Cryptic herbivores mediate the strength and form of ungulate impacts on a long-lived savanna tree

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Abstract. Plant populations are regulated by a diverse array of herbivores that impose demographic filters throughout their life cycle. Few studies, however, simultaneously quantify the impacts of multiple herbivore guilds on the lifetime performance or population growth rate of plants. In African savannas, large ungulates (such as elephants) are widely regarded as important drivers of woody plant population dynamics, while the potential impacts of smaller, more cryptic herbivores (such as rodents) have largely been ignored. We combined a large-scale ungulate exclusion experiment with a five-year manipulation of rodent densities to quantify the impacts of three herbivore guilds (wild ungulates, domestic cattle, and rodents) on all life stages of a widespread savanna tree. We utilized demographic modeling to reveal the overall role of each guild in regulating tree population dynamics, and to elucidate the importance of different demographic hurdles in driving population growth under contrasting consumer communities. We found that wild ungulates dramatically reduced population growth, shifting the population trajectory from increase to decline, but that the mechanisms driving these effects were strongly mediated by rodents. The impact of wild ungulates on population growth was predominantly driven by their negative effect on tree reproduction when rodents were excluded, and on adult tree survival when rodents were present. By limiting seedling survival, rodents also reduced population growth; however, this effect was strongly dampened where wild ungulates were present. We suggest that these complex interactions between disparate consumer guilds can have important consequences for the population demography of long-lived species, and that the effects of a single consumer group are often likely to vary dramatically depending on the larger community in which interactions are embedded.

Key words: Acacia drepanolobium; African savanna; demography; herbivory; Kenya Long-term Exclosure Experiment; lambda; matrix model; Mpala Research Centre, Kenya; rodent; seed predation; tree recruitment; ungulate.

Introduction

When and how herbivores are able to control plant populations are questions of enduring interest in ecology. The assumption that herbivore populations are able to suppress their food plants, at least when the herbivores themselves are not reduced by predators, is at the heart of the original "the world is green" hypothesis (Hairston et al. 1960) and the many extensions and ramifications of food web theory (Paine 1980, Oksanen et al. 1981, Chase et al. 2000). In addition, understanding the contexts under which herbivores are able to reduce plant populations is of key practical importance for the formulation of successful biocontrol strategies

and for the management of human-perturbed communities (Room 1990, McEvoy and Coombs 1999, Post and Pedersen 2008). However, while suppression of growth rates and standing biomass can clearly be achieved by herbivory in some cases (Room 1990, Edkins et al. 2007, Miller et al. 2009), decades of empirical and theoretical work on plant defenses and trophic cascades have shown that it is by no means certain that plants will always, or even often, be appreciably limited by the majority of their herbivores (Murdoch 1966, Chew and Courtney 1991, Hartley and Jones 1997, Stowe et al. 2000).

The mixed evidence for strong herbivore control of their food plants has led to repeated efforts to generalize about when and why herbivore control is sometimes strong and otherwise weak (Crawley 1997, Mcfadyen 1998, McEvoy and Coombs 1999, Davis et al. 2006). Two particularly important strands of argument in this

area involve seed vs. safe site limitation of recruitment, and generalities concerning the importance of adult survival vs. reproductive rates from demographic models. In the first case, considerable evidence suggests that if establishment of seedlings is primarily limited by suitable microsites (safe sites), even high rates of flower or seed predation will have little effect on population dynamics (Andersen 1989, McEvoy and Rudd 1993, Clark et al. 2007). For long-lived species, this general argument is bolstered by the observation that demographic models nearly uniformly show greater sensitivity of population growth to adult survival than to changes in reproduction or recruitment (Heppell et al. 2000, Caswell 2001, Garcia et al. 2008). Together, these results suggest that if long-lived plants are strongly influenced by their enemies, these effects will be driven mostly by changes in adult demographic rates, rather than by reductions in early life stage performance. Nonetheless, if consumers have substantial negative impacts on early life stages, they could potentially overwhelm minor impacts on adult life stages and become important drivers of population growth (Louda and Potvin 1995, Kauffman and Maron 2006).

Unfortunately, there are very few comparative tests of herbivory effects on different life stages or demographic rates that allow a clear test of relative impacts. Most empirical studies target only one species or guild of herbivores, and then often do not distinguish their impacts on different life history stages (Midgley and Bond 2001). In addition, we still have relatively few studies that attempt to estimate the effects of herbivores on population growth or lifetime fitness (e.g., Doak 1992), making it difficult to compare diverse effects of herbivores on, for example, adult growth vs. recruitment of young trees.

African savannas offer unprecedented opportunities to investigate the multiple impacts of diverse consumer guilds on plant demography, by virtue of retaining their complete spectrum of wild mammalian herbivores (from the 5-g pygmy mouse *Mus minutoides* to the 5000-kg African elephant *Loxodonta africana*). Although savanna ecosystems have been intensively studied (Sinclair and Arcese 1995, du Toit et al. 2003), the processes that maintain the tree–grass codominance that typifies these systems remain contentious (van Langevelde et al. 2003, Sankaran et al. 2004). Some studies demonstrate that wild ungulates strongly suppress tree populations (Dublin et al. 1990, Edkins et al. 2007, Fornara and du Toit 2008), whereas others suggest that wild ungulates may have negligible effects on the persistence and overall biomass of tree populations, even with high levels of browsing (Guldemond and van Aarde 2008, Kalwij et al. 2010). Similarly, domestic cattle may have positive (Riginos 2009), negative (Hejcmanova et al. 2009), or negligible (Jeltsch et al. 1997) effects on tree populations.

In stark contrast to the profusion of research on large-ungulate effects, the role of seed and seedling predators (e.g., rodents, birds, insects) in shaping savanna tree populations has been virtually ignored (but see Sharam et al. 2009, Goheen et al. 2010). Even in ecosystems where rodents have been revealed to reduce seed survival and recruitment (Goheen et al. 2010, MacDougall et al. 2010, Norghauer and Newbery 2010), studies rarely consider population-level impacts and fail to incorporate demographic data throughout the plant's life cycle (Kauffman and Maron 2006). To fully understand the role of herbivory in structuring savanna ecosystems, the impact of these unobtrusive consumers on tree demography must be considered alongside their more conspicuous counterparts.

