

# Grasses and browsers reinforce landscape heterogeneity by excluding trees from ecosystem hotspots

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**Abstract** Spatial heterogeneity in woody cover affects biodiversity and ecosystem function, and may be particularly influential in savanna ecosystems. Browsing and interactions with herbaceous plants can create and maintain heterogeneity in woody cover, but the relative importance of these drivers remains unclear, especially when considered across multiple edaphic contexts. In African savannas, abandoned temporary livestock corrals (bomas) develop into long-term, nutrient-rich ecosystem hotspots with unique vegetation. In central Kenya, abandoned corral sites persist for decades as treeless ‘glades’ in a wooded matrix. Though glades are treeless, areas between adjacent glades have higher tree densities than the background savanna or areas near isolated glades. The mechanisms maintaining these distinctive woody cover patterns remain unclear. We asked whether browsing or interactions with herbaceous plants help to maintain landscape heterogeneity by differentially impacting young trees in different locations. We planted the mono-dominant tree species (*Acacia drepanolobium*) in four locations: inside glades, far from glades, at edges of isolated glades and at edges between adjacent glades. Within each location, we assessed the separate and

combined effects of herbivore exclusion (caging) and herbaceous plant removal (clearing) on tree survival and growth. Both caging and clearing improved tree survival and growth inside glades. When herbaceous plants were removed, trees inside glades grew more than trees in other locations, suggesting that glade soils were favorable for tree growth. Different types of glade edges (isolated vs. non-isolated) did not have significantly different impacts on tree performance. This represents one of the first field-based experiments testing the separate and interactive effects of browsing, grass competition and edaphic context on savanna tree performance. Our findings suggest that, by excluding trees from otherwise favorable sites, both herbaceous plants and herbivores help to maintain functionally important landscape heterogeneity in African savannas.

**Keywords** Boma · Grazing lawn · Tree–grass interactions · Spatial heterogeneity · Edge interactions

## Introduction

Understanding heterogeneity in vegetation structure has been a central goal of ecology, particularly in savanna ecosystems where mechanisms of tree–grass coexistence have long been debated (Walter 1971; Walker et al. 1981; Scholes and Archer 1997; Jeltsch et al. 2000; Sankaran et al. 2004). Patterns of woody cover in savannas can be driven by a multitude of factors including rainfall, nutrients, herbivory, fire, interactions with grasses or other woody plants, and interactions among these factors (Dublin et al. 1990; Scholes and Archer 1997; Jeltsch et al. 2000; van Langevelde et al. 2003; Sankaran et al. 2005; Riginos and Grace 2008; van der Waal et al. 2011). Heterogeneity in woody cover is important because it alters and possibly

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enhances biodiversity and ecosystem function (Young et al. 1995; Rietkerk et al. 2004; Riginos and Grace 2008; Lundholm 2009; Gregory et al. 2010).

In African savannas, heterogeneity in woody cover is often associated with heterogeneity in soil quality. Woody cover can be affected by regional-scale nutrient gradients as well as nutrient-rich micro-sites (e.g., termite mounds) (Sankaran et al. 2005; Fox-Dobbs et al. 2010; Levick et al. 2010). Intermediate in scale are nutrient-rich sites derived from traditional livestock corrals (bomas) (Western and Dunne 1979; Blackmore et al. 1990; Lamprey and Reid 2004). Throughout African savannas, former corral sites develop into long-term, nutrient-rich patches with unique vegetation (Blackmore et al. 1990; Reid and Ellis 1995; Young et al. 1995; Augustine 2003; Muchiru et al. 2009; van der Waal et al. 2011), distinctive plant community dynamics (Veblen 2008, 2011; Veblen and Young 2010) and broad-ranging ecological impacts (Augustine 2004; Gregory et al. 2010).

In wooded savannas, corral sites can persist as grass-dominated ‘glades,’ easily recognizable for decades to centuries as large treeless patches (50–100 m in diameter) embedded in a wooded matrix (Young et al. 1995; Muchiru et al. 2009; Veblen and Young 2010). Though glade interiors are treeless, areas between nearby glades (<150 m apart) have higher densities of trees than either the background savanna or areas near isolated glades (Porensky 2011). It is not clear how these distinctive patterns of woody cover associated with glade interiors (no trees) and adjacent glade edges (many trees) are maintained over the long-term. Inside nutrient-rich glades, at glade edges, and in the background savanna, we assessed the relative importance of two mechanisms that may drive heterogeneity in woody cover: herbivory and interactions with herbaceous plants.

Herbivory has major impacts on woody cover in savanna ecosystems (Pellew 1983; Augustine and McNaughton 2004; Goheen et al. 2010) and could play a particularly important role in determining woody cover patterns associated with glades, where use by mid-sized, mixed-feeder herbivores is elevated (Young et al. 1995; van der Waal et al. 2011). Herbivore preference may lead to elevated browsing pressure and reduced tree survival or growth within glades, particularly for young trees (seedlings and saplings) (Goheen et al. 2004; Midgley et al. 2010). Thus, initial anthropogenic disturbance may generate herbivore-mediated feedbacks that help maintain glades in a treeless state over the long term.

Very high densities of trees between nearby glades may also be caused by a combination of anthropogenic legacies and herbivore-mediated feedbacks. During active corral use, intensive livestock activity and human presence between nearby corrals may initiate a burst of tree establishment by reducing grass cover, deterring browsers and

increasing nutrient levels, especially if low grass cover causes reduced fire intensity or frequency (e.g., Tobler et al. 2003; van Langevelde et al. 2003; Augustine and McNaughton 2004; Muchiru et al. 2009; Davies et al. 2010; Goheen et al. 2010). Over the long term, herbivore behaviors may reinforce high tree densities between glades. The mid-sized wildlife species most likely to browse on tree seedlings tend to avoid heavily-treed areas (Riginos and Grace 2008). Reduced browsing pressure in heavily-treed areas between nearby glades could further increase tree density.

Herbaceous plants (hereafter ‘grasses’) can also exert controls over young trees (Riginos and Young 2007). Grasses often compete intensely with young trees (e.g., van der Waal et al. 2009; Cramer et al. 2010). Glades in our study site typically have very high grass cover (Veblen 2008; Porensky 2011), creating an environment in which grass competition may be severe enough to kill young trees (e.g., van der Waal et al. 2011). Areas between nearby glades have unusually low cover of dense glade grasses, which may release young trees from competition and help explain increased tree densities between nearby glades (Porensky 2011). At low-moderate densities (e.g., between nearby glades), grasses may even facilitate young trees by concealing them from herbivores (Western and Maitumo 2004; Riginos and Young 2007). Differences in grass cover can also impact tree density via interactions with fire (van Langevelde et al. 2003; Davies et al. 2010), although fire has been suppressed at our study site for decades.

This work goes beyond previous studies by experimentally testing the separate and combined effects of both herbivory and grasses on the survival and growth of young trees planted in the field in different edaphic contexts. Specifically, we determined the relative importance of herbivores and grasses as drivers of (1) extremely low densities of trees inside glades and (2) high densities of trees between nearby glades.

