INTERACTING EFFECTS OF MULTIPLE HERBIVORE GUILDS ON THE FITNESS AND DEMOGRAPHY OF A SAVANNA TREE

by

JANET ELIZABETH MACLEAN

B.Sc., The University of Aberdeen, 2007

A THESIS SUBMITTED IN THE PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

The Faculty of Graduate Studies

(Zoology)

THE UNIVERSITY OF BRITISH COLUMBIA

(Vancouver)

December 2012

Abstract

Plant populations are limited by a diverse array of herbivores that restrict growth and survival throughout the plant's 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 important drivers of woody plant population dynamics, while the potential impacts of smaller, more cryptic herbivores such as rodents, have largely been ignored. I integrated a five-year manipulation of rodent densities into a large-scale ungulate exclusion experiment to quantify the impacts of three herbivore guilds - wild ungulates, domestic cattle, and rodents - on all life stages of a widespread savanna tree, *Acacia drepanolobium*. I used demographic modeling to determine the overall influence of each guild on tree population dynamics, and to determine the importance of different demographic stages in limiting population growth under contrasting consumer communities. I showed that wild ungulates dramatically reduced population growth (λ_s reduced from 1.06 to 0.98), shifting the population trajectory from increase to decline. The processes that drive these effects, however, 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 (decrease in λ_s from 1.06 to 1.01); however, this effect was strongly dampened where wild ungulates were present (decrease in λ_s from 0.98 to 0.97). I 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.

Preface

I received feedback and editorial assistance from Roy Turkington and Jacob R. Goheen for all three chapters of this thesis.

A version of chapter 2 has been published:

Maclean, J.E., J.R. Goheen, D.F. Doak, T.M. Palmer, and T.P. Young. 2011. Ecology 92:1626-1636.

This work is based on a demographic dataset collected by Jacob R. Goheen from 2004-2009. Abdikadir Ali Hassan and Simon Lima assisted in collecting data for the duration of the project. I assisted in collecting data from a subset of trees in 2009 and I entered and verified the data for 2006-2009. Jacob R. Goheen and Todd M. Palmer determined the sampling protocol for this project, which was conducted within a larger experimental framework (a set of herbivore exclusion plots) established by Truman P. Young. I organized the data and I determined and performed the appropriate statistical analyses, following discussion with Daniel F. Doak. I wrote the manuscript, receiving advice and feedback from Jacob R. Goheen and Daniel F. Doak. The FLORUM discussion group provided helpful comments on a draft manuscript.

My research did not require ethics approval.

Table of Contents

List of Tables

List of Figures

Acknowledgements

1 Introduction

Research concerning the impact of herbivores on their food plants has been a central focus of ecology for decades (Tansley and Adamson 1925; Elton 1927) and has been the subject of extensive debates (Hairston, Smith and Slobodkin 1960; Belsky 1986; Crawley 1987) and reviews (Crawley 1997; Maron and Crone 2006; Turkington 2009). Studies have revealed highly variable results, with clear evidence that herbivores can have negative (Young 1985; Edkins et al. 2007; Miller et al. 2009), negligible (Louda 1983; McNaughton 1986; Stowe et al. 2000), or even positive (Paige 1999; Guidone, Thornber and Field 2010; Olejniczak 2011) impacts on plants. Contemporary research is therefore concerned not so much with *whether* herbivores limit plant populations, but rather with establishing robust generalizations as to the conditions under which such limitation occurs (Maron and Crone 2006; Clark et al. 2007). Important avenues of research include whether herbivore impact is dependent on body size (Crawley 1989), life history stage affected (Midgley and Bond 2001; Davis et al. 2006), timing of tissue damage (Ehrlén 2002; Brody, Price and Waser 2007), and/or local abiotic conditions (Maron and Kauffman 2006; Miller et al. 2009). A plant's lifetime exposure to all herbivores must also be considered to assess the importance of specific interactions to plant fitness and overall success (Caswell 2001; Morris and Doak 2002).

Numerous studies have shown that herbivores can reduce plant survival (Crawley 1997; Edkins et al. 2007; Martin and Meinke 2012), growth (Dharani et al. 2009; Puentes and Agren 2010), seed production (Louda and Potvin 1995; Knight et al. 2009), and seedling/sapling recruitment (Fornara and du Toit 2008; Tanentzap et al. 2009). If a

particular demographic transition is relatively unimportant to plant fitness, however, then

even large reductions in that transition will have little effect at the population level

(Caswell 2001; Ehrlén 2003). For example, Ehrlén (2003) demonstrated that consumption

of a forest understory herb by slugs caused substantial reductions in reproduction and

seedling recruitment, but this had almost no impact on population growth because the

population dynamics were largely driven by adult survival. Other studies have revealed

that the same herbivore impact can have major consequences in some populations but no

effect in others due to context-dependent effects (Horvitz and Schemske 1995; Davis et

al. 2006; Maron et al. 2010). For example, Bonsall et al. (2003) showed that herbivory by

the cinnabar moth (*Tyria jacobaeae*) limits ragwort (*Senecio jacobaea*) population

dynamics in some regions, but has little impact on *Senecio* in other regions. Contextual

differences can be driven by abiotic factors, such as the presence of bare ground (Bonsall

et al. 2003) or light availability (Andrieu et al. 2011). They can also relate to the presence

of other species in the system, such as additional herbivore species, mutualists or

parasites (Ehrlén 2002; Bonsall et al. 2003).

Despite a widespread understanding that the impacts of herbivores on plants need

to be assessed in their life cycle context (Caswell 2001; Maron and Crone 2006), few

studies consider the interacting effects of multiple herbivore species across multiple plant

life stages (but see Ehrlén 2002; Maron and Kauffman 2006). This study seeks to address

this knowledge gap by investigating the contrasting impacts of rodent seed predators and

large ungulates that consume and occasionally kill adult plants. By considering the

effects of these disparate consumers throughout the plant life cycle I am able to

accurately compare and contrast their respective roles in regulating plant population growth.

1.1 Seed Limitation

The degree to which plant populations are limited by seed availability is an issue of prime importance to population ecology, life history theory and community ecology, and can determine the magnitude of herbivore impacts on plant population growth (Eriksson and Ehrlén 1992; Turnbull, Crawley and Rees 2000; Clark et al. 2007). If populations are not seed-limited then they may be limited by the availability of suitable microsites – i.e. locations with appropriate conditions for seed germination and subsequent survival (Eriksson and Ehrlén 1992; Frei, Scheepens and Stocklin 2012). Whilst seed and microsite limitation were formerly seen as dichotomous (Eriksson and Ehrlén 1992; Turnbull, Crawley and Rees 2000), these processes are now viewed as a sliding scale with populations that are primarily seed limited at one end, and populations that are primarily microsite limited at the other (Clark et al. 2007; Duncan et al. 2009). The majority of species are likely limited by a combination of both seeds and microsites, with each being more important than the other at particular locations or points in time (Bonsall et al. 2003; Maron and Crone 2006).

If populations are primarily seed-limited then herbivores that reduce seed production will have a substantial negative impact on the population (Louda 1982; Louda, Potvin and Collinge 1990; Louda and Potvin 1995). Seed predators (that consume post-dispersal seeds) will have a similarly negative impact (Louda, Potvin and Collinge

1990; Maron and Crone 2006; Maron and Kauffman 2006). If populations are primarily limited by microsite availability, however, then seed predators simply consume 'excess' seeds that would never have recruited to the adult population and so have a negligible impact on population growth (Maron and Kauffman 2006; Dybzinski and Tilman 2012). Factors that reduce seed production would also have a negligible impact under this scenario (Louda 1983; Bonsall et al. 2003). The ability of herbivores to reduce plant population growth is thus strongly linked to the relative magnitudes of seed and microsite limitation in the local population (Turnbull, Crawley and Rees 2000; Bonsall et al. 2003). The relative importance of seed predators vs. herbivores that kill or suppress adult life stages is similarly dependent on the strength of seed limitation operating on the population (Maron and Kauffman 2006; Clark et al. 2007).

1.2 Matrix Models and Exclosure Experiments

Matrix population models are popular and convenient tools for assessing the relative importance of multiple impacts on the life history and overall population growth of a study organism (Caswell 2001; Morris and Doak 2002). The asymptotic properties of a correctly parameterized matrix model reveal an organism's long-term population growth rate (λ), which can also be interpreted as a measure of fitness (Louda and Potvin 1995; Caswell 2001; Ehrlén 2002). If the presence of an herbivore reduces λ for a plant population, then this is conclusive evidence that the herbivore has a lasting negative impact and reduces the fitness of the plant. If the herbivore has no impact on λ, however, then we can conclude that it does not reduce overall plant fitness and has no meaningful

impact at the population level, even if it consumes a large volume of foliage, stems or seeds (Louda 1982; Maron and Kauffman 2006). As previously mentioned, this is because certain demographic transitions are more 'important' than others in contributing to population growth (Silvertown et al. 1993; Caswell 2001; Ehrlén 2003).

Because every demographic transition is captured by a specific matrix entry, the sensitivity of λ to changes in that entry reveals the importance of the related demographic transition in determining population growth (Silvertown et al. 1993; Horvitz and Schemske 1995; Caswell 2001). For example, plant populations typically show a far greater sensitivity to adult growth and survival than to seed production and recruitment (Silvertown et al. 1993; Ehrlén 2002). It is therefore often assumed that herbivores impacting adult survival (such as many ungulates) are more important drivers of population growth than are seed predators (Crawley 1990; Silvertown 1993; Caswell 2001). These sensitivities only reveal the theoretical importance of different herbivore guilds, however, based on them causing comparable changes in demographic transitions (Morris and Doak 2002). If, for example, rodent seed predators decimate a seed crop whereas ungulate consumers only cause slight reductions to adult plant growth then rodents may have a greater impact on population growth in that system (Caswell 2001; Morris and Doak 2002). The ultimate contribution of each herbivore guild to limiting plant population growth is therefore a product of both the magnitude of its impact on the relevant demographic transition and the importance of that transition in influencing population growth (i.e. the sensitivity of λ to the related matrix entry) (Morris and Doak 2002; Ehrlén 2003; Bruna and Oli 2005).

A good way to discover the magnitude of herbivore impacts on plant demographic transitions is to use a set of herbivore exclusion plots and measure vital rates in the presence and absence of each herbivore guild (Louda and Potvin 1995; Ehrlén 2003; Maron and Kauffman 2006). A life table response experiment (LTRE) framework can be used to parameterize matrix models using vital rates measured in each experimental plot. This allows us to accurately attribute changes in population growth to different herbivore guilds under their natural densities in the field (Caswell 2001; Ehrlén 2003; Bruna an Oli 2005). Whilst LTREs have widely been used to assess the impact of single herbivore species on plant demography (Ehrlén 2003; Knight et al. 2009; Jacquemyn et al 2012), this framework has rarely been used to compare the role of multiple herbivore guilds in regulating plant population growth. This combination of experimental manipulation and matrix projection models is the most feasible way to understand the lifetime impact of herbivores on long-lived species such as trees (Caswell 2001).

