Large herbivores facilitate savanna tree establishment via diverse and indirect pathways

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Summary

1. Savanna ecosystems are defined largely by tree–grass mixtures, and tree establishment is a key driver of community structure and ecosystem function in these systems. The factors controlling savanna tree establishment are understudied, but likely involve some combination of seed, microsite and predator/fire limitation. In African savannas, suppression and killing of adult trees by large mammals like elephants (*Loxodonta africana* Blumenbach, 1797) and giraffes (*Giraffa camelopardalis* Linnaeus, 1758) can maintain tree–grass co-dominance, although the impacts of even these conspicuous herbivores on tree establishment also are poorly understood.

2. We combined seed addition and predator exclusion experiments with a large-scale, long-term field manipulation of large herbivores to investigate the relative importance of seeds, microsites and predators in limiting establishment of a monodominant tree (*Acacia drepanolobium* Sjostedt) in a Kenyan savanna.

3. Both wild and domestic (i.e. cattle; *Bos taurus* Linnaeus, 1758) large herbivores facilitated tree establishment by suppressing abundances of rodents, the most important seed and seedling predators. However, this indirect, positive effect of wild herbivores was negated by wild herbivores' suppression of seed production. Cattle did not have this direct, negative impact; rather, they further assisted tree establishment by reducing cover of understorey grasses. Thus, the impacts of both groups of large herbivores on tree establishment were largely routed through other taxa, with a negligible net effect of wild herbivores and a positive net effect of cattle on tree establishment.

4. The distinction between the (positive) net effect of cattle and (neutral) net effect of wild herbivores is due to the inclusion of browsers and mixed feeders within the assemblage of wild herbivores. Browsing by wild herbivores limited seed production, which reduced tree recruitment; grazing by cattle was more pronounced than that by wild herbivores, and thus promoted germination and subsequent establishment of small trees.

5. Our study is the first to link seed fates to tree establishment in savanna ecosystems in experimentally-manipulated herbivore communities. Further, our results highlight how large herbivores can modify a suite of independent factors – seed production, competition with understorey species, and seed and seedling predation – to collectively drive tree establishment.

Key-words: facilitation, frailty model, hierarchical model, indirect effect, rodent, savanna, seed predation, seedling predation, tree establishment, ungulate

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Introduction

Herbivory shapes the abundance and distribution of plants by influencing plant survival, growth and reproduction. Through both direct and indirect pathways, herbivores influence plant population growth in ways that vary in magnitude and even direction over the course of a single generation (reviewed in Maron & Crone 2006). The impact of herbivores on plant demography should be particularly strong in ecosystems where herbivores are large, abundant, and have high energetic demands, and therefore function as strong interactors (Paine 1980; Pringle *et al.* 2007).

In many terrestrial ecosystems, large mammalian herbivores exert dramatic effects on plant communities by generating alternate stable states and community-wide indirect effects via consumption of plants (e.g. Dublin, Sinclair & McGlade 1990; Knapp *et al.* 1999; Holdo 2007). In particular, large herbivores often are regarded as critical in maintaining the tree–grass mixture that underlies the structure and function of African savanna ecosystems (Scholes & Archer 1997; Sankaran *et al.* 2005). Large herbivores have been shown to limit tree populations directly by reducing the survival of adult trees (e.g. Laws 1970), the growth of adult trees (e.g. Augustine & McNaughton 2004) and the establishment of young trees (e.g. Prins & Van Der Juegd 1993). However, while the negative impacts of large herbivores on savanna trees are undeniable, our tendency to focus on the direct and readily observed effects of large herbivores may obscure more cryptic, but equally important, demographic processes critical to plants that are mediated by less-conspicuous taxa (Sankaran, Ratnam & Hanan 2004). This knowledge gap hinders our understanding of how savanna ecosystems reorganize in the face of anthropogenic disturbance, particularly in light of the ongoing extirpation and subsequent replacement of wild herbivores by domestic herbivores (Prins 2000).

Establishment of small trees (i.e. saplings) from seeds (hereafter, 'tree establishment') may be a key determinant of the future abundance of adult trees (Janzen 1971; Crawley 2000), but this process is poorly understood in African savannas (Midgley & Bond 2001; but see Moe *et al.* 2009). Elsewhere, plant establishment is thought to be limited by seeds (where too few seeds are produced or dispersed to suitable establishment sites; e.g. Seabloom *et al.* 2003), microsites (where microsites suitable for germination and subsequent seedling survival are occupied by competitors; e.g. Clark, Macklin & Wood 1998; Nathan & Mueller-Landau 2000) or predators (where seeds and/or seedlings are destroyed by consumers; e.g. Orrock *et al.* 2006). Thus, low seed production and dispersal, competition with understorey species, and seed and seedling predation can impose demographic bottlenecks through which seeds and seedlings must pass before transitioning to later life stages. Determining the extent to which large herbivores modify the relative strengths of demographic bottlenecks is a crucial step in developing a mechanistic understanding of tree establishment in African savannas (Midgley & Bond 2001; Sankaran *et al.* 2004).

Across sub-Saharan Africa, and in concert with or exclusive of herbivory, tree abundance is driven by some combination of fire (e.g. Sankaran, Ratnam & Hanan 2008; Holdo, Holt & Fryxell 2009), above-ground competition with grasses for light (e.g. Scheiter & Higgins 2007; Riginos 2009), and below-ground competition with grasses for soil nutrients and water (e.g. Scheiter & Higgins 2007; Riginos 2009), with tree–grass competition typically most intense for seedlings and small trees. In addition, both modelling (Scheiter & Higgins 2009) and empirical (reviewed in Bond 2008) studies suggest or demonstrate that long-term increases in atmospheric CO_2 should favour trees, triggering shifts in savanna-woodland boundaries. In this contribution, we target the role of herbivory in affecting tree establishment, for several reasons. First, fire in our study system (Laikipia, Kenya) has been largely suppressed for upwards of the past 50 years, as it has in many human-occupied rangelands across the globe (Augustine & McNaughton 2004; Dellasala *et al.* 2004). Secondly, many species of wild herbivores in Laikipia and throughout the globe are declining at unprecedented rates (Prins 2000; Georgiadis *et al.* 2007), and we expect such declines to be manifested in tree establishment. Finally, cattle represent the most abundant species of livestock on 'pro-wildlife' ranches, and comprise the highest biomass density of grazers throughout Laikipia (Georgiadis *et al.* 2007). Because wild herbivores are comprised of a diverse assemblage of functional types, including pure grazers (e.g. plains zebra [*Equus burchelli* Gray, 1824], hartebeest [*Alcelaphus buselaphus* Pallas, 1766]), pure browsers (e.g. giraffe), and mixed feeders (e.g. elephant, eland [*Taurotragus oryx* Pallas, 1766], Grant's gazelle [*Gazella granti* Brooke, 1872]), we expect cattle and wild herbivores to affect tree establishment differentially.