In this study, we directly compare the effects of three principal guilds of herbivores (rodents, wild ungulates, and cattle) on the population growth rate of *Acacia drepanolobium*, a moderately long-lived tree that dominates large areas of East African savanna (Pratt and Gwynne 1977, Angassa 2005). Previous efforts (Goheen et al. 2004, 2010), have revealed that rodents are the primary seed and seedling consumers in this system, with birds and insects having negligible effects on recruitment. Combining a series of herbivore exclosures, we monitored tree populations in eight experimentally controlled consumer communities over five years. In our study system, rodents function solely as seed and seedling consumers, with respect to trees. Wild ungulates, in contrast, have the potential to affect tree demography through diverse pathways, including reducing adult growth and survival (Augustine and McNaughton 2004), reducing reproduction (Goheen et al. 2007), and facilitating recruitment (Goheen et al. 2010). Cattle may facilitate tree recruitment (Riginos 2009), but do not browse on adult trees (Odadi et al. 2007). In addition to comparing the relative importance of these herbivore guilds, we also dissect the effects of wild ungulates on four different demographic processes, and examine the potential for interactive effects on the importance of adult vs. juvenile limitations on population growth rates of trees.

METHODS

Study system

We conducted our fieldwork between 2004 and 2009 at the Mpala Research Centre in the Laikipia District of central Kenya (0°17′ N, 37°52′ E, 1800 m a.s.l.). In this region, rain falls in a weakly trimodal pattern, with peaks in April, August, and November. Annual rainfall for the area from 1999 to 2009 was 594 ± 53 mm (mean ± SE). Fires have been actively suppressed in the region since the early 1900s. Additionally, the long-lived tree *A. drepanolobium* is fire tolerant, surviving and coppicing readily following fire (Okello and Young 2000), which suggests that fire is currently of minor importance in regulating tree cover in this system, and may always have been so.

We conducted our study within the Kenya Long-term Exclosure Experiment (KLEE). KLEE was established

in 1995 and is underlain by deep, clayey "black cotton" soils of volcanic origin. *Acacia drepanolobium* has a density of 240–2784 trees/ha in this area and constitutes >95% of the overstory cover (Riginos and Grace 2008). KLEE follows a randomized block design, with three replicate blocks containing a series of 4-ha plots in which combinations of wild ungulates and cattle are permitted access or are selectively excluded using electric fencing and herd management (Young et al. 1998). We targeted the following ungulate treatments, which represent a complete 2 × 2 factorial design of cattle and wild ungulate treatments:

1) full fencing to exclude all large (>15 kg) ungulates;
2) full fencing to exclude wild ungulates, but with cattle grazed 6–8 times per year at intensities approximating the surrounding region (Young et al. 2005);
3) no fencing; wild ungulates have access, but cattle are not allowed to graze;
4) no fencing; wild ungulates have access and cattle are grazed.

KLEE fences exclude the following wild ungulates that browse on *A. drepanolobium*: elephants (*Loxodonta africana*), giraffes (*Giraffa camelopardalis*), elands (*Taurotragus oryx*), and Grant's gazelles (*Gazella granti*). Nonexcluded steinbuck (*Raphicerus campestris*) fall below the 15-kg exclusion limit, and also browse *A. drepanolobium*, but are not abundant. Grazing species excluded by the fences include cape buffalo (*Syncerus caffer*), plains zebra (*Equus quagga*), Grevy's zebra (*Equus grevyi*), and hartebeest (*Alcelaphus buselaphus*). The cattle herds comprise a single domesticated species, zebu cattle (*Bos indicus*). The wild ungulate guild therefore includes both grazers and browsers, whereas the cattle guild includes only a single species of grazer. The dominant rodent in this system is the northern pouched mouse (*Saccostomus mearnsi*), which constitutes 85–90% of captures (Keesing 2000). The diet of the northern pouched mouse mainly consists of fresh, green grasses and forbs and also seeds and seedlings from a variety of plant species including *Acacia* trees (Metz and Keesing 2001). Rodent densities are consistently highest in exclusion plots (treatment 1), intermediate where either wild ungulates or cattle occur (treatments 2 and 3), and least abundant in control plots (treatment 4) (Keesing 2000).

Data collection

In May and June 2004, we tagged 1389 randomly selected *A. drepanolobium* trees and monitored their annual growth, reproduction, and survival over the subsequent five years. These trees were distributed approximately equally among the four herbivore treatments and across the three replicate blocks. For each tree in each year, we recorded mortality, noted whether individuals were reproductive (had produced seed pods), and measured height to the nearest 5 cm.

Additionally, we quantified seed production and seedling survival rates in the presence and absence of rodents around eight focal, reproductive trees in each plot in each year, with the exception of 2007 (when all 1389 trees failed to reproduce) and 2008 (when prolonged drought prevented germination). Flowering in this species is episodic and shows high interannual variation; the precise mechanisms that trigger flowering in *A. drepanolobium* are elusive, but similar interannual variation is common in this genus (Baldock 2007). All seeds produced by these focal trees were collected by hand just prior to dispersal. Seed pods within an individual tree typically mature and dehisce in relative synchrony over a period of 3–4 days, allowing simultaneous collection before seeds detach (Goheen et al. 2007). Seed production was quantified for each tree, after which seeds not damaged by bruchid beetles (64–93%) were sown in the field in close proximity (0.5–3.0 m) to their parent tree. We believe that these methods did not differ significantly from natural dispersal, because *A. drepanolobium* seeds are dispersed by gravity on windy days, and because all recently germinated seedlings noted over the course of this study occurred within 3 m of parent trees.

At each tree, sown seeds were divided equally among four exclusion treatment subplots to assess the role of potential seed predators in limiting recruitment; i.e., each adult tree had four associated subplots, one per seed predator exclusion treatment (for detailed results from this recruitment experiment, see Goheen et al. 2010). Subplots were 1 × 1 m in size and we determined their locations by randomly generating azimuths between 1° and 360° and by randomly generating a distance between 0.5 and 3 m from the parent tree, using 0.5-m increments. The four experimental treatments were:

1) 1 × 1 × 0.4 m cages made from 1 × 1 cm hardware cloth, completely covered with nylon greenhouse screening. These "total exclusion" cages prevented access by rodents, birds, and insects.
2) 1 × 1 × 0.4 m hardware cloth cages (same as treatment 1), but missing greenhouse screening. These cages prevented access by rodents and birds, but allowed insect access.
3) 1 × 1 × 0.4 m hardware cloth cages (same as treatment 2), but with 5 × 5 cm openings cut in each side of the cage. These cages prevented access by birds, but allowed access by rodents and insects.
4) Uncaged control allowing access by insects, rodents, and birds, delineated by colored electrical wire.

Subplots were checked weekly to assess germination and subsequent seedling survival. For the purposes of this study, seeds that failed to germinate and seeds that germinated but failed to survive to the following annual census were both considered as mortality events. We considered this appropriate because previous experiments have demonstrated that *A. drepanolobium* seeds

that do not germinate during their first year are not viable and will not germinate or recruit to the population in subsequent years (Goheen et al. 2010). We therefore calculated seedling mortality for each tree by subtracting the number of surviving seedlings from the total number of viable seeds produced by the tree. Neither germination nor subsequent survival differed with access by birds or insects (i.e., no significant differences between treatments 1 and 2 or treatments 3 and 4), so seedlings surviving to the following year in each of these treatment pairs were pooled to yield seedling survival for individual trees in the presence and absence of rodents.

