When edges meet: interacting edge effects in an African savanna

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Summary

1. Ecological edges (zones separating ecosystems or land cover types) can function as active boundaries, unique habitats and dynamic transition zones. Abiotic factors, species and species interactions exhibit strong responses to edges, and these responses – edge effects – can profoundly impact ecosystem structure and function.

2. Edge effects may be altered by the presence or proximity of other nearby edges. This phenomenon – edge interaction – is poorly understood, though its importance is increasingly recognized. Edge interactions are likely in fragmented or patchy landscapes that contain many edges. In such landscapes, understanding how nearby edges interact may be critical for effective conservation and management.

3. I examined edge interactions in an East African savanna. In this landscape, abandoned cattle corrals develop into treeless, nutrient-rich 'glades' that persist as preferentially grazed areas for decades to centuries. Glades represent important sources of structural and functional landscape heterogeneity and have major impacts on distributional patterns of plant and animals.

4. I used existing variation in inter-glade distance to investigate the importance and strength of glade edge interactions for plants, *Acacia* ants and large herbivores. Specifically, I compared response patterns obtained from transects that extended outward from isolated glades (> 250 m from another glade) and non-isolated glades (< 150 m from another glade).

5. Edge effect patterns between nearby glades differed significantly from patterns around isolated glades. When compared to areas outside isolated glades, areas between glades had almost twice the density of trees, half as much large herbivore use, reduced cover of glade-dominant grasses, and different *Acacia* ant communities. Many of the edge effects observed between non-isolated glades could not be inferred from effects around isolated glades.

6. *Synthesis.* These findings suggest that edge interactions can alter plant and animal distributions in patchy landscapes. Edge effects near multiple edges can be stronger, weaker or qualitatively different from those near isolated edges. Such edge interactions can increase or decrease structural and functional continuity between nearby patches. Appropriate extrapolation of local edge effects in complex and fragmented landscapes will require greater understanding of edge interactions.

Key-words: *Acacia drepanolobium*, boma, continuous response function, *Crematogaster,* edge depth, habitat fragmentation, Kenya, Laikipia, multiple edges, *Tetraponera penzigi*

Introduction

An ecological edge is a zone within a given landscape where ecological traits (e.g. land cover, soil properties or tree density) undergo large changes over a relatively short distance (Cadenasso, Traynor & Pickett 1997). Abiotic factors, species and species interactions often exhibit strong responses to such boundaries (Young, Patridge & Macrae 1995; Fagan, Cantrell

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& Cosner 1999; Ries *et al.* 2004; Harper *et al.* 2005). For example, a forest–field boundary can affect processes such as seed dispersal, nutrient cycling, pollination and herbivory (Cadenasso *et al.* 2003; Osborne *et al.* 2008). Many studies have documented the importance of edges, but it has proved difficult to scale up from isolated edges to large complex landscapes with many edges (but see Ewers & Didham 2007; LaCroix *et al.* 2008). Recent work suggests that edge effects are sensitive to several contextual factors including matrix type or quality, edge orientation, edge contrast, time since disturbance, patch

size and shape and the presence or proximity of other edges (Matlack 1994; Chen, Franklin & Spies 1995; Sisk, Haddad & Ehrlich 1997; Collinge & Palmer 2002; Ewers, Thorpe & Didham 2007; Delattre *et al.* 2009; Reino *et al.* 2009). Relationships between landscape context and edge effects have critical implications for understanding and managing large complex landscapes (Ries *et al.* 2004). This study focuses on one aspect of landscape context and asks the question: how are edge effects modified by the proximity of other, similar edges?

Increases in habitat fragmentation make this question increasingly important. As landscapes become more fragmented, edges become more common. At the same time, edge effects may change (e.g. in strength or extent) as the distance between edges decreases (Ewers, Thorpe & Didham 2007; Harper *et al.* 2007). This process – edge interaction – may lead to fragmented landscapes that have more (or less) connectivity and higher (or lower) quality habitat than would be predicted based on non-interacting edge effects. Several studies using mathematical models and simulations have suggested that edge interactions could have major impacts on ecosystem structure and function (e.g. Fernandez *et al.* 2002; LaCroix *et al.* 2008).

Despite the emerging realization that edge interactions are important, there is little empirical research on the topic. In fact, many studies of edge effects have tried to minimize the risk of encountering edge interactions by focusing on sites that are far from any additional edges. In studies that consider multiple edges or edge density, the most widely known conceptual model of edge interactions is one in which highly fragmented habitats become 'all edge' (e.g. Forman & Godron 1981; Howell, Dijak & Thompson 2007). In this model, edge effects are generally depicted as step functions with a fixed depth or extent (e.g. a specific buffer width). This assumption of fixed edge effects may be problematic, especially if landscapes encompass a gradient from highly intact with low potential for edge interaction to highly fragmented with high potential for edge interaction (e.g. Lofman 2007). Only a handful of empirical studies have directly examined edge interactions (e.g. Malcolm 1994; Fletcher 2005; Laurance *et al.* 2006; Ewers, Thorpe & Didham 2007; Harper *et al.* 2007). Most of these studies have focused on a particular organism or functional group (e.g. trees or birds). Moreover, most previous studies have been patch-based in that they examined interactions between multiple edges of isolated patches or fragments. The work presented here moves beyond prior studies by using an approach with high spatial resolution to document edge interactions for multiple taxa (understorey plants, woody plants, ants and mammalian herbivores) and multiple response types (density, cover and diversity) in a savanna ecosystem. This research also moves beyond a patch-based approach by considering how the configuration of multiple patches can affect the intervening savanna matrix.