1.3 Conclusion

This study addresses the long-standing question of whether, and to what extent, herbivores limit the growth of their food plants (Turkington 2009). I used established herbivore exclusion plots (Young et al. 1998; Goheen et al. 2010) to compare the relative impacts of rodents and large ungulates on the population growth of a ubiquitous savanna tree, *Acacia drepanolobium*. This experimental framework allowed me to conduct a robust test of the hypothesis that seed predators should impact plant population growth less than herbivores that reduce adult growth and survival. Whilst previous studies have

6

addressed the impacts of a single herbivore throughout the life cycle of its food plant (e.g. Louda 1983; Doak 1992; Ehrlén 2003), very few studies have considered the lifetime impacts of multiple herbivore species (but see Maron and Kauffman 2006). This study not only considers the relative effects of multiple herbivore species on plant population growth, but does so within a manipulative experimental framework. This represents a clear advantage over previous studies, which have compared herbivore impacts in different habitats with different herbivore densities (e.g. Maron and Kauffman 2006), rather than manipulating herbivore densities within the same habitat. In chapter 2 I present my results from this demographic analysis, and in chapter 3 I discuss the broader implications of my findings and suggest avenues of future research.

2   Rodent seed predators mediate the strength and form of ungulate impacts on a long-lived savanna tree

2.1 Introduction

When and how herbivores are able to limit plant populations is a question 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 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 involve seed vs. microsite 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, 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 herbivores, 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 herbivore 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, there are 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 them having a uniquely wide spectrum of wild mammalian herbivores (from the 5 g pygmy mouse [*Mus minutoides*] to the 5,000 kg African elephant [*Loxodonta africana*]). While savanna ecosystems have been intensively studied (Sinclair and Arcese 1995; du Toit et al. 2003), the processes that maintain the tree-grass co-dominance 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; Fornara and du Toit 2008; Edkins et al. 2007), while 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 African savannas.

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 domestic cattle – on the population growth rate of *A. drepanolobium*, a moderately long-lived tree that dominates large areas of East African savanna (Pratt and Gwynne 1977; Angassa 2005). Previous efforts have revealed that rodents are the primary seed and seedling consumers in this system, with birds and insects having negligible effects on recruitment (Goheen et al. 2004; Goheen et al. 2010). 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 demographic 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 to alter the importance of adult vs. juvenile limitations to determine tree population growth rates.

2.2 Methods

2.2.1 Study System

This study was conducted between 2004-2009 at the Mpala Research Centre in the Laikipia District of central Kenya (0° 17' N, 37° 52' E, 1800m ASL). The six years of data collection resulted in five inter-annual transition periods for our demographic

analyses. In this region, rain falls in a weakly trimodal pattern with peaks in April, August and November. Mean annual rainfall for the area from 1999 to 2009 was 594 ± 53mm (SE). Fires have been actively suppressed in the region since the early 1900s. Additionally, *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 limiting 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 'black cotton' soils of volcanic origin that contain a high clay content. *Acacia drepanolobium* density ranges from 240-2784 trees ha^{-1} and constitutes >95% of the overstory cover (Riginos and Grace 2008). KLEE follows a randomized block design in which three replicate blocks contain a series of 4-ha plots in which combinations of wild ungulates and cattle are permitted access or selectively excluded using electric fencing and herd management (Young et al. 1998). We targeted the following ungulate treatments, which represent a complete 2 x 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 grazed by cattle six to eight 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 plots are grazed by cattle.

Wild ungulates that browse on *A. drepanolobium* and that are excluded by KLEE fences include elephants (*Loxodonta africana*), giraffes (*Giraffa camelopardalis*), elands (*Taurotragus oryx*), and Grant's gazelles (*Gazella granti*). Non-excluded 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 whilst 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).

2.2.2 Data Collection

In May and June 2004, 1389 randomly selected *A. drepanolobium* trees were tagged and monitored for 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. Mortality, reproduction (whether the tree had produced seed pods), and height to the nearest 5 cm were recorded for each tree in each year.

Additionally, seed production and seedling survival rates were measured 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 in 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 congeneric species (Baldock 2007; Mduma, Sinclair and Turkington 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 (0.5-3.0m) to their parental tree. We believe that these methods did not differ significantly from natural dispersal, because *A. drepanolobium* seeds are wind dispersed, typically falling close to the parental tree. Indeed, all recently germinated seedlings observed during the study occurred within 3m of parent trees.

At each tree, sown seeds were divided equally among four exclusion treatment sub-plots to assess the role of potential seed predators in limiting recruitment - i.e. each adult tree had four associated sub-plots, one per seed predator exclusion treatment (see Goheen et al. 2010 for detailed results from this recruitment experiment). The four experimental exclusion treatments were:

1) 1m × 1m × 0.4m cages made from 1 × 1cm hardware cloth, completely covered with nylon greenhouse screening. These 'total exclusion' cages prevented access by rodents, birds and insects.

2) 1m × 1m × 0.4m hardware cloth cages (same as treatment #1), but without greenhouse screening. These cages prevented access by rodents and birds, but allowed insect access.

3) 1m × 1m × 0.4m hardware cloth cages (same as treatment #2), but with 5cm × 5cm 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.

Sub-plots were checked weekly to assess germination and subsequent seedling survival. 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 as 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.

2.2.3 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 normalize the data and 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 (with the lowest AIC value) 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] X two cattle treatments [presence/absence] X two rodent treatments [presence/absence] X 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 0.5-7m, increasing by 0.1m 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 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.

The above analysis included the varying effect of wild ungulates on individual trees of different sizes, and thus summarized and partitioned the overall impacts of wild ungulates on tree demography. We complemented this analysis with results from a Life Table Response Experiment (LTRE; Caswell 2001; Bruna and Oli 2005) that 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 ($\Delta\lambda$) (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 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 2008) and the add-on packages 'popbio' (Stubben and Milligen 2007) and 'akima' (Akima et al. 2009).

2.3 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. 2.1). 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. 2.1, 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 (Appendix A); however, the effects of rodents and wild ungulates were qualitatively unchanged when alternative models were used (Appendix A). The models revealed large inter-annual variation in λ, especially in the absence of all herbivore guilds (λ=1.10 in 2005, λ=0.99 in 2007, standard deviation over all years=0.05). This variation was reduced in the presence of herbivores (with all herbivore guilds present: λ=1.00 in 2005, λ=0.97 in 2008, standard deviation over all years=0.01). Despite this variation, the pattern of major herbivore impacts remained constant each year.
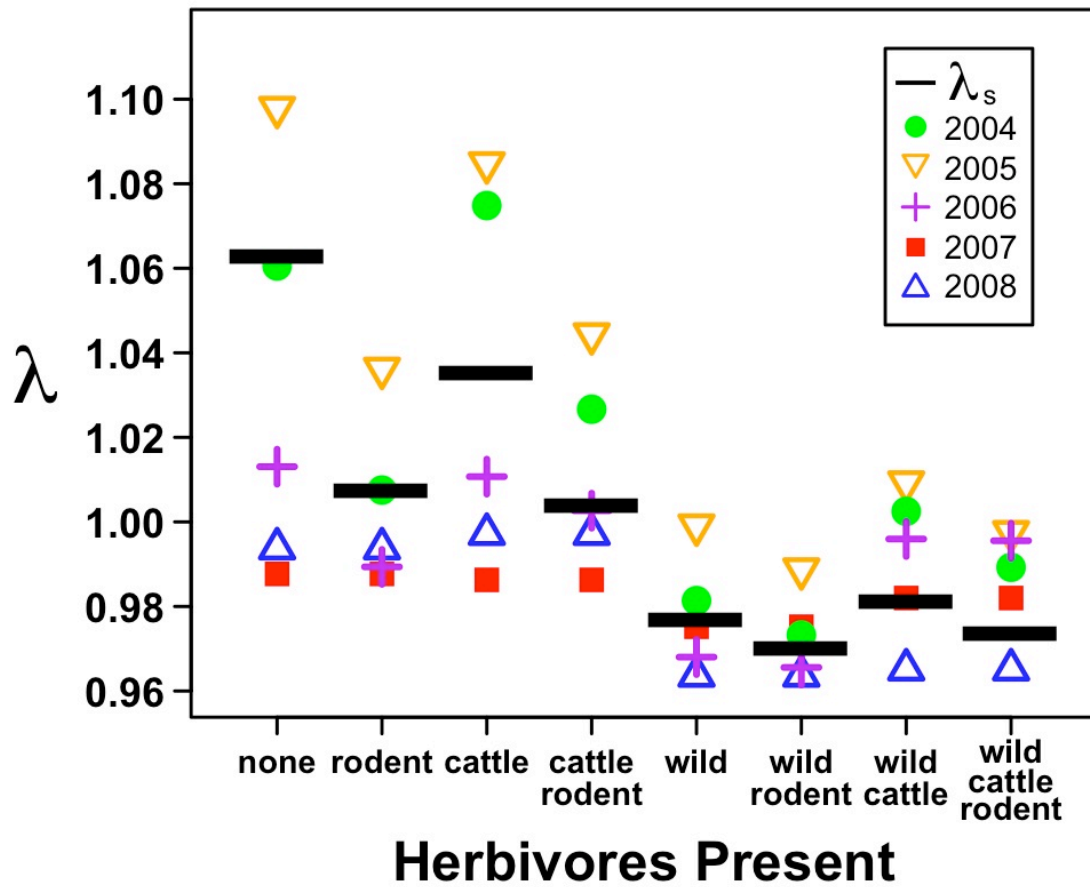
Figure 2.1: Rates of *Acacia drepanolobium* population growth (λ) for each wild ungulate ('wild'), cattle, and rodent treatment. Colored symbols denote estimates of λ for individual years, and black bars represent overall treatment estimates of stochastic lambda (λs). Both wild ungulates (four rightmost columns vs. four leftmost columns) and rodents (every second column) cause clear decreases in λs. (This figure is reproduced from Maclean et al. [2011])