Demographic models

We used the five years of demographic data to fit a series of statistical models describing the effects of herbivore treatment and tree size on *A. drepanolobium* vital rate functions (sensu Easterling et al. 2000). We pooled data across replicate plots within each treatment to maximize the information used to parameterize models, and thus better reflect the average demographic patterns and treatment effects across the study region (sensu Horvitz and Schemske 1995, Bruna and Oli 2005). In addition, block effects were weak relative to treatment effects for all demographic rates and had negligible effects on estimates of vital rate model coefficients (e.g., for tree growth, block $F_{2, 6606} = 0.334$, $P = 0.716$), thus making this pooling reasonable. We fit logistic regressions to model three binomial vital rates: adult survival probability, probability of reproduction, and the probability of a seed germinating and surviving as a seedling to the following annual census (modeled as a single rate, hereafter referred to as "seedling survival"; Appendix A). We fit general linear models for three continuous vital rates: mean annual tree growth, variance in annual growth, and the mean number of seeds produced by reproducing trees. A suite of 62–72 candidate models was constructed for each vital rate, consisting of models with the main effects and two-way interactions of year, tree height, presence/absence of wild ungulates, and presence/absence of cattle (Appendix A). In addition, models for seedling survival included presence/absence of rodents as a main effect, and all possible two-way interactions with the previously listed main effects. Tree height and number of seeds produced were log-transformed to meet model assumptions. We used AIC criteria to select the best-supported model for each vital rate, and repeated all subsequent analyses using the top five models for each vital rate to confirm that our results were not qualitatively changed by alternative model selection (see Appendix A for details of model selection and results of analyses using alternative models, and Appendix B for coefficients of our best-supported models for each vital rate).

We then used these best-supported models to construct a stage-structured population matrix (Caswell 2001) for each treatment combination in each year,

giving a total of 40 matrices (two wild ungulate treatments [presence/absence] × two cattle treatments [presence/absence] × two rodent treatments [presence/absence] × five years). Each matrix comprised 67 stage classes, consisting of a seedling class (trees germinating and recruiting to the population during the previous year from seed produced by the parent tree) and 66 post-seedling classes containing trees from 0.5 m to 7 m, increasing by 0.1-m increments. We estimated fecundities (i.e., the first row in each matrix) by multiplying the predicted probability of reproduction with the predicted seed production and predicted seedling survival (using relevant coefficients from the statistical models for each vital rate) for a tree of mean height in each stage class for the given treatment–year combination. All other matrix elements were calculated as the probability of survival multiplied by the probability of growing/shrinking to a given stage class for individuals of mean height in each stage class (using cumulative probability functions described by coefficients taken from the statistical models of annual growth and variance in growth [sensu Easterling et al. 2000]). In addition to estimating a population growth rate (λ) for each annual matrix, we also used Tuljapurkar's approximation (Tuljapurkar 1982, Caswell 2001, Morris and Doak 2002) to calculate the stochastic population growth rate (λ_s) as an overall measure of population growth for each treatment.

To explore which effects of wild ungulates were most important in generating between-treatment differences, we next created a series of matrices that included between zero and four different effects of wild ungulates on *Acacia* demography. We first created matrices that included no rodent effects and that ranged from the complete absence of wild ungulate effects (using vital rate functions from the full exclusion treatment), through inclusion of wild ungulate effects on only one vital rate (i.e., growth, reproduction [combining probability of reproduction with seed production], adult survival, or seedling survival), to effects on each combination of two or of three rates, and ending with all four observed effects. We used λ_s to summarize the expected population growth for all 16 combinations of vital rates affected by wild ungulates. We then conducted a full four-way ANOVA to quantify how much of the variance in λ_s was explained by including each of the four vital rates in the model (i.e., by calculating the sum of squares associated with each variable and interaction term; Appendix C). Finally, we repeated this same procedure including rodent effects on seedling survival in all 16 models. Because cattle had a very small effect on λ_s (see *Results*), none of these models included the effects of cattle on any vital rate and we did not use these methods to further investigate the importance of cattle impacts.

This analysis included the varying effect of wild ungulates on individual trees of different sizes, and thus summarized and partitioned the overall impacts of wild
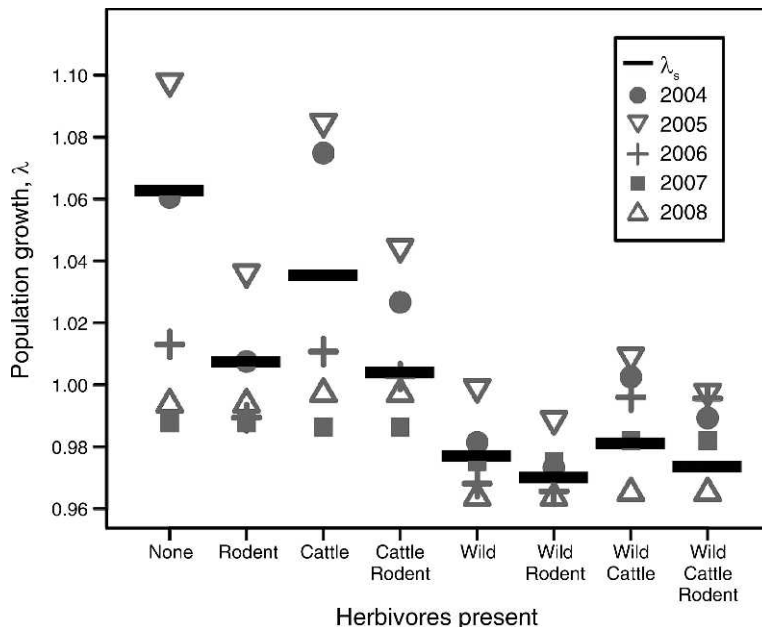
FIG. 1.   Rates of *A. drepanolobium* population growth (λ) for each wild ungulate ("wild"), cattle, and rodent treatment for the years 2004–2008. Gray symbols denote estimates of λ for individual years, and black bars represent overall treatment estimates of stochastic lambda (λ_s). Both wild ungulates (four rightmost columns vs. four leftmost columns) and rodents (every second column) cause clear decreases in λ_s.

ungulates on tree demography. We complemented this analysis with results from a life table response experiment (LTRE; Caswell 2001, Bruna and Oli 2005), which revealed the contribution of each matrix element to the difference in population growth observed between all eight treatments in each of the five years. Contributions are assessed by multiplying the sensitivities of matrix elements (calculated for a matrix midway between the two treatment matrices under comparison) by the difference between associated elements for each of the two matrices in the LTRE, thereby revealing the demographic transitions underlying differences in population growth, Δλ (Caswell 2001, Bruna and Oli 2005; see Appendix D for a full discussion of LTRE procedures). We compared treatment effects using the "mean matrix" for each treatment, where each matrix entry was calculated from the mean vital rate values for that entry over the five transition years.