Previous efforts by our research group have documented that (1) wild herbivores, but not cattle, suppress seed production of trees (Goheen *et al.* 2007); (2) cattle, much more than wild herbivores, suppress the abundance of herbaceous plants in the understorey (Young, Palmer & Gadd 2005), which competitively suppress saplings (Riginos & Young 2007); (3) exclusion of all large herbivores is accompanied by compensatory increases in rodent abundance, probably because of competitive release (Keesing 2000) and similar to results from other systems (e.g. Smit *et al.* 2001); and (4) rodents (and not insects or large herbivores) are responsible for the majority of seedling consumption (Goheen *et al.* 2004). Thus, large herbivores have the potential to influence tree establishment through some combination of seed, microsite, and predator limitation, with the latter two arising indirectly through the effects of large herbivores on putative competitors and predators of tree seeds and seedlings.

Using our prior results as a foundation, we investigated how both wild herbivores and cattle altered germination and subsequent sapling survival of the whistling-thorn tree (*Acacia drepanolobium*), a species that forms monodominant stands throughout large areas of East Africa. Between 2004 and 2006, we combined seed addition experiments and exclusions of seed and seedling predators with an ongoing, large-scale manipulation of large herbivores (both wild herbivores

and cattle) to address the following questions: (1) How do wild herbivores and cattle modify seed, microsite and predator limitation by affecting seed production, understorey biomass, and rodent abundance?; and (2) What are the relative roles of seeds, microsites and predators in limiting germination and subsequent establishment of *A. drepanolobium*?

Materials and methods

STUDY SITE AND THE KENYA LONG-TERM EXCLOSURE EXPERIMENT (KLEE)

We monitored the fates of *A. drepanolobium* seeds and seedlings in 2004, 2005 and 2006 in the KLEE (Young *et al.* 1998) at the Mpala Research Centre in central Kenya (0°17′N, 37°52′E, 1800 m a.s.l). Mean annual rainfall at the study site from 1998 to 2007 was 618 ± 56 mm (SE); rainfall was 744 mm in 2003, 854 mm in 2004, 576 mm in 2005 and 645 mm in 2006. Starting in the early 1900s, and especially since the 1970s, pastoral and commercial ranching use of fire has been essentially eliminated, and accidental wildfires have been actively suppressed throughout most of Laikipia (Augustine & McNaughton 2004).

The study site is characterized by deep, clay 'black cotton' soils of volcanic origin. Five to 10 T dry biomass ha^{-1} year^{-1} are produced in these soils (Otieno 2004), with five species of perennial bunchgrasses comprising over 90% of the herbaceous layer (Young *et al.* 1998). *Acacia drepanolobium* comprises a virtual monoculture in the overstorey of KLEE (making up more than 97% of the woody vegetation), as it does in many East African ecosystems underlain with black cotton soils. KLEE is comprised of three replicated blocks of six 4-ha plots. Each plot is associated with an herbivore treatment, from which a different combination of large mammalian herbivores have been excluded or permitted access since 1995 using a combination of electrified fencing and visual barriers (see Young *et al.* 1998 for further details). In this study, we used the following four treatments:

1 Full fencing to exclude all large (> 15 kg) mammalian herbivores.
2 Full fencing to exclude wild, large mammalian herbivores, but cattle are grazed six to eight times per year at stocking rates approximating the surrounding ranch (Young *et al.* 2005).
3 No fencing; wild herbivores have access but cattle are not allowed to graze.
4 No fencing; wild herbivores have access and cattle are grazed.

Wild herbivores common in KLEE include elephant, giraffe, eland, Grant's gazelle, hartebeest, plains zebra and oryx (*Oryx gazella* Linnaeus, 1758).

SEED COLLECTION OF *A. DREPANOLOBIUM*

Within KLEE in 2004–2006, *A. drepanolobium* flowered in February and March and produced fruits in May. Seeds mature for *c.* 2 months, after which time fruits dehisce and dry seeds dangle from thread-like arils attached to the inner walls of pods. Within an individual tree, fruits produced in a single season typically dehisce within 3–4 days in relative synchrony. Seeds then are dispersed passively on windy days (Goheen *et al.* 2007), after which they germinate following rain (Okello 2008). Consumption and subsequent dispersal of viable *A. drepanolobium* seeds by large herbivores is negligible (Goheen *et al.*

2007; Okello 2008; K. E. Veblen, unpublished data). *Acacia drepanolobium* apparently does not have a seed bank (Okello & Young 2000).

Within each of the 12 monitored KLEE plots, we harvested dehisced pods from eight randomly pre-selected individuals of *A. drepanolobium* (Goheen *et al.* 2007), subject to the constraint that different individuals were selected in subsequent years. Heights of focal trees ranged from 1·7 to 4·4 m across years and did not differ significantly among plots ($P \geq 0.31$ for all years). Seed traps traditionally used to estimate seed rain are not feasible at KLEE because elephants destroy them and they are not easily replaced. Seeds were instead collected from dehisced pods, sun-dried for 7–10 days, counted, weighed, and assessed for damage by bruchid beetles (*Bruchus* spp.). Individual seeds weighed 0·060 ± 0·003 g (SE). Bruchids infest and bore holes in seeds upon emergence and can reduce greenhouse germination rates from nearly 80% to 10% (Okello & Young 2000; see also Miller 1994). Thus, we excluded seeds with exit holes and used only seeds without exit holes in our subsequent seed additions. Bruchid infestation ranged between 7% and 36% in different years but did not differ significantly by herbivore treatment ($P > 0.19$ for all years).