## Materials and methods

### Study site

This research took place in central Kenya on Mpala Conservancy (36°52'E, 0°17'N) and neighboring Jessel Ranch. These properties are managed for livestock production as well as biodiversity conservation, and host a full complement of wildlife species including native ungulates and their predators (see Young et al. 1998). Soils are ‘black cotton’ vertisols characterized by high clay content and poor drainage (Deckers et al. 2001). Mean annual rainfall is 500–600 mm. Topography is relatively uniform, and vegetation is dominated by a single tree species (*Acacia*

*drepanolobium*, comprising 97% of total woody cover) and five grass species (Young et al. 1998). The study area includes dozens of glades that are irregularly distributed throughout the landscape, creating variability in inter-glade distance (Fig. 1). Fire has not been an active part of this ecosystem since the 1960s, although small portions of the study site have been experimentally burned in recent years (R.L. Sensenig, personal communication).

#### Seed collection and germination

Between September 2008 and January 2009, we collected seeds from 33 adult *A. drepanolobium* trees located throughout the study site. Source trees were all greater than 3 m tall and occupied by the same symbiotic *Acacia* ant species (*Crematogaster mimosae*). Source trees were separated from each other by at least 60 m. In total, we collected 1,518 seeds, or  $46 \pm 3$  (1SE) seeds per source tree. We randomly assigned half the seeds from each source tree to a ‘sapling’ treatment and the other half to a ‘seedling’ treatment.

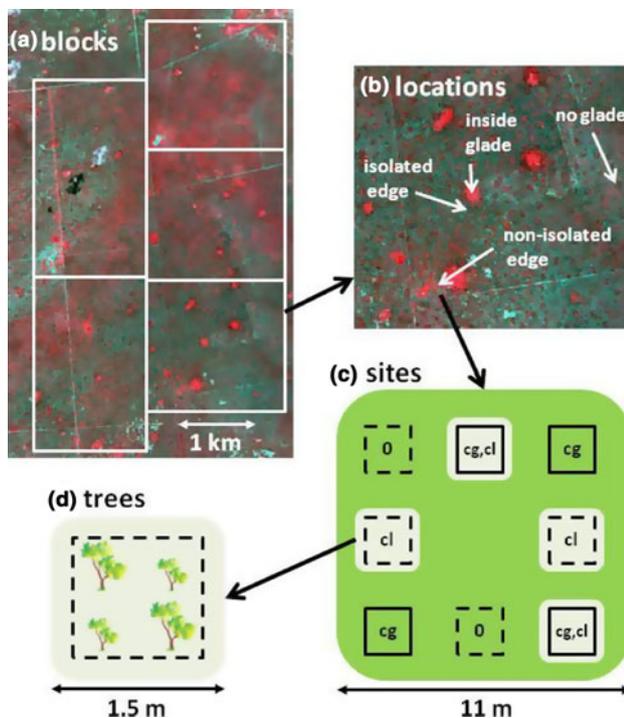
Germination and initial tree growth took place in a tree nursery operated by Kiwi Consultants in Nanyuki, Kenya,

40 km from the study site. Seeds assigned to the sapling treatment were germinated in February 2009, and seeds assigned to the seedling treatment were germinated in June 2009. All trees were grown in potting soil and fertilized once during initial growth. Trees were kept outdoors under shade cloth for the first 2–3 months of growth and then moved into full sun. On 15 August 2009, we clipped the top 3 cm of each sapling to simulate natural browsing and induce allocation to defense structures (cf. Young et al. 2003). In October 2009, we retrieved 484 saplings and 245 seedlings from the nursery. Most saplings had well-developed woody stem tissue, while seedlings were just beginning to form woody tissue. Trees were individually tagged. For each tree, we measured stem length (length of the longest stem, measured while straightening the stem as much as possible), diameter at 3 cm height (hereafter ‘basal diameter’), and number of branches.

#### Experimental design and data collection

We split the study area into five blocks based on property ownership and geographic position (Fig. 1). Within each block, we randomly chose a relatively isolated glade (>250 m from any other glade), a non-isolated glade (<150 m from a second glade), and a ‘no glade’ area (>300 m from any glade). We planted trees in four  $11 \times 11$  m plots in each block: within the isolated glade, 25 m outside the edge of the isolated glade, 25 m outside the edge of the non-isolated glade, and at a random location within the ‘no-glade’ area (Fig. 1). The 25-m edge distance was chosen to match the observed location of peak tree densities between nearby glades (Porensky 2011). Glade edges were defined as in previous work (Porensky 2011). We used aerial photographs from 1961 to ensure that all glades were >45 years old. Plots inside glades were all located in areas dominated by the grass *Pennisetum stramineum* to reduce variability caused by differences in glade vegetation (Veblen 2008).

Within each plot, we created two replicates of a  $2 \times 2$  factorial design that included mammalian herbivore exclusion (caging) and herbaceous vegetation removal (clearing). The four treatments included caged, cleared, caged + cleared, and control (no caging or clearing). We randomly assigned treatments to eight  $1.5 \times 1.5$  m ‘sites’ within each  $11 \times 11$  m plot (Fig. 1). Sites were arranged in a grid and separated from one another by 1.5 m. Sites assigned to caged and caged + cleared treatments were covered by a  $1 \times 1 \times 1$  m chicken-wire cage. To reduce rodent incursions, we covered the bottom half-meter of each cage with  $\leq 1.3$ -cm mesh. At sites assigned to cleared and caged + cleared treatments, we clipped all non-woody plants (almost entirely grasses) at ground level. At intervals throughout the experiment (0.5, 1.5, 3 and 6 months after



**Fig. 1** The experimental design. **a** The study area was divided into five blocks. Glades are visible as round spots in this Quickbird image (DigitalGlobe 2003). **b** Each block contained four locations: far from glade, inside glade, isolated glade edge and non-isolated glade edge. **c** Within each location, two replicates of four treatments were randomly assigned to eight sites. Treatments included control (0), caging (cg), clearing (cl), and both caging and clearing (cg, cl). **d** Saplings and seedlings were randomly assigned to each site

planting), grass regrowth was sprayed with herbicide. Although the goal of caging was to protect trees from browsing, the cages also eliminated herbivory on herbaceous vegetation. In order to separate the direct effects of reduced browsing (the factor of interest) from indirect effects of reduced grazing inside cages (e.g., shading of trees by tall grasses), caged herbaceous plants were occasionally clipped so that average vegetation height inside cages matched that of surrounding, uncaged vegetation.

