. Before boma establishment and

≥ 18 months after boma abandonment, we sampled soil nutrients, foliar nutrients, plant communities, and large herbivore use at each plot.

Results Bomas developed into glade hotspots with elevated nutrient concentrations, altered vegetation, and elevated use by large herbivores. Few edge effects were detectable at distances ≥ 50 m. Both glade density and matrix type affected the development of edge effects around experimental glades. When compared to patterns around single glades, the presence of a second glade 100 m away strengthened glade edge effects (more difference between glade and matrix), but the presence of a second glade 200 m away weakened edge effects. Vegetation edge effects were stronger in bushland areas than open plains, while wildlife shifts were strongest along the bushland-plain interface.

Conclusions Our results highlight the potential for edge effect variability in complex landscapes, and show that manipulative experiments can help illuminate causes and consequences of that variability.

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Introduction

Human alterations of landscape pattern have major consequences for biodiversity, ecosystem function,

and ecosystem service provision (Fahrig et al. 2011; Tschardt et al. 2012). One consequence of human land use change is an increased prevalence of ecological edges, or boundaries separating adjacent patches or habitat types (Cadenasso et al. 2003). For example, urban and agricultural developments, roads, oil rigs, timber harvests, and water points can all produce ecological boundary zones (e.g., edges separating roads, houses or clear cuts from adjacent forest) (Fletcher 2005; Harper et al. 2005; Laurance et al. 2009). As edges become more abundant, it is increasingly important to understand their effects on ecological processes. Ecological edge effects occur when abiotic factors, species, or species interactions respond to edges (Cadenasso et al. 1997; Ries et al. 2004). Edge effects can result in altered species distributions, community dynamics, biodiversity, and species interactions (Fagan et al. 1999; Ries et al. 2004; Harper et al. 2005; Laurance et al. 2011), and therefore have major implications for ecosystem structure, function, and services.

Edge effects are sensitive to landscape context. For example, the strength and extent of a given edge effect can vary based on matrix type or quality (Sisk et al. 1997; Pauchard and Alaback 2004; Santos-Barrera and Urbina-Cardona 2011; Wilkerson 2013) and the degree of contrast between adjacent patches (Collinge and Palmer 2002; Campbell et al. 2011). Moreover, recent studies suggest that edge effects can be sensitive to the presence and proximity of other, nearby edges, a phenomenon called *edge effect interaction* (e.g., Malcolm 1994; Fletcher 2005; Laurance et al. 2006; Harper et al. 2007; Porensky 2011; Donihue et al. 2013; Porensky and Young 2013). By magnifying or diminishing edge effects, these kinds of context-dependence can influence distributions of species and the habitat patches they rely on. To maximize ecosystem function and ecological service provision in increasingly complex landscapes, we need to understand how landscape configuration influences edge effects.

Despite the potential importance of landscape context, only a few studies have carried out controlled, replicated manipulations of landscape configuration to experimentally investigate relationships between landscape context and edge effects (examples include Collinge and Palmer 2002; Damschen et al. 2008; Ewers et al. 2011; Laurance et al. 2011; Orrock et al. 2011). In this study, we took advantage of a unique

aspect of African savanna ecosystems to create a series of patch configurations within replicated plots and then assess the emergence of edge effects within these plots. This work builds on descriptive studies of edge effects in our study system (Young et al. 1995; Porensky 2011). Our experimental design allowed us to quantify the effects of both landscape composition and landscape configuration on edge effect development while controlling for potentially confounding factors that accompany the vast majority of descriptive studies on edge effects (e.g., non-random patch locations in existing landscapes).

To create landscapes with different patch configurations, we manipulated the density of temporary livestock corrals, or “bomas”, in a semi-arid savanna ecosystem. Throughout eastern and southern Africa, cattle are corralled in bomas at night for protection against predation and theft (Western and Dunne 1979; Blackmore et al. 1990). Before boma establishment, boma sites (10–100 m in diameter) are structurally and functionally similar to the background savanna landscape, and sites are traditionally 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). As a result of intense livestock and herder use (including grazing, dung and seed deposition, and fuelwood cutting), boma sites develop after abandonment into ecological hotspots characterized by high nutrient availability, high productivity, unique plant communities, and preferential use by wildlife (e.g., Stelfox 1986; Reid and Ellis 1995; Young et al. 1995; Augustine 2003, 2004; Treydte et al. 2006; Muchiru et al. 2009; van der Waal et al. 2011; Veblen 2012; Donihue et al. 2013; Vuorio et al. 2014). In central Kenya, these boma-derived hotspots take the form of treeless, highly productive “glades” that persist for more than 50 years via a combination of legacy effects and herbivore-mediated feedbacks (Young et al. 1995; Augustine 2003; Augustine et al. 2003; Veblen and Young 2010; Porensky and Veblen 2012; Veblen 2012). Management practices that create wildlife hotspots such as glades may help combat large mammal defaunation and associated problems (Dirzo et al. 2014; Young et al. 2014, 2015).

In this landscape, as in many other agricultural landscapes, a critical question is how management activities (e.g., bomas) should be spatially configured to maximize agricultural production, biodiversity

conservation, and the provision of other ecosystem services (Fahrig et al. 2011). Boma-derived glades have edge effects that can extend at least 100 m into the surrounding savanna landscape (Reid and Ellis 1995; Young et al. 1995; Muchiru et al. 2009; Söderström and Reid 2010; Porensky 2011; Veblen 2013; Vuorio et al. 2014). These edge effects presumably result from livestock use patterns (e.g., central place foraging during boma use) and subsequent wildlife foraging patterns, and include more palatable and productive vegetation, unique plant species, and increased animal use (e.g., Young et al. 1995; Donihue et al. 2013; Veblen 2013). However, descriptive research suggests that glade edge effects can be modified by the presence of other, nearby glades (Porensky 2011; Donihue et al. 2013). Compared to areas around isolated glades, areas between glades that are 150–200 m apart (center-to-center) have higher tree densities, less glade-specialist grass, and less animal use (Porensky 2011; Donihue et al. 2013). These previous findings suggest that high glade densities can have negative consequences for wildlife conservation, biodiversity and forage availability. However, it remains unclear what is driving these patterns (e.g., wildlife foraging decisions, legacy effects of boma use), or even whether they are driven by boma configuration instead of other correlated factors (e.g., herders selectively placing more bomas in sites with more trees).

To identify boma presence and density as causative factors driving glade edge effects, we manipulated boma densities and then documented the development of edge effects in eight directions around abandoned boma sites. Hereafter, we use the term “boma” when referring to the time period when the experimental sites were being actively used by cattle, and the term “glade” to refer to the same experimental sites after cattle removal. Experimental glades were located at pre-existing boundaries between dense bushlands and open, grassy plains. We asked three research questions:

- (1) Do experimental glades have edge effects that extend into the surrounding savanna?
- (2) Are glade edge effects altered by the presence and proximity of additional nearby glades?
- (3) Are glade edge effects altered by matrix type (i.e. whether the edge effect extends into bushland or open plain)?

We hypothesized that experimental glades would develop edge effects, and that for some response variables these edge effects would extend >100 m into the surrounding savanna. We expected that glade edge effect development would be sensitive to glade density, and that higher densities would be associated with weaker edge effects (c.f., Porensky 2011). Due to predator avoidance and forage availability, most wild herbivores in this region (except black rhinos, elephants and duikers, which are relatively uncommon) tend to use open areas or bush-plain edges more than bushy areas (Riginos and Grace 2008; Riginos 2015), and we therefore expected that experimental glades would cause larger magnitude ecological changes in areas closer to open plains.

Methods

Study region

This research was conducted at Ol Pejeta Conservancy (36.87°E, 0.04°N), a 36,500 ha property managed for both cattle production and wildlife conservation on the southern end of the Laikipia plateau in Kenya (~1800 m asl). Ol Pejeta has a mean annual rainfall of 700–900 mm (Wahungu et al. 2011). In addition to ~6000 Boran cattle, the Conservancy is home to a wide variety of large wild herbivores, including zebras (*Equus burchelli*), impalas (*Aepyceros melampus*), elephants (*Loxodonta africana*), giraffes (*Giraffa camelopardalis reticulata*), hares (*Lepus capensis*), African buffalos (*Syncerus caffer*), Grant’s gazelles (*Nanger [Gazella] granti*), Thompson’s gazelles (*Eudorcas [Gazella] thomsonii*), elands (*Taurotragus oryx*), hartebeests (*Alcelaphus buselaphus*), warthogs (*Phacochoerus africanus*), bush duikers (*Sylvicapra grimmia*), and waterbucks (*Kobus ellipsiprymnus*).

Ol Pejeta conservancy includes a mosaic of open, grassy plains (<10 % canopy cover; on clay loam soils), open *Acacia drepanolobium* woodlands (~15–30 % canopy cover; on soils intermediate between clay and clay loam), and dense bushlands co-dominated by the shrubs *Euclea divinorum*, *Scutia myrtina*, and *Rhamnus staddo* (>30 % canopy cover; on clayey soils; nomenclature from Agnew and Agnew 1994). The open plains serve as important foraging areas for both wild and domestic herbivores and are dominated by five grass species: *Themeda*

triandra, *Pennisetum stramineum*, *Pennisetum mezianum*, *Cynodon plectostachyus*, and *Sporobolus nervosus* (nomenclature from Agnew 2006).