ASSESSING GERMINATION AND ESTABLISHMENT OF *A. DREPANOLOBIUM*

We divided seeds collected from each individual tree into four equal groups and scattered by hand each group of seeds into one of four subplots near their source tree (see below). Seed production per reproductive tree ranged from 12 to 1868 (2004), 26 to 6596 (2005) and 9 to 1092 (2006). We did not standardize the number of seeds added to subplots for two reasons. First, we were interested in comparing results from our study against tree establishment in KLEE to better understand the processes underlying natural establishment of *A. drepanolobium* (see 'Assessing establishment of *A. drepanolobium*'). Secondly, both seed and seedling predation may depend on numbers of seeds and seedlings (e.g. Russo 2005; Kauffman & Maron 2006; Paine & Beck 2007; Poulsen *et al.* 2007), and we wanted to account for any density dependence across the natural range of individual variation in seed production by *A. drepanolobium* (Clark *et al.* 2007). In addition, we explored whether density dependence affected germination by regressing numbers of germinants against numbers of seeds in subplots where germination occurred by testing for decreasing slopes (i.e. a significant quadratic term in regressions). If germination were density-dependent, the numbers of germinants should asymptote or decline with increasing numbers of seeds. In no year were quadratic terms statistically significant ($P > 0.43$ in all years). Dehiscent *Acacia* typically germinate on the soil surface without burial (Cavanagh 1980), so we did not attempt to bury seeds. We used latex gloves when handling seeds to reduce scent contamination.

Prior to seed addition, the locations of subplots for seed additions were determined by randomly generating azimuths between 1° and 360° and by randomly generating a distance between 0·5 and 3·0 m using 0·5 m increments from the parent tree. We constrained subplots to these distances because recently germinated natural saplings occurred 0·56–3·36 m from adult trees (mean = 1·85 m, see 'Assessing sapling establishment of *A. drepanolobium*'). For each tree, three subplots were assigned to 1 m × 1 m × 0·4 m experimental cages to exclude different combinations of putative seed and seedling predators (hereafter 'cages'): (1) insect + rodent + bird exclusion (cages made of 1 × 1 cm hardware cloth and covered with nylon greenhouse screening, hereafter 'total exclusion cages'); (2) rodent + bird exclusion (same as #1, but not covered with screening, hereafter 'rodent + bird exclusion cages') and (3) bird exclusion (same as #2,

but with 5 cm × 5 cm openings cut in each side of the cage to permit access by rodents, hereafter 'bird exclusion cages'). Cage edges were secured *c*. 15 cm into the ground and cages were stabilized with heavy-duty bailing wire. Cages were quickly repaired if they were kicked or stepped on by large herbivores. The fourth subplot was an uncaged 1 m × 1 m control area delineated by coloured electrical wire. See Fig. S1 (Supporting Information) for a schematic representation of our experimental layout.

Seeds of *A. drepanolobium* and other dehiscent *Acacia* species are dispersed primarily by gravity (Miller & Coe 1993). However, to further ensure that seeds were not blowing into or out of subplots, we used coloured straws to mark every seed produced for two out of eight trees in every plot in 2004. In no case did we observe germination of unmarked seeds, suggesting secondary dispersal of seeds by wind into cages was minimal. Secondary dispersal by animals may result in erroneous conclusions for studies that use seed removal as a proxy for seed predation (Vander Wall, Kuhn & Beck 2005; Moore & Swihart 2008). However, we are unaware of any scatterhoarding species of rodents (the primary agents of seed removal, see Results) at our sites (Kingdon 1974), based on over 50 000 trap nights over 10 years. Further, seed removal by *Saccostomus* rodents (the overwhelmingly dominant genus at this site) can be equated with seed mortality, as members of this genus larderhoard foods > 0·5 m below-ground in burrows excavated in termite mounds (Kingdon 1974; Keesing 2000; Bradley J. Bergstrom, personal communication). Thus, and in light of the fact that recently germinated saplings occurred in close proximity to adult trees, we believe that our methods did not differ significantly from natural dispersal.

Once established, subplots were visited weekly for 6 months to assess seed germination. In 2006, and following the termination of the experiment, we collected soil to a depth of *c*. 30 cm over the 1 × 1 m area associated with each subplot. We sifted this soil and attempted to germinate seeds in a screenhouse to further ensure that remaining seeds were not viable. No seeds germinated from these trials, confirming Okello & Young's (2000) conclusion that *A. drepanolobium* has no seed bank.

Following germination, we marked each seedling with a coloured, uniquely numbered straw to identify them across successive surveys. We monitored seedling survival every week for 24 weeks following germination. All seedlings that survived this 24-week time period had accumulated woody tissue around their basal stems. These individuals ranged in height from 20 to 36 cm. For the purposes of our study, we considered these individuals to be established saplings, because mortality of trees this size due to herbivory, drought, or fire is low (*c*. 7%) compared to seedlings (i.e. small individuals with herbaceous stems; Riginos & Young 2007; Okello *et al.* 2008; Goheen & Riginos, unpublished manuscript).

In March 2006, 7 months after the largest bout of seed production, we conducted a survey for naturally establishing saplings in a single 50 m × 50 m (0·25 ha) square in the centre of each of the 12 KLEE plots. Three observers walked single file along sixteen 50 m transects per square, spaced *c*. 3 m apart. Established saplings were categorized as individuals ≤30 cm with basal diameters ≤5 mm, because these were the approximate upper bounds for *A. drepanolobium* 6–9 months old from a separate seedling transplant experiment (Goheen & Riginos, unpublished manuscript). We used data from these surveys to estimate natural establishment. Excavations of established saplings of similar sizes elsewhere on Mpala and on neighbouring properties confirmed that trees of this size are unlikely to be coppices or resprouts. Prior to this survey, in August 2005, we had recorded the number of trees reproducing in the same 0·25 ha area. We combined these data to estimate the number of recently established sap-

lings per reproductive tree in each plot. In addition, a single germinant from 2004 and seven germinants from 2005 (representing the total number of seeds germinating naturally in control plots in 2004 and 2005) were monitored every 2–3 months through March 2007 in attempt to further inform our conclusions regarding tree establishment.

STATISTICAL ANALYSES

We used a 10-point pin frame to assess understorey biomass of herbaceous plants associated with each subplot. Frames were placed in the middle of each subplot and the number of individual green leaves hitting the pins was counted. This estimate of understorey biomass was used as a predictor for seedling germination in Hierarchical Generalized Linear Models (HGLM) (see Statistical analyses). In subplots where germination occurred, we repeated these methods following the death or establishment of the last seedling in the subplot and used this index as a predictor for tree establishment in proportional hazards models (see Statistical analyses). The same method was used in each year to estimate understorey biomass for all subplots under three randomly selected trees per plot. Understorey biomass never differed significantly between control and caged subplots within a given herbivore treatment (Mann–Whitney *U* tests; $P > 0·10$ in each year).