Within each  $1.5 \times 1.5$  m site, we planted two randomly chosen saplings and either one or two randomly chosen seedlings (for a total of 16 saplings and 12 seedlings per plot, Fig. 1). Due to unexpectedly high mortality at the nursery, we were unable to plant two seedlings at every site, but within each plot we planted three seedlings per treatment. For each plot, we randomly chose which of the two sites assigned to a given treatment would receive two seedlings and which would receive one seedling. The orientation of seedlings and saplings within each site was also assigned randomly. Within each site, trees were planted  $\sim 70$  cm apart (the maximum amount of separation possible given the size of the cages). Trees were planted in mid-October 2009, just before a short rainy season. At the time of planting, we watered each seedling or sapling with 1 L. We did not add any more water after planting. In total, we planted 320 saplings and 240 seedlings.

Trees were monitored in late August 2010. For each individually tagged tree, we recorded survival, stem length, basal diameter and number of branches (measured as described above). Of the 457 surviving trees, 6 were excluded from basal diameter analysis because the main stem had died or been severely browsed or broken.

#### Statistical analysis

The experiment had a blocked split-split-plot design with location as the main plot effect, treatment (caging and/or clearing) as the subplot effect, and tree age class as the sub-subplot effect. To evaluate factors responsible for reduced tree density inside glades, we compared three locations: far from glade, isolated glade edge and inside glade. To evaluate factors responsible for increased tree density between nearby glades, we compared isolated glade edges to non-isolated glade edges.

We analyzed tree survival using a generalized linear mixed model with a binary conditional probability distribution and residual pseudo-likelihood estimation. For trees that survived, we analyzed three different growth responses (stem length growth, basal diameter growth and branch production) using linear mixed models with restricted maximum-likelihood estimation. We analyzed each growth response separately because we expected stem length, basal

diameter and branch production to be differently affected by our treatments. In all cases, we used Satterthwaite's approximation of degrees of freedom and a 'variance components' covariance structure. For all models, fixed predictors included location, treatment, tree age class and all two-way interactions. If interactions were significant, we analyzed simple effects (e.g., differences among treatments within each location and differences among locations within each treatment). Random factors included block, location  $\times$  block and site nested within location  $\times$  block. We used transformations or variance-weighting when necessary in order to meet the assumptions of the models. We used Tukey's HSD method ( $\alpha = 0.05$ ) for post hoc mean comparisons. All analyses were conducted in SAS 9.2 (SAS Institute, Cary, NC, USA).

## Results

### Baseline tree sizes

For seedlings, baseline stem length (measured just prior to planting) was  $15.6 \pm 0.4$  (1SE) cm and baseline basal diameter was  $2.2 \pm 0.04$  mm. For saplings, baseline stem length was  $25.0 \pm 0.5$  cm and baseline basal diameter was  $3.4 \pm 0.06$  mm. For both size classes, baseline branch number was  $1.1 \pm 0.02$  branches.

### Part I: inside and outside of isolated glades

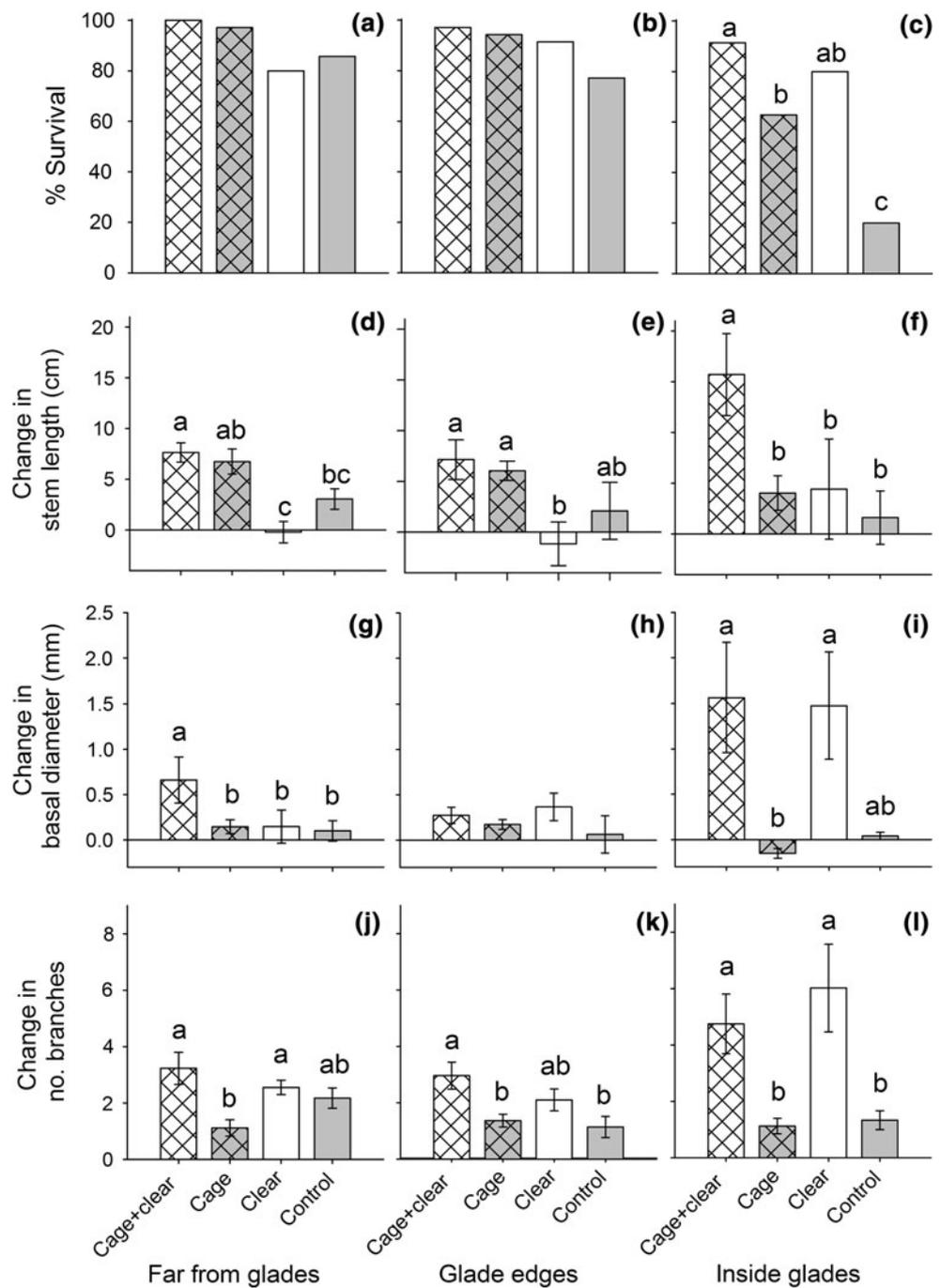
#### Survival

Saplings had significantly higher survival than seedlings (85 vs. 77%,  $F_{1,402} = 3.55$ ,  $P = 0.04$ ). Interactions involving age class were not significant, but the interaction between location (far from glade, glade edge, or inside glade) and treatment (caging and/or clearing) significantly affected survival ( $F_{6,402} = 3.06$ ,  $P = 0.006$ ).