We additionally calculated the elasticity of lambda to seedling survival for each of these treatment "mean matrices." Elasticities reveal the proportional change in λ generated by a proportional change in a vital rate, and thus reflect the potential for herbivores to influence λ through their effects on a single life stage. Herbivores that reduce vital rates with a high elasticity value have a greater potential to negatively impact λ than herbivores that impact vital rates with a low elasticity. We calculated elasticity values for each treatment matrix by perturbing seedling survival values simultaneously for all height classes. Seedling survival values were first increased by 1%, then decreased by 1%, to center the

calculation around the current vital rate estimates (Morris and Doak 2002). We recalculated λ for both of these new matrices, and divided the proportional change in λ by the proportional change in the vital rates (in this case, 0.02) to determine the elasticity values (Morris and Doak 2002). We then calculated the stage-specific reproductive values and stable stage distribution for each treatment "mean matrix" to reveal herbivore-induced changes to predicted tree population structure (Caswell 2001).

All analyses were carried out using R version 2.8.1 (R Development Core Team 2010) and the add-on packages "popbio" (Stubben and Milligan 2007) and "akima" (Akima et al. 2009).

RESULTS

Our models revealed substantial variation in λ_s across treatments (0.97–1.06). This variation was largely driven by dramatic reductions in λ_s in the presence of wild ungulates and rodents (Fig. 1). In the absence of all herbivores, λ_s was high (1.06), projecting substantial population increase. In the presence of all three herbivore guilds, λ_s was reduced to 0.97, indicating population decline. By themselves, rodents reduced λ_s from 1.06 to 1.01, and wild ungulates alone reduced λ_s to 0.98. In contrast to wild ungulates and rodents, cattle had negligible, inconsistent effects on λ_s (Fig. 1, Appendix A: Table A2). By themselves, cattle reduced λ_s to 1.04, but had a positive effect when wild ungulates were present. These negative effects of cattle in the absence of wild ungulates depended on model selection
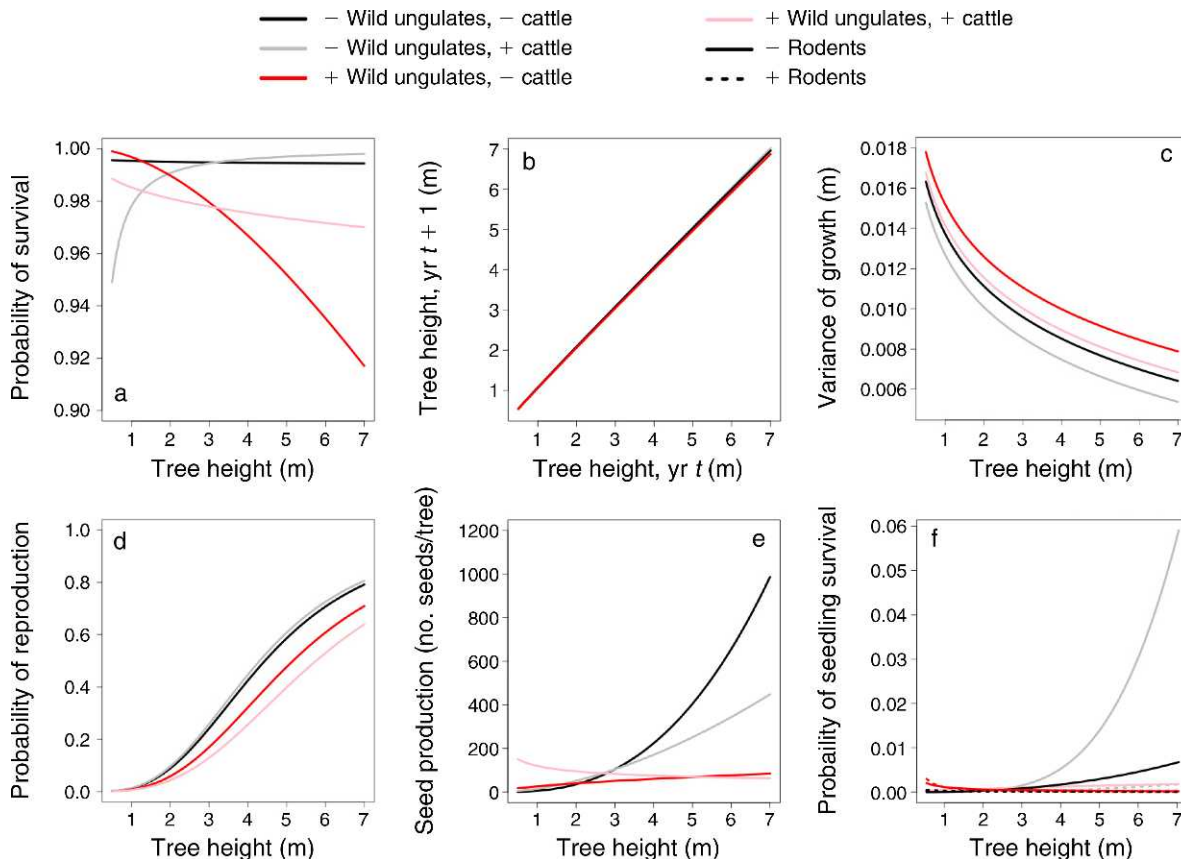
FIG. 2. Vital rate functions estimated from general linear models with parameters averaged over all five years: (a) probability of survival; (b) annual growth; (c) variance in growth; (d) probability of reproduction; (e) seed production; and (f) seedling survival. In panel (f), models that include the effects of rodents (dashed lines) all have slopes and intercepts fractionally greater than zero, but they are difficult to distinguish due to overlap.

(Appendix A); however, the effects of rodents and wild ungulates were qualitatively unchanged when alternative models were used (Appendix A).

Although the effects of rodents in isolation and wild ungulates in isolation were dramatic, our models predicted sub-additive effects when these two guilds were considered together. In particular, while rodents alone strongly suppressed λ_s, the reduction in λ_s by rodents in combination with wild ungulates was only slightly greater than that of wild ungulates alone. Two factors probably contribute to this sub-additivity. First, wild ungulates reduce rodent densities (Keesing 2000, Goheen et al. 2010), dampening effect of rodents on seedling survival. Second, in the absence of wild ungulates, total per capita seedling production has the potential to be higher (Fig. 2), and seedlings constitute a greater proportion of the population (Fig. 3). Because the negative impact of rodents on tree fecundity is constrained by seed and seedling abundance, rodents have the capacity to induce greater decreases in λ_s in the absence of wild ungulates. This greater potential for rodents to negatively impact tree population growth is

also reflected in the increased elasticity of λ to seedling survival in the absence of wild ungulates (Fig. 3).