RODENT SAMPLING

We sampled rodents in each replicate plot of all four herbivore treatments between July 2004 and July 2006. Sampling was conducted in 3–4 plots simultaneously, with no more than 10 days elapsing between sampling bouts in plots. Sampling was conducted every 4–5 months. We live-trapped rodents using baited large Sherman traps for three consecutive nights on each 10 × 10 grid with 10 m spacing between trap stations (100 traps per plot). Northern pouched mice (*Saccostomus mearnsi* Heller, 1910) comprised 85–90% of captures in every sampling bout. Captured individuals of all species were marked with unique fingerling ear tags and released. (See Keesing 2000 for more details on trapping methods.) We used program CAPTURE to estimate abundances of *Saccostomus*. Other species of rodents were captured too infrequently to reliably estimate abundances through mark–recapture techniques.

STATISTICAL ANALYSES

We used mixed-model repeated measures analysis of variance (rmANOVA) to separately analyse the effects of herbivore treatment on seed production, understorey vegetation, and rodent abundance. For each rmANOVA, fixed effects (wild herbivore occurrence and cattle occurrence) were crossed and block was specified as random. All two-way interactions between wild herbivores, cattle, and time were included in each rmANOVA. If dependent variables did not vary as a function of a fixed effect, we pooled data between levels of a fixed effect. We used planned pairwise contrasts to examine differences between herbivore treatments, controlling for time. We used SAS 9.1 for these analyses (SAS Institute Inc 2004).

Seed production, understorey biomass and seed predators (i.e. rodents; see Results) varied consistently by herbivore treatment, and through time (see Results). We used Poisson regression to evaluate how seed predation, seed production and understorey biomass affected germination of *A. drepanolobium* (see also Holdo 2007). We constructed a separate set of regression models for each year and calculated Akaike's Information Criterion for over-dispersed count

data and small samples (QAIC$_c$). Each set comprised models of every possible combination of main effects and two-way interactions, for a total of 18 models per year. In these analyses, subplots were used as sampling units, with the number of germinants per subplot as the response variable. For each year, we tested for over-dispersion from zero-inflation (i.e. an abundance of zeroes resulting in greater variability than expected under a Poisson distribution) in the data by comparing the full (i.e. global) Poisson model to a negative binomial model using likelihood ratio tests (Cameron & Trivedi 1998). In all three years, there was evidence of over-dispersion ($P < 0.001$). We accounted for over-dispersion by rescaling the covariance matrix from every model to its estimated dispersion parameter (McCullagh & Nelder 1999). We used QAIC$_c$ and Akaike weights (w_i) to evaluate support for regression models. The latter of these ranges from 0 to 1 for each model, and represents the relative likelihood that a model is 'best', given the data and a candidate set of models (Burnham & Anderson 2002). We used SAS 9.1 for these analyses.

Because subplots were used as sampling units in the above analyses, the same herbivore treatment and estimate of rodent abundance were assigned to each subplot within the same plot. To address these potential correlations among predictors within plots, we fit HGLMs (Raudenbusch & Bryk 2002) to seedling production in each year. Each HGLM incorporated a Poisson (log link) subplot-level sampling model with an over-dispersion term with a linear, plot-level model. When random effects associated with plots were significant predictors of numbers of germinants per subplot, we treated plots as sampling units. When random effects of plots had negligible effects on numbers of germinants, we treated subplots as sampling units (Raudenbusch & Bryk 2002). In each year, HGLMs were constructed using variables from our lowest-QAIC$_c$ Poisson regression model for that particular year, as HGLMs generate pseudo-likelihoods that are difficult to compare using traditional model selection procedures (Goheen *et al.* 2007). In 2004 and 2005, lowest-QAIC$_c$ models included interaction terms between subplots and seed production, and rodents were responsible for the majority of seed predation. Thus, we stratified HGLMs based on rodent exclusion in 2004 and 2005. We used program HLM for these analyses (Raudenbusch and Bryk 2002). See Appendix S1 (Supporting Information) for further justification of HGLMs.

We used Cox proportional hazards regression (Fox 2001; Jansen, Bongers & Hemerik 2004) to investigate how understorey biomass, type of subplot, number of seedlings per subplot, and weeks to germination influenced the probability of tree establishment from germinated seedlings. Similar to our germination analyses, we first fit models using all combinations of these three subplot-level covariates, then used AIC$_c$ and w_i to select the best model within a given year. We ensured that covariates in the best regression model met assumptions of proportional hazards (Grambsch & Therneau 1994). After identifying the best regression model using only subplot-level covariates, we investigated how occurrence of cattle, occurrence of wild herbivores, and rodent abundance influenced the probability of establishment. However, in no year did any combination of plot-level covariates improve model fit, so these terms subsequently were excluded from the models.

Field experiments must contend with spatial and temporal variability in unmeasured variables that bear on plant establishment, and spatial heterogeneity in tree establishment can be particularly striking for savanna trees (Hochberg, Menault & Gignoux 1994). Thus, we used frailty models (Therneau & Grambsch 2000) to ask whether heterogeneity among subplots and plots modified coefficients from proportional hazards models. In the event that random effects within these sampling units are negligible, associated frailties are dropped

from subsequent models. See Fox *et al.* 2006 for an example of this approach in an ecological context. We used the R statistical package to analyse survival data. See Appendix S1 (Supporting Information) for further justification of frailty models.

Results

Wild herbivores, but not cattle ($P = 0.67$), significantly reduced *A. drepanolobium* seed production in each year of the study ($F_{1,8} = 19.55$, $P < 0.01$; Fig. 1a), with trees producing more viable seeds in 2005 than in 2004 or 2006 ($F_{2,10} = 20.45$, $P < 0.001$; Fig. 1a). Cattle, but not wild herbivores ($P = 0.84$), significantly reduced understorey biomass in each year of the study ($F_{1,10} = 38.24$, $P < 0.001$; Fig. 1b). Understorey biomass was lower in 2006 than
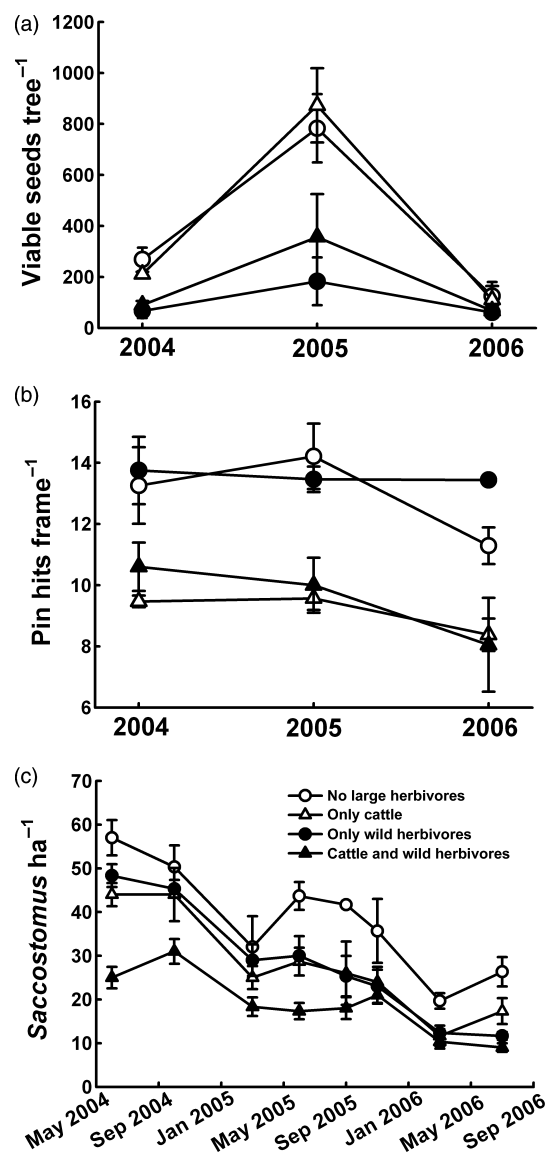