Experimental design

Within a 10×15 km study region we chose eleven 400×400 m areas for experimental plots (Supplementary Material). For most of the wild herbivore species present in this region, characteristic home ranges are >10 times larger than the area of a single plot. For some of the smaller species (hare, duiker), characteristic home ranges are similar in scale to a single plot. Plots were randomly located along pre-existing boundaries separating (1) bushland or open woodland areas from (2) large, open plains (Fig. 1). Each plot was centered at a point where tree cover was $>10\%$ but $<15\%$. Plots were separated by at least 600 m center-to-center. Each plot's center was located >500 m from existing bomas, glades, and other significant landscape features (e.g. rivers, houses, etc.) to minimize potential interference from non-focal patch types. Boundaries between plains and other land cover types are sharp, with shifts in plant species composition and vegetation structure occurring over distances of 5–20 m. Thus, the area within 500 m of each plot's center included only three, distinct patch types: (1) either bushland or open woodland (hereafter lumped as “bushland”), (2) a narrow edge zone bisecting the plot, and (3) open plain. Plots were randomly assigned to one of three density treatments (Fig. 1): one experimental boma (“single”, $N = 3$), two experimental bomas located 200 m apart center-

to-center (“double-far”, $N = 4$), or two experimental bomas located 100 m apart (“double-close”, $N = 4$). In February and March 2009, each boma (circular, 17.2 ± 0.8 m in diameter) was used by approximately 200 cows for one continuous month, then abandoned. While each boma was being used to hold cattle (nightly), herders lived in adjacent portable houses. Instead of more traditional thorn-fence bomas, we used metal-fenced “mobile bomas” that are becoming more common in the area (Porensky and Veblen 2015). For the duration of the study (32 months), no additional bomas were created within 600 m of any plot's center. All plots were grazed periodically (at similar intensities) by cattle. For more details on bomas and cattle use, please see Porensky and Veblen (2015).

Vegetation and dung sampling

We quantified vegetation and large herbivore dung immediately before initiating the experiment (“baseline”, January–February 2009) and at 1, 6, 12, 18 and 32 months (October–November 2011) after the experimental bomas were abandoned. We collected data at 16 8×14 m subplots within each plot (Fig. 1). Subplots extended in eight directions out from the central, or focal, glade. Hereafter, references to “plot-level” results imply data averaged across all 16 subplots. We also monitored one subplot 200 m away from the focal glade as a plot-specific control, or reference (Fig. 1). Previous studies indicate that glade edge effects rarely extend as far as 200 m (Young et al. 1995; Muchiru et al. 2009; Porensky 2011).

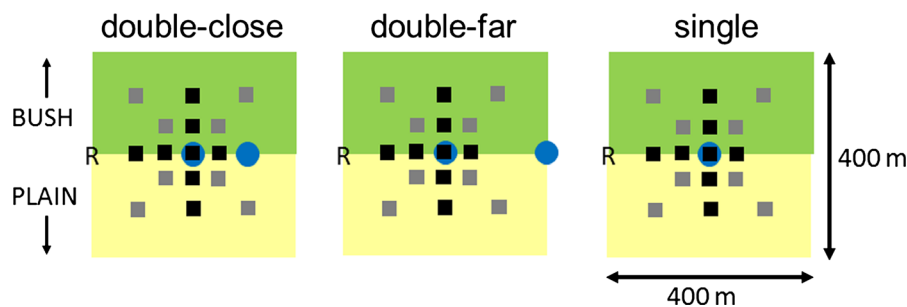


Fig. 1 Sampling design for each of the three glade density treatments: one experimental glade (“single”, $N = 3$), two experimental glades located 200 m apart center-to-center (“double-far”, $N = 4$), or two experimental glades located 100 m apart (“double-close”, $N = 4$). Circles represent

experimental glades and small squares represent 8×14 m sampling subplots. Soil and foliar nutrient samples were taken at black but not grey subplots. R's represent 8×14 m reference (site-specific control) subplots

At each subplot, we recorded the number of large herbivore dung piles and identified each to species. Dung piles were then crushed in place to prevent re-counting in subsequent surveys. We used dung counts as indicators of relative animal use. This method has been shown to be effective when making comparisons within study regions and within seasons, both in this ecosystem (including across glades edges; Young et al. 1995, 2005; Riginos 2015) and in others (Barnes 2001; Rasmussen et al. 2005; Daniels 2006). The dung piles of buffalo and cattle were indistinguishable, and although cattle are far more abundant than buffalo in the study region, these two species were lumped as “cattle + buffalo”. Similarly, we did not distinguish between dung of Grevy’s zebras and the far more common plains zebras. Wildlife species (i.e. all but cattle + buffalo) were classified as either grazers (zebra, hare, hartebeest, warthog, waterbuck, and white rhino) or mixed feeders/browsers (elephant, eland, giraffe, Grant’s gazelle, Thompson’s gazelle, impala, steinbuck, black rhino, and duiker). Previous work indicated that dung decomposition rates did not differ significantly among patch types (LMP unpublished data). To account for plot-level differences in baseline dung abundance, we report dung results using graphs that show changes over time. In these graphs, values can be compared across space (e.g., more increase inside than outside glades), but the actual change values should be interpreted cautiously as dung decomposition rates can vary over time. For example, an overall decline in dung abundance between 0 and 32 months should not be interpreted as an actual decline in animal use. Spurious dung patterns can also be caused by detection differences if dung piles are easier to detect in certain patch types. We conducted several re-surveys to address this possibility and determined that our detection rates did not differ measurably among patch types. Hereafter, when we mention wildlife we are referring to dung data, and we assume that dung is a reasonable (though clearly imperfect) proxy for wildlife use.

In one 1×1 m quadrat placed at the center of each subplot, we visually estimated aerial percent cover of each understory plant species (plant parts located >0.5 m above ground level were excluded during visual estimation). Percent cover of vegetation, litter and bare ground/rock totaled 100 %. We counted all *A. drepanolobium* trees present within each 8×14 m subplot. For each *A. drepanolobium* individual, we recorded its height class ($<$ or >0.5 m).

We calculated Shannon-Wiener species diversity (Shannon 1948) for two guilds at each subplot: understory plants (aerial cover, calculated at the scale of 1×1 m quadrats) and wild herbivores (dung piles, calculated at the scale of 112 m^2 subplots). For each of these communities, we also calculated the Czekanowski proportional similarity index (Bloom 1981) to quantify the magnitude of overall community change between baseline and 32 months.

Soil and foliar nutrient sampling

Immediately before the bomas were installed and 18 months after they were abandoned, we collected soil and plant samples from half of the subplots (Fig. 1), and analyzed these samples for nutrient concentrations. We collected four 10-cm-deep by 8-cm-diameter soil cores (0–10 cm depth) within each subplot. Each core was taken 2 m from the center of the subplot (N, E, S and W directions for the baseline survey, and NE, NW, SE and SW directions for the 18-month survey). The clay-rich soils at our plots exhibited shrink-swell dynamics, causing dung to be quickly incorporated into surface soils. During the 18-month survey, we observed that dung was no longer visible as a distinct soil layer, though surface soils inside glades probably contained large amounts of partially-decomposed dung. Within each subplot, soil from the four cores was pooled and a subsample of the homogenized material was extracted for analysis. Sub-samples were dried to constant weight in a solar drying oven. Roots >1 mm in diameter were removed before analysis.

To evaluate plant nutrient quality, we harvested material from each grass species with more than five percent aerial cover as measured in the 1×1 m quadrat located at the center of each subplot. Grass blades were harvested within 10 m of the center of the subplot, but were not harvested from within the 1×1 m quadrat. For the baseline survey, which took place during a dry season, we were only able to collect dry grass leaves. For the 18-month survey, we collected only green grass leaves. Samples were dried to constant weight in a solar drying oven.

Soil and foliar nutrient analyses were carried out by Crop Nutrition Laboratory Services in Nairobi, Kenya. Soils were analyzed for exchangeable K, Ca, Mg and Na using a Mehlich-3 extractant and atomic emission spectrometry (ICP). Available inorganic phosphorous was measured using a modified Olsen method. Soils

were also analyzed for pH and CEC (meq/100 g, potentiometric method in water); % total nitrogen (Kjeldahl digestion); and % total organic carbon (Walkley–Black procedure). Plant samples were analyzed for total % N (Kjeldahl digestion), % P and % K (Dry Ashing and ICP). For each subplot, a separate nutrient analysis was carried out for each grass species with more than five percent cover. We then calculated a weighted average “nutrient quality index” based on relative species abundance at each subplot.

Statistical analyses

We analyzed data in R 2.12.2 (package nlme, Pinheiro et al. 2013) using linear mixed models (LMMs) with plot included as a random factor. Dependent variables are listed in Tables 1 and 2.