In contrast to the highly specific effects of rodents (which only impacted seedling survival), wild ungulates reduced tree population growth through several diverse demographic pathways, suppressing adult survival, adult growth, probability of reproduction, and seed production (Fig. 2). Where rodents were excluded, wild ungulates primarily impacted tree population growth by suppressing reproduction (Fig. 4). However, where rodents could consume seeds and seedlings, wild ungulates primarily impacted tree population growth by killing adult trees (Fig. 4). This result is mostly driven by alterations in the demographic patterns of the trees in the presence of rodents, and not by differences in the per capita effects of ungulates on trees. In particular, rodents reduce the proportion of trees in the seedling class of the stable stage distribution, and, by altering survival rates of seeds and seedlings, lower the reproductive value of adult trees (Appendix E: Fig. E1). These altered demographic parameters combine to reduce the potential of wild ungulates to impact λ through their effects on reproductive parameters.
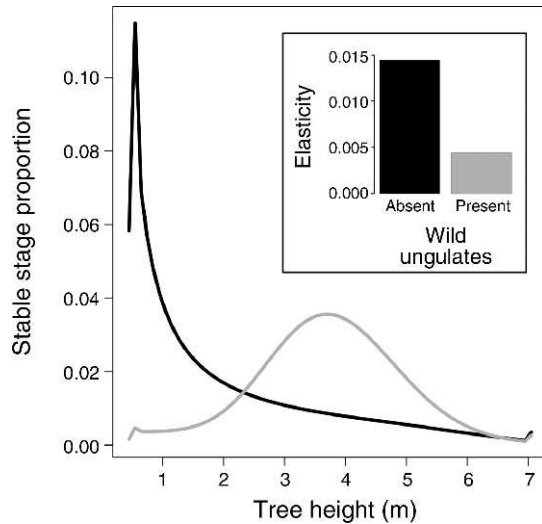
Fig. 3. Stable stage distributions and (inset) elasticity of λ to seedling survival for *A. drepanolobium* populations growing in the presence and absence of wild ungulates. Distributions and elasticities are calculated for a tree population in the absence of rodents and cattle, using mean estimates of vital rates over all five transition years. The black line and bar represent populations growing in the absence of wild ungulates; the gray line and bar represent populations growing in the presence of wild ungulates. Juvenile stages constitute a higher proportion of the population, and the elasticity of λ to sapling recruitment is substantially higher, in the absence of wild ungulates than in their presence. These patterns show why the ability of rodents to negatively impact tree population growth by decreasing seedling survival is increased by the absence of wild ungulates.

Correspondingly, the increased proportion of trees in large stage classes in the presence of rodents magnifies the negative effects of wild ungulates on adult tree survival (Appendix E: Fig. E1).

Results from our LTRE confirm the previous analysis: following exclusion of rodents, reduced fecundities drove the reduction in tree population growth imposed by wild ungulates (Appendix D: Fig. D1). However, in the presence of rodents, decreased adult growth and survival were responsible for the reduction in tree population growth (Appendix D: Fig. D1).

DISCUSSION

Our study reveals that populations of savanna trees can be regulated through alternative demographic pathways, contingent on the full spectrum of herbivores to which trees are exposed. In the presence of rodents, wild ungulates affected tree population growth via adult tree survival; however, in the absence of rodents, wild ungulates principally regulated population growth by suppressing tree reproduction. Similarly, the extent to which rodents served as barriers to tree recruitment depended on the presence of ungulates. Rodents caused substantial decreases to tree population growth in the absence of wild ungulates, and probably play a large role in determining tree population dynamics in areas where

wild ungulates have been extirpated. In the presence of wild ungulates, however, rodents had greatly reduced impacts. The combined effects of rodents and wild ungulates were therefore sub-additive, and tree population growth rate in the presence of wild ungulates and rodents was only fractionally lower than that in the presence of wild ungulates alone. Tree populations will therefore be subject to contrasting demographic pressures as herbivore communities change both spatially and temporally across African savannas, because different herbivore communities will alter the vital rates (e.g., survival, reproduction) that have the scope to strongly influence population growth.

That reproduction and seedling survival strongly influenced population growth in the majority of our manipulations runs contrary to the conventional wisdom on the demography of long-lived species. For such species, adult growth and survival are typically ascribed primacy in driving population growth because of the greater sensitivity of λ to adult vital rates (Heppell et al. 2000, Caswell 2001). However, our results demonstrate that, in natural systems, reductions in vital rates to which λ is insensitive can be large enough to outweigh even reasonably large reductions in vital rates to which λ is highly sensitive, cautioning against overinterpretation of sensitivity analysis results (see also Finkelstein et al. 2010). In particular, our models revealed that the effects of rodents on seedling survival and the isolated effects of wild ungulates on reproduction caused far greater decreases in estimated tree population growth than the isolated effects of wild ungulates on adult survival. This occurred because reproductive output and seedling survival were markedly reduced in the presence of wild ungulates and rodents, but browsing by wild ungulates caused only a minor decrease in adult tree survival.