I investigated edge interactions in a semi-arid Kenyan savanna. Specifically, this work focused on long-term, functionally important spatial heterogeneity in the form of treeless 'glades' created by temporary livestock corrals, also called 'bomas.' Throughout the savannas of sub-Saharan Africa, pastoralist herders have been creating and abandoning bomas for centuries (Blackmore, Mentis & Scholes 1990). Today, bomas are still widely used as a management tool on both private and communally managed lands. Bomas are *c.* 50–100 m in diameter and are ringed by *Acacia* thorn fences. Livestock graze in surrounding areas during the day but are corralled within bomas at night for protection. Bomas are used for months or years and then abandoned. Abandoned bomas develop into structurally distinct, nutrient-rich landscape hotspots that persist for decades to centuries (Blackmore, Mentis & Scholes 1990; Reid & Ellis 1995; Young, Patridge & Macrae 1995; Augustine 2003, 2004; Muchiru, Western & Reid 2009; Veblen & Young 2010). In central Kenya, abandoned bomas develop into 'glades' which, compared to the savanna matrix, have much lower tree density (glades are virtually treeless), higher concentrations of phosphorus, nitrogen and potassium in the soil, higher grass productivity and quality, higher cover of two grass species (*Cynodon plectostachyus* and *Pennisetum stramineum*), and preferential use by livestock and wild herbivores (Young, Patridge & Macrae 1995; Augustine 2003, 2004; Veblen & Young 2010). The word 'boma' will be used hereafter to refer to an actively used corral, while 'glade' will be used to refer to an abandoned corral site.

The spatial arrangement of glades varies widely across African savannas. In the study area examined here, inter-glade distance ranges from > 500 m to < 50 m. The ecological effects of glade density and spatial arrangement remain poorly understood. Areas surrounding active bomas are characterized by heavy grazing, trampling and dung deposition, intensive tree harvesting (for fuelwood and boma fences) and human presence, which deters many large, wild herbivores (Lamprey & Reid 2004; Muchiru, Western & Reid 2009). These anthropogenically mediated impacts are especially pronounced in areas between several bomas (Muchiru, Western & Reid 2009). As glades develop at these sites, large wild herbivores may enhance interactions between nearby glade edges. For example, disproportionate use of areas between nearby glades could promote the establishment of disturbance-tolerant grasses such as the glade specialist *C. plectostachyus* (Muchiru, Western & Reid 2009). Thus, glade configuration could have large and persistent ecological impacts.

In this study, I used pre-existing variation in glade density to (i) investigate glade edge effects and (ii) determine whether these edge effects differ in the presence of a second, nearby glade. I predicted that the mechanisms outlined above would lead to the emergence of edge interactions for a variety of different taxa and response types. Specifically, I hypothesized that with decreasing distance between glades, edge effects would build on one another and inter-glade areas would become more similar to glade interiors. These changes would imply a strengthening of edge effects and increased structural and functional continuity between nearby glades.

Materials and methods

STUDY AREA

This research was carried out in the Laikipia district of central Kenya. Many properties in Laikipia – both communally managed pastoralist

areas and commercial ranches – are managed jointly for livestock and wildlife. The study was conducted on two such properties: Mpala Conservancy (36°52′E, 0°17′N) and neighbouring Jessel Ranch. In addition to cattle, common large herbivores include plains zebra (*Equus burchelli*), Grant's gazelle (*Gazella granti*), eland (*Taurotragus oryx*), hartebeest (*Alcelaphus buselaphus*), oryx (*Oryx gazella*), elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), warthog (*Phacochoerus africanus*), steinbuck (*Raphicerus campestris*) and occasionally impala (*Aepyceros melampus*) or buffalo (*Syncerus caffer*). Soils are 'black cotton' vertisols characterized by very high clay content and poor drainage (Deckers, Sppargaren & Nachtergaele 2001). Mean annual rainfall ranges from 400 to 600 mm. The 15-km^2 study site includes dozens of glades that are irregularly distributed throughout the landscape, creating variability in inter-glade distance. The background savanna matrix is quite homogeneous: soil type and topography are uniform and vegetation is dominated by one tree species – *Acacia drepanolobium*, comprising 97% of total woody cover (Young *et al.* 1998). Although fire has not played an active part in this ecosystem for several decades, small portions of the study site have been experimentally burned in recent years.

Overlying the glade mosaic is a finer-scale mosaic produced by colonies of four symbiotic *Acacia* ant species (*Tetraponera penzigi*, *Crematogaster nigriceps*, *C. mimosae* and *C. sjostedti*, Stanton, Palmer & Young 2002). *Crematogaster sjostedti* is competitively dominant and often found on the largest trees, while *T. penzigi* and *C. nigriceps* are competitively subordinate and tend to be found on smaller trees (Young, Stubblefield & Isbell 1997; Stanton, Palmer & Young 2002). Different ants have different impacts on *A. drepanolobium* growth, reproduction, architecture, herbivory and parasitism (Stanton *et al.* 1999; Palmer, Young & Stanton 2002; Riginos & Young 2007; Palmer *et al.* 2008). For example, *C. sjostedti* colonies are poor defenders against herbivory by large mammals and actively facilitate parasitic cerambycid beetles that are likely to weaken trees (Palmer & Brody 2007; Palmer *et al.* 2008). In contrast, *C. nigriceps* colonies are very aggressive in defending against large herbivores (Young, Stubblefield & Isbell 1997; Stanton *et al.* 1999). Ants play a central role in this system's ecology via their impacts on the dominant tree species and its herbivores.

DATA COLLECTION

From August to December 2008, I measured glade edge effects in areas that differed in terms of their likelihood of edge interactions. Specifically, I surveyed continuously along 8-m-wide belt transects of three types: no glade (control), isolated glade and non-isolated glade. 'No glade' transects were 200 m long, and located more than 300 m from any glade. Previous work indicated that glade edge effects should extend no more than 175–225 m (Western & Dunne 1979; Young, Patridge & Macrae 1995; Muchiru, Western & Reid 2009). Each 'isolated' transect extended 200 m in a random direction (excluding directions that intersected man-made tracks or firebreaks) from the centre of a relatively isolated glade (more than 250 m from any other glade). 'Non-isolated' transects started at the centre of glades that had a neighbouring glade within 150 m and extended from the centre of the focal glade to the centre of the closest neighbouring glade (excluding pairs separated by tracks or firebreaks). I sampled all isolated and non-isolated glades in the study area that had been abandoned for more than 45 years (i.e. those that were visible in aerial photographs from 1961), and were less than 400 m from a track or firebreak and more than 200 m from another significant landscape feature (e.g. a fenced or previously burned area). This strategy yielded nine isolated glades and five non-isolated glades. One

transect was surveyed per glade. Six 'no glade' transects were located randomly within regions chosen to provide adequate spatial representation across the study area.