Fig. 1. (a) Production of viable seeds per reproductive tree by herbivore treatment. (b) Understorey vegetation biomass by herbivore treatment. (c) Abundances of *Saccostomus mearnsi* per ha by herbivore treatment. Error bars represent SE.

in 2004 or 2005 ($F_{2,10} = 25.54$, $P < 0.001$; Fig. 1b). Abundances of pouched mice declined from 2004 to 2006 ($F_{7,8} = 191.33$, $P < 0.001$; Fig. 1c) and, in keeping with previous findings, differed among herbivore treatments ($F_{3,8} = 21.56$, $P < 0.01$; Fig. 1c). Consistently, pouched mice were most abundant in plots from which all large herbivores were excluded, intermediate in plots accessible only to cattle or wild herbivores, and lowest in plots accessible both to cattle and wild herbivores (Fig. 1c). See Table S1 (Supporting Information) for estimates and standard errors for pairwise comparisons of differences between treatments and years for rmANOVAs.

Between 2004 and 2006, we recorded fates (germinated vs. not germinated) for 92 484 seeds of *A. drepanolobium*. Across herbivore and subplot treatments, 1·9%, 3·1% and 0·8% of seeds germinated in 2004, 2005 and 2006 respectively (2407 in total). Our values are comparable to germination rates reported by Okello *et al.* (2008) in the field. Across herbivore and subplot treatments, 0·98 ± 0·27 (SE), 5·32 ± 0·04 (SE) and 0·17 ± 0·04 (SE) seeds germinated in each 1 × 1 m subplot in 2004, 2005 and 2006 respectively. Most (94%) germination occurred in August and September of each year, following the first rains after seed production. Reduced germination in 2006 likely was due in part to low rainfall at KLEE, with 74 mm falling in August and September of 2006 compared to 121 and 101 mm in 2004 and 2005 respectively. In no year did germination differ significantly between control and bird cage subplots, and in no year did germination differ significantly between rodent + bird and total cages (all $P > 0.15$). Thus, within each year we pooled data from control subplots and bird exclusion cages, and from rodent + bird and total exclusion cages. In 2004 and 2005, the best regression models for germination included terms for seed production, understorey biomass, rodent
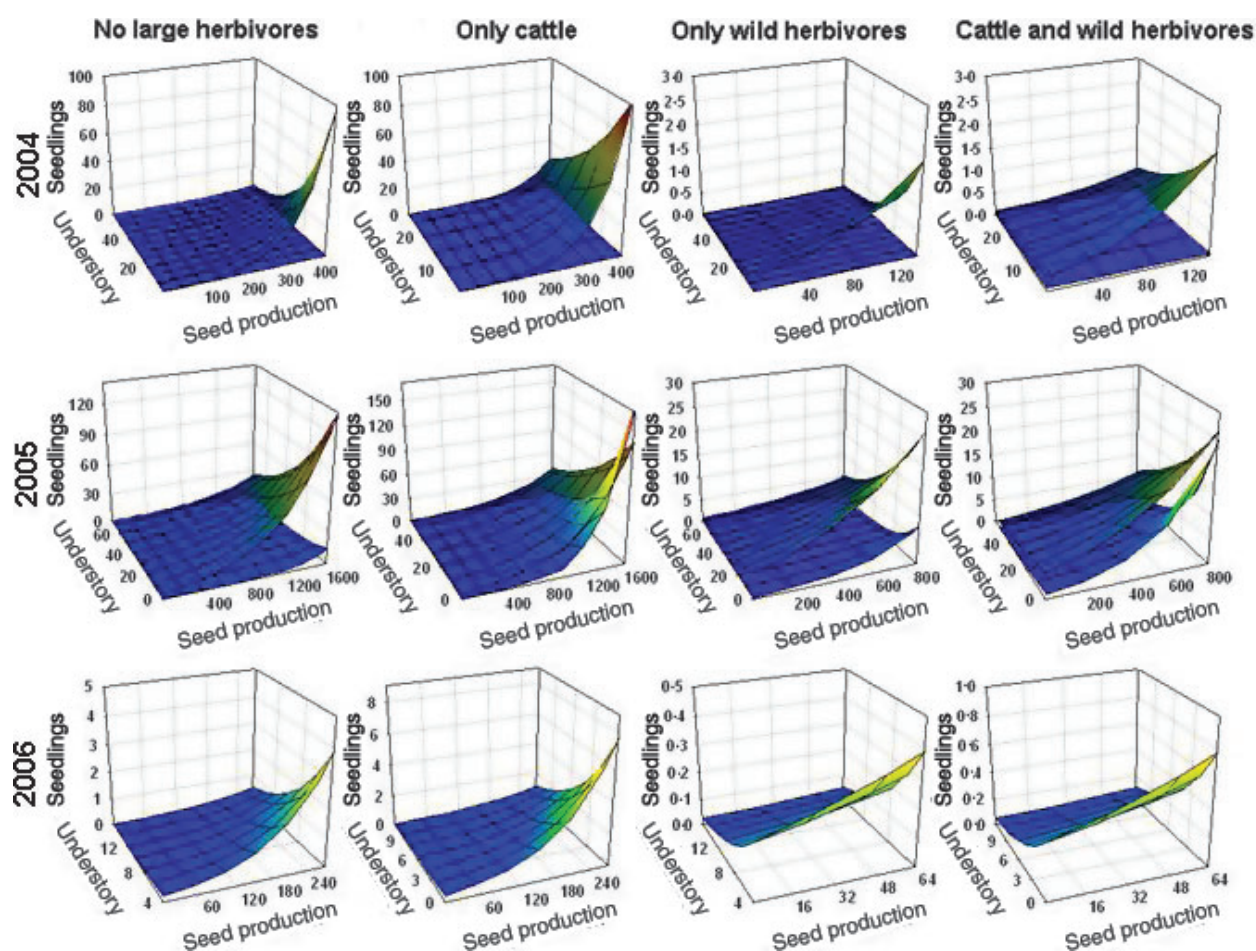