To simplify analysis, we used response values from the final sampling date (32 months for vegetation and dung; 18 months for soil and foliar nutrients). Inspection of intermediate time steps indicated that patterns developed consistently through time and the general effects of treatments were not sensitive to season (see also Porensky and Veblen 2015). To investigate effects of experimental glades and glade density treatments, we included distance from glade, squared distance from glade, density treatment, treatment \times distance, and treatment \times distance² as fixed factors. To investigate anisotropic edge effects (e.g. different edge effects on the plain and bushland sides of the plot), we also included matrix type (plain, bush, or edge), matrix \times distance, and matrix \times distance² as fixed factors. For soil and forage analyses, matrix \times distance² was omitted due to lack of spatial resolution). Although many edge response shapes appeared asymptotic, models more complex than a quadratic polynomial were not investigated to avoid overfitting the data, which had relatively low spatial resolution. Quadratic models did seem to provide good fits within the spatial range of our data. When available, baseline (pre-boma) values were included as covariates; although the experiment had relatively small sample sizes, the inclusion of random effects and baseline data in statistical models should minimize the chance that our results are spurious. For soil sodium and soil cation exchange capacity, baseline data were not available. For all other response variables, main effects of treatment or matrix type suggest that the magnitude of change from baseline differed across treatments or matrix types. Values were transformed or

variance-weighted when necessary to meet model assumptions. Due to the low replication of this broad-scale experiment, we report patterns that were significant at the $\alpha = 0.10$ level (Peterman 1990). Because reference data were only collected in one direction (Fig. 1), these were excluded from LMMs.

To further quantify edge effect development around glades, we calculated edge magnitude (the amount of change across the edge) and edge depth (the spatial extent of glade-induced changes) for each response variable. Edge magnitude and depth results allow for comparisons of edge effect patterns across multiple studies and ecosystems, but should be interpreted somewhat cautiously because data in this experiment have low spatial resolution. For models with significant density treatment \times distance interactions, we calculated edge magnitude and depth separately for each treatment. To calculate edge magnitude, we extracted fitted values from each LMM and back-transformed when necessary. For each plot, we averaged fitted values across subplots to get one value per distance class, then calculated the magnitude of the edge effect as the largest value minus the smallest value. To estimate edge effect depth, we calculated the 90 % confidence interval associated with fitted values at each distance. We then compared these 90 % confidence intervals against a reference 90 % confidence interval, which was calculated using data from the 200 m reference subplots ($N = 11$). Edge depth was defined as the distance beyond which the model and reference confidence intervals always overlapped.

Results

Soil nutrients

All nine soil properties were significantly elevated inside 32-month-old experimental glades (Supplementary Material). For soil responses, glade edge effects had relatively large magnitudes, but soil nutrient enrichment was not detectable at distances ≥ 50 m from glade center (Tables 1, 2). For pH and Ca, edge effects differed among glade density treatments. Within-glade (Distance = 0 m) and near-glade (50 m) elevations in pH were more pronounced in the single treatment than the double treatments (Table 2; Fig. 2a; treatment $F_{2,8} = 0.18, P = 0.8$; distance \times treatment $F_{2,66} = 5.40, P = 0.007$; distance² \times treatment $F_{2,66} = 0.19, P = 0.8$).

Table 1 Edge magnitude, edge depth and statistical results for responses without significant treatment × distance interactions

Response variable (units, <i>df</i>)	Edge magnitude (max–min)	Edge depth (m)	Distance from glade	Distance ² from glade	Baseline
Soils					
Nitrogen (%; <i>df</i> = 1,66)	0.36 ± 0.03	48	F = 147, P < 0.0001	F = 152, P < 0.0001	F = 64, P < 0.0001
Organic carbon (%; <i>df</i> = 1,66)	1.95 ± 0.08	41	F = 72, P < 0.0001	F = 101, P < 0.0001	F = 71, P < 0.0001
Phosphorous (Olsen ppm; <i>df</i> = 1,66)	80 ± 14	44	F = 95, P < 0.0001	F = 120, P < 0.0001	F = 109, P < 0.0001
Potassium (ppm; <i>df</i> = 1,66)	3530 ± 350	48	F = 262, P < 0.0001	F = 290, P < 0.0001	F = 28, P < 0.0001
Magnesium (ppm; <i>df</i> = 1,66)	660 ± 98	36	F = 77, P < 0.0001	F = 90, P < 0.0001	F = 16.2, P < 0.0001
Sodium (ppm; <i>df</i> = 1,67) ^a	165 ± 14	40	F = 123, P < 0.0001	F = 81, P < 0.0001	NA
Cation exchange capacity (meq/100 g; <i>df</i> = 1,67) ^a	23 ± 1.2	44	F = 53, P < 0.0001	F = 81, P < 0.0001	NA
Forage quality					
Percent phosphorous index (<i>df</i> = 1,61)	0.18 ± 0.02	15	F = 22, P < 0.0004	F = 52, P < 0.0001	F = 62, P < 0.0001
Percent potassium index (<i>df</i> = 1,61)	0.58 ± 0.03	0	F = 2.18, P = 0.15	F = 20, P < 0.0001	F = 3.91, P = 0.05
Understorey plants					
Total understorey cover (%; <i>df</i> = 1,152)	34 ± 5.7	24	F = 0.55, P = 0.5	F = 21, P < 0.0001	F = 31, P < 0.0001
<i>P. stramineum</i> cover (%; <i>df</i> = 1,152)	7.3 ± 0.9	4	F = 2.37, P = 0.13	F = 2.01, P = 0.16	F = 261, P < 0.0001
<i>S. nervosus</i> cover (%; <i>df</i> = 1,152)	7.5 ± 2.0	9	F = 4.20, P = 0.04	F = 3.01, P = 0.08	F = 185, P < 0.0001
<i>T. triandra</i> cover (%; <i>df</i> = 1,152)	39 ± 3.4	21	F = 17.2, P = 0.0001	F = 73, P < 0.0001	F = 184, P < 0.0001
Understorey community similarity (<i>df</i> = 1,153)	0.47 ± 0.02	28	F = 16.2, P = 0.0001	F = 24, P < 0.0001	NA
Understorey species diversity (S-W index; <i>df</i> = 1,149)	1.35 ± 0.10	38	F = 15.9, P = 0.0001	F = 49, P < 0.0001	F = 92, P < 0.0001
<i>Acacia drepanolobium</i>					
Height < 0.5 m (no. per 112 m ² ; <i>df</i> = 1,152)	6.27 ± 0.59	0	F = 0.73, P = 0.4	F = 1.98, P = 0.16	F = 2888, P < 0.0001
Height > 0.5 m (no. per 112 m ² ; <i>df</i> = 1,152)	3.65 ± 0.90	0	F = 0.07, P = 0.8	F = 1.43, P = 0.2	F = 1228, P < 0.0001
Dung					
Grazers (per 112 m ² ; <i>df</i> = 1,152)	4.8 ± 0.7	0	F = 0.54, P = 0.5	F = 3.08, P = 0.08	F = 102, P < 0.0001
Dung species diversity (S-W index; <i>df</i> = 1,149)	1.01 ± 0.06	49	F = 38, P < 0.0001	F = 30, P < 0.0001	F = 0.94, P = 0.3
Dung community similarity (<i>df</i> = 1,153)	0.28 ± 0.02	3	F = 1.37, P = 0.2	F = 12.8, P = 0.0005	NA

Predicted values from associated models were used to calculate edge magnitude (difference between maximum and minimum response value when plotted vs. distance to glade) and depth (distance beyond which glade and reference confidence intervals overlapped). See Supplementary Material for average response values at each distance from glade

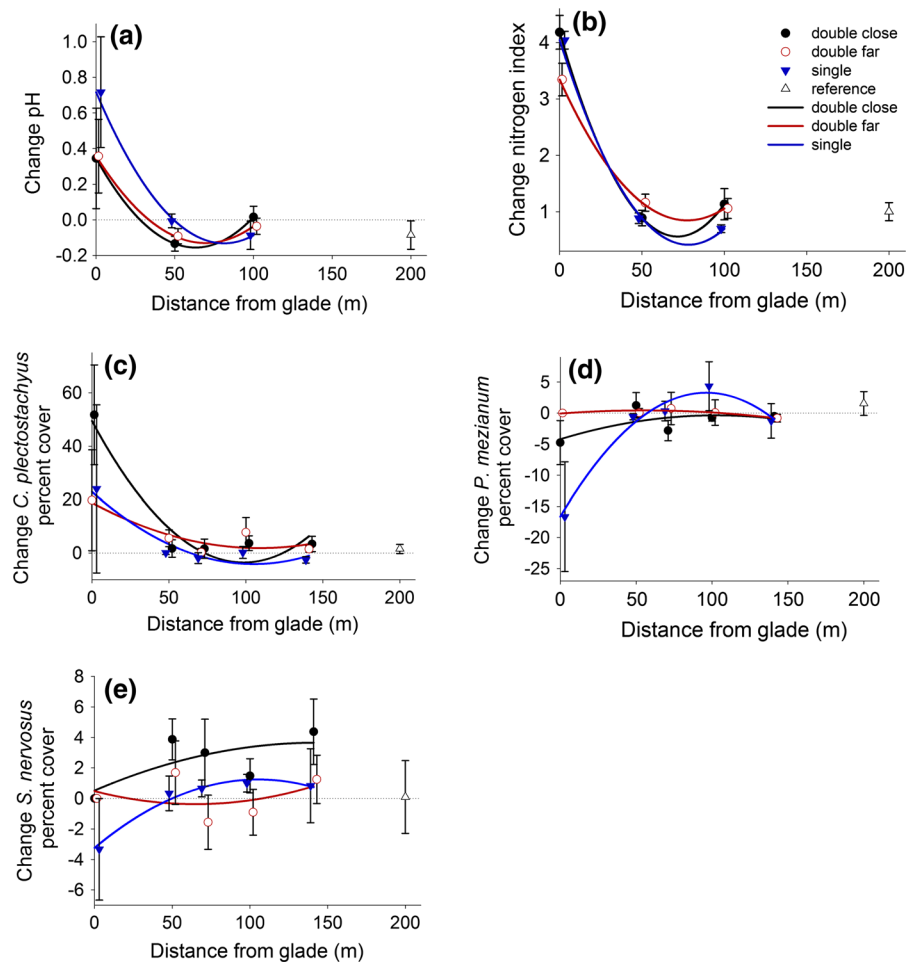
^a Interpret results cautiously due to lack of baseline data