Along each transect, I measured the location of all *A. drepanolobium* trees and all dung piles produced by large wildlife (mammals > 5 kg and ostriches). I identified the species of animal that produced each dung pile. For each *A. drepanolobium* tree, I recorded height class (< 2 m, 2–4 m, or > 4 m) and which of the four symbiotic *Acacia* ant species was present. I also recorded the locations of *Lycium europaeum* shrubs. *Lycium europaeum* is an uncommon species that specializes in glade edges (Muchiru, Western & Reid 2009; K.E. Veblen, unpublished data). For each response variable along each transect, data were binned into 5-m intervals. This made it possible to obtain a continuous value (e.g. the number of trees or dung piles) for each 5-m distance interval. For wildlife, species richness was calculated for each 5-m interval as the number of species whose dung was found within the interval. Species evenness was calculated using Pielou's index (Pielou 1966) based on relative abundances of different types of dung in each interval. Understorey plants (largely herbaceous, though small shrubs were infrequently encountered) were sampled at 5-m intervals along each transect by visually estimating percentage cover of each species within 1 × 1 m quadrats centred on the transect line. Understorey species richness and species evenness values were calculated separately for each quadrat using the methods described above. Due to the addition of new bomas during the sampling period, I was able to sample seven of the nine isolated glades for dung, understorey vegetation and *L. europaeum*; all nine were sampled for tree density and ants.

DATA ANALYSIS

Defining the edge

To compare edge effects across glade types and response variables, it was necessary to standardize transects based on a common spatial anchor point. The most obvious structural trait of glades is their treelessness, so transects were standardized using tree density. For each glade transect, I identified the beginning of the first 5-m interval (starting from the glade centre) in which I found four or more *A. drepanolobium* trees within 4 m of the transect line. This structurally defined location generally corresponded to the physical boundary of the original boma and is hereafter called the 'glade edge'. This location is not intended to reflect the functional location of the edge (Cadenasso, Traynor & Pickett 1997). For analysis, this 'glade edge' location along each transect was denominated 0 m. Areas inside the glade were given negative values with respect to the edge, and areas outside the glade were given positive values. This standardization procedure confirmed that mean diameters of isolated and non-isolated glades were similar (radii were 37.8 ± 4.6 m and 42.0 ± 11.6 m, respectively; $t = -0.34$, $P = 0.75$). Because 'no glade' transects were only used to generate reference values (see below), I did not define any 'edge' for these transects. For non-isolated transects, I only included data from ≤50% of the distance between the two glade edges in order to focus on dynamics in the edge closest to the focal glade. I excluded the neighbouring glade's edge from analyses to reduce spatial dependency and because in three of five cases the neighbouring glade was younger than 45 years.

Analysing edge responses

To compare glade edge effects between transect types, I carried out a three-step analytical process. First, I fitted a nonlinear model for each

response variable along each transect. Secondly, I used fitted models to determine edge effect parameters. Finally, I compared these parameters between the different types of transects.

Theory and empirical evidence suggest that when ecological variables such as tree density or light intensity are plotted against physical distance from an edge, responses will take one of the following forms (Ries *et al.* 2004; Ewers & Didham 2006): sigmoid curves (i.e. monotonic, asymptotic increase or decrease with rate of change highest at some distance from the edge, Fig. 1a,b), unimodal curves (i.e. peak or trough near the edge, Fig. 1c,d) or straight lines (i.e. constant rate of change across the sampled area). The shape of an edge response can provide insight into the mechanisms driving it. For example, a unimodal peak in animal density near an edge may suggest that the edge environment provides optimal access to complementary resources in adjacent patches (Ries *et al.* 2004).

Often, edge response data have a form that would be best fit by some combination of the curves listed above (e.g. Fig. 1e,f), presumably because edge responses are governed by a combination of several mechanisms. In order to obtain realistic and ecologically meaningful fits to the data, I modelled each response using an equation that includes linear, sigmoid and unimodal components:

$$y = a + \underbrace{bX}_{\text{linear}} + \underbrace{\frac{b1}{1 + e^{(b2-X)*b3}}}_{\text{sigmoid}} + \underbrace{h * e^{\frac{-(X-x0)^2}{2W^2}}}_{\text{unimodal}}$$

where X is distance from the edge and the other variables are fitted constants. I fitted this model using the nonlinear platform in JMP (version 8.0, SAS Institute, Inc., Cary, NC, USA), which numerically estimates parameter values based on minimization of the sum of squared errors. For each response variable along each transect, I fitted the overall model using an expectation maximization approach in which the three shape components were fitted sequentially and cyclically until the entire model converged. In other words, I began by estimating parameter values for the linear component of the overall model while holding the sigmoid and unimodal parameters constant. I then estimated the sigmoid parameters while holding the linear and unimodal parameters constant. I repeated this process until parameter values for all
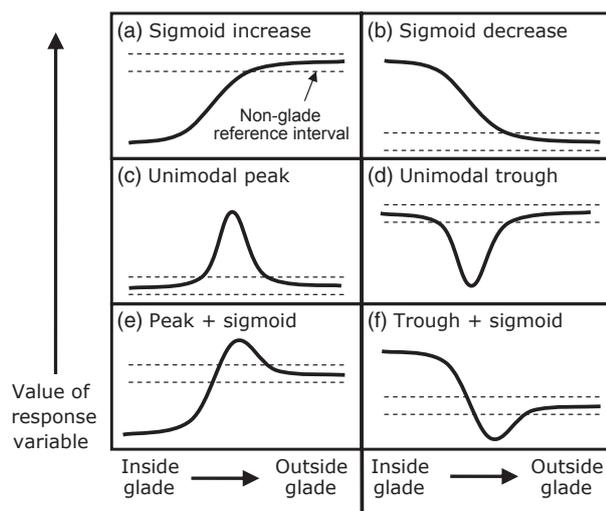
components converged. This procedure produces unbiased maximum likelihood solutions while also making it easier to fit a complex model with multiple components. In order to avoid local minima, I repeated the entire process with different starting values for the parameters and chose the final model with the best overall fit. The fitted models had an average r^2 of 0.50 ± 0.22 (SD). All variables were retained in each fitted model regardless of significance (Smith *et al.* 2009).