Fig. 2. Hierarchical Generalized Linear Model (HGLM) predictions for numbers of seedlings per subplot (1 × 1 m) by ungulate treatment, 2004–2006. Note differences in axes between ungulate treatments and years, for clarity. Axes for independent variables represent the range for understorey biomass and seed production recorded in each ungulate treatment for each year. Because wild ungulates did not significantly influence understorey biomass, the modelled range in understorey biomass is identical for 'no ungulates' and 'only wild ungulates' treatments. Because cattle did not significantly influence seed production, the modelled range in seed production is identical for 'only cattle' and 'cattle and wild ungulates' treatments. In 2004 and in 2005, two surfaces are modelled in each year representing rodent exclusion and control subplots. In each year × ungulate treatment combination, the surface associated with rodent exclusion subplots always exceeds the surface associated with control subplots. Only a single surface is plotted in 2006 because germination did not differ significantly between rodent exclusion and control subplots.

exclusion, and a rodent exclusion × seed production interaction. In 2006, the best model included only a term for seed production, although uncertainty existed between this model and the model including only a term for understorey biomass ($w_i = 0.30$ for both models). See Table S2 (Supporting Information) for $QAIC_c$ and w_i for Poisson regression models.

Generally, our HGLMs were congruent with model selection using only subplot-level predictors (i.e. not herbivore treatments themselves). The number of seeds germinating was lower in subplots with greater understorey biomass in all 3 years (Fig. 2) and was related positively to seed production in 2005 and 2006 irrespective of rodent exclusion (Fig. 2). In 2004, when *Saccostomus* were most abundant, seed production affected germination in rodent exclusion but not in control subplots. In addition, HGLMs revealed a negative relationship between *Saccostomus* abundance and germination in 2004 and 2005, as the intercepts (γ_{01}s) of the relationships between germination and understorey biomass and seed production declined with increasing *Saccostomus* abundance in control subplots (Table S3, Supporting Information). After controlling for variation in understorey biomass and seed production among herbivore treatments, rodents were predicted to reduce germination from 54% (in 2005 in plots accessible to all large herbivores) up to nearly 100% (in 2004 in plots excluding all large herbivores), based on estimated coefficients in HGLMs (Fig. 2; Table S3, Supporting Information). Thus, large herbivores influenced germination mostly via indirect pathways and seed production, as neither the occurrence of cattle nor wild herbivores was a significant predictor of germination after accounting for *Saccostomus* abundance, understorey biomass and seed production (Fig. 2).

Patterns of seedling survival and subsequent tree establishment were similar to germination patterns. In no year did seedling survival and establishment of saplings differ significantly between control and bird cage subplots, and in no year did seedling survival and establishment of saplings differ between rodent + bird and total cages (z-tests, $P > 0.54$). Thus, we considered only whether seedlings were exposed to rodents, similar to our germination analyses. In 2004, our best proportional hazards model included terms for rodent exclusion and understorey biomass (Table 1). There was no evidence that rodent exclusion increased sapling establishment from germinated seedlings in 2005 or 2006, potentially reflecting lower abundances of *Saccostomus* in these years relative to 2004. In both 2004 and 2005 (but not in 2006), understorey biomass reduced establishment (Table 1). In both 2005 and 2006 (but not in 2004), our best models included a term for the number of weeks to emergence (Table 1). In 2005, early germinating seedlings experienced higher survival; in 2006, however, early germinating seedlings incurred higher mortality (Table 1). Weeks to emergence did not differ by herbivore treatment (Mann–Whitney U tests, $P > 0.26$). In no year was there any evidence of density-dependent recruitment; our best models never included a term for seedling density as a predictor of seedling survival. Thus, large herbivores appear to have influenced sapling establishment from germinated seedlings indirectly – by suppressing rodents in 2004 and by suppressing understorey biomass in 2004 and in 2005. See Table S4 (Supporting Information) for AIC_c and w_i values, and Fig. S2 (Supporting Information) for figures for graphical depictions of Cox regression models.

Incorporating frailty terms to account for heterogeneity in tree establishment within subplots significantly reduced proportional hazards model deviance in 2004 ($\chi^2_2 6 = 92.66$, $P < 0.001$) and in 2005 ($\chi^2_1 16 = 1175.84$, $P < 0.001$), and marginally reduced model deviance in 2006 ($\chi^2_8 = 14.08$, $P = 0.08$). In all 3 years, incorporating frailties for subplots

Table 1. Analysis of deviance for best-fitting Cox proportional hazards models for survival of *A. drepanolobium* seedlings by year

Predictor	Model without subplot frailty					Model with subplot frailty			
	Coef	SE	*P*	Residual deviance	d.f.	Coef	SE	*P*	Residual deviance
2004									
Null model	NA	NA	NA	3002	26	NA	NA	NA	2880
Understorey	0·05	0·01	<0·001	2987	1	0·03	0·01	0·02	2865
Rodent exclusion	−0·75	0·32	0·02	2983	1	−0·98	0·46	0·04	2861
2005									
Null model	NA	NA	NA	25 822	116	NA	NA	NA	24 756
Understorey	0·02	0·003	<0·001	25 775	1	0·04	0·006	<0·001	24 709
Emergence	0·03	0·01	0·02	25 770	1	0·05	0·034	0·18	24 704
2006									
Null model	NA	NA	NA	420	8	NA	NA	NA	398
Emergence	−0·12	0·06	0·04	416	1	−0·16	0·07	0·04	394

Sample sizes: 2004 = 292 dead individuals, 46 recruited saplings; 2005: 1913 dead individuals, 90 recruited saplings; 2006: 62 dead individuals, four recruited saplings. Coefficients are log hazard ratios, representing the log of the change in mortality for a one-unit increase for understorey biomass and emergence, or the log of the change in mortality from excluding rodents. Heterogeneity in survival was significant ($P < 0.001$) among subplots for 2004 and 2005, and heterogeneity in survival time was marginally significant ($P = 0.08$) for 2006. Incorporating Gaussian-distributed frailty terms reduced model deviance in each year. Degrees of freedom listed for null models represent the number of subplots in which germination occurred and represent subplot frailties.

reduced model deviance more than did modelling frailties for plots, and Gaussian frailties resulted in lower model deviance than did gamma-distributed frailties. In general, inclusion of frailty terms in hazard models increased the magnitude of hazard ratios associated with predictor variables, although the number of weeks to emergence was no longer an important predictor of establishment in 2005 after adding a frailty term to the proportional hazards model (Table 1).