Simple effects analysis revealed that caging and clearing did not significantly impact survival far from glades ( $F_{3,136} = 2.55$ ,  $P = 0.06$ ) or at glade edges ( $F_{3,38.9} = 2.10$ ,  $P = 0.12$ ), but strongly affected survival inside glades ( $F_{3,136} = 11.16$ ,  $P < 0.0001$ ). Inside glades, trees in the control treatment had less than one-third the survival of trees in any other treatment (Fig. 2a–c; Table 1).

Tree survival did not differ significantly across locations within the cleared ( $F_{2,7.18} = 0.84$ ,  $P = 0.5$ ) or caged + cleared ( $F_{2,36.26} = 1.06$ ,  $P = 0.4$ ) treatments. However, survival did differ by location within the caged ( $F_{2,27.11} = 4.65$ ,  $P = 0.02$ ) and control ( $F_{2,6.61} = 9.17$ ,  $P = 0.01$ ) treatments. Survival far from glades was 55% higher than survival inside glades for the cage treatment and over 300% higher for the control treatment (Fig. 2a–c; Table 1).

**Fig. 2** Survival (a–c) and growth (d–l) of trees planted a, d, g, j far from glades, b, e, h, k at glade edges, and c, f, i, l inside glades. For growth responses, means ± SE were calculated across blocks ( $n = 5$ ) after averaging over all seven trees present within each block × location × treatment combination. Within each panel, treatments with shared letters are not significantly different (Tukey’s HSD method,  $\alpha = 0.05$ )



*Stem length growth*

Seedling stem lengths grew significantly more than those of saplings ( $8.6 \pm 0.8$  vs.  $3.4 \pm 0.6$  cm;  $F_{1,272} = 31.95$ ,  $P < 0.0001$ ). Interactions involving age class were not significant. The interaction between location and treatment significantly affected stem length growth ( $F_{6,104} = 3.28$ ,  $P = 0.005$ ).

Treatment significantly affected stem length growth at all three locations (far from glades  $F_{3,120} = 10.73$ ,

$P < 0.0001$ ; glade edge  $F_{3,31.3} = 9.18$ ,  $P = 0.0002$ ; inside glades  $F_{3,24.5} = 7.51$ ,  $P = 0.001$ ). Far from glades and at glade edges, caged + cleared trees grew about 8 cm more than cleared trees, while caged and control trees had intermediate growth (Fig. 2d–f; Table 1). Inside glades, growth of caged + cleared trees was over three times that of trees in other treatments (Fig. 2d–f; Table 1).

Stem length growth did not differ significantly across locations within any treatments (cage  $F_{2,82.9} = 0.33$ ,

**Table 1** Survival and growth of *A. drepanolobium* trees planted far from glades, at isolated glade edges and inside glades

Treatment	Location	Survival	Stem length growth (cm)	Basal diameter growth (mm)	No. of new branches
Cage + Clear	Far from glade	100	7.6 ± 0.9	0.7 ± 0.3	3.2 ± 0.6
	Glade edge	97	7.1 ± 1.9	0.3 ± 0.1	3.0 ± 0.5
	Inside glade	91	15.7 ± 4.0	1.6 ± 0.6	4.7 ± 1.1
Cage	Far from glade	97 a	6.8 ± 1.2	0.1 ± 0.1 ab	1.1 ± 0.3
	Glade edge	94 ab	6.0 ± 0.9	0.2 ± 0.1 a	1.4 ± 0.2
	Inside glade	63 b	4.0 ± 1.7	−0.2 ± 0.1 b	1.1 ± 0.3
Clear	Far from glade	80	−0.2 ± 1.0	0.1 ± 0.2 b	2.6 ± 0.3 ab
	Glade edge	91	−1.2 ± 2.1	0.4 ± 0.2 ab	2.1 ± 0.4 b
	Inside glade	80	4.4 ± 4.9	1.5 ± 0.6 a	6.0 ± 1.6 a
Control	Far from glade	86 a	3.1 ± 1.0	0.1 ± 0.1	2.2 ± 0.4
	Glade edge	77 a	2.1 ± 2.8	0.1 ± 0.2	1.1 ± 0.4
	Inside glade	20 b	1.6 ± 2.6	0.04 ± 0.04	1.3 ± 0.3

For growth responses, mean ± SE were calculated across blocks ( $n = 5$ ) after averaging over all seven trees present within each block × location × treatment combination. Within each combination of treatment and response variable, locations with shared letters are not significantly different (Tukey's HSD method,  $\alpha = 0.05$ )

$P = 0.7$ ; caged + cleared  $F_{2,7.16} = 4.07$ ,  $P = 0.07$ ; clear  $F_{2,7.39} = 1.49$ ,  $P = 0.3$ ; control  $F_{2,5.86} = 0.01$ ,  $P = 0.99$ ; Fig. 2d–f; Table 1).

#### Basal diameter growth

Seedling basal diameters increased significantly more than those of saplings ( $0.8 \pm 0.1$  vs.  $0.2 \pm 0.1$  mm;  $F_{1,269} = 46.15$ ,  $P < 0.0001$ ). Interactions involving age class were not significant, but growth was significantly affected by the interaction between location and treatment ( $F_{6,116} = 6.56$ ,  $P < 0.0001$ ).

Treatment significantly affected basal diameter growth far from glades ( $F_{3,119} = 4.04$ ,  $P = 0.009$ ) and inside glades ( $F_{3,28.5} = 6.61$ ,  $P = 0.002$ ). Far from glades, growth of caged + cleared trees was over 4.5 times that of trees in other treatments (Fig. 2g–i; Table 1). Inside glades, cleared and caged + cleared trees grew significantly more than caged trees, while control trees had intermediate growth (Fig. 2g–i; Table 1). Treatment did not significantly affect basal diameter growth at glade edges ( $F_{3,118} = 1.87$ ,  $P = 0.1$ ).

Within the cage treatment, basal diameter growth differed significantly among locations ( $F_{2,84.5} = 3.45$ ,  $P = 0.04$ ). Caged trees inside glades grew significantly less than caged trees in glade edges, while caged trees far from glades had intermediate growth (Fig. 2g–i; Table 1). Locations also differed significantly within the cleared treatment ( $F_{2,9.65} = 4.01$ ,  $P = 0.05$ ). Cleared trees inside glades grew over 10 times as much as cleared trees far from glades, while cleared trees at glade edges had intermediate growth (Fig. 2g–i; Table 1). Basal diameter growth did not differ significantly across locations within the caged + cleared ( $F_{2,7.16} = 3.97$ ,  $P = 0.07$ ) or control ( $F_{2,9.66} = 0.02$ ,  $P = 0.98$ ) treatments.

#### Branch production

Saplings produced significantly more new branches than seedlings ( $2.9 \pm 0.2$  vs.  $2.3 \pm 0.2$  new branches;  $F_{1,257} = 13.14$ ,  $P = 0.0003$ ). Interactions involving age class were not significant. Branch production was significantly affected by the interaction between location and treatment ( $F_{6,86.4} = 3.29$ ,  $P = 0.006$ ).