This model fitting approach is grounded in mechanistic edge effect theory (unlike smoothing techniques, e.g. Kratzer, Hayes & Thompson 2006) but does not force a potentially unrealistic model (e.g. pure sigmoid or pure unimodal) onto complex data. On the other hand, if data are perfectly unimodal or sigmoid, the model will collapse appropriately to a unimodal or sigmoid fit. Like other continuous response functions (e.g. Ewers & Didham 2006), fitted models can be used to quantitatively determine edge effect parameters, which can then be compared across transect types (see below). Finally, fitted models can be used to evaluate the relative importance of different shape components (and related mechanisms) in determining edge responses. For this study, I used nonlinear modelling to examine how isolated versus non-isolated glades differ in two edge parameters: edge effect magnitude and edge effect depth.

Edge effect magnitude

I used fitted models to obtain 'inside glade' and 'outside glade' values that could be compared between glade types. Specifically, I obtained the minimum and maximum fitted value from each nonlinear model. Whichever extreme value (either the minimum or the maximum) was located closer to the glade centre was defined as the 'inside glade' value; the other extreme value was defined as the 'outside glade' value. I compared 'inside glade' and 'outside glade' values between the glade types using ANOVA and MANOVA models in JMP (version 8.0, SAS Institute, Inc.) with glade type as the predictor and either 'inside glade' or 'outside glade' values for tree density, wildlife dung density and other variables as the responses.

Edge effect depth

I defined edge effect depth as the distance to which glade edge effects extended into the surrounding savanna. To compare edge effect depth between glade types, I first used the six 'no glade' transects to generate a reference interval for each response variable. I averaged the fitted model for each 'no glade' transect to generate six transect means and then used these six values to calculate a 90% 'reference confidence interval.' For isolated and non-isolated glade transects, I averaged all the fitted models for each glade type to generate overall 'average models' and 90% confidence intervals. Models were weighted equally during averaging. For each glade type, I defined edge effect depth as the distance from the glade edge beyond which the confidence intervals for the average model and the reference always overlapped. I used jack-knifing to estimate edge depth mean and variance within each glade type, and non-parametric Wilcoxon tests in JMP (version 8.0, SAS Institute, Inc.) to compare edge depths between glade types.

Lycium europaeum *analysis*

The low density of *L. europaeum* shrubs made model-fitting unrealistic. *Lycium europaeum* is known to specialize in glade edges, and my goal was to evaluate the impact of glade proximity on this pattern. I therefore analysed *L. europaeum* density using ANOVA with glade type

Fig. 1. Potential edge response patterns. Dashed lines represent the bounds of the 'no glade' (reference) confidence interval. Table 2 identifies the specific patterns shown by response variables measured in this study.

Table 1. Response values (mean ± 1 SE) and statistical test results for magnitudes of edge effects. Fitted nonlinear models were used to obtain 'inside glade' and 'outside glade' values for each transect; these values were then compared between glade types. Significant results are in bold. For each fitted model, whichever extreme value (either the minimum or the maximum) was located closer to the glade centre was defined as the 'inside glade' value; the other extreme value was designated as the 'outside glade' value. Isolated glades were > 250 m and non-isolated glades were < 150 m from a second glade

	Inside glades					Outside glades				
	Isolated glades	Non-isolated glades	F	n	P	Isolated glades	Non-isolated glades	F	n	P
Tree density (# of trees ha⁻¹)										
Overall	65 ± 58	145 ± 75	0.68	9,5	0.42	2825 ± 240	4775 ± 873	8.11*	9,5	**0.01**
MANOVA by size class	n/a	n/a	0.09*	9,5	0.96	n/a	n/a	6.75†	9,5	**0.009**
<2 m tall (protected ANOVA)						2085 ± 275	3775 ± 850	5.53*	9,5	**0.04**
2–4 m tall (protected ANOVA)						1253 ± 130	1265 ± 438	0.16*	9,5	0.69
>4 m tall (protected ANOVA)						570 ± 68	163 ± 80	13.8	9,5	**0.003**
Ant density (# of trees occupied ha⁻¹)										
Total (all species)	18 ± 50	128 ± 93	1.33	9,5	0.27	2160 ± 195	3743 ± 638	9.47*	9,5	**0.01**
MANOVA by species	n/a	n/a	0.66‡	9,5	0.63	n/a	n/a	15.33*	9,5	**0.0005**
Tetraponera penzigi (protected ANOVA)						1188 ± 215	2128 ± 568	3.37*	9,5	0.09
Crematogaster nigriceps (protected ANOVA)						508 ± 133	1228 ± 353	6.42*	9,5	**0.03**
C. mimosae (protected ANOVA)						985 ± 250	1665 ± 370	2.96*	9,5	0.11
C. sjostedti (protected ANOVA)						1053 ± 145	843 ± 288	1.07*	9,5	0.32
Wildlife dung density (# of dung piles ha⁻¹)										
Dung density	4055 ± 1530	2120 ± 550	0.56*	7,5	0.47	808 ± 223	273 ± 93	6.47*	7,5	**0.03**
Wildlife dung diversity (per 40m²)										
Species richness	3.24 ± 0.31	2.54 ± 0.63	1.20	7,5	0.30	1.25 ± 0.19	1.03 ± 0.26	0.53	7,5	0.48
Species evenness	0.82 ± 0.06	0.79 ± 0.07	0.08	7,5	0.78	0.85 ± 0.07	0.93 ± 0.07	Z = 1.79¶	7,5	0.07
Understorey cover (% cover)										
Overall	80.50 ± 3.30	87.42 ± 3.76	1.89	7,5	0.20	42.66 ± 3.26	47.59 ± 2.22	1.30	7,5	0.28
MANOVA by group	n/a	n/a	0.88§	7,5	0.49	n/a	n/a	0.19*	7,5	0.90
Understorey diversity (per 1 m²)										
Species richness	4.95 ± 0.65	3.83 ± 0.65	1.40	7,5	0.26	12.83 ± 1.09	13.65 ± 1.04	0.28	7,5	0.61
Species evenness	0.19 ± 0.04	0.29 ± 0.05	2.83	7,5	0.12	0.68 ± 0.01	0.73 ± 0.02	3.57	7,5	0.09

*Response variable(s) log-transformed for analysis.

†<2 m tree density and 2–4 m tree density log-transformed for analysis.

‡*Crematogaster mimosae* values log-transformed for analysis.

¶Nonparametric Wilcoxon test used because errors were not normally distributed.

§Non-graminoid cover values log-transformed for analysis.

as the predictor and *L. europaeum* density in the immediate glade edge (−5 to 5 m) as the response variable.