While 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, per capita seedling production has the potential to be higher (Fig. 2.2), and seedlings constitute a greater proportion of the population (Fig. 2.3). As 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. 2.3).
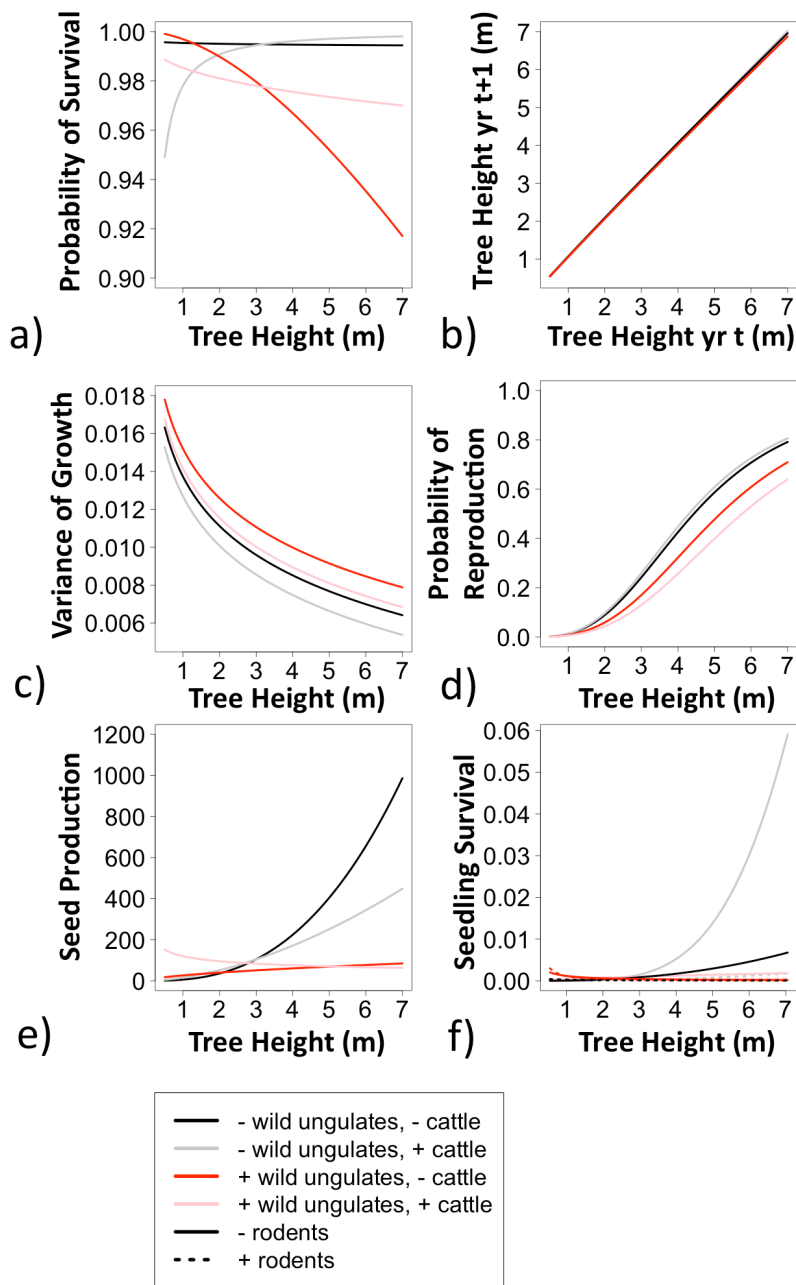
Figure 2.2: Vital rate functions estimated from general linear models with parameters averaged over all five years: a) probability of survival; b) annual growth; c) variance in growth; d) probability of reproduction; e) seed production per tree; f) probability of seedling survival. In figure 2f, models that include the effects of rodents (dashed lines) all have slopes and intercepts fractionally greater than zero, but that are difficult to distinguish due to overlap. (This figure is reproduced from Maclean et al. [2011])
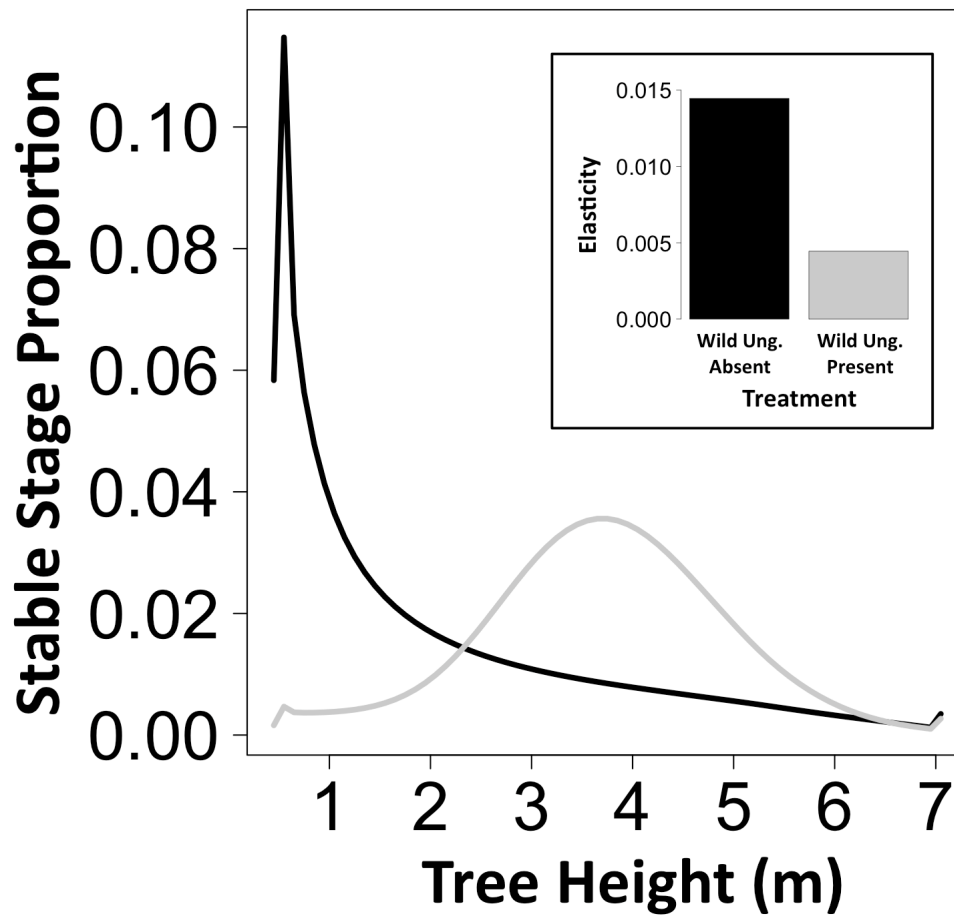
Figure 2.3: Stable stage distributions and elasticity of λ to seedling survival (inset); for *Acacia drepanolobium* populations growing in the presence and absence of wild ungulates. Distributions and elasticities are calculated for a tree population in the absence of rodents and cattle, using mean estimates of vital rates over all five transition years. The black line and bar represent populations growing in the absence of wild ungulates, the grey 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. (This figure is reproduced from Maclean et al. [2011])

In contrast to the highly specific effects of rodents (which only impact 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. 2.2). Where rodents were excluded, wild ungulates primarily impacted tree population growth by suppressing reproduction (Fig. 2.4). However, where rodents could consume seeds and seedlings, wild ungulates primarily impacted tree population growth by killing adult trees (Fig. 2.4). 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. 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).

The 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).
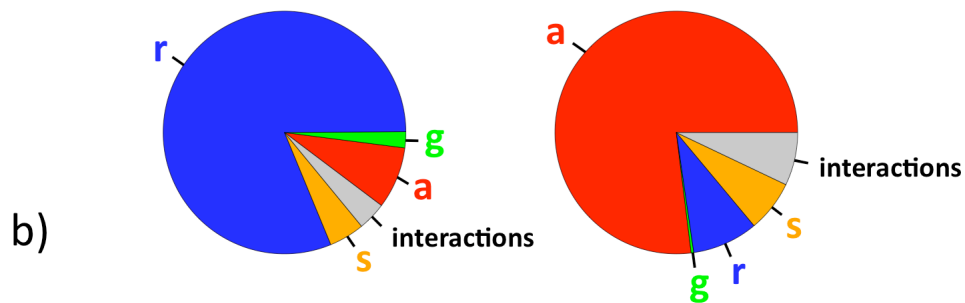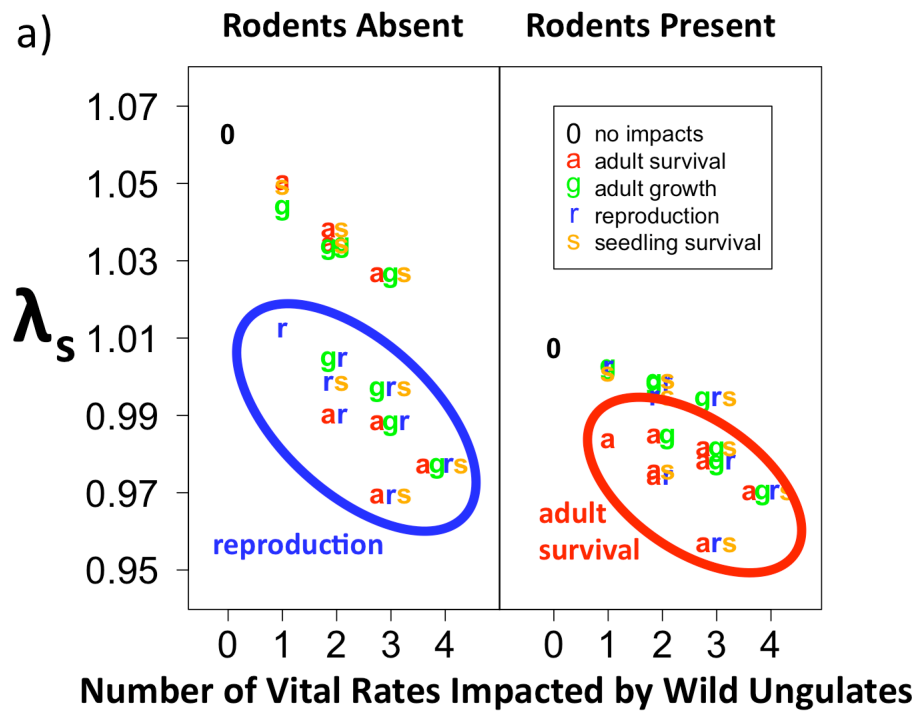
Figure 2.4: a) Stochastic population growth rates (λ_s) estimated for matrix models incorporating different combinations of effects from wild ungulates on vital rates, both in isolation from (left panel) or in the presence of (right panel) rodents. Colored letters denote which vital rate, or combination 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 (left panel), wild ungulates impacted λ_s principally by suppressing reproduction. In the presence of rodents (right panel), wild ungulates impacted λ_s principally by reducing adult survival. (This figure is reproduced from Maclean et al. [2011])

2.4 Discussion

This study reveals that populations of savanna trees can be limited 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 limited 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 which vital rates (e.g. survival, reproduction) strongly influence population growth.

That reproduction and seedling survival strongly influenced population growth in the majority of our manipulations is contrary to conventional wisdom on the demography of long-lived species. For such species, it is typically assumed that adult growth and survival place the strongest limits on population growth because of the greater sensitivity of λ to these 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 over-interpretation of sensitivity analysis results (see also Finkelstein et al. 2009). 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.

Browsing had a negligible effect on adult survival and this is likely attributable to defensive ant symbionts that attack herbivores as they come into contact with the host tree (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).

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% SE higher) as plots from which they were excluded. In contrast, tree density in plots accessible to wild ungulates was 26% ± 11% SE lower 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. Deveny and Fox 2006; Smit et al. 2001; Yarnell et al. 2007) and we therefore believe 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 show no indication of either bird or insect effects on post-dispersal seed and seedling performance. Also, 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

have previously been demonstrated (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, this 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. While 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 limited, and will increase awareness of the critical impacts of inconspicuous consumers on largely cryptic life stages.

3   Conclusions and Future Directions

Herbivore populations around the world are experiencing dramatic changes in the face of increasing anthropogenic impacts (Ceballos and Ehrlich 2002; Beschta and Ripple 2009). Populations of many native species, especially large ungulates, face precipitous declines caused by unsustainable levels of hunting (Sinclair and Arcese 1995; Barrett and Arcese 1998; Hillborn et al. 2006; MacDougall 2008), urbanization (Paudel and Kindlmann 2012), pollution (Rodriguez-Estival, Taggart and Mateo 2011) and climate change (Ogutu and Owen-Smith 2003). Other species show marked increases in certain locations due to the elimination of their natural predators (Beschta and Ripple 2009), or active management for the purpose of tourism (Guldemond and van Aarde 2008). Additionally, numerous domestic herbivores are progressively encroaching into otherwise natural areas (Spear and Chown 2009). These fluctuating herbivore populations may have dramatic impacts on their food plants. For example, altered herbivore densities have been blamed for widespread shrub encroachment or decline in areas across the globe (Bond 2008; Guldemond and van Aarde 2008; Naito and Cairns 2011).

The research reported here has clearly shown that the effect of one herbivore group on plant population regulation is highly dependent on the other herbivore groups present in the local community. This indicates that the impact of fluctuating herbivore populations on shrub encroachment will be highly context-dependent. Interestingly, I discovered that the underlying demographic pathways through which an herbivore limits its food plant can change under different community contexts, in addition to the absolute magnitude of its effect on plant population growth. Thus elephant regulation of the *A.*

drepanolobium population in this study was mediated through adult survival in the presence of rodents, but through reproduction in their absence. I discuss the implications of these findings and potential avenues of future research in the following sections.