Treatment significantly affected branch production in all locations (far from glades  $F_{3,120} = 9.02$ ,  $P < 0.0001$ ; glade edges  $F_{3,31} = 7.04$ ,  $P = 0.001$ ; inside glades  $F_{3,26.9} = 14.58$ ,  $P < 0.0001$ ). Far from glades and at glade edges, caged + cleared trees produced over twice as many branches as caged trees, while cleared and control trees produced an intermediate number of branches (Fig. 2j–l; Table 1). Inside glades, cleared and caged + cleared trees produced more than three times as many branches as caged and control trees (Fig. 2j–l; Table 1).

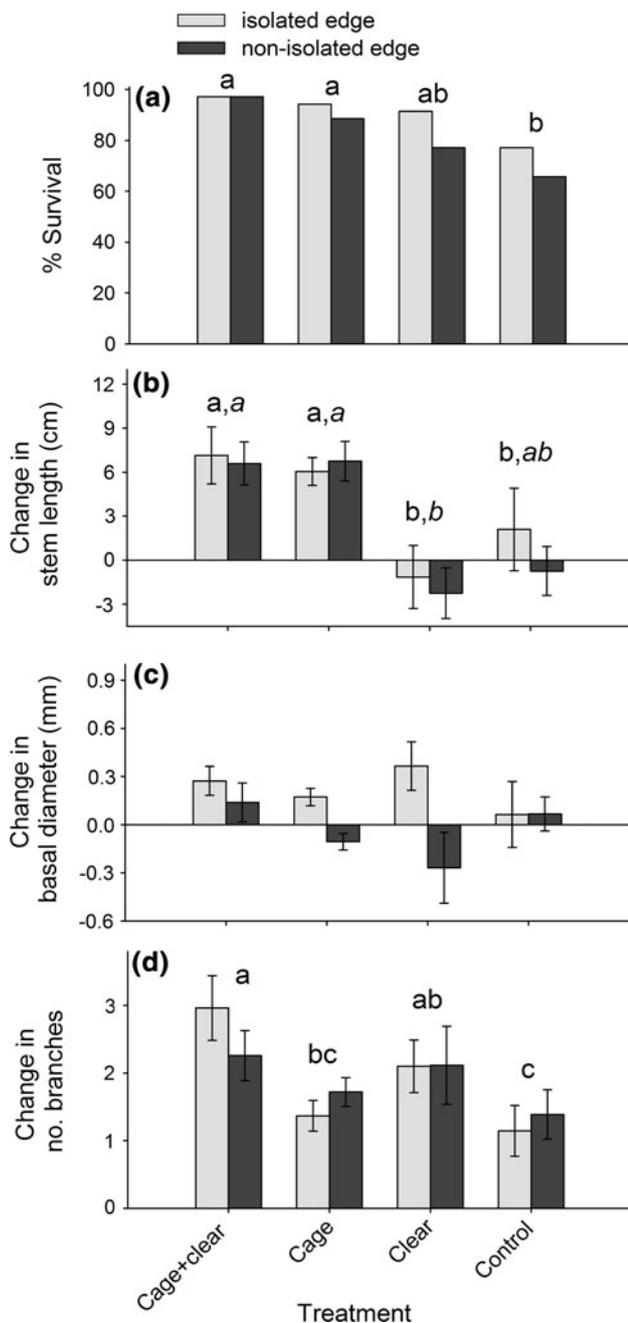
Branch production was not significantly affected by location in the cage ( $F_{2,24.9} = 0.40$ ,  $P = 0.7$ ), caged + cleared ( $F_{2,11.7} = 1.82$ ,  $P = 0.2$ ) or control ( $F_{2,7.62} = 1.47$ ,  $P = 0.3$ ) treatments. In the cleared treatment, location had significant effects on branch production ( $F_{2,8.36} = 6.62$ ,  $P = 0.02$ ). Cleared trees inside glades produced almost three times as many branches as cleared trees at glade edges, and cleared trees far from glades produced an intermediate number of branches (Fig. 2j–l; Table 1).

#### Part II: isolated versus non-isolated glade edges

##### Survival

When we compared isolated and non-isolated edges, tree survival was only affected by treatment ( $F_{3,85.28} = 5.68$ ,  $P = 0.001$ ). Caged and caged + cleared trees had about

30% higher survival than control trees, and cleared trees had intermediate survival (Fig. 3a). Edge type, tree age class, and interactions had no significant impact on survival.



**Fig. 3** Survival (a) and growth (b–d) of trees planted in isolated and non-isolated glade edges. For growth responses, bars are mean ± SE calculated across blocks ( $n = 5$ ) after averaging over all seven trees present within each block × location × treatment combination. Within each panel, across both edge types, treatments with shared letters are not significantly different (Tukey’s HSD method,  $\alpha = 0.05$ ). For stem length growth, non-italicized letters indicate significance groups for saplings, while italicized letters indicate significance groups for seedlings (tree age × treatment  $F_{3,182} = 2.72$ ,  $P = 0.046$ )

*Stem length growth*

Stem growth was not significantly affected by edge type, but was affected by the interaction between treatment and tree age class ( $F_{3,182} = 2.72$ ,  $P = 0.046$ ). Treatments had significant effects on stem length growth for both saplings ( $F_{3,55.3} = 16.54$ ,  $P < 0.0001$ ) and seedlings ( $F_{3,57.3} = 6.94$ ,  $P = 0.0005$ ). Saplings that were caged or caged + cleared grew significantly more than control or cleared trees (Fig. 3b). Seedling results were similar except that growth in the control treatment was intermediate between the cleared treatment and the other treatments (Fig. 3b). In three out of four treatments, seedlings grew significantly more than saplings (caged:  $8.5 \pm 1.0$  vs.  $4.9 \pm 1.1$  cm,  $F_{1,55.1} = 5.64$ ,  $P = 0.02$ ; cleared:  $1.3 \pm 1.2$  vs.  $-2.9 \pm 1.2$  cm,  $F_{1,51} = 6.91$ ,  $P = 0.01$ ; control:  $5.5 \pm 1.5$  vs.  $-0.8 \pm 1.5$  cm;  $F_{1,35.4} = 9.88$ ,  $P = 0.003$ ). In the caged + cleared treatment, stem length growth did not differ significantly between tree age classes ( $6.7 \pm 1.2$  cm for seedlings vs.  $7.1 \pm 1.1$  cm for saplings;  $F_{1,49.1} = 0.04$ ,  $P = 0.8$ ).

*Basal diameter growth*

Across edge types, basal diameters of seedlings grew significantly more than those of saplings ( $0.4 \pm 0.05$  vs.  $-0.1 \pm 0.05$  mm;  $F_{1,217} = 49.61$ ,  $P < 0.0001$ ). Edge type, treatment and all interactions had no significant impact on growth, though we observed a trend towards more growth in isolated than non-isolated edges ( $F_{1,8.37} = 4.35$ ,  $P = 0.07$ ; Fig. 3c).