Results

EDGE PATTERNS AROUND RELATIVELY ISOLATED GLADES

As expected, there were strong edge patterns around isolated glades (> 250 m from another glade) for most response variables. Tree density was over 40 times lower inside than outside glades (Table 1; matched pairs $t = 10.61$, $P < 0.0001$, $n = 9$). Total tree density increased sigmoidally to background values at the glade edge (Fig. 2a, Table 2). This general pattern was echoed by small trees, intermediate-sized trees and all the *Acacia* ant species (Fig. 2b,c, Table 2). For large trees (> 4 m), there was a prominent peak in density near the glade edge, with density remaining significantly above reference values until 90 m beyond the edge (Fig. 2d, Table 2).

Wildlife dung pile densities were more than five times higher inside than outside glades (Fig. 2e, Table 1; matched pairs $t = 1.99$, $P = 0.09$, $n = 7$). Similarly, wildlife species richness was 2.6 times greater inside glades than outside (Fig. 2f, Table 1; matched pairs $t = 7.81$, $P = 0.0002$, $n = 7$). Wildlife species evenness did not respond significantly to glade edges (Table 1; matched pairs $t = 0.26$, $P = 0.80$, $n = 7$). Of the 2194 dung piles found, 99.6% were produced by the 11 large herbivore species listed in Materials and Methods.

Cover of understorey vegetation was 1.9 times higher inside than outside glades (Fig. 3a, Table 1; matched pairs $t = 12.59$, $P < 0.0001$, $n = 7$). The percentage cover of glade-dominant grasses (*Cynodon* spp. and *P. stramineum*) remained significantly above reference values until 23 ± 5 m beyond the glade edge. Percentage cover of other graminoids remained below reference values until 56 ± 1 m beyond the edge (Fig. 3b,c, Table 2). Understorey species richness was over 2.5 times higher outside glades than inside (Fig. 3e, Table 1; matched pairs $t = 7.58$, $P = 0.0001$, $n = 7$), and
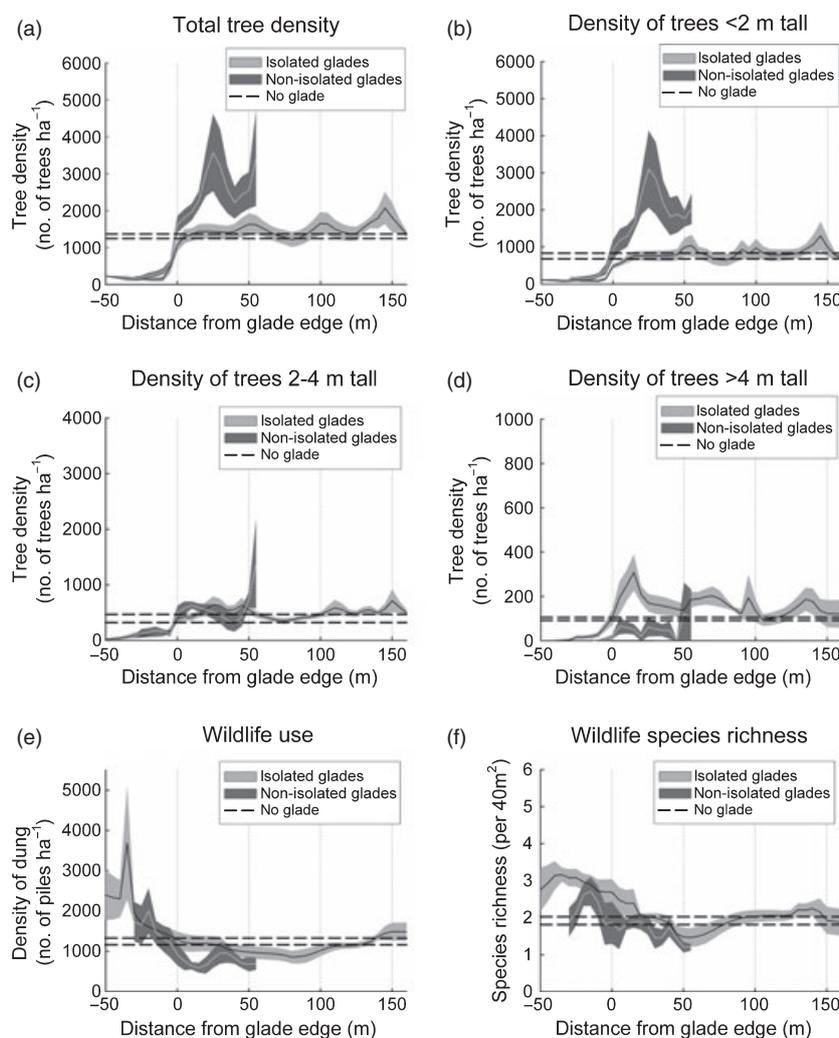

Fig. 2. Edge effects for tree density and wildlife (average models ± 1 SE). Isolated glades ($n = 9$ for tree data and 7 for wildlife data) were > 250 m from another glade. Non-isolated glades ($n = 5$) were < 150 m from a second glade. 'No glade' reference values (±1 SE) were generated from the fitted models of 'no glade' transects (> 300 m from a glade, $n = 6$).

Table 2. Response values (mean ± 1 SE) and statistical test results for depths of edge effects. Edge depth was defined as the distance from the glade edge at which the average fitted model's confidence interval no longer diverged from the reference confidence interval. Jack-knifing and nonparametric tests were used to compare edge depth values between glade types. Significant results are in bold. Isolated glades were > 250 m and non-isolated glades were < 150 m from a second glade. Edge response patterns are displayed in Fig. 1