3.1 Plant Demography

The overwhelming majority of studies demonstrate that plant populations are more sensitive to changes in adult growth and survival than to changes in reproduction (Silvertown et al. 1993; Ehrlén 2002). Conventional demographic wisdom therefore indicates that the impacts of herbivores on adult growth and survival should play a greater role in regulating plant population growth than impacts on seed production and recruitment (Silvertown et al. 1993; Caswell 2001). My work adds to a small but growing body of research demonstrating that population growth can, however, be driven by seed predators, if their impact is of far greater magnitude than that of consumers of adult plants (Maron and Crone 2006; Maron and Kauffman 2006). Indeed, recent work on life history evolution suggests that species may guard against large variation in demographic transitions to which λ is highly sensitive (Ehrlén 2003). Ontogenetic shifts in anti-herbivore defenses may therefore represent finely tuned evolutionary strategies designed to maximize the long-term fitness of plant populations (Tucker and Avila-Sakar 2010; Boege, Barton and Dirzo 2011).

A key meta-analysis by Pfister (1998) revealed that natural populations show a strong negative correlation between the sensitivity of λ to changes in a particular demographic transition and the inter-annual variability of that transition. This buffers

populations against large fluctuations in population growth between years. Such buffering represents a beneficial life history strategy because long-term population growth depends on the geometric mean of λ for each year, which is negatively correlated with inter-annual variance in λ (Pfister 1998; Ehrlén 2003). In addition to guarding against inter-annual variability, plants should minimize the risk of being eaten during life stages that strongly influence λ (Ehrlén 2003). They can achieve this by investing most resources in defense during key life stages (Tucker and Avila-Sakar 2010; Boege, Barton and Dirzo 2011). If this defensive investment effectively reduces herbivory then this will increase λ each year in addition to reducing the variance in λ between years, both of which benefit long-term population growth and overall fitness (Ehrlén 2003).

Mature *A. drepanolobium* trees display extensive investment in anti-herbivore defenses. These are both direct – growing large thorns, and indirect – supporting aggressive ant mutualists that deter herbivores by attacking them when they damage the host tree (Goheen and Palmer 2010; Stanton and Palmer 2011). This considerable investment in adult defense demonstrates that these trees are effectively adapted to reduce herbivore damage to the life history transitions that have the greatest impact on lifetime fitness (λ). Because ungulate herbivory greatly reduces the probability that a tree will reproduce (Fig. 2.2d), this suggests that the trees also 'choose' to invest their resources in compensatory regrowth rather than in reproduction. This again represents the optimal investment of resources because maintaining growth has a greater positive effect on λ than does increasing reproduction. Altogether, these results suggest that the *A. drepanolobium* population is so well adapted to minimizing the most detrimental herbivore impacts (on adult growth and survival) that it has switched to being limited by

what were initially much less important herbivore impacts (on reproduction). This work therefore supports the growing evidence that the evolution of plant defenses must be considered in the light of impacts throughout the entire plant life cycle (Boege and Marquis 2005; Tucker and Avila-Sakar 2010; Boege, Barton and Dirzo 2011).

Acacia drepanolobium individuals are induced to invest more resources in anti-herbivore defenses following periods of intensive browsing (Young, Stanton and Christian 2003; Huntzinger et al. 2004). Inducible defenses are highly beneficial when populations face variable herbivore pressure. This means that valuable resources are not wasted in anti-herbivore defense until they are needed (Boege, Barton and Dirzo 2011; Karban, Ishizaki and Shiojiri 2012). Savannas are highly variable ecosystems where ungulate and rodent populations all show dramatic fluctuations in space and time (Dublin, Sinclair and McGlade 1990; Keesing 2000; Edkins et al. 2007; Shorrocks 2007). In addition to variable herbivore pressure, plant populations may face changes in the underlying sensitivity of λ to different demographic transitions under different abiotic conditions (Horvitz and Schemske 1995). Altogether, the high variability of factors influencing savanna tree population regulation suggests that possessing inducible defenses should be a highly successful life history strategy. Indeed, *A. drepanolobium* is so successful that it constitutes over 95% of woody vegetation in our study region (Riginos and Grace 2008). However, a variety of additional woody species are now found inside the KLEE exclusion plots following 15 years of herbivore exclusion (T.P. Young, unpublished data). This suggests that ungulate herbivores exert intense pressure on trees in this region and may indicate the importance of inducible ant defenses in allowing *A.*

drepanolobium to persist in this region where other species fail (see also Goheen and Palmer 2010).

3.2 Seed Limitation

The ability of rodents and ungulates to reduce *A. drepanolobium* population growth by reducing seed production and recruitment demonstrates a high degree of seed limitation is operating on the tree population (Clark et al. 2007). This is in keeping with previous work suggesting that most plant populations exhibit some degree of seed limitation (Turnbull, Crawley and Rees 2000). Even in the absence of both herbivore guilds, however, only a small fraction of seeds survived and recruited as saplings the following year. This suggests that the population also faces strong microsite limitation. Savanna ecosystems regularly suffer drought conditions that hinder seedling recruitment and thus we would anticipate this scarcity of suitable microsites in both space and time (Midgley and Bond 2001). Further seed sowing experiments under a range of abiotic conditions and in the presence and absence of seed predators will be needed to fully assess the relative roles of seed limitation and microsite limitation in regulating the *A. drepanolobium* population. It is clear, however, that the demographic importance of seed vs. microsite limitation is strongly dependent on the local herbivore community.

Reductions in seed production caused by ungulate herbivory only impacted population growth in the absence of rodents. In the presence of rodents the differences in seed production between exclusion and control plots had no impact on population growth. This reveals that enhancing seed production – and therefore reducing seed

limitation – only benefits plant populations under certain consumer communities (i.e. the absence of rodents). This work therefore supports the conclusions of Clark et al. (2007) that the importance of seed limitation for most species will vary greatly through space and time and needs to be assessed under a range of contexts.

One important factor that I did not consider in this study is the role of seed dispersal in altering seed and microsite limitation (Clark et al. 2007; Satterthwaite 2007). Under the same level of seed production, increased dispersal would likely lead to greater recruitment because more seeds would be able to find suitable microsites with reduced intraspecific competition (Brodie et al. 2009; Poulsen, Clark and Bolker 2012). Dispersal may also reduce recruitment, however, if seeds are typically deposited in unsuitable sites (Watkinson and Sutherland 1995; Leibold et al. 2004; Kang and Armbruster 2011). Even very occasional dispersal events can be highly important in increasing plant population growth and range expansion (Vellend, Knight and Drake 2006). Although rodents do not act as dispersal agents in this system (Keesing 2000; Goheen et al. 2010), it is possible that large ungulates occasionally play an important role as a seed disperser. Elephants have been implicated in increasing dispersal and germination of other *Acacia* species, because the small proportion of seeds that survive passage through the elephant gut display increased recruitment once deposited due to receiving nutrients from elephant faeces and suffering reduced exposure to bruchid beetles (Miller 1994; Miller 1995). However, the importance of this role is currently under debate, especially when compared to the large number of seeds lost to elephant damage (Midgley and Bond 2001). Further work is needed to quantify the importance of occasional dispersal events in this study system.

3.3 Tree Encroachment in African Savannas

Increased densities of large ungulates have frequently been blamed for dramatic declines in tree cover, especially where their numbers are artificially elevated by providing dry-season watering holes, or where their natural dispersal is restricted by fences (Guldemonde and van Aarde 2008). Reciprocally, reductions in ungulate density have been linked to tree encroachment – although other factors such as increased atmospheric CO_2, fire suppression, and altered rainfall regimes have also been implicated in this phenomenon (Sankaran, Ratnam and Hanan 2004; Bond 2008; Midgley, Lawes and Chamaillé-Jammes 2010). Although an overwhelming array of studies link ungulates to changes in woody cover in savannas, there is a scarcity of robust experimental evidence to support these claims (Midgley and Bond 2001; Bond 2008; Midgley, Lawes and Chamaillé-Jammes 2010).

I provide conclusive evidence that large ungulates can cause a shift from population growth to population decline in *A. drepanolobium*. I also demonstrate that rodents can induce large decreases in tree population growth of a similar magnitude to ungulate impacts. Rodent seed predators are seldom studied in relation to tree population regulation, likely due to their inconspicuous appearance and the widely accepted low sensitivity of λ to seed survival (Silvertown et al. 1993; Ehrlén 2002). This study strongly suggests that rodents can meaningfully limit tree population growth and should be given greater attention in a variety of systems.

Domestic cattle are also frequently associated with tree encroachment in rangeland environments (Roques, O'Connor and Watkinson 2001; Riginos and Young

2007). This has been attributed to reductions in grass cover following cattle grazing that reduces the competitive influence of grass on the trees (Riginos and Young 2007). Reduced grass cover also reduces fire frequency and so cattle will likely have a greater impact on tree population dynamics in areas subject to frequent fires (Holdo, Holt and Fryxell 2009). However, increased cattle densities are typically associated with a suite of anthropogenic impacts, such as reduced wildlife densities, and so disentangling the direct impacts of cattle from those that are correlated with cattle abundance can be problematic (Young, Palmer and Gadd 2005; Riginos and Young 2007). Alternatively, saplings may benefit from reduced evapotranspiration and concealment from herbivores within a grass layer, and cattle could also negatively impact the tree population by removing grass (Western and Maitumo 2004). Our results indicate that cattle have a negligible impact on *A. drepanolobium* in this region. Indeed, even the direction of their impact (i.e. positive or negative) was variable between plots and years. It seems likely that differences in local water stress could switch the impact of cattle from beneficial to detrimental, and the variability of these results may relate to genuine differences in space and time. Regardless, this research is strongly indicative that native herbivores have a much greater influence on tree dynamics than their domestic counterparts.

3.4 Future Directions

This research has shown important new insights into the ability of different herbivore guilds to limit plant population growth both in isolation and in concert. Our results may act as a foundation for future research to explore these complex and dynamic

relationships. Perhaps the most important avenue of further enquiry is to examine the role

of the abiotic environment in directly limiting plant population growth, and also in

altering the magnitude of each herbivore impact. I discovered large differences in

population growth in different years of the study (Fig. 2.1). A large part of these

differences is doubtless driven by variable climatic conditions, principally rainfall.

Indeed, in one year seed production failed entirely, and in another year there were no

successful seedling recruits due to drought conditions. Continuing this experiment over a

greater period of time would allow us to observe plant-herbivore interactions over a

greater range of climatic conditions and advance our understanding of how frequently

drought substantially alters plant population dynamics.

Seed predators will have no impact on population growth in years when

recruitment fails due to drought. In drought years the population is entirely limited by

microsite availability because seeds left unconsumed by rodents will not germinate. The

role of rodents in regulating population growth over the long term will therefore depend

on the frequency of drought conditions. Once the impact of drought conditions on *A.*

drepanolobium has been properly assessed it will be possible to project the effect of

predicted regional climate change on tree population growth and woody cover across the

study region. Although climate models are subject to large degrees of error (Hegerl and

Zwiers 2011), exploration of a range of possible scenarios would be very useful

information to help advise preparations to mitigate the impacts of future climate change.