*Branch production*

Branch production in glade edges was affected by tree age class and treatment. Saplings produced about 30% more branches than seedlings ( $2.2 \pm 0.1$  vs.  $1.6 \pm 0.2$  new branches;  $F_{1,179} = 13.57$ ,  $P = 0.0003$ ). Caged + cleared trees produced significantly more branches than caged and control trees, and cleared trees produced significantly more branches than control trees ( $F_{3,63.5} = 8.11$ ,  $P < 0.0001$ ; Fig. 3d). Edge type and all interactions did not significantly affect branch production.

**Discussion**

Previous studies have identified herbivores, grass competition and soil nutrients—along with other factors such as fire and rainfall regime—as important drivers of woody vegetation cover and density in savanna landscapes (Knoop and Walker 1985; Augustine and McNaughton 2004; Sankaran et al. 2005; Goheen et al. 2007, 2010; Bond 2008;

Riginos 2009; Cramer et al. 2010; van der Waal et al. 2011). To our knowledge, our study is the first to experimentally test the separate and combined impacts of browsing, competition with herbaceous plants, and edaphic context on tree survival and growth in a field setting. We examined these factors in the absence of fire, which is not a major factor at our study site, although fire is a critical driver of tree cover in many savannas (Sankaran et al. 2005; Bond 2008). The lack of fire in our system provides an opportunity to distinguish direct impacts of grasses and browsing from more indirect, fire-mediated impacts on tree cover (e.g., Roques et al. 2001; van Langevelde et al. 2003; Staver et al. 2009).

### Impacts of grasses and browsing

Our results provide field-based evidence that the influence of grass and browsers on woody cover depends strongly on edaphic context. Both browsing and grass competition reduced *A. drepanolobium* survival, but only inside nutrient-rich glades. Grass removal improved survival inside glades more than herbivore exclusion, and the combination of grass removal and herbivore exclusion led to the highest survival rates. Outside glades, however, browsing and grasses had no significant impacts on survival. These results differ from those of van der Waal et al. (2011), who planted young trees in field plots in South Africa and found that fertilization, but neither herbivory nor the interaction of fertilizer and herbivory, reduced tree survival.

Grass competition emerged as the major factor limiting basal diameter growth and branch production inside glades, and to a lesser degree, it also limited growth outside glades. These results support previous studies in our system (Riginos and Young 2007; Riginos 2009) and other savannas (Knoop and Walker 1985; van der Waal et al. 2009; Cramer et al. 2010; Ward and Esler 2011) which found that grass competition can significantly restrict tree growth and recruitment. In a pot experiment, van der Waal et al. (2011) went a step further by showing that competition between grasses and trees was more intense when plants were grown in glade-derived, nutrient-rich soil. Our results support these findings, in that growth reductions due to grass competition were greater inside than outside glades.

In contrast to basal diameter and branch production results, which suggested that grass removal overwhelmingly benefits trees, stem length growth results revealed a trade-off between the benefits (release from competition) and costs (e.g., increased visibility to herbivores; Riginos and Young 2007) of grass removal. Inside glades, cleared and control trees had similar stem length growth, and this growth was significantly less than that of caged + cleared trees. This result suggests that the benefits of grass removal were offset by negative impacts of increased visibility.

Outside glades, the negative impacts of grass removal were even more prominent. Caged and cleared + caged trees had significantly higher stem length growth than cleared trees, while control trees had intermediate growth. Thus, outside glades, the negative impacts of increased apparency seemed to significantly outweigh any benefits of release from competition. By continually reducing tree height, browsers can have large impacts on three-dimensional landscape structure in this ecosystem (see also Levick et al. 2009). Continual browsing is also likely to keep small trees in the grass layer, making them more susceptible to damage and mortality during fire (Okello et al. 2008; Staver et al. 2009; Midgley et al. 2010).

As mentioned previously, glades are only one of several major sources of edaphic variation in savanna ecosystems. Our work and that of van der Waal et al. (2011) suggest that, at intermediate spatial scales, edaphic context can modify the importance of grass competition and browsing as drivers of tree survival and growth. Findings from both studies support the hypothesis that tree establishment is more limited by grass competition in nutrient-rich patches. The two studies differ in their conclusions about the role of browsing and its interactions with nutrient context. These findings add to the existing body of work on how edaphic context influences savanna tree cover (e.g., Eckhardt et al. 2000; Dickie et al. 2007; Levick et al. 2010), and suggest that future research is necessary in other landscapes and at multiple scales.

### Tree age

We found significant and consistent differences in survival and growth between seedlings and saplings. Saplings had higher survival and branch production, but seedlings had higher stem length growth and basal diameter growth. These results parallel those of previous studies on other plant species (Horvitz and Schemske 2002; Hodar et al. 2008). Although some studies (e.g., Hodar et al. 2008) identified interactions between age and experimental treatments, we found that seedlings and saplings generally displayed similar responses across herbivore, grass competition, and planting location treatments.

To establish inside glades, trees must disperse into glades as seeds, avoid seed death (via predation, pathogens, or desiccation), germinate, emerge, and survive seedling and sapling growth stages. In this study, we focused on the latter two stages, but processes during other life stages may also limit tree establishment inside glades. Predation by rodents may be important for seeds and young seedlings (Goheen et al. 2004, 2010; Walters et al. 2005), especially given high rodent densities inside glades (Veblen, unpublished data). In this study, rodents likely contributed to seedling mortality in uncaged treatments, especially in the control treatment where grasses provided protective cover

from predation (Peles and Barrett 1996). Rodents are unlikely to have caused mortality of saplings, and this may have contributed to the higher survival rates of saplings compared to seedlings.

#### Isolated versus non-isolated glade edges

Tree survival and growth did not differ significantly between isolated and non-isolated glade edges, suggesting that high densities of trees between nearby glades are not maintained via reduced impacts of grass or herbivores on trees at the seedling or sapling stages. However, reduced grass competition and herbivory may help maintain high tree densities between glades by impacting other tree life stages. For example, reduced wildlife use of areas between nearby glades (Porensky 2011) may cause increased *A. drepanolobium* seed production (Goheen et al. 2007), which may then result in higher tree recruitment. Alternatively, high tree densities may be a legacy of past events. Livestock and human impacts create a region of intensive use (i.e., low grass cover, high livestock use and low wildlife use) around active corrals, and impacts are especially pronounced between active corrals and nearby glades (unpublished data; see also Muchiru et al. 2009). The combination of low browser density, low grass cover and ample fertilization in areas between active corrals and nearby glades may initiate a burst of tree establishment, especially if low grass cover causes reduced fire intensity or frequency (e.g., Tobler et al. 2003; van Langevelde et al. 2003; Augustine and McNaughton 2004; Goheen et al. 2007, 2010). Increased tree establishment during boma use could have long-term consequences for local tree densities.