That browsing imparted a negligible effect on survival is probably attributable to defensive ant symbionts, which render adult *A. drepanolobium* unpalatable relative to its congeners (Goheen and Palmer 2010). If trees face ontogenetic trade-offs in allocations to resistance (sensu Boege and Marquis 2005), pronounced defensive investment by adult trees may increase the potential for alterations in the vital rates of early demographic stages (seeds, seedlings) and other rates with typically low elasticities (reproductive output) to drive most of the variation in population dynamics. Browsing by wild ungulates induces increased production of direct (spines) and indirect (extra-floral nectaries and swollen thorn domatia) defenses, highlighting the ability of *A. drepanolobium* to respond to increased browsing pressure (Young et al. 2003, Huntzinger et al. 2004). Our ongoing research seeks to better quantify anti-herbivore defense trade-offs throughout the tree's life cycle. We hope to better understand how defensive investment strategies may vary spatiotemporally under different local consumer communities, and to further elucidate how interannual variation in abiotic conditions may influence these strategies.
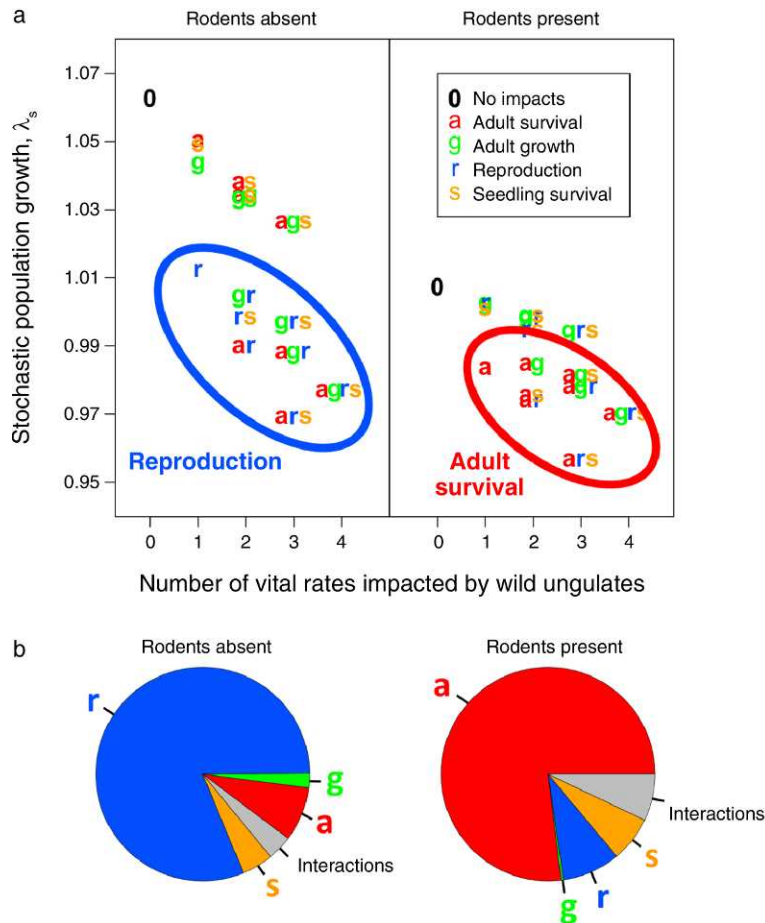
FIG. 4. (a) Stochastic population growth rates (λ_s) estimated for matrix models incorporating different combinations of effects from wild ungulates on vital rates, both in isolation from (left panel) or in the presence of (right panel) rodents. Colored letters denote which vital rate, or combination of vital rates, include the effects of wild ungulates in the matrix model. (b) Proportion of the variance (sum of squares) in λ_s accounted for by including each vital rate in the model. In the absence of rodents, wild ungulates impacted λ_s principally by suppressing reproduction. In the presence of rodents, wild ungulates impacted λ_s principally by reducing adult survival.

Although the negative effect of rodents on seedling survival caused a greater decrease in tree population growth than did wild ungulates through any single vital rate, the combined impact of wild ungulates on multiple vital rates was greater than that due to rodents alone. Indeed, wild ungulates were the only herbivore guild that suppressed λ_s to below replacement level ($\lambda_s < 1$). These findings support the widely held view that declining populations of wild ungulates (especially elephants) can trigger shrub encroachment in savannas (Dublin et al. 1990, Fornara and du Toit 2008). Our results also suggest that rodents can reduce, but not reverse, rates of tree population growth and subsequent encroachment following ungulate declines. These inconspicuous consumers should therefore be carefully considered as biologists work to understand how ecosystems will reorganize in the face of ongoing, global declines in populations of wild ungulates (Ceballos and Ehrlich 2002).

A widespread increase in the abundance of domestic cattle has also been implicated as a cause of tree encroachment (Midgley and Bond 2001, Riginos 2009). It is likely that grazing by cattle reduces the competitive effects of grasses, leading to increased tree population growth (Riginos 2009). We found support for this hypothesis where wild ungulates also occurred, but discovered an unexpected negative effect of cattle on λ_s in the absence of wild ungulates. However, this result is not robust to use of alternative vital rate models, and so may be erroneous (see Appendix A). Under all model scenarios, cattle had minimal influence on tree population growth compared to the resounding effects of wild ungulates and rodents.

The negligible impact of cattle on tree population growth is reflected in current patterns of tree density across our ungulate exclusion plots. In 2011 (i.e., 15 years since the plots were established), plots accessible to cattle had essentially the same density of trees (6% ±

12% higher, mean ± SE) as plots from which they were excluded. In contrast, tree density in plots accessible to wild ungulates was 26% ± 11% lower (mean ± SE) than in wild ungulate exclusion plots (T. P. Young, *unpublished data*). If differences in tree density across treatments were strongly affecting our results, we would expect higher population growth in plots associated with lower tree density (i.e., stronger negative density dependence in plots from which wild ungulates were excluded), but we find the opposite pattern. We are therefore reasonably confident that our conclusions are robust to these differences in tree density.

Rodent abundance also varied predictably across the ungulate treatments, with rodents occurring at higher abundance in the absence of wild ungulates (Keesing 2000, Goheen et al. 2010). Indeed, the heightened impact of rodents on λ_s in the absence of wild ungulates was partially driven by the higher abundance of rodents in ungulate exclusion plots. The design of KLEE precludes orthogonal treatments (where rodent abundances are held constant under varying ungulate treatments), thus limiting our ability to attribute changes in λ_s solely to rodents or to the indirect effects of large ungulates mediated through rodents. However, increases in rodent density following exclusion or extirpation of ungulates have been demonstrated elsewhere (e.g., Smit et al. 2001, Deveny and Fox 2006, Yarnell et al. 2007) and we therefore believe that our experiment generates realistic changes in rodent abundance that typically occur in the absence of native ungulates. As such, our results represent real changes to tree population dynamics that would occur following ungulate extirpations.

A second caveat is that it is logistically impossible to allow insects and birds to access seedling subplots while excluding rodents by themselves. However, our results here show no indication of either bird or insect effects on post-dispersal seed and seedling performance. Also, we previously demonstrated (1) negligible impacts of insects on recruitment in the absence of rodents and birds; and (2) negligible impacts of birds above and beyond those of rodents (Goheen et al. 2010). It is possible that pre-dispersal seed consumption by bruchid beetles has an additional impact on tree population growth not captured by our models. Bruchid attack rates on seeds can be high (7%–36% across the five years of our study), and they therefore have the ability to reduce the quantity of viable seed dispersed by acacias. However, we have found no evidence of differences in bruchid seed predation between our herbivore treatment plots (Goheen et al. 2010), and it is therefore unlikely that they would alter our conclusions relating to the comparative effects of rodents, wild ungulates, and cattle.

To our knowledge, ours is the first "cradle to grave" study of tree population dynamics to simultaneously investigate the role of both large and small herbivores in driving tree demography. Although the capacity of rodents to reduce survival of tree seeds and seedlings has been documented across a range of systems (Weltzin et

al. 1997, Kauffman and Maron 2006, Goheen et al. 2010), our results provide an important advance by demonstrating that rodents can limit overall population growth by serving as demographic filters to recruitment. In African savannas, landscape change is often manifested by altered browsing regimes stemming from the extirpation or overabundance of large mammals, particularly elephants (Dublin et al. 1990, Augustine and McNaughton 2004). Our study suggests that seed and seedling consumers also play a large role in regulating tree populations, and may buffer against or exacerbate fluctuating tree population dynamics following ungulate extirpations or reintroductions. We hope that our study will lead to an enhanced appreciation of the multiple diverse pathways through which plant populations are regulated, and will increase awareness of the critical impacts of inconspicuous consumers on largely cryptic life stages.