Climatic conditions are one factor affecting the relative importance of seed and

microsite limitation acting on the population, and thus determining the capacity of

different herbivore guilds to limit plant population growth. Density dependence and

dispersal are two more factors that have the capacity to alter this relationship. Our experiment was carried out under natural levels of density dependence and dispersal, allowing us to replicate typical conditions for seedling recruitment and calculate realistic estimates of population growth. An interesting extension to this work, however, would be to artificially manipulate seed density in our sowing experiments to assess the importance of density dependence in regulating recruitment and population growth. This would also reveal the potential for increased seed dispersal to reduce intraspecific competition for the same microsites and consequently to enhance the ability of seeds to find suitable areas for recruitment. Sowing seeds at a range of densities in each experimental plot (presence and absence of large ungulates crossed with presence and absence of rodents) would reveal how the different herbivore guilds alter the importance of density dependent recruitment. This would reveal the potential role of occasional longer-distance dispersal events in boosting recruitment. It would also provide insight into the evolutionary pressure acting on *A. drepanolobium* seed production. If strong density dependence reduces recruitment when hundreds of seeds fall very close to the parent tree, then lower annual seed production should show a selective advantage. If, however, there is limited density dependence, or if rodents consume the majority of seeds, then trees should produce seeds at saturating densities and higher seed production should be at a selective advantage.

A final important extension to this work would be to test how well the model predictions from our study area apply to *A. drepanolobium* populations growing elsewhere. It would be particularly interesting to calculate tree population growth rate in a range of study sites along a gradient of large ungulate density. This would allow us to verify that rodent seed predators act as a buffer to increased population growth under

reduced ungulate densities in real-world situations. It would also allow us to confirm that our model predictions are generalizable across a larger area rather than reliant on some unusual circumstance that may be particular to our local study site. Our work demonstrates that *A. drepanolobium* is well adapted to intense pressure from large ungulate herbivores and is able to persist in our study site where other, more poorly defended, species fail. It would also be intriguing to survey tree community composition along this same gradient of large ungulate density. If observations from our study site hold then I would expect *A. drepanolobium* to dominate in areas of high ungulate density, but to be joined – and perhaps outcompeted – by other species in areas of lower herbivore pressure.

3.5 Final Conclusions

The research presented here constitutes strong evidence that seed predators can play a substantial role in restricting plant population growth. This finding runs contrary to the received demographic theory that seed predators should minimally impact plant populations because population growth is typically far more sensitive to adult growth and survival than to recruitment (Silvertown et al. 1993; Ehrlén 2002). Indeed, my study population also conformed to this typical sensitivity structure. The enormity of rodent seed consumption overwhelmed this low sensitivity, however, and resulted in a substantial barrier to population growth. Perhaps even more surprising was my discovery that large ungulate impacts were also mediated principally through their effects on reproduction, rather than on adult growth and survival, when considered in isolation.

Large ungulates (principally elephants) are frequently blamed for reducing tree cover due to their occasional, but highly visible, destruction of adult trees (Edkins et al. 2007; Dharani et al. 2009). Their role in reducing reproductive output has been largely overlooked until now (but see Goheen et al. 2007), and this is the first study to irrefutably demonstrate that it can have a meaningful impact on overall population growth. Although I confirm that ungulate impacts on adult tree survival are also important drivers of population growth, it is the unexpected importance of herbivore impacts on tree reproduction that constitutes one of my most novel and important findings.

Another important finding is that the effect of one herbivore guild can be mediated through different demographic pathways in the presence versus the absence of another herbivore guild. My demographic models clearly show that ungulate impacts were mediated through their effect on reproduction in the absence of rodents and their effect on adult survival in the presence of rodents. To my knowledge this is the first time that such a context dependent switch in demographically important pathways has been demonstrated.

My third key finding is that the effects of the two main herbivore guilds were sub-additive. Thus large ungulates induced greater reductions in *A. drepanolobium* population growth in the absence of rodents than in their presence. Reciprocally, rodents induced greater reductions in population growth in the absence of large ungulates than in their presence. It is likely that the sub-additive nature of the interaction between two disparate herbivore guilds will be highly system-specific, depending on the species considered and the nature of their impacts on the plant population. Similar studies will have to be

conducted in a range of communities to draw conclusions about the generality of this result.

In addition to these important conclusions pertaining to ecological theory, I have revealed a number of smaller-scale conclusions of great relevance to our study system. I have demonstrated that rodents can form important barriers to tree encroachment following large ungulate declines. I have revealed that cattle have little impact on *A. drepanolobium* population growth in this region, and therefore increased cattle grazing should not directly precipitate extensive shrub encroachment. Finally, I have shown that although elephants do occasionally kill adult trees, this should not lead to a rapid decline in tree cover in this area. These results will be of interest to local land managers and also provide evidence to contribute to a general understanding of fluctuating tree cover in savanna ecosystems across the continent.

This research has provided a number of valuable insights of relevance to both ecological theory and local rangeland management. It also provides a strong scientific basis for making effective decisions on conservation issues, especially those relating to elephant impacts on tree cover. These results are a useful foundation for further research into the rodent-ungulate-*Acacia* interactions in this fascinating ecosystem. I also hope that they will be more broadly valuable for the insights they provide into how interactions within multi-guild consumer communities determine the population dynamics of their shared food source.

Literature Cited

Akima, H., A. Gebhardt, and T. Petzoldt. 2009. Akima: Interpolation of irregularly
spaced data. R package version 0.5-4. 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.

Andrieu, E., M. Debussche, F. Munoz, and J.D. Thompson. 2011. How does herbivory
affect individuals and populations of the perennial herb *Paeonia officinalis*? Flora
206:544-549.

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. The Journal of Applied Ecology
41:45-58.

Baldock, K.C.R. 2007. Multi-species pollination interactions in a Kenyan savannah
ecosystem. Ph.D. thesis. University of Edinburgh.

Barrett, C.B. and P. Arcese. 1998. Wildlife harvest in integrated conservation and
development projects: Linking harvest to household demand, agricultural production,
and environmental shocks in the Serengeti. Land Economics 74: 449-465.

Belsky, A.J. 1986. Does herbivory benefit plants? A review of the evidence. The
American Naturalist 127:870-892.

Beschta, R.L. and W.J. Ripple. 2009. Large predators and trophic cascades in terrestrial
ecosystems of the western United States. Biological Conservation 142:2401-2414.

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.

Boege, K, K.E. Barton and R. Dirzo. 2011. Influence of tree ontogeny on plant-herbivore interactions. In *Size- and Age-related changes in tree structure and function, Tree Physiology 4* (eds. F.C. Meinzer et al.), pp193-214. Springer Science and Business Media.

Bond, W.J. 2008. What limits trees in C4 grasslands and savannas? The Annual Review of Ecology, Evolution, and Systematics 39:641-659.

Brodie, J.F., O.E. Helmy, W.Y. Brockelman, and J.L. Maron. 2009. Functional differences within a guild of tropical mammalian frugivores. Ecology 90:688-698.

Brody, A., M.V. Price, and N.M. Waser. 2007. Life-history consequences of vegetative damage in scarlet gilia, a monocarpic plant. Oikos 116:975-985.

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.

Bonsall, M.B., E. van der Meijden, and M.J. Crawley. 2003. Contrasting dynamics in the same plant-herbivore interaction. Proceedings of the National Academy of Sciences of the United States of America 100: 14932-14936.

Caswell, H. 2001. Matrix population models. Sinauer Associates, 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. The 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. The American Naturalist 170:128-142.

Crawley, M.J. 1987. Benevolent herbivores? Trends in Ecology and Evolution 2:167-168.

Crawley, M.J. 1989. Insects and plant population dynamics. Annual review of Entomology 34: 531-564.

Crawley, M.J. 1990. The population dynamics of plants. Philisophical Transactions of the Royal Society of London B 330:125-140.

Crawley, M.J. 1997. Plant-herbivore dynamics. In *Plant Ecology* (ed. M.J. Crawley), pp. 401-474. 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.

Dharani, N., J.I. Kinyamario, P.W. Wagacha, and A.J. Rodrigues. 2009. Browsing impact of large herbivores on *Acacia xanthophloea* Benth in Lake Nakuru National Park, Kenya. African Journal of Ecology 47:184-191.

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.

Duncan, R.P., J.M. Diez, J.J. Sullivan, S. Wangen, and A.L. Miller. 2009. Safe sites, seed supply, and the recruitment function in plant populations. Ecology 90:2129-2138.

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

Dybzinski, R., and D. Tilman. 2012. Seed and microsite limitation in a late-successional old field: the effects of water, adults, litter, and small mammals on seeds and seedlings. Plant Ecology 213: 1003-1013.

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.

Ehrlén, J. 2002. Assessing the lifetime consequences of plant-animal interactions for the perennial herb *Lathyrus vernus* (Fabaceae). Perspectives in Plant Ecology, Evolution and Systematics 5:145-163.

Ehrlén, J. 2003. Fitness components versus total demographic effects: evaluating herbivore impacts on a perennial herb. The American Naturalist 162:796-810.

Elton, C. 1927 Animal Ecology. University of Chigaco Press, U.S.A. Chapter 5.

Eriksson, O., and J. Ehrlén. 1992. Seed and microsite limitation of recruitment in plant populations. Oecologia 91:360-364.

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. Écoscience 15:129-135.

Frei, E.S., J.F. Scheepens, and J. Stocklin. 2012. Dispersal and microsite limitation of a rare alpine plant. Plant Ecology 213:395-406.

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., 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.

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.

Guidone, M., C.S. Thornber and E. Field. 2010. Snail grazing facilitates growth of a bloom-forming alga. Marine Ecology Progress Series 420:83-89.

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. The American Naturalist 94:421-424.

Hartley, S.E. and C.G. Jones. 1997. Plant chemistry and herbivory, or why the world is green. In *Plant Ecology* (ed. M.J. Crawley), pp. 284-324. Blackwell Science, Oxford, UK.

Hegerl, G. and F. Zwiers. 2011. Use of models in detection and attribution of climate change. Wiley Interdisciplinary Reviews – Climate Change 2:570-591.

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.

Hilborn, R., P. Arcese, M. Borner, J. Hando, G. Hopcraft, M. Loibooki, S. Mduma and A.R.E. Sinclair. 2006. Effective enforcement in a conservation area. Science 314:1266-1266.

Holdo, R., R.D. Holt, and J.M. Fryxell. 2009. Grazers, browsers, and fire influence the extent and spatial pattern of tree cover in the Serengeti. Ecological Applications 19: 95-109.

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

Jacquemyn, H., R. Brys, R. Davidson, S. Tuljapurkar, and E. Jongejans. 2012. Stochastic LTRE analysis of the effects of herbivory on the population dynamics of a perennial grassland herb. Oikos 121:211-281.

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.

Kang, Y. and D. Armbruster. 2011. Dispersal effects on a discrete two-patch model for plant-insect interactions. Journal of Theoretical Biology 268:84-97.

Karban, R., S. Ishizaki, and K. Shiojiri. 2012. Long-term demographic consequences of eavesdropping for sagebrush. Journal of Ecology 100:932-938.

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

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

Knight, T.M., H. Caswell, and S. Kalisz. 2009. Population growth rate of a common understory herb decreases non-linearly across a gradient of deer herbivory. Forest Ecology and Management 257:1095-1103.

Leibold, M.A., M. Holyoak, N. Mouquet, P. Amarasekare, J.M. Chase, M.F. Hoopes, R.D. Holt, J.B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. Ecology Letters 7:601-613.

Louda, S.M. 1982. Seed predation and seedling mortality in the recruitment of a shrub, *Haplopappus venetus* (Asteraceae), along a climatic gradient. Ecology 64:511-521.