Patterns of natural tree establishment in 0·25 ha areas within each herbivore treatment plot generally mirrored those from seeds monitored in our study. When rodents were not excluded, tree establishment from monitored seeds differed by occurrence of cattle, but not wild herbivores. 2005 was the only year in which sapling establishment was sufficiently high in rodent-accessible subplots for statistical analyses; in this year, establishment was higher in plots to which cattle had access (Mann–Whitney U test, $P = 0.04$). In March 2006, surveys of naturally occurring, recently established saplings likewise tended to be more abundant in plots accessible to cattle (1·68 vs. 0·48 saplings established ha^{-1}; Mann–Whitney U test, $P = 0.07$; Fig. 3). Naturally occurring saplings were 21·59 ± 1·47 cm (SE) tall and 3·76 ± 0·94 cm (SE) in diameter. The number of established saplings in subplots from focal trees in 2005 did not differ significantly from the number of naturally occurring, recently established saplings from reproductive trees in 2005 in either cattle exclusion ($P = 0.19$) or cattle accessible ($P = 0.52$) plots within KLEE (Fig. 3). Further, 100% of the eight seeds that germinated in control subplots between 2004 and 2005 survived through March 2007, at which point they were 35·11 ± 3·58 cm tall and 6·11 ± 0·72 cm in diameter. Trees of this size closely match those of established saplings from other studies (Riginos & Young 2007; Okello 2008; Okello *et al.* 2008). Taken together, our results suggest that our study and analyses accounted for the important drivers of tree establishment in this system.
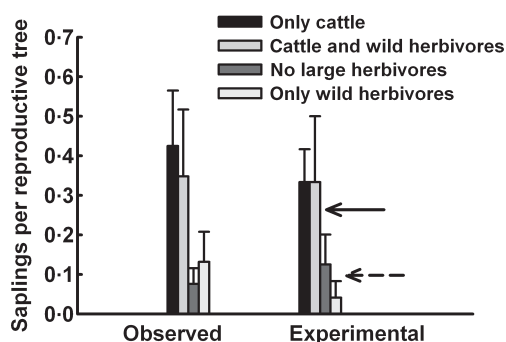

Fig. 3. Numbers of recently established saplings naturally occurring in Kenya long-term exclosure experiment (KLEE) ('observed') and from seeds exposed to rodents that were monitored in our study ('experimental') for 2005. Arrows represent predicted values from multiplying the predicted number of germinants (from HGLMs) with the probability of recruitment (from frailty models) depicted in Table 1. The solid arrow depicts the predicted number of saplings in the presence of cattle. The dashed arrow depicts the predicted number of saplings in the absence of cattle.

Discussion

Seed, microsite and predator limitation often interact strongly to determine patterns of plant establishment (Clark *et al.* 2007). In our system, the magnitude of each source of limitation was modified by interannual variation in rodent abundance, seed production, and understorey vegetation, as well as the compositions of the different herbivore communities in which our experiments were embedded (Fig. 4; see also Asquith, Wright & Clauss 1997). Predator (rodent) limitation on tree establishment was intensified where all large herbivores had been excluded, particularly in 2004 when pouched mice were sufficiently abundant to limit both germination and seedling survival by consuming tree seeds and seedlings. Because wild herbivores and cattle suppressed abundances of pouched mice, predator limitation was relatively weak in plots accessible to all large herbivores, as well as in 2006 when abundances of pouched mice were low across herbivore treatments. Microsite limitation was diminished in the presence of cattle: cattle reduced understorey vegetation, thereby increasing rates of germination in all 3 years and decelerating seedling mortality in 2004 and 2005. Presumably, understorey plants both physically impeded the arrival of seeds at suitable microsites and competed with recent germinants for light, water or nutrients. Germination always increased proportionately with seed production, except when seeds were exposed to rodents in 2004. While seedlings of many species increase when seeds are added (Turnbull, Crawley & Rees 2000), our results are novel in highlighting the fact that the strength of seed limitation varies for a species exposed to demographic filters that change across space and through time (see also Clark *et al.* 2007).

Following a seedling transplant experiment conducted previously in this system (Goheen *et al.* 2004), we concluded that large herbivores accelerated tree establishment largely by suppressing rodents. The results of the current study are qualitatively similar to this conclusion, and add two key findings to our previous results. First, large herbivores (both wild herbivores and cattle) are likely to enhance tree establishment when annual abundances of seed and seedling predators (in our system, rodents) are high, as they were in 2002 (Goheen *et al.* 2004) and 2004. When rodents are rare (e.g. in 2006), predator limitation of tree establishment is minimal (see also DeMattia, Curran & Rathcke 2004), and large herbivores influence establishment via their effects on understorey biomass and seed production. Secondly, our study highlights the interaction among a suite of largely independent factors (seed production, understorey biomass, rodents) in collectively driving tree establishment, with all three being independently impacted by large herbivores (Fig. 4).