	Edge depth (m)					Response pattern (Fig. 1)	
	Isolated glades	Non-isolated glades	Wilcoxon Z-value	n	P	Isolated glades	Non-isolated glades
Tree density							
Overall	**0 ± 0**	**36 ± 6**	**3.42**	**9,5**	**0.0006**	a	e
< 2 m tall	2 ± 1	**> 55**	n/a			a	e
2–4 m tall	−4 ± 1	−11 ± 6	−0.16	9,5	0.9	a	a
> 4 m tall	**90 ± 0**	**50 ± 0***	**−3.37**	**9,5**	**0.0008**	e	a
Density of trees occupied by *Acacia* ants							
Total (all species)	**1 ± 1**	**39 ± 5***	**3.08**	**9,5**	**0.002**	a	e
Tetraponera penzigi	62 ± 25	−6 ± 14	−2.35	9,5	0.02‡	a	e
Crematogaster nigriceps	4 ± 4	6 ± 5	0.93	9,5	0.4	a	a
C. mimosae	**8 ± 1**	**55 ± 0***	**2.84**	**9,5**	**0.005**	a	e
C. sjostedti	**−16 ± 2**	**15 ± 5***	**2.86**	**9,5**	**0.004**	a	a
Wildlife							
Dung density	−19 ± 20	**> 55**	n/a			b	f
Species richness	26 ± 24	**> 55**	n/a			b	f
Species evenness	Never differs significantly	Never differs significantly	n/a			n/a	n/a
Understorey cover							
Overall	13 ± 11	−11 ± 7	−1.33	7,5	0.2	b	b
Glade-dominant grass	**23 ± 5**	**11 ± 1**	**−2.62**	**7,5**	**0.009**	b	b
Other graminoid	**56 ± 1**	**19 ± 8**	**−2.97**	**7,5**	**0.003**	a	a
Non-graminoid	**4 ± 12**	**−24 ± 1***	**−2.71**	**7,5**	**0.007**	a	a
Understorey diversity							
Species richness	**35 ± 15†**	**5 ± 2**	**−2.45**	**7,5**	**0.01**	a	a
Species evenness	8 ± 1	7 ± 2	−0.49	7,5	0.6	a	a

*One jack-knifing iteration was excluded from analysis because edge depth was > 55 m.
†One jack-knifing iteration was excluded from analysis because edge depth was > 165 m.
‡Not significant due to multiple tests.

species evenness was more than 3.5 times higher outside glades than inside (Fig. 3f, Table 1; matched pairs $t = 12.93$, $P < 0.0001, n = 7$).

EDGE INTERACTIONS

Inside glades there were no detectable effects of glade type (isolated vs. non-isolated) on plant, ant or large herbivore communities (Table 1). However, areas between two proximate glades differed from areas outside isolated glades.

Trees and L. europaeum

Maximum total tree densities between two glades were 1.7 times higher than outside isolated glades, and this overall difference was driven by the smallest trees (Table 1, Fig. 2a–d). Non-isolated glade edges had 1.8 times as many small trees (< 2 m tall) as isolated edges. These differences in edge magnitude were accompanied by shifts in edge depth. Between two glades, tree density exhibited a peak at 25 m outside glades and remained significantly higher than the reference interval until $36 ± 6$ m outside the glade edge (Fig. 2a, Table 2). This overall pattern was also driven by small trees (Fig. 2b, Table 2).

Finally, non-isolated glade edges had over three times as high a density of *L. europaeum* bushes as isolated edges (1150 ± 258 vs. 358 ± 163 bushes ha^{-1}; $F_{5,7} = 7.54, P = 0.02$).

Large trees (> 4 m tall) showed a pattern opposite to that of smaller trees and *L. europaeum*. Densities of large trees were around three times greater outside isolated glades than between two glades (Table 1). The peak in large tree density observed near isolated glades was completely absent in areas between two glades, and in fact large tree density remained below reference values until 50 m beyond the glade edge (Fig. 2d, Table 2). Densities of intermediate-sized trees (2–4 m tall) did not differ significantly between glade types (Fig. 2c, Tables 1 and 2).

Wildlife

Although glades typically attract wildlife, areas between two glades had half as many dung piles as areas outside isolated glades (Fig. 2e, Table 1). This shift was also apparent in edge depth analysis. For isolated glades, wildlife dung density inside glades was significantly higher than in the 'no glade' reference interval. In areas between two glades, dung density values remained significantly lower than reference values until the
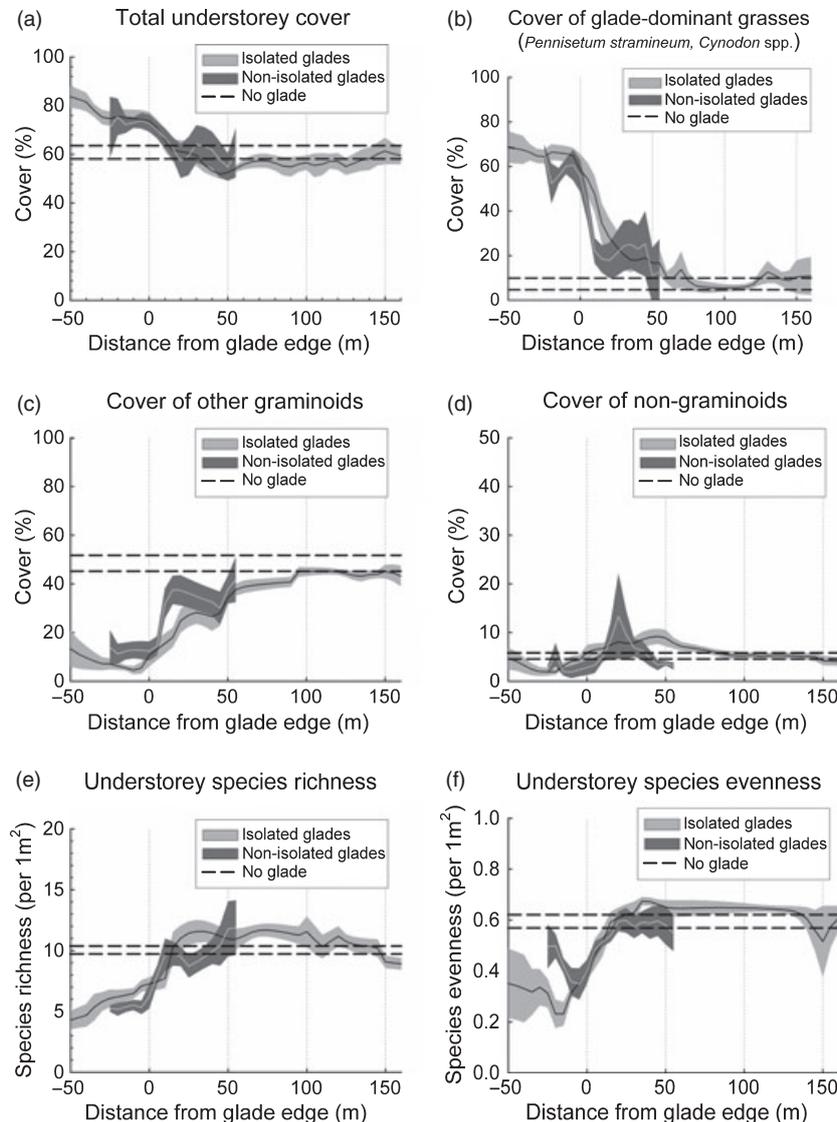
Fig. 3. Edge effects for understorey vegetation (average models $\pm$ 1 SE). Isolated glades ($n = 7$) were > 250 m from another glade. Non-isolated glades ($n = 5$) were < 150 m from a second glade. 'No glade' reference values ($\pm$ 1 SE) were generated from the fitted models of 'no glade' transects (> 300 m from a glade, $n = 6$).