Table 2 Edge magnitude, edge depth and statistical results for response variables with significant treatment \times distance interactions

Response variable (units, <i>df</i>)	Edge magnitude (max–min)		Edge depth (m)		Distance from glade		Distance ² from glade	Baseline
	Single	Double-far	Double-close	Single	Double-far	Double-close		
Soils								
pH (<i>df</i> = 1,66)	0.86 \pm 0.09	0.53 \pm 0.04	0.30 \pm 0.03	33	14	0	F = 44, P < 0.0001	F = 49, P < 0.0001
Calcium (ppm, <i>df</i> = 1,66)	2000 \pm 450	1730 \pm 320	1540 \pm 490	0	5	4	F = 45, P < 0.0001	F = 227, P < 0.0001
Forage quality								
Percent nitrogen index (<i>df</i> = 1,61)	3.3 \pm 0.13	2.3 \pm 0.16	3.2 \pm 0.12	38	38	37	F = 127, P < 0.0001	F = 124, P < 0.0001
Understory plants								
<i>C. plectostachyus</i> cover (%; <i>df</i> = 1, 152)	17 \pm 12	5.7 \pm 2.4	37 \pm 16	0	0	0	F = 7.26, P = 0.008	F = 15.0, P = 0.0002
<i>Acacia drepanolobium</i>								
All trees (no. per 112 m ² , <i>df</i> = 1, 152)	14 \pm 6.4	6.8 \pm 1.4	9.2 \pm 2.4	0	0	9	F = 0.01, P = 0.9	F = 3.83, P = 0.05
Dung								
All wild herbivores (no. per 112 m ² , <i>df</i> = 1, 152)	28 \pm 2.0	7.5 \pm 1.4	21 \pm 2.7	19	20	37	F = 6.56, P = 0.01	F = 14.0, P = 0.0003
Browsers/mixed feeders (no. per 112 m ² , <i>df</i> = 1, 152)	26 \pm 1.2	8.6 \pm 0.4	24 \pm 0.9	106	42	52	F = 59, P < 0.0001	F = 75, P < 0.0001
Cattle + buffalo (per 112 m ² , <i>df</i> = 1, 152)	13 \pm 1.2	2.3 \pm 0.2	19 \pm 2.0	21	0	29	F = 8.53, P = 0.004	F = 26, P < 0.0001

Predicted values from associated models were used to calculate edge magnitude (difference between maximum and minimum response value when plotted vs. distance to glade) and depth (distance beyond which glade and reference confidence intervals overlapped). See Supplementary Material for average response values at each distance from glade

Fig. 2 Glade density treatment effects on soils, forage quality and the understory plant community. **a** Soil pH, **b** foliar nitrogen content, **c** *C. plectostachyus* cover, **d** *P. mezianum* cover, and **e** *S. nervosus* cover. Points (jittered) represent average subplot-specific changes from baseline to 18 months (for soils and forage) or 32 months (for understory plants) \pm 1 SE. Lines represent simple quadratic functions fit to the raw data



Calcium showed a similar pattern (Table 2; treatment $F_{2,8} = 0.29$, $P = 0.8$; distance \times treatment $F_{2,66} = 2.63$, $P = 0.08$; distance² \times treatment $F_{2,66} = 0.38$, $P = 0.7$). For both responses, edge effect magnitude was largest in the single treatment and smallest in the double-close treatment (Table 2). For phosphorous, concentrations increased most in double-close plots and least in single plots (mean change for double-close plots: 7.04 ± 3.34 , double-far: 4.56 ± 5.64 , single: 4.28 ± 2.52 ppm; treatment $F_{2,8} = 6.62$, $P = 0.02$; distance \times treatment $F_{2,66} = 0.03$, $P = 0.97$; distance² \times treatment $F_{2,66} = 0.003$, $P = 0.997$). Glade density treatments did not significantly affect other soil nutrients (all treatment, distance \times treatment and distance² \times treatment P -values > 0.22).

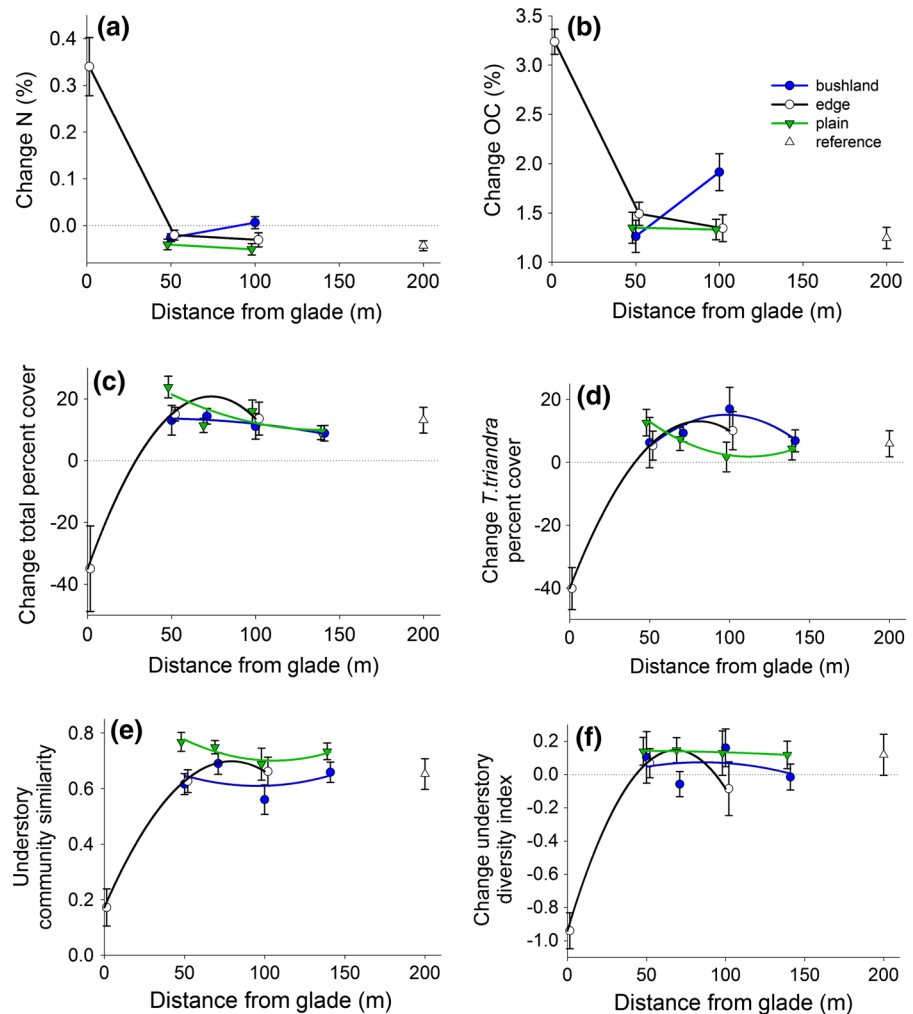
For total soil nitrogen and organic carbon, experimental glade edge effect patterns were different in different matrix types (N: matrix $F_{2,66} = 4.31$,

$P = 0.02$, distance \times matrix $F_{2,66} = 2.42$, $P = 0.10$; OC: matrix $F_{2,66} = 1.54$, $P = 0.2$, distance \times matrix $F_{2,66} = 5.86$, $P = 0.005$). In edges and plains, nutrient levels declined with distance from glade, but bushlands did not follow the same pattern and instead displayed unusually high nutrient values at 100 m from glade (Fig. 3a, b). The main effect of matrix type was also significant for sodium and CEC (P values < 0.03), but this result likely reflects pre-existing variation since baseline data were lacking for these response variables. Other soil parameters did not differ significantly based on matrix type (all matrix and distance \times matrix P values > 0.11).

Plant nutrients

All of the foliar nutrient index values increased substantially between 0 and 18 months, likely because

Fig. 3 Edge effect development in plains versus bushland for soil and understory plant responses. **a** Soil nitrogen, **b** soil organic carbon, **c** total plant cover, **d** *T. triandra* cover, **e** understory community similarity, and **f** understory species diversity. Points (jittered) represent average subplot-specific changes from baseline to 32 months \pm 1 SE. Lines in **c–f** represent simple quadratic functions fit to the raw data



of the switch from brown leaf collection to green leaf collection. However, we also observed significant effects of glades and glade density treatments. Foliar nutrient increases were highest inside glades (Distance = 0), and glades had edge effects with large magnitudes and moderate depths (Tables 1 and 2). For foliar nitrogen, edge magnitude was smallest in the double-far treatment (Table 2). Compared to the other treatments, nitrogen concentrations in the double-far treatment were slightly lower inside experimental glades and higher at 50 m from glades (Fig. 2b; treatment $F_{2,8} = 0.20$, $P = 0.8$; distance \times treatment $F_{2,61} = 1.91$, $P = 0.16$; distance² \times treatment $F_{2,61} = 2.89$, $P = 0.06$). Glade density treatments did not significantly affect foliar potassium and phosphorous (treatment P values > 0.16).