LITERATURE CITED

Akima, H., A. Gebhardt, and T. Petzoldt. 2009. Akima: interpolation of irregularly spaced data. R package version 0.5-4. R Foundation for Statistical Computing, Vienna, Austria. ⟨http://CRAN.R-project.org/package=akima⟩

Andersen, A. N. 1989. How important is seed predation to recruitment in stable populations of long-lived perennials? Oecologia 81:310–315.

Angassa, A. 2005. The ecological impact of bush encroachment on the yield of grasses in Borana rangeland ecosystem. African Journal of Ecology 43:14–20.

Augustine, D. J., and S. J. McNaughton. 2004. Regulation of shrub dynamics by native browsing ungulates on East African rangeland. Journal of Applied Ecology 41:45–58.

Baldock, K. C. R. 2007. Multi-species pollination interactions in a Kenyan savannah ecosystem. Dissertation. University of Edinburgh, Edinburgh, Scotland, UK.

Boege, K., and R. J. Marquis. 2005. Facing herbivory as you grow up: the ontogeny of resistance in plants. Trends in Ecology and Evolution 20:441–448.

Bruna, E. M., and M. K. Oli. 2005. Demographic effects of habitat fragmentation on a tropical herb: life-table response experiments. Ecology 86:1816–1824.

Caswell, H. 2001. Matrix population models. Sinauer Associates, Sunderland, Massachusetts, USA.

Ceballos, G., and P. R. Ehrlich. 2002. Mammal population losses and the extinction crisis. Science 296:904–907.

Chase, J. M., M. A. Leibold, A. L. Downing, and J. B. Shurin. 2000. The effects of productivity, herbivory, and plant species turnover in grassland food webs. Ecology 81:2485–2497.

Chew, F. S., and S. P. Courtney. 1991. Plant apparency and evolutionary escape from insect herbivory. American Naturalist 138:729–750.

Clark, C. J., J. R. Poulsen, D. J. Levey, and C. W. Osenberg. 2007. Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. American Naturalist 170:128–142.

Crawley, M. J. 1997. Plant–herbivore dynamics. Pages 401–474 in M. J. Crawley, editor. Plant ecology. Blackwell Science, Oxford, UK.

Davis, A. S., D. A. Landis, V. Nuzzo, B. Blossey, E. Gerber, and H. L. Hinz. 2006. Demographic models inform selection of biocontrol agents for garlic mustard (Alliaria petiolata). Ecological Applications 16:2399–2410.

Deveny, A. J., and L. R. Fox. 2006. Indirect interactions between browsers and seed predators affect the seed bank dynamics of a chaparral shrub. Oecologia 150:69–77.

Doak, D. F. 1992. Lifetime impacts of herbivory for a perennial plant. Ecology 73:2086–2099.

Dublin, H. T., A. R. E. Sinclair, and J. McGlade. 1990. Elephants and fire as causes of multiple stable states in the Serengeti Mara woodlands. Journal of Animal Ecology 59:1147–1164.

du Toit, J., H. C. Biggs, and K. H. Rogers. 2003. The Kruger experience; ecology and management of savanna heterogeneity. Island Press, Chicago, Illinois, USA.

Easterling, M. R., S. P. Ellner, and P. M. Dixon. 2000. Size-specific sensitivity: applying a new structured population model. Ecology 81:694–708.

Edkins, M. T., L. M. Kruger, K. Harris, and J. J. Midgley. 2007. Baobabs and elephants in Kruger National Park: nowhere to hide. East African Journal of Ecology 46:119–125.

Finkelstein, M. E., D. F. Doak, M. Nakagawa, P. R. Sievert, and J. Klavitter. 2010. Assessment of demographic risk factors and management priorities: impacts on juveniles substantially affect population viability of a long-lived seabird. Animal Conservation 13:148–156.

Fornara, D. A., and J. T. du Toit. 2008. Responses of woody saplings exposed to chronic mammalian herbivory in an African savanna. Ecoscience 15:129–135.

Garcia, M. B., F. X. Picó, and J. Ehrlén. 2008. Life span correlates with population dynamics in perennial herbaceous plants. American Journal of Botany 95:258–262.

Goheen, J. R., F. Keesing, B. F. Allan, D. Ogada, and R. S. Ostfeld. 2004. Net effects of large mammals on Acacia seedling survival in an African savanna. Ecology 85:1555–1561.

Goheen, J. R., and T. M. Palmer. 2010. Defensive plant-ants stabilize megaherbivore-driven landscape change in an African savanna. Current Biology 20:1768–1772.

Goheen, J. R., T. M. Palmer, F. Keesing, C. Riginos, and T. P. Young. 2010. Large herbivores facilitate savanna tree establishment via diverse and indirect pathways. Journal of Animal Ecology 79:372–382.

Goheen, J. R., T. P. Young, F. Keesing, and T. M. Palmer. 2007. Consequences of herbivory by native ungulates for the reproduction of a savanna tree. Journal of Ecology 95:129–138.

Guldemond, R., and R. van Aarde. 2008. A meta-analysis of the impact of African elephants on savanna vegetation. Journal of Wildlife Management 72:892–899.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist 94:421–425.

Hartley, S. E., and C. G. Jones. 1997. Plant chemistry and herbivory, or why the world is green. Pages 284–324 in M. J. Crawley, editor. Plant ecology. Blackwell Science, Oxford, UK.

Hejcmanova, P., M. Hejcman, A. A. Camara, and M. Antoninova. 2009. Exclusion of livestock grazing and wood collection in dryland savannah: an effect on long-term vegetation succession. African Journal of Ecology 48:408–417.

Heppell, S. S., H. Caswell, and L. B. Crowder. 2000. Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. Ecology 81:654–665.

Horvitz, C. C., and D. W. Schemske. 1995. Spatiotemporal variation in demographic transitions of a tropical understory herb: projection matrix analysis. Ecological Monographs 65:155–192.

Huntzinger, P. M., R. Karban, T. P. Young, and T. M. Palmer. 2004. Relaxation of induced indirect defenses of acacias following exclusion of mammalian herbivores. Ecology 85:609–614.

Jeltsch, F., S. J. Milton, W. R. J. Dean, and N. Van Rooyen. 1997. Analysing shrub encroachment in the southern Kalahari: a grid-based modeling approach. Journal of Applied Ecology 34:1497–1508.