#### Landscape heterogeneity

At our study site, grasses and browsers may be able to maintain the conversion of wooded savanna to treeless grassland even in the absence of fire, but only in edaphically distinct landscape patches. Grasses and browsing, separately and especially in combination, reduced the survival and growth of *A. drepanolobium* seedlings and saplings inside glades, but not outside glades. When grasses were removed (in cleared and caged + cleared treatments), survival rates inside glades were high and statistically indistinguishable from survival rates outside glades. Moreover, when grasses were removed, trees inside glades had higher basal diameter growth and produced more branches than trees planted in other locations. Thus, in the absence of grass competition, *A. drepanolobium* actually grows better in glade-like conditions. Herbivores consume trees (a top-down mechanism), while grasses reduce the availability of resources required by trees (a bottom-up mechanism). In our system, both mechanisms

appear to increase landscape heterogeneity by helping to maintain glades in a treeless state.

#### Implications for management

In general, spatial heterogeneity tends to be good for biodiversity (e.g., Lundholm 2009; Tamme et al. 2010), and heterogeneity created via glades is no exception (e.g., Young et al. 1995; Augustine 2004; Gregory et al. 2010; van der Waal et al. 2011). Glade treelessness is initiated by anthropogenic activities and attracts herbivores (especially mid-sized species such as Grant's gazelles and oryx), probably by allowing for improved predator detection (Riginos and Grace 2008). Grazers attracted to glades could potentially promote tree establishment by reducing grass competition and fire frequency or intensity (Roques et al. 2001; van Langevelde et al. 2003; Riginos and Young 2007). However, the mixed-feeder herbivores most attracted to glades probably contribute to the maintenance of these treeless sites both directly, by browsing on *A. drepanolobium* seedlings, and indirectly, by increasing grass productivity through fertilization (Odadi 2010; Augustine et al. 2011; van der Waal et al. 2011). Thus, our results suggest that loss of either livestock (which initiate glade formation) or wildlife (which help to maintain glades) from this savanna ecosystem could lead to homogenization of the landscape, with negative consequences for biodiversity. Many livestock–wildlife interactions have negative impacts on human livelihoods or conservation objectives (e.g., Young et al. 2005; Laporte et al. 2010). When managed sustainably, glades appear to represent an example of positive synergy between livestock production and biodiversity conservation.

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#### References

- Augustine DJ (2003) Long-term, livestock-mediated redistribution of nitrogen and phosphorus in an East African savanna. *J Appl Ecol* 40:137–149
- Augustine DJ (2004) Influence of cattle management on habitat selection by impala on central Kenyan rangeland. *J Wildl Manag* 68:916–923
- Augustine DJ, McNaughton SJ (2004) Regulation of shrub dynamics by native browsing ungulates on East African rangeland. *J Appl Ecol* 41:45–58

- Augustine DJ, Veblen KE, Goheen JR, Riginos C, Young TP (2011) Pathways for positive cattle–wildlife interactions in semi-arid rangelands. In: Georgiadis N (ed) *Conserving wildlife in African Landscapes: Kenya's Ewaso Ecosystem*, vol Smithsonian Contributions to Zoology no. 632. Smithsonian Institution Scholarly Press, Washington, D.C., pp 55–71
- 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* 17:463–470
- Bond WJ (2008) What limits trees in C-4 grasslands and savannas? *Annu Rev Ecol Evol Syst* 39:641–659
- Cramer MD, van Cauter A, Bond WJ (2010) Growth of N-2-fixing African savanna *Acacia* species is constrained by below-ground competition with grass. *J Ecol* 98:156–167
- Davies KW, Bates JD, Svejcar TJ, Boyd CS (2010) Effects of long-term livestock grazing on fuel characteristics in rangelands: an example from the sagebrush steppe. *Rangel Ecol Manag* 63:662–669
- Deckers J, Spargaren O, Nachtergaele F (2001) Vertisols: genesis, properties and soilscape management for sustainable development. In: Syers JK, Penning de Vries FWT, Nyamudeza P (eds) *The sustainable management of vertisols*. CABI, Wallington, pp 3–20
- Dickie IA, Schnitzer SA, Reich PB, Hobbie SE (2007) Is oak establishment in old-fields and savanna openings context dependent? *J Ecol* 95:309–320
- DigitalGlobe (2003) QuickBird scene 000000058088\_01\_P001, Level Standard 2A. DigitalGlobe, Longmont, Colorado, 6/20/2003
- Dublin HT, Sinclair ARE, McGlade J (1990) Elephants and fire as causes of multiple stable states in the Serengeti Mara woodlands. *J Anim Ecol* 59:1147–1164
- Eckhardt HC, van Wilgen BW, Biggs HC (2000) Trends in woody vegetation cover in the Kruger National Park, South Africa, between 1940 and 1998. *Afr J Ecol* 38:108–115
- Fox-Dobbs K, Doak DF, Brody AK, Palmer TM (2010) Termites create spatial structure and govern ecosystem function by affecting N-2 fixation in an East African savanna. *Ecology* 91:1296–1307
- Goheen JR, Keesing F, Allan BF, Ogada DL, Ostfeld RS (2004) Net effects of large mammals on *Acacia* seedling survival in an African savanna. *Ecology* 85:1555–1561
- Goheen JR, Young TP, Keesing F, Palmer TM (2007) Consequences of herbivory by native ungulates for the reproduction of a savanna tree. *J Ecol* 95:129–138
- Goheen JR, Palmer TM, Keesing F, Riginos C, Young TP (2010) Large herbivores facilitate savanna tree establishment via diverse and indirect pathways. *J Anim Ecol* 79:372–382
- Gregory NC, Sensenig RL, Wilcove DS (2010) Effects of controlled fire and livestock grazing on bird communities in east African savannas. *Conserv Biol* 24:1606–1616
- Hodar JA, Zamora R, Castro J, Gomez JM, Garcia D (2008) Biomass allocation and growth responses of Scots pine saplings to simulated herbivory depend on plant age and light availability. *Plant Ecol* 197:229–238
- Horvitz CC, Schemske DW (2002) Effects of plant size, leaf herbivory, local competition and fruit production on survival, growth and future reproduction of a neotropical herb. *J Ecol* 90:279–290
- Jeltsch F, Weber GE, Grimm V (2000) Ecological buffering mechanisms in savannas: a unifying theory of long-term tree-grass coexistence. *Plant Ecol* 161:161–171
- Knoop WT, Walker BH (1985) Interactions of woody and herbaceous vegetation in a southern African savanna. *J Ecol* 73:235–253
- Lamprey R, Reid RS (2004) Expansion of human settlement in Kenya's Maasai Mara: what future for pastoralism and wildlife? *J Biogeogr* 31:997–1032
- Laporte I, Muhly TB, Pitt JA, Alexander M, Musiani M (2010) Effects of wolves on elk and cattle behaviors: implications for livestock production and wolf conservation. *Plos One* 5(8):e11954
- Levick SR, Asner GP, Kennedy-Bowdoin T, Knapp DE (2009) The relative influence of fire and herbivory on savanna three-dimensional vegetation structure. *Biol Conserv* 142:1693–1700
- Levick SR, Asner GP, Kennedy-Bowdoin T, Knapp DE (2010) The spatial extent of termite influences on herbivore browsing in an African savanna. *Biol Conserv* 143:2462–2467
- Lundholm JT (2009) Plant species diversity and environmental heterogeneity: spatial scale and competing hypotheses. *J Veg Sci* 20:377–391
- Midgley JJ, Lawes MJ, Chamaille-Jammes S (2010) Savanna woody plant dynamics: the role of fire and herbivory, separately and synergistically. *Aust J Bot* 58:1–11
- 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
- Odadi WO (2010) Competitive and facilitative interactions between cattle and wild ungulates in a semi-arid savanna rangeland in Laikipia, Kenya. PhD dissertation, Egerton University, Njoro, Kenya
- Okello BD, Young TP, Riginos C, Kelly D, O'Connor TG (2008) Short-term survival and long-term mortality of *Acacia drepanolobium* after a controlled burn. *Afr J Ecol* 46:395–401
- Peles JD, Barrett GW (1996) Effects of vegetative cover on the population dynamics of meadow voles. *J Mammal* 77:857–869
- Pellew RAP (1983) The impacts of elephant, giraffe and fire upon the *Acacia tortilis* woodlands of the Serengeti. *Afr J Ecol* 21:41–74
- Porensky LM (2011) When edges meet: interacting edge effects in an African savanna. *J Ecol* 99:923–934
- Reid RS, Ellis JE (1995) Impacts of pastoralists on woodlands in South Turkana, Kenya: livestock-mediated tree recruitment. *Ecol Appl* 5:978–992
- Rietkerk M, Dekker SC, de Ruiter PC, van de Koppel J (2004) Self-organized patchiness and catastrophic shifts in ecosystems. *Science* 305:1926–1929
- Riginos C (2009) Grass competition suppresses savanna tree growth across multiple demographic stages. *Ecology* 90:335–340
- Riginos C, Grace JB (2008) Savanna tree density, herbivores, and the herbaceous community: bottom-up versus top-down effects. *Ecology* 89:2228–2238
- Riginos C, Young TP (2007) Positive and negative effects of grass, cattle, and wild herbivores on *Acacia* saplings in an East African savanna. *Oecologia* 153:985–995
- Roques KG, O'Connor TG, Watkinson AR (2001) Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *J Appl Ecol* 38:268–280
- Sankaran M, Ratnam J, Hanan NP (2004) Tree-grass coexistence in savannas revisited—insights from an examination of assumptions and mechanisms invoked in existing models. *Ecol Lett* 7:480–490
- Sankaran M, Hanan NP, Scholes RJ, Ratnam J, Augustine DJ, Cade BS, Gignoux J, Higgins SI, Le Roux X, Ludwig F, Ardo J, Banyikwa F, Bronn A, Bucini G, Caylor KK, Coughenour MB, Diouf A, Ekaya W, Feral CJ, February EC, Frost PGH, Hiernaux P, Hrabar H, Metzger KL, Prins HHT, Ringrose S, Sea W, Tews J, Worden J, Zambatis N (2005) Determinants of woody cover in African savannas. *Nature* 438:846–849
- Scholes RJ, Archer SR (1997) Tree-grass interactions in savannas. *Annu Rev Ecol Syst* 28:517–544
- Staver AC, Bond WJ, Stock WD, van Rensburg SJ, Waldram MS (2009) Browsing and fire interact to suppress tree density in an African savanna. *Ecol Appl* 19:1909–1919