In areas around experimental glades, foliar nitrogen increased less in bushlands than edges or plains (mean change in index value for bushland: 0.75 ± 0.09 , edge: 1.08 ± 0.12 , plain: 1.14 ± 0.13 ; matrix $F_{2,61} = 4.49$, $P = 0.02$, distance \times matrix $F_{2,61} = 0.66$, $P = 0.5$), and foliar potassium increased less in plains than bushlands (mean change for bushland: 1.25 ± 0.10 , edge: 1.06 ± 0.09 , plain: 0.96 ± 0.11 ; matrix $F_{2,61} = 4.33$, $P = 0.02$, distance \times matrix $F_{2,61} = 0.60$, $P = 0.6$). Foliar phosphorous was not significantly affected by matrix type (P values > 0.13).

Understory plant community

For three common grass species, glades developed stronger edge effects in the double-close or single

treatments than the double-far treatment (Table 2). Relative to baseline values, cover of the glade-specialist grass *Cynodon plectostachyus* increased inside of experimental glades and stayed stable or declined far from glades, but the magnitude of these changes was smaller for the double-far and single treatments than the double-close treatment (Fig. 2c; treatment $F_{2,8} = 0.81$, $P = 0.5$; distance \times treatment $F_{2,152} = 2.00$, $P = 0.14$; distance² \times treatment $F_{2,152} = 4.94$, $P = 0.008$). Cover of *Pennisetum mezianum* declined inside glades and remained stable or increased far from glades, but the magnitude of these changes was largest for the single treatment and smallest for the double-far treatment (Fig. 2d; we were unable to statistically analyze this response variable because data did not meet model assumptions). Finally, cover of *Sporobolus nervosus* increased more in double-close plots than other plots (Fig. 2e; treatment $F_{2,8} = 4.29$, $P = 0.05$; distance \times treatment $F_{2,152} = 0.43$, $P = 0.6$; distance² \times treatment $F_{2,152} = 0.94$, $P = 0.4$). For *Themeda triandra*, total understory cover, understory species diversity, and understory community similarity, experimental glades had lower values than surrounding areas (Table 1, Supplementary Material), but patterns did not vary significantly among glade density treatments (all treatment P values > 0.16). The grass *Pennisetum stramineum* did not respond significantly to distance from glade (Table 1) or glade density treatments (P values > 0.6).

In plains, total cover and *T. triandra* cover increased more at 50 m than 100 m from glade, but this pattern was absent or reversed in bushland and edge environments (Fig. 3c, d; total cover: matrix $F_{2,152} = 5.35$, $P = 0.006$, distance \times matrix $F_{2,152} = 1.12$, $P = 0.3$, distance² \times matrix $F_{2,152} = 6.60$, $P = 0.002$; *T. triandra* matrix $F_{2,152} = 0.75$, $P = 0.5$, distance \times matrix $F_{2,152} = 1.59$, $P = 0.2$, distance² \times matrix $F_{2,152} = 8.65$, $P = 0.0003$). The understory plant community changed more and species diversity declined more in bushland than open plains subplots (Fig. 3e, f; community similarity: matrix $F_{2,153} = 7.33$, $P = 0.0009$, distance \times matrix $F_{2,153} = 0.82$, $P = 0.4$, distance² \times matrix $F_{2,153} = 3.39$, $P = 0.04$; SW index: matrix $F_{2,149} = 0.29$, $P = 0.7$, distance \times matrix $F_{2,149} = 0.01$, $P = 0.99$, distance² \times matrix $F_{2,149} = 8.49$, $P = 0.0003$). Changes in other understory response variables were not affected by matrix type (all P values > 0.14).

Acacia drepanolobium trees

Compared to double glade plots, single glade plots lost more *A. drepanolobium* trees inside glades and gained more trees outside glades (Fig. 4a; treatment $F_{2,8} = 1.55$, $P = 0.3$; distance \times treatment $F_{2,152} = 0.44$, $P = 0.6$; distance² \times treatment $F_{2,152} = 4.18$, $P = 0.02$). Edge magnitude was largest in the single treatment and smallest in the double-far treatment (Table 2). At the plot scale, the double-far treatment gained the most trees over the course of the experiment (mean change for double-close plots: -0.66 ± 0.22 , double-far: 0.16 ± 0.17 , single: 0.08 ± 0.58 trees per 112 m²).

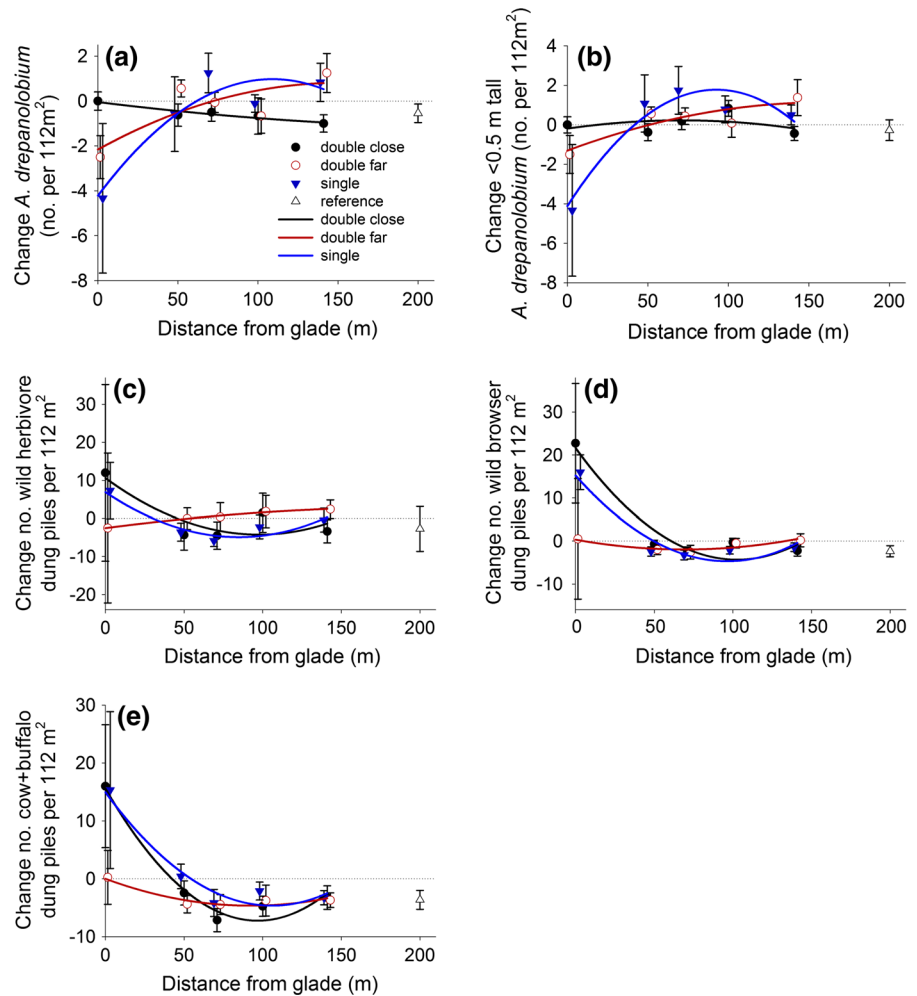
Separating trees by height class showed that small trees (<0.5 m tall) drove overall density patterns. Small trees accounted for 60–70 % of all trees, and small tree edge effect patterns were similar to those of all trees (Fig. 4b; treatment $F_{2,8} = 0.13$, $P = 0.9$; distance \times treatment $F_{2,152} = 0.24$, $P = 0.8$; distance² \times treatment $F_{2,152} = 2.25$, $P = 0.11$). At the plot scale, double-far plots lost slightly fewer large trees (>0.5 m tall) than other plots (mean change for double-close = -0.59 ± 0.25 , double-far = -0.47 ± 0.24 , single = -0.56 ± 0.38 trees per 112 m²; treatment $F_{2,8} = 3.25$, $P = 0.09$; distance \times treatment $F_{2,152} = 0.07$, $P = 0.9$; distance² \times treatment $F_{2,152} = 0.96$, $P = 0.4$).

Stronger edge effects developed in bushlands than plains for all trees (Fig. 5a; matrix $F_{2,152} = 3.52$, $P = 0.03$, distance \times matrix $F_{2,152} = 3.62$, $P = 0.03$, distance² \times matrix $F_{2,152} = 3.21$, $P = 0.04$), small trees (Fig. 5b; matrix $F_{2,152} = 6.99$, $P = 0.001$, distance \times matrix $F_{2,152} = 4.02$, $P = 0.02$, distance² \times matrix $F_{2,152} = 4.29$, $P = 0.02$) and large trees (Fig. 5c; matrix $F_{2,152} = 1.68$, $P = 0.2$, distance \times matrix $F_{2,152} = 0.16$, $P = 0.9$, distance² \times matrix $F_{2,152} = 2.95$, $P = 0.06$).