limit of measurement (55 m, Fig. 2e, Table 2). These edge depth patterns were paralleled by wildlife species richness (Fig. 2f, Table 2), but species evenness showed no signs of significant edge interaction (Tables 1 and 2).

Understorey

The total percentage cover of understorey plants in edges, as well as cover values for different functional groups, did not differ significantly between glade types (Fig. 3a–d, Table 1). However, the presence of a second glade was associated with reductions in edge depth for all functional groups (Fig. 3b–d, Table 2). In other words, between nearby glades, the understorey community converted more quickly to dominance by non-glade species. For understorey diversity measures, edge magnitude values did not differ significantly between glade types (Fig. 3e,f, Tables 1 and 2). However, for understorey

species richness, the presence of a second glade was associated with a 30-m reduction in edge depth (Table 2).

Acacia ants

Areas between two glades had 1.7 times as many ant-occupied trees as areas outside isolated glades; this difference parallels the total difference in tree density (Table 1). However, the proportional occupancy of each ant species differed depending on glade type. The number of trees occupied by *C. nigriceps* (a small tree specialist) was 2.4 times higher between glades than outside isolated glades. The numbers of trees occupied by *T. penzigi* and *C. mimosae* did not differ significantly between glade types (*P*-values = 0.09 and 0.11 respectively), although trends suggested higher values near non-isolated glades. Finally, despite the increased tree density between glades, the number of trees occupied by *C. sjostedti* (a large-tree specialist)

did not differ significantly between glade types (Table 1). For total occupancy, *T. penzigi* and *C. mimosae* occupancy, edge depth patterns paralleled those of small trees (Table 2). For *C. sjostedti*, as for large trees, edge depth in non-isolated glade edges was significantly larger than in isolated edges (Table 2).

Discussion

In this tropical savanna landscape, edge effects around treeless glades were significantly affected by the presence of a second glade within 150 m, indicating the presence of edge interactions. Contrary to predictions, the majority of interaction patterns did not indicate increased continuity between nearby glades.

Glades are anthropogenic features, and many of the observed edge interactions are at least partially mediated by current or past human activities. African savannas (like many other landscapes) have a long history of human use. Explicitly studying human activities and their ecological impacts will be critical for understanding, conserving and managing these landscapes. Moreover, findings from this and other studies suggest that although the mechanisms driving edge interactions are often system-specific, the existence of interactions is common and ecologically significant (e.g. Fletcher 2005; Laurance *et al.* 2006).

In this study, transects near isolated glades extended 164 ± 10 m beyond the glade edge. Some edge effects have been shown to extend for kilometres (Ewers & Didham 2008), although previous work suggests that such long-range effects are unlikely in this system (Muchiru, Western & Reid 2009). Finally, as with many large-scale studies, these findings are based on small sample sizes. The fact that edge interactions were detected consistently across many response variables, despite sample size limitations, points to the importance of this phenomenon.

EDGE EFFECTS AROUND ISOLATED GLADES

Tree density, wildlife habitat use, and the cover and diversity of understorey vegetation all changed significantly across isolated glade edges. Most edge effects were only detectable within a few metres of the glade edge, but for two variables (large tree density and cover of non-glade-dominant graminoids) edge effects extended at least 50 m into the surrounding landscape (Table 2). This depth implies a 4- to 9-fold increase in glade-affected area across the landscape, when compared to the within-glade footprint. These results add to the growing evidence (e.g. Blackmore, Mentis & Scholes 1990; Young, Patridge & Macrae 1995; Augustine 2003; Muchiru, Western & Reid 2009; Veblen & Young 2010) that glades are important features in African savanna ecosystems.

EDGE EFFECTS AROUND NON-ISOLATED GLADES

Tree and shrub patterns

Tree density between glades was 1.7 times higher than tree density outside isolated glades – a pattern driven by the smallest (< 2 m tall) trees. Areas near two glades presumably experience more tree harvesting (for boma fence material and fuelwood) than areas near only one glade. *Acacia drepanolobium* trees are known to regrow readily after cutting (Okello, O'Connor & Young 2001). Some of the small trees found between nearby glades could be regrowing individuals (formerly tall but now short), but new recruits must also be present to explain the 70% increase in overall tree density. High tree densities between glades are probably the result of a legacy effect reinforced by on-going feedback loops. Cattle and human impacts create a region of intensive use (i.e. low grass cover, high cattle use and low wildlife use) around bomas, and impacts are especially pronounced between bomas and nearby glades (see also Muchiru, Western & Reid 2009; L.M. Porensky, unpublished data). Experimental manipulations in this ecosystem have demonstrated that both competition with grasses and browsing, especially by megaherbivores, can reduce the growth, survival and reproduction of *A. drepanolobium* (Goheen *et al.* 2007; Riginos & Young 2007; Riginos 2009). Moreover, in the absence of large herbivores, cattle tend to facilitate *A. drepanolobium* establishment (Goheen *et al.* 2010). Thus, the combination of low browser density, high cattle density, low grass cover and ample fertilization in areas between bomas and nearby glades probably initiates a burst of tree establishment (e.g. Tobler, Cochard & Edwards 2003; Augustine & McNaughton 2004). The shrub *L. europaeum*, which had significantly higher densities in non-isolated glade edges, may experience a similar establishment burst. Initial increases in tree and shrub density probably lead to shifts in understorey and ant communities as well as large herbivore behaviour, which then promote even more woody plant establishment (see below).