- Tamme R, Hiiesalu I, Laanisto L, Szava-Kovats R, Partel M (2010) Environmental heterogeneity, species diversity and co-existence at different spatial scales. *J Veg Sci* 21:796–801
- Tobler MW, Cochard R, Edwards PJ (2003) The impact of cattle ranching on large-scale vegetation patterns in a coastal savanna in Tanzania. *J Appl Ecol* 40:430–444
- van der Waal C, de Kroon H, de Boer WF, Heitkonig IMA, Skidmore AK, de Knecht HJ, van Langevelde F, van Wieren SE, Grant RC, Page BR, Slotow R, Kohi EM, Mwakiwa E, Prins HHT (2009) Water and nutrients alter herbaceous competitive effects on tree seedlings in a semi-arid savanna. *J Ecol* 97:430–439
- van der Waal C, Kool A, Meijer S, Kohi E, Heitkonig I, de Boer W, van Langevelde F, Grant R, Peel M, Slotow R, de Knecht H, Prins H, de Kroon H (2011) Large herbivores may alter vegetation structure of semi-arid savannas through soil nutrient mediation. *Oecologia* 165:1095–1107
- van Langevelde F, van de Vijver C, Kumar L, van de Koppel J, de Ridder N, van Andel J, Skidmore AK, Hearne JW, Stroosnijder L, Bond WJ, Prins HHT, Rietkerk M (2003) Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* 84:337–350
- Veblen KE (2008) Season- and herbivore-dependent competition and facilitation in a semiarid savanna. *Ecology* 89:1532–1540
- Veblen KE (2011) Savanna glade hotspots: plant community development and synergy with large herbivores. *J Arid Environ* (in revision)
- 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
- Walker B, Ludwig D, Holling CS, Peterman RM (1981) Stability of semi-arid savanna grazing systems. *J Ecol* 69:473–498
- Walter H (1971) Ecology of tropical and subtropical vegetation. Oliver and Boyd, Edinburgh
- Walters M, Milton SJ, Somers MJ, Midgley JJ (2005) Post-dispersal fate of *Acacia* seeds in an African savanna. *S Afr J Wildl Res* 35:191–199
- Ward D, Esler KJ (2011) What are the effects of substrate and grass removal on recruitment of *Acacia mellifera* seedlings in a semi-arid environment? *Plant Ecol* 212:245–250
- Western D, Dunne T (1979) Environmental aspects of settlement site decisions among pastoral Maasai. *Hum Ecol* 7:75–98
- Western D, Maitumo D (2004) Woodland loss and restoration in a savanna park: a 20-year experiment. *Afr J Ecol* 42:111–121
- Young TP, Patridge N, Macrae A (1995) Long-term glades in *Acacia* bushland and their edge effects in Laikipia, Kenya. *Ecol Appl* 5:97–108
- Young TP, Okello BD, Kinyua D, Palmer TM (1998) KLEE: a longterm multi-species herbivore exclusion experiment in Laikipia, Kenya. *Afr J Range Forage Sci* 14:94–102
- Young TP, Stanton ML, Christian CE (2003) Effects of natural and simulated herbivory on spine lengths of *Acacia drepanolobium* in Kenya. *Oikos* 101:171–179
- 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* 122:351–359