Large herbivore community

Wild herbivores were attracted to experimental glades, and this attraction was stronger in the single and double-close treatments than in the double-far treatment (Table 2; Fig. 4c; treatment $F_{2,8} = 1.18$, $P = 0.4$; distance \times treatment $F_{2,152} = 2.37$, $P = 0.10$; distance² \times treatment $F_{2,152} = 4.25$, $P = 0.02$). Splitting herbivores into feeding guilds revealed that

Fig. 4 Glade density treatment effects on trees and large herbivores. **a** *Acacia drepanolobium* density, **b** small (<0.5 m tall) *Acacia drepanolobium* density, **c** wild herbivore use, **d** browser/mixed feeder use, and **e** cattle + buffalo use. *Points* (jittered) represent average subplot-specific changes from baseline to 32 months \pm 1 SE. *Lines* represent simple quadratic functions fit to the raw data

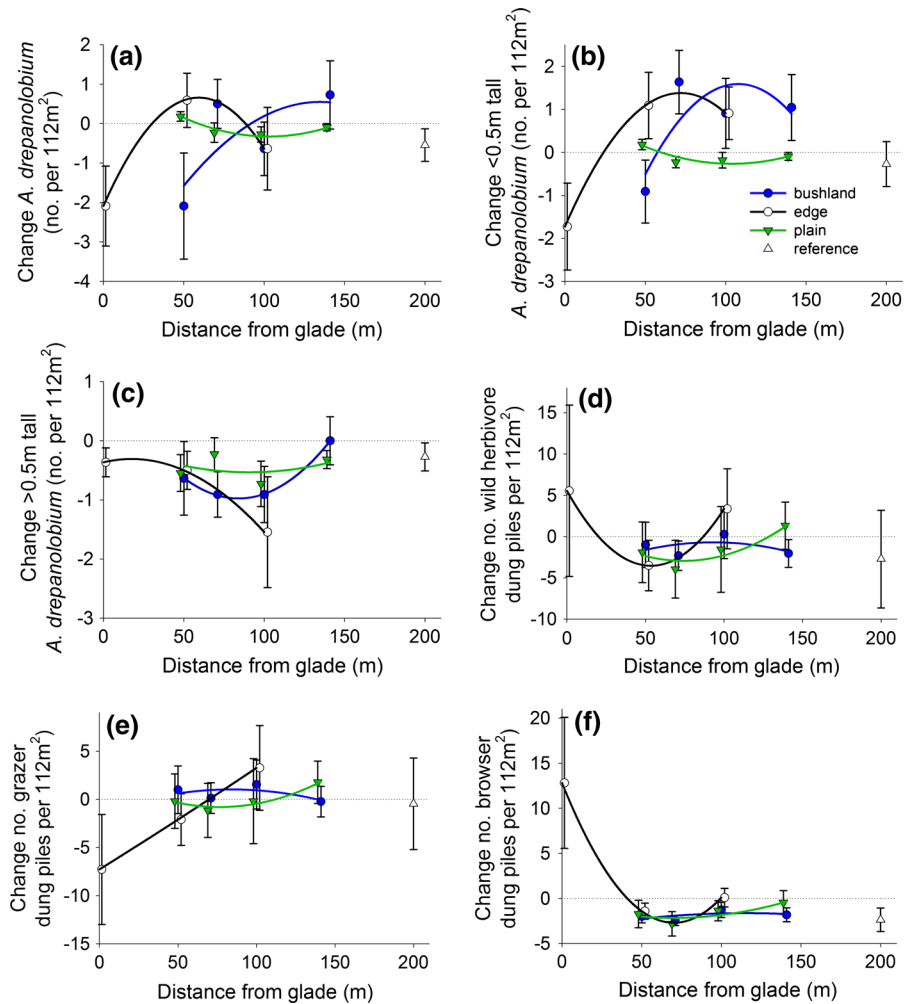


wild herbivore patterns were driven by browsers/mixed feeders (Table 2; Fig. 4d; treatment $F_{2,8} = 2.45$, $P = 0.15$; distance \times treatment $F_{2,152} = 8.15$, $P = 0.0004$; distance² \times treatment $F_{2,152} = 4.44$, $P = 0.01$). Wild grazing herbivores did not respond strongly to density treatments (P values > 0.29) and tended to avoid glades (Table 1, Supplementary Material). Cattle and buffalo (primarily grazers, but not included in the wild herbivore analysis) showed the same significant pattern as browsers and total wild herbivores (Fig. 4e; treatment $F_{2,8} = 0.72$, $P = 0.5$; distance \times treatment $F_{2,152} = 2.14$, $P = 0.12$; distance² \times treatment $F_{2,152} = 4.36$, $P = 0.01$).

Along edges between bushland and plains, wild herbivore use declined at 50 m from glades and increased at 100 m from glades, but this edge effect pattern was not present in plain or bushland matrix

types (Fig. 5d–f; all wild herbivores: matrix $F_{2,152} = 14.5$, $P < 0.0001$, distance \times matrix $F_{2,152} = 2.67$, $P = 0.07$, distance² \times matrix $F_{2,152} = 0.99$, $P = 0.4$; grazers: matrix $F_{2,152} = 7.44$, $P = 0.0008$, distance \times matrix $F_{2,152} = 3.76$, $P = 0.03$, distance² \times matrix $F_{2,152} = 0.13$, $P = 0.9$; browsers: matrix $F_{2,152} = 0.78$, $P = 0.5$, distance \times matrix $F_{2,152} = 0.03$, $P = 0.97$, distance² \times matrix $F_{2,152} = 4.22$, $P = 0.02$). In areas around experimental glades, cattle and buffalo use declined less in edges and bushlands than open plains (mean change for bushland: -3.1 ± 0.7 , edge: -2.4 ± 1.2 , plain: -5.0 ± 1.0 dung piles per 112 m²; matrix $F_{2,152} = 6.77$, $P = 0.002$, distance \times matrix $F_{2,152} = 0.30$, $P = 0.7$, distance² \times matrix $F_{2,152} = 1.41$, $P = 0.2$). As distance from glade increased, wildlife species diversity (Shannon–Weiner index) declined and

Fig. 5 Edge effect development in plains versus bushland for tree and wildlife responses. **a** *Acacia drepanolobium* density, **b** small (<0.5 m tall) *A. drepanolobium* density, **c** large (>0.5 m tall) *A. drepanolobium* density, **d** total wildlife use, **e** browser use, and **f** grazer use. Points (jittered) represent average subplot-specific changes from baseline to 32 months \pm 1 SE. Lines represent simple quadratic functions fit to the raw data



community similarity increased (Table 1, Supplementary Material), but these responses did not differ significantly across glade density treatments or matrix types (all P values > 0.11).

Discussion/conclusion

Edge effects around experimental glades

Consistent with previous observational work (e.g., Stelfox 1986; Young et al. 1995; Augustine 2003; Treydte et al. 2006; Muchiru et al. 2009; Porensky 2011; van der Waal et al. 2011; Veblen 2012; Vuorio et al. 2014), experimental cattle corrals in our study developed into ecosystem hotspots with elevated soil and plant nutrient content, reduced plant diversity,

altered plant species composition, increased cover of *C. plectostachyus*, reduced tree density, altered wildlife species composition, elevated wildlife use and wildlife diversity, and elevated cattle (+buffalo) use (Tables 1 and 2, Figs. 2, 3, 4, 5). Experimental glades developed edge effects with large magnitudes and relatively shallow depths (Tables 1, 2). In other words, experimental glades differed strongly from the surrounding savanna, but glade effects did not penetrate far into the surrounding landscape. Edge magnitudes were particularly large for browser use and soil phosphorous concentrations, which were more than 10 times as high inside glades (Distance = 0) as at reference subplots (see Supplementary Material and Porensky and Veblen 2015).

Previous descriptive research (e.g., Young et al. 1995; Muchiru et al. 2009; Porensky 2011) suggested

that glade edge depths vary broadly depending on the response variable. In our experimental study, most response variables had edge depths <50 m (our sampling strategy did not include subplots at distances between 0 and 50 m), but we did observe edge depths >50 m for browsing and mixed feeding herbivores, which are strongly attracted to glades. It is likely that edge effects around these young glades will become more spatially extensive as the glades continue to age (Veblen 2012). Increased sampling in areas <50 m from experimental glades is an important goal for future research on this topic. This experiment was not designed to detect edge effects with depths greater than 200 m. Edge effects operating over very large spatial scales have been documented in some ecosystems (Laurance 2000; Ewers and Didham 2008), though previous work suggests that large-scale edge effects around glades are rare for the traits studied here (Young et al. 1995; Muchiru et al. 2009; Porensky 2011; Veblen 2012).

Edge effect interactions

The presence and proximity of other glades within 200 m had significant effects on the development of glade edge effects. Differences between response values inside the glades (0 m) and values at 50–100 m from glades drove many of the edge effect interactions, indicating that boma configuration influences cattle use patterns and, after abandonment, the attractiveness of glades to large herbivores.

A few ecological variables responded monotonically to experimentally increased glade density. For example, soil phosphorous increased most in double-close plots and least in single glade plots. Soil pH and Ca displayed the opposite trend, increasing more inside single than double-close glades (Table 2; Fig. 2). These findings suggest that in the first 18 months after boma abandonment, the magnitude of soil nutrient enrichment inside and around developing glades is directly (or inversely) proportional to the density of cattle during boma use.

For most response variables, however, we observed a very different and counterintuitive pattern. Compared to plots with a single glade, the presence of a second glade 100 m away led to similar or even strengthened glade effects and glade edge effects, but the presence of a second glade 200 m away led to weakened edge effects. Below, we describe this

surprising result in more detail. Briefly, our results suggest that in the double-far treatment, the moderately intense impacts of cattle and herders led to moderate degradation and bush encroachment. In the double-close treatment, cattle and herder impacts were even more intense, but rather than causing degradation, these intense impacts initiated a threshold shift towards glade-like conditions.