Unlike small trees, very large (> 4 m) *A. drepanolobium* trees were less common near non-isolated than isolated glades. Although intensive tree cutting around bomas is unlikely to kill individual trees, it may have lasting effects on size structure in this long-lived species. The loss of large trees (and their replacement by more, smaller trees) may have important ecological impacts. For example, large trees are more likely to reproduce than small trees (Goheen *et al.* 2007). Reduced fruiting could have cascading effects on other taxa, as the fruits and seeds of *A. drepanolobium* are eaten by a variety of animals, from bruchid beetles to rodents and large mammalian browsers (Coe & Beentje 1991; Walters *et al.* 2005; Palmer & Brody 2007). Furthermore, large trees provide shade and high-quality forage, which may be important for large herbivores (Ludwig, De Kroon & Prins 2008; Treydte, Grant & Jeltsch 2009).

Cascading effects of tree patterns on other species

Densities of wildlife dung were very low in areas between adjacent glades. Most large herbivore species in this ecosystem avoid areas with a higher density of trees because of reduced predator visibility (Riginos & Grace 2008). Thus, high tree densities between glades may deter large herbivores. Wildlife diversity patterns suggest that proportional reductions in dung density were similar between species. These findings are important for managers, who often use glades to attract wildlife for

ecotourism or conservation (G. Prettejohn, pers. comm.). Moreover, low browser densities between glades may facilitate further tree establishment (Goheen *et al.* 2007), and thus initiate a positive feedback loop. This positive feedback may help explain why edge interaction patterns persist for decades after boma abandonment.

For much of the understorey plant community, the presence of a second glade was associated with reduced edge depth (i.e. a 'compression' of edge effects). In other parts of the landscape, high tree density and glades are both associated with high cover of the grass *P. stramineum* (Riginos *et al.* 2009; Veblen & Young 2010), so the low cover of this species in inter-glade areas (with especially high tree density) is surprising. However, previous work suggests that *P. stramineum* cover is positively correlated with soil nitrogen (Riginos & Grace 2008). The small trees that dominate inter-glade areas are unlikely to be supplying large quantities of nitrogen to the soil (Ludwig *et al.* 2004), and very likely to be competing directly with grasses for nitrogen (Cramer, van Cauter & Bond 2010). Thus, inter-glade areas may be less suitable habitat for *P. stramineum*.

Patterns in *Acacia* ant community composition showed that edge interactions indirectly affect organisms other than plants and wildlife. *Crematogaster nigriceps*, the one species found on a significantly higher proportion of trees in inter-glade areas, is a competitive subordinate known to colonize small trees (Young, Stubblefield & Isbell 1997; Stanton, Palmer & Young 2002). *Crematogaster sjostedti*, the only species found on a lower proportion of trees in inter-glade areas, is a competitive dominant that colonizes the largest *A. drepanolobium* individuals along with many smaller 'satellite' trees (Young, Stubblefield & Isbell 1997). Thus, the replacement of large trees by more, smaller trees between glades may lead to reduced *C. sjostedti* occupation and increased *C. nigriceps* occupation. Because *C. nigriceps* is more aggressive than *C. sjostedti* (see Study Area), altered ant composition may further deter large herbivores from inter-glade areas, and thus reinforce a positive feedback leading to greater tree establishment. In total, these results suggest that the proximity of glade edges has complex, cascading, and intricately linked impacts on a range of taxa, from trees and grass to mammalian herbivores and ants.

TYPES OF EDGE INTERACTIONS

These results reveal a rich diversity of edge interactions. For *C. sjostedti* ants, the presence of a second glade seemed to *strengthen* edge effects by increasing edge effect depth (e.g. Malcolm 1994). For large trees, a second glade seemed to make edges more glade-like; in the presence of a second glade, low densities of large trees (typical of the glade environment) extended out to 50 m beyond the glade edge, and the glade edge density peak was entirely absent. For most response variables, however, edge interactions implied a *weakening* of the edge effects observed around isolated glades (see also Harper *et al.* 2007). The presence of a second glade was associated with reduced edge depth (i.e. a compression of the focal edge) for understorey species richness and the percentage cover of glade-dominant grasses, other graminoids and non-graminoids. These compression

effects probably represent cascading consequences of increased tree density between glades and suggest that for some response variables, increased glade density may actually lead to decreases in glade-affected area across the landscape.

In several cases, the presence of a second edge led to emergent patterns in which the inter-glade environment was even less glade-like than the matrix (Fig. 1). These patterns are emergent in that they would have been very hard to infer from edge effect patterns around isolated glades. For example, tree density was low inside isolated glades and then increased sigmoidally at the glade edge. When a second glade was present, tree density was still low inside glades, but densities in the glade edge region were significantly *higher* than reference values. This pattern was echoed by densities of small trees, total ant occupancy, and densities of *T. penzigi* ants and *C. mimosae* ants. Wildlife dung density and wildlife species richness displayed similar interaction patterns, in that values were significantly *below* reference levels in inter-glade areas. These responses were probably a cascading consequence of high tree density and the associated shift in habitat structure.

Finally, these results demonstrate another emergent property of adjacent edges. For most response variables, edges interacted despite the fact that the inter-glade distance was several times larger than the depth of the edge effect, as observed around isolated glades.

IMPLICATIONS FOR AFRICAN SAVANNAS AND OTHER COMPLEX LANDSCAPES

In this semi-arid *Acacia* savanna, glade edge effects appear to be very sensitive to glade proximity. Areas around closely-spaced glades may experience less wildlife use and have less glade grass than areas around more widely-spaced glades. These results suggest that glade configuration should be an important consideration in ongoing land management decisions, especially considering the fact that glade density is currently increasing in many parts of East Africa (Lamprey & Reid 2004; Muchiru, Western & Reid 2009).

More generally, these findings suggest that edge interactions are important to consider in the study of complex and fragmented landscapes. Interactions may lead to either increases or decreases in structural and functional continuity between nearby patches. Interaction patterns may not be easy to infer from edge effects around isolated glades. Finally, edges may interact even when features are far apart relative to edge effect depths. For all of these reasons, appropriate extrapolation of local edge effects to complex landscapes will require greater understanding of edge interactions. As fragmentation and landscape complexity increase, consideration of edge effects and their context-dependence will be increasingly critical for effective conservation and management.

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