Louda, S.M. 1983. Seed predation and seedling mortality in the recruitment of a shrub, *Haplopappus venetus* (Asteraceae), along a climatic gradient. Ecology 64:511-521.

Louda, S.M., M.A. Potvin, and S.K. Collinge. 1990. Predispersal seed predation, postdispersal seed predation and competition in the recruitment of seedlings of a native thistle in Sandhills Prairie. American Midland Naturalist 124:105-113.

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. 2008. Herbivory, hunting and long-term vegetation change in degraded savanna. Biological Conservation 141:2174-2183.

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

Maclean, J.E., J.R. Goheen, D.F. Doak, T.M. Palmer, and T.P. Young. 2011. Cryptic herbivores mediate the strength and form of ungulate impacts on a long-lived savanna tree. Ecology 92:1626-1636.

Maron, J.L., and E. Crone. 2006. Herbivory: effects on plant abundance, distribution and population growth. Proceedings of the Royal Society B 273:2575-2584.

Maron, J.L., and M.J. Kauffman. 2006. Habitat-specific impacts of multiple consumers on plant population dynamics. Ecology 87:113-124.

Maron, J.L., C.C. Horvitz, and J.L. Williams. 2010. Using experiments, demography and population models to estimate interaction strength based on transient and asymptotic dynamics. Journal of Ecology 98:290-301.

Martin, E.F., and R.J. Meinke. 2012. Variation in the demographics of a rare central Oregon endemic, *Astragalus peckii* Piper (Fabaceae), with fluctuating levels of herbivory. Population Ecology 54:381-390.

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.

McNaughton, S.J. 1986. On plants and herbivores. The American Naturalist 128:765-770.

Mduma, S.A.R, A.R.E. Sinclair, and R. Turkington. 2007. What is the role of seasonality and synchrony in reproduction of savanna trees in Serengeti? Journal of Ecology 95:184-196.

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.

Midgley, J.J., M.J. Lawes, and S. Chamaillé. 2010. Savanna woody plant dynamics: the role of fire and herbivory, separately and synergistically. Australian Journal of Botany 58:1-11.

Miller, M.F. 1994. The costs and benefits of acacia seed consumption by ungulates. Oikos 71:181-187.

Miller, M.F. 1995. *Acacia* seed survival, seed germination and seedling growth following pod consumption by large herbivores and seed chewing by rodents. African Journal of Ecology 33:194-210.

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, Massachusetts, USA.

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

Naito, A.T. and D. M. Cairns. 2011. Patterns and processes of global shrub expansion.
    Progress in Physical Geography 35:423-442.

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.

Ogutu, J.O. and N. Owen-Smith. ENSO, rainfall and temperature influences on extreme
    population declines among African savanna ungulates. Ecology Letters 6:412-419.

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

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.

Olejniczak, P. 2011. Overcompensation in response to simulated herbivory in the
    perennial herb *Sedum maximum*. Plant Ecology 212:1927-1935.

Paige, K.N. 1999. Regrowth following ungulate herbivory in *Ipomopsis aggregata*:
    Geographic evidence for overcompensation. Oecologia 118:316-323.

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

Paudel, P.K. and P. Kindlmann. 2012. Human disturbance is a major determinant of wildlife distribution in Himalayan midhill landscapes of Nepal. Animal Conservation 15:283-293.

Pfister, C.A. 1998. Patterns of variance in stage-structured populations: Evolutionary predictions and ecological implications. Proceedings of the National Acadamy of Sciences, USA 95:213-218.

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

Poulsen, J.R., C.J. Clark, and B.M. Bolker. 2012. Experimental manipulation of seed shadows of an Afrotropical tree determines drivers of recruitment. Ecology 93:500-510.

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

Puentes, A., and J. Agren. 2012. Additive and non-additive effects of simulated leaf and inflorescence damage on survival, growth and reproduction of the perennial herb *Arabidopsis lyrata*. Oecologia 169:1033-1042.

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. and T. Young. 2007. Positive and negative effects of grass, cattle, and wild herbivores on *Acacia* saplings in an East African savanna. Oecologia 153:985-995.

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.

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

Rodriguez-Estival, J., M.A. Taggart, and R. Mateo. 2011. Alterations in vitamin A and E
levels in liver and testis of wild ungulates from a lead mining area. Archives of
Environmental Contamination and Toxicology 60:361-371.

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

Roques, K.G., T.G. O'Connor, and A.R. Watkinson. 2001. Dynamics of shrub
encroachment in an African savanna: relative influences of fire, herbivory, rainfall
and density dependence. Journal of Applied Ecology 38:268-280.

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.

Satterthwaite, W.H. 2007. The importance of dispersal in determining seed versus safe
site limitation of plant populations. Plant Ecology 193:113-130.

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

Shorrocks, B. 2007. The biology of African savannas. Oxford University Press, U.K.

Silvertown, J., M. Franco, I. Pisanty, and A. Mendoza. 1993. Comparative plant
demography – Relative importance of life-cycle components to the finite rate of
increase in woody and herbaceous perennials. Journal of Ecology 81:465-476.

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

Spear, D. and S.L. Chown. 2009. Non-indigenous ungulates as a threat to biodiversity. Journal of Zoology 279:1-17.

Stanton, M.L. and T.M. Palmer. 2011. The high cost of mutualism: effects of four species of East African ant symbionts on their myrmecophyte host tree. Ecology 92:1073-1082.

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.

Tanentzap, A.J., L.E. Burrows, W.G. Lee, G. Nugent, J.M. Maxwell, and D.A. Coomes. 2009. Landscape-level vegetation recovery from herbivory: progress after four decades of invasive red deer control. Journal of Applied Ecology 46:1064-1072.

Tansley, A.G., and R.S. Adamson. 1985 Studies of the vegetation of the English chalk: III. The chalk grasslands of Hampshire-Sussex border. Journal of Ecology 13:177-223.

Tucker C. and G. Avila-Sakar. 2010. Ontogenetic changes in tolerance to herbivory in *Arabidopsis*. Oecologia 164:1005-1015.

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

Turnbull, L.A., M.J. Crawley, and M. Rees. 2000. Are populations seed-limited? A review of seed sowing experiments. Oikos 88:225-238.

Turkington, R. 2009. Top-down and bottom-up forces in mammalian herbivore-vegetation systems: an essay review. Botany 87:723-739.

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.

Vellend, M., T.M. Knight, and J.M. Drake. 2006. Antagonistic effects of seed dispersal and herbivory on plant migration. Ecology Letters 9:319-326.

Watkinson, A.R. and W.J. Sutherland. 1995. Sources, sinks and pseudo-sinks. Journal of Animal Ecology 64:126-130.

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

Western, D. and D. Maitumo. 2004. Woodland loss and restoration in a savanna park: a 20-year experiment. African Journal of Ecology 42:111-121.

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. 1985 *Lobelia telekii* herbivory, mortality, and size at reproduction: variation with growth rate. Ecology 66:1879-1883.

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., 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.

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.

Appendices

Appendix A. Model selection for *Acacia drepanolobium* vital rates

Table A1: Model selection to identify the best model for each *A. drepanolobium* vital rate. Results are presented for the top ten models for each vital rate, from the suite of candidate models containing all possible combinations of main effects and their two-way interactions (giving 62-72 potential models per vital rate). The top ten models for each vital rate all contain main effects for tree height ('height'), wild ungulate presence/absence ('wild'), cattle presence/absence ('cattle'), and year ('year'); the seed survival models contain the additional main effect of rodent presence/absence ('rodent'). Because all models contain these main effects, only the interaction terms included in each model are presented. Models for adult growth and seed production also potentially included height^2 as a variable to allow for a non-linear relationship. Top-ranking models for each vital rate were used in subsequent matrix analysis, and analyses were repeated using coefficients from each of the top five models to verify that alternative model selection would not qualitatively alter our results.

Dependant variable: Adult *A. drepanolobium* survival.

Model Rank	Included Interaction Terms						AIC	Akaike Weight	Summed Weight
	height: wild	height: cattle	height: year	wild: cattle	wild: year	cattle: year			
1	X	X	X		X		1022.90	0.280	0.280
2	X	X	X	X	X		1024.85	0.106	0.386
3	X		X		X		1024.93	0.101	0.487
4		X	X		X		1025.31	0.084	0.571
5	X	X	X				1025.80	0.066	0.637
6	X	X	X		X	X	1026.03	0.059	0.695
7	X		X	X	X		1026.91	0.038	0.733
8			X		X		1027.03	0.036	0.769
9	X	X	X	X	X	X	1027.24	0.032	0.801
10		X	X	X	X		1027.27	0.032	0.832

Dependant variable: *A. drepanolobium* growth (tree height in the following year).

Model Rank	height²	Included Interaction Terms						AIC	Akaike Weight	Summed Weight
		height: wild	height: cattle	height: year	wild: cattle	wild: year	cattle: year			
1			X	X	X	X	X	-16543.70	0.089	0.089
2			X	X	X	X		-16543.70	0.088	0.178
3		X	X	X	X	X	X	-16543.12	0.066	0.243
4		X	X	X	X	X		-16543.10	0.066	0.309
5			X	X		X		-16543.06	0.064	0.373
6			X	X		X	X	-16543.03	0.063	0.437
7	X		X	X	X	X	X	-16542.60	0.062	0.499
8	X		X	X	X	X		-16542.58	0.061	0.560
9	X	X	X	X	X	X	X	-16540.09	0.053	0.613
10	X	X	X	X	X	X		-16539.8	0.052	0.665

Dependant variable: *A. drepanolobium* variance in growth (residuals from growth model 1 above).

Model Rank	Included Interaction Terms						AIC	Akaike Weight	Summed Weight
	height: wild	height: cattle	height: year	wild: cattle	wild: year	cattle: year			
1			X		X		-32368.17	0.271	0.271
2		X	X		X		-32367.58	0.202	0.473
3	X		X		X		-32366.44	0.114	0.588
4			X	X	X		-32366.18	0.100	0.688
5	X	X	X		X		-32365.78	0.082	0.770
6		X	X	X	X		-32365.58	0.074	0.845
7	X		X	X	X		-32364.45	0.042	0.887
8	X	X	X	X	X		-32363.78	0.030	0.917
9		X	X		X	X	-32363.21	0.022	0.940
10	X		X	X		X	-32362.49	0.016	0.956

Dependant variable: *A. drepanolobium* probability of reproduction.

Model Rank	Included Interaction Terms						AIC	Akaike Weight	Summed Weight
	height: wild	height: cattle	height: year	wild: cattle	wild: year	cattle: year			
1			X	X	X		3551.49	0.319	0.319
2	X		X	X	X		3553.47	0.119	0.437
3		X	X	X	X		3553.48	0.118	0.555
4			X		X		3554.82	0.060	0.616
5	X		X	X			3554.91	0.058	0.673
6		X	X	X			3554.97	0.056	0.729
7	X	X	X	X			3555.45	0.044	0.773
8			X	X	X	X	3556.07	0.032	0.805
9			X				3556.43	0.027	0.833
10		X	X	X			3556.75	0.023	0.856

Dependant variable: *A. drepanolobium* seed production, if reproducing.