For many response variables, glades in the double-far treatment (two glades 200 m apart) had weaker edge effects than glades in other treatments. Edge magnitude was smallest in the double-far treatment for foliar nitrogen content, *C. plectostachyus* increase, *P. mezianum* extirpation, total tree density, total wildlife use, browser/mixed feeder use, and cattle + buffalo use (Table 2; Figs. 2 and 4). The double-far treatment also tended to have narrower edge depths than other treatments (Table 2). In other words, double-far glades were more similar to the background savanna, and the impacts of double-far glades extended less far into the surrounding landscape. At the plot scale, double-far plots had relatively low cover of a palatable grass species (*S. nervosus*), and more *A. drepanolobium* trees.

These results are consistent with the findings of a previous observational study at a different ranch (Porensky 2011), in which glades were 177 ± 16 m apart center-to-center. In that study, the presence of a nearby glade was associated with less glade-specialist grass, higher tree densities, and less wildlife use both inside and nearby glades. In this study's double-far treatment, as in the previous study, areas around active bomas experienced fertilization combined with moderate cattle grazing and low browsing pressure. The current study shows experimentally that these impacts cause areas within and around the resultant glade to have lower forage quality, higher relative abundance of unpalatable grasses, more trees, and less herbivore use. Thus, differences between the single and double-far experimental treatments fit well with previous descriptive work, and provide experimental demonstration that edge interactions are not caused by pre-existing site differences (e.g., herders placing more bomas at sites with more trees). The current study also bolsters previous results by detecting these same edge effect interactions after averaging data from eight directions around experimental glades, rather than only looking at edge effects in the zone between two adjacent glades.

Even as results from the double-far treatment reinforce previous findings, they raise another question. Why weren't double-close results more similar to double-far results? In most cases, double-close edge effects were similar to or even stronger than single edge effects (Table 2). At double-close sites, plant nitrogen increased, unpalatable grasses declined, palatable grasses (*Cynodon* and *Sporobolus*) established, large trees declined, and wildlife use was high (Figs. 2 and 4). Glades in the double-close treatment were closer together than the glades studied in previous work (Porensky 2011). Cattle impacts and phosphorous fertilization at double-close sites may have been strong enough to kill existing vegetation and facilitate the establishment of the palatable, nitrogen-rich grass species that are most abundant in cattle dung (particularly *Cynodon*). In other words, the more intense cattle impacts at double-close sites initiated different ecological feedbacks than the moderate cattle impacts at double-far sites.

Together, these results demonstrate that increasing glade density has complex, nonlinear consequences for savanna ecology. Wild herbivores and cattle are attracted to glades in landscapes that have high or low glade densities, but not intermediate glade densities. On the other hand, *A. drepanolobium*, a species of special concern in this study system (Okello et al. 2001; Wahungu et al. 2011), may have the highest chance of persistence and recruitment when glade densities are intermediate. Palatable grasses appear to do best when glade densities are high. Depending on their objectives, managers may want to avoid certain glade densities, or intentionally include a range of densities. These results add nuance to the intermediate landscape complexity hypothesis (Fahrig et al. 2011; Tscharrntke et al. 2012) by suggesting that in our system, intermediate landscape complexity favors some components of biodiversity (trees) but has negative effects on other components (wildlife).

More broadly, our results provide experimental evidence for the idea that edge effects can be altered by the presence and proximity of other nearby edges (see also Fletcher 2005; Harper et al. 2007), and also show that the direction of edge effect interactions can be reversed as the density of edges (and associated landscape complexity) increases. Our experimental design was able to isolate glade density as the causal factor behind these variable edge effects, but further research is needed to better elucidate underlying

mechanisms (e.g., the intensity and spatial distribution of cattle and herder use around active bomas arranged at multiple densities).

The importance of matrix type: bush versus plain

Our results support previous work (e.g., Sisk et al. 1997; Pauchard and Alaback 2004; Rand et al. 2006; Santos-Barrera and Urbina-Cardona 2011; Wilkerson 2013) suggesting that edge effects are sensitive to matrix type. Our study did not include experimental glades located far from bushland—plain boundaries, but we still observed strong differences between edge effects extending into bushland and those extending into plains. For most response variables, glade-induced changes were stronger in bushland or edge subplots (which were less glade-like before the experiment) than in plains subplots (which started out more similar to glades, in that they had some *C. plectostachyus* cover and few trees). For example, bushland plant communities near experimental glades tended to become more glade-like (e.g., loss of trees, altered understory plant species composition, reduced plant diversity) but plant communities in open plains did not change very much (Figs. 3, 5). Our results support previous studies (e.g., Campbell et al. 2011) showing that higher contrast edges (e.g., glades vs. bushland) are associated with stronger edge effects than lower contrast edges (e.g. glades vs. plains).

Along edges between bushland and plains, wild herbivores appeared to avoid areas close to experimental glades in favor of areas inside glades (for browsers) or far from glades (for grazers; Fig. 5). Shifts in wildlife use were less pronounced in plain and bushland than edge subplots, suggesting that wildlife moving towards (or away from) glades generally did so by shifting their location along the plain-bush edge rather than moving from plain or bushland towards (or away from) the edge. This result suggests that for wildlife, attraction to experimental glades may be regulated by some degree of “matrix fidelity” (see also Wolf et al. 2009; Merkle et al. 2014).

We also observed a shift in cattle use towards bushlands and away from plains. Combined with transient fertilization during boma use, reduced cattle use in open plains could be the driver of the observed

increases in total plant cover and *T. triandra* cover at plains subplots located close to experimental glades (Fig. 3). Increased cattle use of bushlands could be the driver of anisotropic patterns of plant community change (described above), as well as marked increases in soil nitrogen, soil organic carbon, and small tree density at bushland subplots located 100 m from glades (Figs. 3, 5).

Despite their complexity, the results from this experimental study demonstrate that edge effects are strongly impacted by landscape context, including both matrix type and the presence of other nearby edges. In complex landscapes, the strength and character of any given edge effect is likely to be variable and potentially unpredictable. In order to maximize ecosystem function and desired ecosystem services in such landscapes, ecologists and managers need a better understanding of how landscape configuration can alter ecological responses to landscape boundaries (Fahrig et al. 2011).

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References

- Agnew A, Agnew S (1994) Upland Kenya Wild Flowers. East African Natural History Society, Nairobi, Kenya
- Agnew ADQ (2006) A field key to upland Kenya grasses. *J East Afr Nat Hist* 95(1):1–83
- Augustine DJ (2003) Long-term, livestock-mediated redistribution of nitrogen and phosphorus in an East African savanna. *J Appl Ecol* 40(1):137–149
- Augustine DJ (2004) Influence of cattle management on habitat selection by impala on central Kenyan rangeland. *J Wildl Manag* 68(4):916–923
- Augustine DJ, McNaughton SJ, Frank DA (2003) Feedbacks between soil nutrients and large herbivores in a managed savanna ecosystem. *Ecol Appl* 13(5):1325–1337
- Barnes RFW (2001) How reliable are dung counts for estimating elephant numbers? *Afr J Ecol* 39(1):1–9
- Blackmore AC, Mentis MT, Scholes RJ (1990) The origin and extent of nutrient-enriched patches within a nutrient-poor savanna in South-Africa. *J Biogeogr* 17(4–5):463–470
- Bloom SA (1981) Similarity indexes in community studies: potential pitfalls. *Mar Ecol Prog Ser* 5(2):125–128
- Cadenasso ML, Pickett STA, Weathers KC, Jones CG (2003) A framework for a theory of ecological boundaries. *BioScience* 53(8):750–758
- Cadenasso ML, Traynor MM, Pickett STA (1997) Functional location of forest edges: gradients of multiple physical factors. *Can J For Res* 27(5):774–782
- Campbell RE, Harding JS, Ewers RM, Thorpe S, Didham RK (2011) Production land use alters edge response functions in remnant forest invertebrate communities. *Ecol Appl* 21(8):3147–3161
- Collinge SK, Palmer TM (2002) The influences of patch shape and boundary contrast on insect response to fragmentation in California grasslands. *Landscape Ecol* 17(7):647–656
- Damschen EI, Brudvig LA, Haddad NM, Levey DJ, Orrock JL, Tewksbury JJ (2008) The movement ecology and dynamics of plant communities in fragmented landscapes. *Proc Natl Acad Sci U S A* 105(49):19078–19083
- Daniels M (2006) Estimating red deer *Cervus elaphus* populations: an analysis of variation and cost-effectiveness of counting methods. *Mammal Rev* 36:235–247
- Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB, Collen B (2014) Defaunation in the Anthropocene. *Science* 345:401–406
- Donihue CM, Porensky LM, Foufopoulos J, Riginos C, Pringle RM (2013) Glade cascades: indirect legacy effects of pastoralism enhance the abundance and spatial structuring of boreal fauna. *Ecology* 94(4):827–837
- Ewers RM, Didham RK (2008) Pervasive impact of large-scale edge effects on a beetle community. *Proc Natl Acad Sci U S A* 105(14):5426–5429
- Ewers RM, Didham RK, Fahrig L, Ferraz G, Hector A, Holt RD, Kapos V, Reynolds G, Sinun W, Snaddon JL, Turner EC (2011) A large-scale forest fragmentation experiment: the stability of altered forest ecosystems project. *Philos Trans R Soc B* 366(1582):3292–3302
- Fagan WF, Cantrell RS, Cosner C (1999) How habitat edges change species interactions. *Am Nat* 153(2):165–182
- Fahrig L, Baudry J, Brotons L, Burel FG, Crist TO, Fuller RJ, Sirami C, Siriwardena GM, Martin JL (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecol Lett* 14(2):101–112
- Fletcher RJ (2005) Multiple edge effects and their implications in fragmented landscapes. *J Anim Ecol* 74(2):342–352
- Harper KA, Macdonald SE, Burton PJ, Chen JQ, Brosfolske KD, Saunders SC, Euskirchen ES, Roberts D, Jaiteh MS, Esseen PA (2005) Edge influence on forest structure and composition in fragmented landscapes. *Conserv Biol* 19(3):768–782
- Harper KA, Mascarua-Lopez L, Macdonald SE, Drapeau P (2007) Interaction of edge influence from multiple edges: examples from narrow corridors. *Plant Ecol* 192(1):71–84