Fire is a critical determinant of tree abundances in many African savannas (Scholes & Archer 1997; Sankaran *et al.* 2005), although it has been suppressed since the 1960s in Laikipia. *Acacia drepanolobium* seems to be adapted to fire (*sensu* Higgins, Bond & Trollope 2000). Okello *et al.* (2008) demonstrated low mortality of *A. drepanolobium* saplings following fire over both short-term (9-month) and long-term (8-
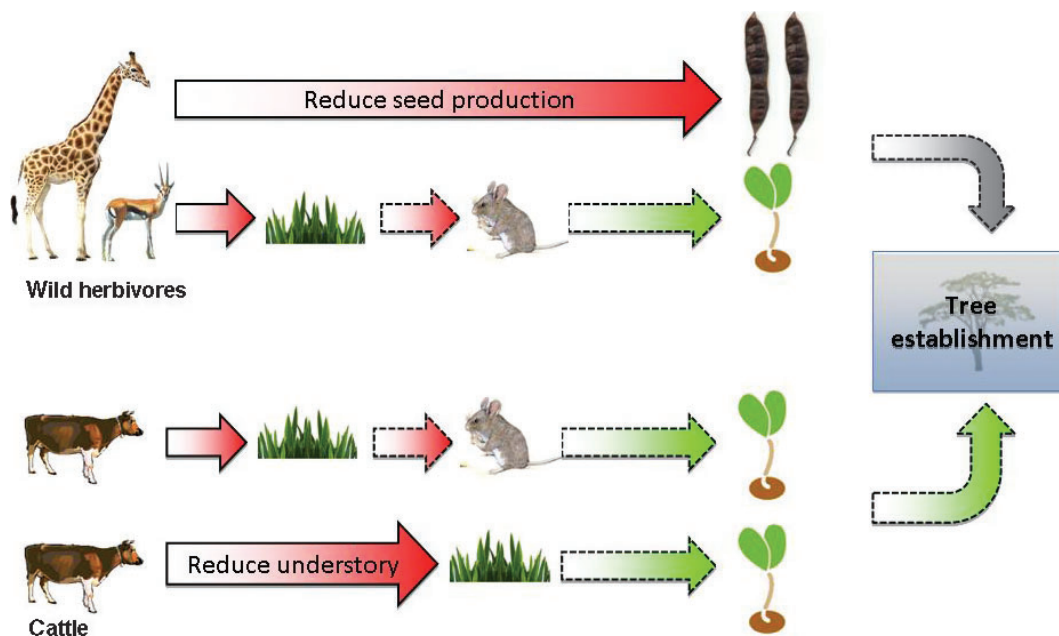
Fig. 4. Schematic showing direct (solid line arrows) and indirect (dashed line arrows) effects (positive effects, green arrows; negative effects, red arrows; neutral effects, gray arrows) of wild vs. domestic herbivores on tree establishment.

year) periods, with virtually all fire-damaged saplings coppicing readily in the months immediately following a controlled burn. Thus, while fire was not studied as a determinant of tree recruitment in our investigation, we suspect that our results and conclusions regarding tree establishment are robust to the occurrence of at least occasional fire.

In African savannas, tree establishment often is envisaged as episodic, with narrow windows of recruitment occurring in years of high rainfall (Scholes & Archer 1997; Sankaran *et al.* 2004; and references therein). While the spatial extent of our study precluded water manipulations, it seems unlikely that episodic recruitment of *A. drepanolobium* is mediated entirely by water stress in our system. Rainfall at Mpala exceeded the long-term mean (618 mm) during the 2 years of our study [2004 (854 mm) and 2006 (645 mm)] when tree establishment was lowest. In particular, rainfall in 2004 was the highest recorded in the 11-year time series of rainfall data at Mpala. Also, our experiments demonstrate that sapling establishment can be bolstered significantly by protecting seeds (in 2004 and 2005) and seedlings (in 2004) from rodents. Growth rates (but not survival) of established saplings are negatively correlated with neighbourhood tree density (Riginos & Young 2007); however, we were unable to detect any influence of seed or seedling density on germination and subsequent establishment. Thus, while natural sapling establishment may be pulsed in our system, we show these pulses are modulated by cumulative filters imposed by seed limitation, seed and seedling predation, and competition with understorey vegetation, in addition to rainfall.

Wild herbivores reduced both seed production (which negatively influenced germination) and rodent abundances (which positively influenced germination); these two impacts effectively negated one another. In other African savannas (Prins & Van Der Juegd 1993; Moe *et al.* 2009), wild herbivores (particularly impala [*Aepyceros melampus* Lichtenstein 1812]) directly limit tree establishment by consuming seedlings. Consistent with previous work (Goheen *et al.* 2004), we noted negligible direct consumption of tree seedlings by wild herbivores. This discrepancy between systems may be due to differences in abundances and compositions of wild herbivores between sites, differences in the abilities of trees to compensate following browsing (*A. drepanolobium* compensates relatively quickly following natural and simulated herbivory; Gadd, Young & Palmer 2001), or differences in palatability between tree species (*A. drepanolobium* are unpalatable, relative to other woody species in Laikipia; Goheen and Palmer, unpublished manuscript). Cattle had no effect on seed production but reduced both rodent abundances and understorey biomass and thereby facilitated tree establishment. Thus, the overall net effect of wild herbivores on tree establishment was negligible, while the overall net effect of cattle herbivores was positive. The positive net effect of cattle on tree establishment resulted from two sources: the higher stocking densities of cattle, relative to pure grazers (e.g. plains zebra, buffalo) within the wild herbivore assemblage (Young *et al.* 2005), and the counterbalancing reductions of seed production and seed predators by wild herbivores.

Our study focused on how large herbivores influence tree populations through indirect facilitation of sapling establishment. We do not report on direct impacts of large herbivores on adult trees, but elsewhere these effects have been shown to be context dependent (see Guldemond & Van Aarde 2008 for a recent meta-analysis of elephant impacts on savanna trees).

Within a site, the influence of sapling establishment on tree population growth should depend on the relative sensitivity of tree populations to seed and seedling numbers, and the extent to which large herbivores limit growth and survival of adult trees. Relative to other congeners with which it coexists, adult *A. drepanolobium* are unpalatable, employing ants, spines, and possibly secondary compounds as effective deterrents against browsing herbivores (Goheen & Palmer, unpublished manuscript). Thus, germination, seedling survival, and sapling establishment are likely more important for this species than for other tree species that are less well-protected as adults. We suggest that the primary effects of large herbivores on the population dynamics of *A. drepanolobium* and other similarly unpalatable species are transmitted primarily through indirect facilitation of sapling establishment, rather than through direct effects (e.g. browsing) on adult trees. Given the ubiquity of human disturbances in tropical savannas, testing this hypothesis is an important research priority with significant implications for guiding management decisions within these sensitive areas.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online ver-sion of this article.

Appendix S1. Details and justification for HGLMs.

Fig. S1. Schematic of experimental design.

Fig. S2. Hazard functions for probabilities of tree establishment, 2004–2006.

Table S1. Pairwise comparisons for seed production between herbi-vore treatment × year combinations.

Table S2. Results for selection of Poisson regression models for the number of seedlings germinating using subplot-level predictors, used to formulate hierarchical generalized linear models.

Table S3. Coefficient estimates for hierarchical generalized linear models (HGLM) fit to seedling production in 3 years.

Table S4. Results for selection of Cox proportional hazards models for seedling survival using subplot-level predictors, used to formulate frailty models.

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