Kalwij, J. M., W. F. de Boer, L. Mucina, H. H. T. Prins, C. Skarpe, and C. W. Winterbach. 2010. Tree cover and biomass increase in a southern African savanna despite growing elephant population. Ecological Applications 20:222–233.

Kauffman, M. J., and J. L. Maron. 2006. Consumers limit the abundance and dynamics of a perennial shrub with a seed bank. American Naturalist 168:454–470.

Keesing, F. 2000. Cryptic consumers and the ecology of an African savanna. BioScience 50:205–215.

Louda, S. M., and M. A. Potvin. 1995. Effect of inflorescence-feeding insects on the demography and lifetime fitness of a native plant. Ecology 76:229–245.

MacDougall, A. S., A. Duwyn, and N. T. Jones. 2010. Consumer-based limitations drive oak recruitment failure. Ecology 91:2092–2099.

McEvoy, P. B., and E. M. Coombs. 1999. Biological control of plant invaders: regional patterns, field experiments, and structured population models. Ecological Applications 9:387–401.

McEvoy, P. B., and N. T. Rudd. 1993. Effects of vegetation disturbances on insect biological control of tansy ragwort, Senecio jacobaea. Ecological Applications 3:682–698.

McFadyen, R. E. C. 1998. Biological control of weeds. Annual Review of Entomology 43:369–393.

Metz, M. R., and F. Keesing. 2001. Dietary choices of the pouched mouse (Saccostomus mearnsi) in central Kenya. Biotropica 33:182–187.

Midgley, J. J., and W. J. Bond. 2001. A synthesis of the demography of African acacias. Journal of Tropical Ecology 17:871–886.

Miller, T. E. X., S. M. Louda, K. A. Rose, and J. O. Eckberg. 2009. Impacts of insect herbivory on cactus population dynamics: experimental demography across an environmental gradient. Ecological Monographs 79:155–172.

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology. Sinauer Associates, Sunderland, Massachusetts, USA.

Murdoch, W. W. 1966. "Community structure, population control, and competition"—a critique. American Naturalist 100:219–226.

Norghauer, J. M., and D. M. Newbery. 2010. Recruitment limitation after mast-seeding in two African rain forest trees. Ecology 91:2303–2312.

Odadi, W. O., T. P. Young, and J. B. Okeyo-Owuor. 2007. Effects of wildlife on cattle diets in Laikipia rangeland, Kenya. Rangeland Ecology and Management 60:179–185.

Okello, B. D., and T. P. Young. 2000. Effects of fire, bruchid beetles, and soil type on the germination and seedling

establishment of *Acacia drepanolobium*. African Journal of Range and Forest Science 17:46–51.

Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemla. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist 118:240–261.

Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. Journal of Animal Ecology 49:667–685.

Post, E., and C. Pedersen. 2008. Opposing plant community responses to warming with and without herbivores. Proceedings of the National Academy of Sciences USA 105:12353–12358.

Pratt, D. J., and M. D. Gwynne. 1977. Rangeland management and ecology in East Africa. Hodder and Stoughton, London, UK.

R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ⟨http://www.R-project.org⟩

Riginos, C. 2009. Grass competition suppresses savanna tree growth across multiple demographic stages. Ecology 90:335–340.

Riginos, C., and J. B. Grace. 2008. Savanna tree density, herbivores, and the herbaceous community: bottom-up vs. top-down effects. Ecology 89:2228–2238.

Room, P. M. 1990. Ecology of a simple plant–herbivore system: biological control of *Salvinia*. Trends in Ecology and Evolution 5:74–79.

Sankaran, M., J. Ratnam, and N. P. Hanan. 2004. Tree–grass coexistence in savannas revisited—insights from an examination of assumptions and mechanisms invoked in existing models. Ecology Letters 7:480–490.

Sharam, G. J., A. R. E. Sinclair, and R. Turkington. 2009. Serengeti birds maintain forests by inhibiting seed predators. Science 325:51–51.

Sinclair, A. R. E., and P. Arcese. 1995. Serengeti II: Dynamics, management and conservation of an ecosystem. Chicago University Press, Chicago, Illinois, USA.

Smit, R., J. Bokdam, J. den Ouden, H. Olff, H. Schot-Opschoor, and M. Schrijvers. 2001. Effects of introduction and exclusion of large herbivores on small rodent communities. Plant Ecology 155:119–127.

Stowe, K. A., R. J. Marquis, C. G. Hochwender, and E. L. Simms. 2000. The evolutionary ecology of tolerance to consumer damage. Annual Review of Ecology and Systematics 31:565–595.

Stubben, C. J., and B. G. Milligan. 2007. Estimating and analyzing demographic models using the popbio Package in R. Journal of Statistical Software 22:11.

Tuljapurkar, S. D. 1982. Population dynamics in variable environments. III. Evolutionary dynamics of *r*-selection. Theoretical Population Biology 21:141–165.

van Langevelde, F., C. A. D. M. van de Vijver, L. Kumar, J. van de Koppel, N. de Ridder, J. van Andel, A. K. Skidmore, J. W. Hearne, L. Stroosnijder, W. J. Bond, H. H. T. Prins, and M. Rietkerk. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. Ecology 84:337–350.

Weltzin, J. F., S. R. Archer, and R. K. Heitschmidt. 1997. Small-mammal regulation of vegetation structure in a temperate savanna. Ecology 78:751–763.

Yarnell, R. W., D. M. Scott, C. T. Chimimba, and D. J. Metcalfe. 2007. Untangling the roles of fire, grazing and rainfall on small mammal communities in grassland ecosystems. Oecologia 154:387–402.

Young, T. P., B. Okello, D. Kinyua, and T. M. Palmer. 1998. KLEE: a long-term multi-species herbivore exclusion experiment in Laikipia, Kenya. African Journal of Range and Forage Science 14:92–104.

Young, T. P., T. M. Palmer, and M. E. Gadd. 2005. Competition and compensation among cattle, zebras, and elephants in a semi-arid savanna in Laikipia, Kenya. Biological Conservation 122:351–359.

Young, T. P., M. L. Stanton, and C. E. Christian. 2003. Effects of natural and simulated herbivory on spine lengths of *Acacia drepanolobium* in Kenya. Oikos 101:171–179.

APPENDIX A

Model selection for *Acacia drepanolobium* vital rates (*Ecological Archives* E092-137-A1).

APPENDIX B

Coefficients for the best-supported model for each vital rate (*Ecological Archives* E092-137-A2).

APPENDIX C

Calculating the proportion of variance in λ_s associated with including the effects of wild ungulates on each vital rate (*Ecological Archives* E092-137-A3).

APPENDIX D

Life table response experiment (LTRE) details (*Ecological Archives* E092-137-A4).

APPENDIX E

Stable stage distribution and stage-specific reproductive value for tree populations growing in the presence and absence of rodents (*Ecological Archives* E092-137-A5).