- Laurance WF (2000) Do edge effects occur over large spatial scales? *Trends Ecol Evol* 15(4):134–135
- Laurance WF, Camargo JLC, Luizao RCC, Laurance SG, Pimm SL, Bruna EM, Stouffer PC, Williamson GB, Benitez-Malvido J, Vasconcelos HL, Van Houtan KS, Zartman CE, Boyle SA, Didham RK, Andrade A, Lovejoy TE (2011) The fate of Amazonian forest fragments: a 32-year investigation. *Biol Conserv* 144(1):56–67
- Laurance WF, Goosem M, Laurance SGW (2009) Impacts of roads and linear clearings on tropical forests. *Trends Ecol Evol* 24(12):659–669
- Laurance WF, Nascimento HEM, Laurance SG, Andrade AC, Fearnside PM, Ribeiro JEL, Capretz RL (2006) Rain forest fragmentation and the proliferation of successional trees. *Ecology* 87(2):469–482
- Malcolm JR (1994) Edge effects in central Amazonian forest fragments. *Ecology* 75(8):2438–2445
- Merkle JA, Fortin D, Morales JM (2014) A memory-based foraging tactic reveals an adaptive mechanism for restricted space use. *Ecol Lett* 17:924–993
- Muchiru AN, Western D, Reid RS (2009) The impact of abandoned pastoral settlements on plant and nutrient succession in an African savanna ecosystem. *J Arid Environ* 73:322–331
- Okello BD, O'Connor TG, Young TP (2001) Growth, biomass estimates, and charcoal production of *Acacia drepanolobium* in Laikipia, Kenya. *For Ecol Manag* 142(1–3):143–153
- Orrock JL, Curler GR, Danielson BJ, Coyle DR (2011) Large-scale experimental landscapes reveal distinctive effects of patch shape and connectivity on arthropod communities. *Landscape Ecol* 26(10):1361–1372
- Pauchard A, Alaback PB (2004) Influence of elevation, land use, and landscape context on patterns of alien plant invasions along roadsides in protected areas of south-central Chile. *Conserv Biol* 18(1):238–248
- Peterman RM (1990) Statistical power analysis can improve fisheries research and management. *Can J Fish Aquat Sci* 47:2–15
- Pinheiro J, Bates D, DebRoy S, Sarkar D, the R Development Core Team (2013) nlme: linear and nonlinear mixed effects models. R package version 3
- Porensky LM (2011) When edges meet: interacting edge effects in an African savanna. *J Ecol* 99(4):923–934
- Porensky LM, Veblen KE (2012) Grasses and browsers reinforce landscape heterogeneity by excluding trees from ecosystem hotspots. *Oecologia* 168(3):749–759
- Porensky LM, Veblen KE (2015) Generation of ecosystem hotspots using short-term cattle corrals in an African savanna. *Rangel Ecol Manag* 68(2):131–141
- Porensky LM, Young TP (2013) Edge-effect interactions in fragmented and patchy landscapes. *Conserv Biol* 27(3):509–519
- Rand TA, Tylianakis JM, Tscharntke T (2006) Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. *Ecol Lett* 9(5):603–614
- Rasmussen HB, Kahindi O, Vollrath F, Douglas-Hamilton I (2005) Estimating elephant densities from wells and droppings in dried out riverbeds. *Afr J Ecol* 43:312–319
- Reid RS, Ellis JE (1995) Impacts of pastoralists on woodlands in south Turkana, Kenya—livestock-mediated tree recruitment. *Ecol Appl* 5(4):978–992
- Ries L, Fletcher RJ, Battin J, Sisk TD (2004) Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annu Rev Ecol Evol Syst* 35:491–522
- Riginos C (2015) Climate and the landscape of fear in an African savanna. *J Anim Ecol* 84:124–133
- Riginos C, Grace JB (2008) Savanna tree density, herbivores, and the herbaceous community: bottom-up versus top-down effects. *Ecology* 89:2228–2238
- Santos-Barrera G, Urbina-Cardona JN (2011) The role of the matrix-edge dynamics of amphibian conservation in tropical montane fragmented landscapes. *Rev Mex Biodivers* 82(2):679–687
- Shannon CE (1948) A mathematical theory of communication. *Bell Syst Tech J* 27:379–423 and 623–656
- Sisk TD, Haddad NM, Ehrlich PR (1997) Bird assemblages in patchy woodlands: modeling the effects of edge and matrix habitats. *Ecol Appl* 7(4):1170–1180
- Söderström B, Reid RS (2010) Abandoned pastoral settlements provide concentrations of resources for savanna birds. *Acta Oecol* 36(2):184–190
- Stelfox JB (1986) Effects of livestock enclosures bomas on the vegetation of the Athi Plains, Kenya. *Afr J Ecol* 24:41–45
- Treydte AC, Halsdorf SA, Weber E, Edwards PJ (2006) Habitat use of warthogs on a former cattle ranch in Tanzania. *J Wildl Manag* 70(5):1285–1292
- Tscharntke T, Tylianakis JM, Rand TA, Didham RK, Fahrig L, Batáry P, Bengtsson J, Clough Y, Crist TO, Dormann CF, Ewers RM, Fründ J, Holt RD, Holzschuh A, Klein AM, Kleijn D, Kremen C, Landis DA, Laurance W, Lindenmayer D, Scherber C, Sodhi N, Steffan-Dewenter I, Thies C, van der Putten WH, Westphal C (2012) Landscape moderation of biodiversity patterns and processes—eight hypotheses. *Biol Rev* 87(3):661–685
- van der Waal C, Kool A, Meijer S, Kohi E, Heitkönig I, de Boer W, van Langevelde F, Grant R, Peel M, Slotow R, de Knegt H, Prins H, de Kroon H (2011) Large herbivores may alter vegetation structure of semi-arid savannas through soil nutrient mediation. *Oecologia* 165(4):1095–1107
- Veblen KE (2012) Savanna glade hotspots: plant community development and synergy with large herbivores. *J Arid Environ* 78:119–127
- Veblen KE (2013) Impacts of traditional livestock corrals on woody plant communities in an East African savanna. *Rangel J* 35(3):349–353
- Veblen KE, Young TP (2010) Contrasting effects of cattle and wildlife on the vegetation development of a savanna landscape mosaic. *J Ecol* 98:993–1001
- Vuorio V, Muchiru A, Reid RS, Ogutu JO (2014) How pastoralism changes savanna vegetation: impact of old pastoral settlements on plant diversity and abundance in southwestern Kenya. *Biodivers Conserv* 23:3219–3240
- Wahungu GM, Mureu LK, Kimuyu DM, Birkett A, Macharia PG, Burton J (2011) Survival, recruitment and dynamics of *Acacia drepanolobium* Sjöstedt seedlings at Olpejeta Conservancy, Kenya, between 1999 and 2009. *Afr J Ecol* 49(2):227–233

- Western D, Dunne T (1979) Environmental aspects of settlement site decisions among pastoral Maasai. *Hum Ecol* 7(1):75–98
- Wilkerson ML (2013) Invasive plants in conservation linkages: from conceptual model to understanding real-world patterns. PhD Dissertation, University of California, Davis
- Wolf M, Frair J, Merrill E, Turchin P (2009) The attraction of the known: the importance of spatial familiarity in habitat selection in wapiti *Cervus elaphus*. *Ecography* 32:401–410
- Young HS, Dirzo R, Helgen KM, McCauley DJ, Billeter SA, Kosoy MY, Osikowicz LM, Salkeld DJ, Young TP, Dittmar K (2014) Declines in large wildlife increase landscape-level prevalence of rodent-borne disease in Africa. *Proc Natl Acad Sci* 111(19):7036–7041
- Young HS, McCauley DJ, Dirzo R, Goheen JR, Agwanda B, Castillo EO, Ferguson A, Kinyua SN, McDonough M, Palmer TM, Pringle RM, Young TP, Helgen KM (2015) Context-dependent effects of large mammal declines on small mammal communities in central Kenya. *Ecol Appl* 25(2):348–360
- Young TP, Palmer TA, Gadd ME (2005) Competition and compensation among cattle, zebras, and elephants in a semi-arid savanna in Laikipia, Kenya. *Biol Conserv* 122(2):351–359
- Young TP, Patridge N, Macrae A (1995) Long-term glades in *Acacia* bushland and their edge effects in Laikipia, Kenya. *Ecol Appl* 5(1):97–108