Model Rank	height^2	Included Interaction Terms						AIC	Akaike Weight	Summed Weight
		height: wild	height: cattle	height: year	wild: cattle	wild: year	cattle: year			
1		X	X		X	X		1897.91	0.145	0.145
2		X	X	X	X	X		1898.18	0.126	0.271
3		X			X	X		1898.42	0.112	0.383
4		X		X	X	X		1899.06	0.081	0.465
5	X	X	X		X	X		1899.31	0.072	0.537
6	X	X	X	X	X	X		1899.60	0.062	0.599
7		X	X	X		X		1899.79	0.057	0.655
8		X	X			X		1900.29	0.044	0.700
9	X	X		X	X	X		1900.42	0.041	0.741
10		X		X		X		1900.92	0.032	0.773

Dependant variable: *A. drepanolobium* seed survival.

Model Rank	Included Interaction Terms										AIC	Akaike Weight	Summed Weight
	height: seeds	height: wild	height: cattle	height: rodent	seeds: wild	seeds: rodent	wild: cattle	wild: rodent	cattle: year	rodent: year			
1		X	X		X	X			X	X	338.32	0.143	0.143
2		X	X			X				X	339.34	0.086	0.229
3		X	X		X	X		X	X	X	339.54	0.078	0.307
4		X	X			X				X	339.58	0.076	0.383
5	X	X	X		X	X		X	X	X	339.87	0.066	0.449
6		X	X		X	X	X		X	X	340.04	0.060	0.509
7		X	X		X	X				X	340.47	0.049	0.558
8		X	X			X		X	X	X	341.17	0.034	0.592
9	X	X	X	X	X	X		X	X	X	341.61	0.028	0.620
10	X	X	X	X		X			X	X	341.71	0.026	0.646

Table A2: Influence of alternative model selection on calculation of stochastic population growth (λ_s). Values reported for the 'best model' are those presented in the manuscript using models with the lowest AIC value for each vital rate. Subsequent table entries denote measures of λ_s where alternative glms were used for certain vital rates (e.g. values reported under 'Survival 2' are calculated from matrices utilizing coefficients from the adult survival logistic regression attaining the second highest support [second lowest AIC value]). The difference in population growth ($\Delta\lambda_s$) between the best model and the alternative model are reported for each treatment ($_0$ – absence of herbivore guild; W – wild ungulates present; C – cattle present; R– rodents present). Mean $\Delta\lambda_s$ over all eight treatments is presented in the final column, revealing that alternative model selection causes a maximum mean $\Delta\lambda_s$ of 0.0038 (alternative Survival model 5). The maximum $\Delta\lambda_s$ for any treatment was of -0.011 using alternative Adult Survival model 3 for treatment 000 (i.e., wild ungulates, cattle, and rodents all absent).

Alternative Model	Treatment																Average $\Delta\lambda_s$
	000		00R		0C0		0CR		W00		W0R		WC0		WCR		
	λ_s	$\Delta\lambda_s$	λ_s	$\Delta\lambda_s$	λ_s	$\Delta\lambda_s$	λ_s	$\Delta\lambda_s$	λ_s	$\Delta\lambda_s$	λ_s	$\Delta\lambda_s$	λ_s	$\Delta\lambda_s$	λ_s	$\Delta\lambda_s$	
Best Model	1.063	$0.00e^{00}$	1.007	$0.00e^{00}$	1.035	$0.00e^{00}$	1.004	$0.00e^{00}$	0.977	$0.00e^{00}$	0.970	$0.00e^{00}$	0.981	$0.00e^{00}$	0.974	$0.00e^{00}$	$0.00e^{00}$
Survival 2	1.062	$-5.20e^{-04}$	1.007	$-3.52e^{-04}$	1.035	$-8.40e^{-05}$	1.004	$9.92e^{-05}$	0.977	$4.18e^{-04}$	0.970	$4.03e^{-04}$	0.981	$-5.04e^{-04}$	0.973	$-4.93e^{-04}$	$-1.29e^{-04}$
Survival 3	1.052	$-1.13e^{-02}$	1.004	$-3.77e^{-03}$	1.051	$1.59e^{-02}$	1.011	$6.79e^{-03}$	0.978	$5.10e^{-04}$	0.972	$2.08e^{-03}$	0.982	$8.98e^{-04}$	0.971	$-2.93e^{-03}$	$1.02e^{-03}$
Survival 4	1.067	$4.10e^{-03}$	1.007	$-1.11e^{-04}$	1.056	$2.06e^{-02}$	1.013	$9.43e^{-03}$	0.977	$-6.93e^{-05}$	0.971	$1.12e^{-03}$	0.977	$-4.41e^{-03}$	0.973	$-4.38e^{-04}$	$3.77e^{-03}$
Survival 5	1.061	$-1.71e^{-03}$	1.006	$-1.40e^{-03}$	1.031	$-4.06e^{-03}$	1.002	$-1.99e^{-03}$	0.977	$-3.15e^{-05}$	0.970	$2.10e^{-05}$	0.981	$-1.83e^{-04}$	0.973	$-1.11e^{-04}$	$-1.18e^{-03}$
Growth 2	1.063	$3.90e^{-05}$	1.007	$6.43e^{-06}$	1.035	$-3.49e^{-05}$	1.004	$-2.67e^{-05}$	0.977	$-3.04e^{-06}$	0.970	$-2.08e^{-06}$	0.981	$-2.17e^{-05}$	0.974	$-7.13e^{-06}$	$-6.27e^{-06}$
Growth 3	1.063	$2.10e^{-04}$	1.008	$1.09e^{-04}$	1.035	$-6.61e^{-04}$	1.004	$-3.15e^{-04}$	0.977	$3.91e^{-04}$	0.971	$7.53e^{-04}$	0.982	$8.28e^{-04}$	0.975	$9.36e^{-04}$	$2.81e^{-04}$
Growth 4	1.063	$2.51e^{-04}$	1.008	$1.17e^{-04}$	1.035	$-6.96e^{-04}$	1.004	$-3.42e^{-04}$	0.977	$3.88e^{-04}$	0.971	$7.50e^{-04}$	0.982	$8.02e^{-04}$	0.975	$9.23e^{-04}$	$2.74e^{-04}$
Growth 5	1.061	$-1.82e^{-03}$	1.007	$-4.13e^{-04}$	1.038	$2.36e^{-03}$	1.005	$6.75e^{-04}$	0.976	$-9.31e^{-04}$	0.969	$-1.54e^{-03}$	0.981	$-1.34e^{-04}$	0.974	$3.92e^{-04}$	$-1.77e^{-04}$
Grow Var 2	1.063	$-3.67e^{-04}$	1.007	$-2.55e^{-04}$	1.037	$1.82e^{-03}$	1.005	$7.27e^{-04}$	0.977	$3.14e^{-05}$	0.970	$8.87e^{-05}$	0.981	$2.18e^{-04}$	0.974	$6.12e^{-05}$	$2.91e^{-04}$
Grow Var 3	1.063	$-7.95e^{-05}$	1.007	$-7.56e^{-05}$	1.035	$-7.81e^{-04}$	1.004	$-3.02e^{-04}$	0.977	$2.25e^{-06}$	0.970	$-2.76e^{-05}$	0.981	$1.24e^{-04}$	0.974	$3.96e^{-05}$	$-1.38e^{-04}$
Grow Var 4	1.063	$4.17e^{-05}$	1.007	$2.03e^{-07}$	1.035	$-4.51e^{-05}$	1.004	$-1.04e^{-05}$	0.977	$6.89e^{-06}$	0.970	$3.51e^{-06}$	0.981	$2.44e^{-06}$	0.974	$1.57e^{-06}$	$9.91e^{-08}$
Grow Var 5	1.062	$-4.77e^{-04}$	1.007	$-3.32e^{-04}$	1.037	$1.33e^{-03}$	1.005	$5.35e^{-04}$	0.977	$1.22e^{-05}$	0.970	$3.48e^{-05}$	0.981	$2.81e^{-04}$	0.974	$7.01e^{-05}$	$1.82e^{-04}$
Prob Rep 2	1.063	$-2.45e^{-05}$	1.007	$-1.22e^{-05}$	1.035	$-1.52e^{-05}$	1.004	$-7.10e^{-06}$	0.977	$1.86e^{-05}$	0.970	$1.22e^{-05}$	0.981	$3.70e^{-05}$	0.974	$2.66e^{-05}$	$4.43e^{-06}$
Prob Rep 3	1.063	$2.31e^{-05}$	1.007	$1.18e^{-05}$	1.035	$-1.92e^{-05}$	1.004	$-9.36e^{-06}$	0.977	$1.05e^{-05}$	0.970	$6.95e^{-06}$	0.981	$-2.65e^{-05}$	0.974	$-1.89e^{-05}$	$-2.70e^{-06}$
Prob Rep 4	1.063	$2.02e^{-04}$	1.008	$9.28e^{-05}$	1.035	$-1.09e^{-04}$	1.004	$-4.61e^{-05}$	0.976	$-6.07e^{-04}$	0.970	$-4.38e^{-04}$	0.982	$4.71e^{-04}$	0.974	$2.62e^{-04}$	$-2.16e^{-05}$
Prob Rep 5	1.063	$-2.68e^{-04}$	1.007	$-1.02e^{-04}$	1.035	$-1.04e^{-04}$	1.004	$-1.79e^{-05}$	0.977	$4.87e^{-04}$	0.970	$3.56e^{-04}$	0.981	$2.58e^{-04}$	0.974	$1.39e^{-04}$	$9.35e^{-05}$
Seed Prod 2	1.064	$9.98e^{-04}$	1.007	$2.14e^{-05}$	1.037	$1.59e^{-03}$	1.004	$1.80e^{-05}$	0.978	$7.71e^{-04}$	0.970	$1.06e^{-04}$	0.982	$1.17e^{-03}$	0.974	$-1.50e^{-05}$	$5.83e^{-04}$
Seed Prod 3	1.057	$-5.94e^{-03}$	1.007	$-4.69e^{-04}$	1.040	$4.72e^{-03}$	1.004	$2.98e^{-04}$	0.976	$-1.11e^{-03}$	0.970	$-2.53e^{-04}$	0.985	$3.44e^{-03}$	0.974	$8.01e^{-04}$	$1.85e^{-04}$
Seed Prod 4	1.057	$-5.64e^{-03}$	1.007	$-4.98e^{-04}$	1.042	$6.51e^{-03}$	1.004	$3.26e^{-04}$	0.976	$-5.99e^{-04}$	0.970	$-1.87e^{-04}$	0.986	$4.92e^{-03}$	0.974	$8.14e^{-04}$	$7.05e^{-04}$
Seed Prod 5	1.068	$5.46e^{-03}$	1.008	$4.32e^{-04}$	1.050	$1.47e^{-02}$	1.005	$8.94e^{-04}$	0.978	$1.23e^{-03}$	0.970	$2.15e^{-04}$	0.978	$-3.62e^{-03}$	0.973	$-7.57e^{-04}$	$2.31e^{-03}$
Seed Surv 2	1.061	$-2.23e^{-03}$	1.007	$-8.51e^{-04}$	1.039	$3.40e^{-03}$	1.006	$1.74e^{-03}$	0.978	$6.68e^{-04}$	0.970	$-1.63e^{-04}$	0.984	$2.61e^{-03}$	0.975	$1.23e^{-03}$	$8.01e^{-04}$
Seed Surv 3	1.063	$2.69e^{-04}$	1.005	$-2.07e^{-03}$	1.035	$-2.63e^{-04}$	1.003	$-1.27e^{-03}$	0.977	$-4.90e^{-04}$	0.972	$2.27e^{-03}$	0.981	$-4.75e^{-04}$	0.975	$1.87e^{-03}$	$-1.90e^{-05}$
Seed Surv 4	1.058	$-5.35e^{-03}$	1.005	$-2.91e^{-03}$	1.044	$9.01e^{-03}$	1.008	$4.49e^{-03}$	0.976	$-7.20e^{-04}$	0.969	$-1.25e^{-03}$	0.985	$3.66e^{-03}$	0.976	$2.46e^{-03}$	$1.17e^{-03}$
Seed Surv 5	1.060	$-2.76e^{-03}$	1.004	$-3.85e^{-03}$	1.033	$-1.98e^{-03}$	1.002	$-2.03e^{-03}$	0.979	$1.77e^{-03}$	0.974	$4.31e^{-03}$	0.984	$2.58e^{-03}$	0.978	$4.32e^{-03}$	$2.96e^{-04}$

Appendix B. Coefficients for the best-supported model for each vital rate

Table B1: Coefficients for best-supported logistic regression describing probability of survival.

Variable	Coefficient	SE
Intercept	5.733	1.382
log(height)	0.397	1.238
wild ungulates present	-0.272	1.080
cattle present	-1.576	0.752
year 2005	3.411	1.987
year 2006	1.048	1.596
year 2007	-3.270	1.366
year 2008	-2.967	1.363
log(height):wild ungulates present	-1.637	0.782
log(height):cattle present	1.362	0.683
log(height):year 2005	-2.565	1.442
log(height):year 2006	-2.056	1.327
log(height):year 2007	0.971	1.223
log(height):year 2008	1.170	1.194
wild ungulates present:year 2005	-0.545	1.324
wild ungulates present:year 2006	1.199	0.957
wild ungulates present:year 2007	1.865	0.866
wild ungulates present:year 2008	0.857	0.877

Table B2: Coefficients for best-supported linear model describing tree growth.

Variable	Coefficient	SE
Intercept	0.076	0.008
log(height)	0.959	0.007
wild ungulates present	-0.010	0.004
cattle present	-0.020	0.007
year 2005	-0.029	0.011
year 2006	-0.049	0.011
year 2007	0.006	0.011
year 2008	0.052	0.011
log(height):cattle present	0.014	0.006
log(height):year 2005	0.025	0.009
log(height):year 2006	0.043	0.009
log(height):year 2007	-0.015	0.009
log(height):year 2008	-0.044	0.010
wild ungulates present:cattle present	0.006	0.003
wild ungulates present:year 2005	0.002	0.005
wild ungulates present:year 2006	0.003	0.005
wild ungulates present:year 2007	0.010	0.005
wild ungulates present:year 2008	-0.026	0.005
cattle present:year 2005	0.001	0.005
cattle present:year 2006	0.001	0.005
cattle present:year 2007	-0.008	0.005
cattle present:year 2008	0.008	0.005

Table B3: Coefficients for best-supported variance in tree growth linear model.

Variable	Coefficient	SE
Intercept	$3.763e^{-3}$	$2.164e^{-3}$
log(height)	$-1.699e^{-3}$	$1.975e^{-3}$
wild ungulates present	$-3.716e^{-5}$	$1.148e^{-3}$
cattle present	$-1.040e^{-3}$	$5.196e^{-4}$
year 2005	$-8.220e^{-4}$	$3.124e^{-3}$
year 2006	$-1.491e^{-3}$	$3.178e^{-3}$
year 2007	$8.232e^{-3}$	$3.231e^{-3}$
year 2008	$2.019e^{-2}$	$3.325e^{-3}$
log(height):year 2005	$6.487e^{-4}$	$2.837e^{-3}$
log(height):year 2006	$1.097e^{-3}$	$2.852e^{-3}$
log(height):year 2007	$-1.694e^{-3}$	$2.858e^{-3}$
log(height):year 2008	$-1.053e^{-2}$	$2.914e^{-3}$
wild ungulates present:year 2005	$1.414e^{-4}$	$1.629e^{-3}$
wild ungulates present:year 2006	$2.700e^{-4}$	$1.636e^{-3}$
wild ungulates present:year 2007	$7.894e^{-4}$	$1.651e^{-3}$
wild ungulates present:year 2008	$6.324e^{-3}$	$1.678e^{-3}$

Table B4: Coefficients for best-supported logistic regression describing probability of reproduction.

Variable	Coefficient	SE
Intercept	-4.491	0.304
log(height)	3.451	0.261
wild ungulates present	-0.609	0.164
cattle present	0.091	0.106
year 2005	0.090	0.422
year 2006	0.325	0.532
year 2007	-15.106	1203
year 2008	-15.104	1273
log(height):year 2005	0.277	0.372
log(height):year 2006	-1.867	0.442
log(height):year 2007	-3.460	1034
log(height):year 2008	-3.462	1077
wild ungulates present:cattle present	-0.410	0.178
wild ungulates present:year 2005	-0.132	0.197
wild ungulates present:year 2006	0.634	0.252
wild ungulates present:year 2007	0.800	595.1
wild ungulates present:year 2008	0.799	615.7

Table B5: Coefficients for best-supported linear model describing seed production.

Variable	Coefficient	SE
Intercept	1.176	0.690
log(height)	2.649	0.548
wild ungulates present	1.539	0.789
cattle present	1.019	0.723
year 2005	1.966	0.215
year 2006	-0.273	0.206
log(height):wild ungulates present	-2.051	0.612
log(height):cattle present	-0.929	0.592
wild ungulates:cattle	0.494	0.238
wild ungulates present:year 2005	-0.564	0.296
wild ungulates present:year 2006	0.547	0.297

Table B6: Coefficients for best-supported logistic regression describing probability of seedling survival.

Variable	Coefficient	SE
Intercept	-10.09	1.252
log(height)	1.454	1.031
log(seed production)	0.374	0.156
wild ungulates present	1.322	2.077
cattle present	-1.518	1.825
rodents present	2.238	1.690
year 2005	-0.373	0.388
year 2006	-1.273	1.079
log(height):wild ungulates present	-2.803	1.212
log(height):cattle present	2.311	1.353
log(seeds):wild ungulates present	0.342	0.200
log(seeds):rodents present	-1.171	0.295
cattle present:year 2005	-1.063	0.441
cattle present:year 2006	-0.206	1.217
rodents present:year 2005	2.747	1.172
rodents present:year 2006	1.700	1.546

Appendix C. Calculating the proportion of variance in λ_s associated with including the effects of wild ungulates on each vital rate

We conducted a full four-way ANOVA using the data presented in Fig. 4a with λ_s as our response variable and the inclusion/exclusion of wild ungulate effects on each of the four vital rates: 1) adult survival, 2) adult growth (by changing appropriate parameters in both the adult growth and variance in growth glms), 3) tree reproduction (by changing appropriate parameters in both the probability of reproduction logistic regression and the seed production glm), and 4) seedling survival: as our explanatory variables. This approach allowed us to calculate the sum of squares associated with each vital rate as a measure of its 'importance' in driving changes in λ_s. This procedure was strictly used to partition the variance associated with each vital rate, and cannot be viewed as a conventional ANOVA as we used 16 measures of λ_s to calculate the 15 parameters in the model. There are therefore no F-values or P-values denoting the significance of each explanatory term.

Table C1: Sum of squares associated with including the effects of wild ungulates on each vital rate in the absence of rodents. Effects on reproduction explain the greatest proportion of the variance (in bold). Dotted lines separate main effects, two-way, three-way, and four-way interactions.

Explanatory Variable	Sum Sq.
adult survival	$1.023e^{-3}$
adult growth	$2.670e^{-4}$
reproduction	**$1.007e^{-2}$**
seedling survival	$5.858e^{-4}$
adult survival:adult growth	$3.163e^{-5}$
adult survival:reproduction	$1.454e^{-4}$
adult growth:reproduction	$2.244e^{-4}$
adult survival:seedling survival	$3.347e^{-6}$
adult growth:seedling survival	$3.721e^{-5}$
reproduction:seedling survival	$6.224e^{-6}$
adult survival:adult growth:reproduction	$3.921e^{-6}$
adult survival:adult growth:seedling survival	$6.671e^{-7}$
adult survival:reproduction:seedling survival	$1.156e^{-5}$
adult growth:reproduction:seedling survival	$2.898e^{-6}$
adult survival:adult growth: reproduction:seedling survival	$7.367e^{-7}$

Table C2: Sum of squares associated with including the effects of wild ungulates on each vital rate in the presence of rodents. Effects on adult survival explain the greatest proportion of the variance (in bold). Dotted lines separate main effects, two-way, three-way, and four-way interactions.

Explanatory Variable	Sum Sq.
adult survival	**$2.372e^{-3}$**
adult growth	$1.084e^{-5}$
reproduction	$2.702e^{-4}$
seedling survival	$2.114e^{-4}$
adult survival:adult growth	$8.141e^{-5}$
adult survival:reproduction	$4.625e^{-5}$
adult growth:reproduction	$1.175e^{-5}$
adult survival:seedling survival	$1.448e^{-5}$
adult growth:seedling survival	$3.000e^{-5}$
reproduction:seedling survival	$1.638e^{-5}$
adult survival:adult growth:reproduction	$2.986e^{-6}$
adult survival:adult growth:seedling survival	$3.115e^{-6}$
adult survival:reproduction:seedling survival	$8.799e^{-6}$
adult growth:reproduction:seedling survival	$1.493e^{-6}$
adult survival:adult growth: reproduction:seedling survival	$1.152e^{-6}$

Appendix D. Life Table Response Experiment (LTRE) details

Life Table Response Experiments (LTREs) are a form of retrospective matrix analysis that reveal the relative importance of individual demographic transitions to the difference in population growth rate ($\Delta\lambda$) caused by the application of some treatment to the population (Caswell 2001). Projection matrices are constructed for populations in each treatment, the projected population growth rate of each is compared, and then these differences among populations are decomposed into the contributions from each matrix entry to $\Delta\lambda$. The contributions are calculated as:

$$\Delta\lambda = \lambda^t - \lambda^c$$

$$\approx \sum_{ij} (a^t_{ij} - a^c_{ij}) \times \left(\frac{\partial\lambda}{\partial a_{ij}}\right)\Bigg|_{(A^i + A^c)/2}$$

Where λ^t and λ^c are measures of λ from treatment 1 and treatment 2 (control) matrices (e.g. matrices constructed for populations in the presence and absence of wild ungulates, in our study); a^t_{ij} and a^c_{ij} represent each corresponding matrix element of the treatment 1 and treatment 2 matrices, and ($\partial\lambda/\partial a_{ij}$) signifies the sensitivity of that entry for the mean matrix with each entry averaged across the two treatment matrices ($[A^t + A^c]/2$). Thus, the contributions of each of the matrix elements a_{ij} to $\Delta\lambda$ are evaluated using the sensitivities calculated for the mean matrix midway between the two treatment matrices (Caswell 2001, Bruna and Oli 2005).

This approach reveals the relative importance of the demographic transitions that underlie differences in λ observed between the treatments. This can be contrasted with prospective matrix analysis, which entails calculating λ for a single population and then observing which matrix entries have the highest sensitivities or elasticities with respect to λ (Caswell 2000). In prospective analysis it is then inferred that treatments which influence matrix elements to which λ is most

sensitive should have the greatest impact on population growth. Thus, LTREs integrate experimental observations with projections of asymptotic growth rate to reveal the true impacts of applying a specified treatment to a population (Caswell 2001).

As the contribution to $\Delta\lambda$ of a specific matrix element is determined by the magnitude of both 1) the difference between that element over the two matrices under comparison; and 2) the sensitivity of that element, matrix elements can be associated with a large contribution either if λ is highly sensitive to that element, or if the treatment under comparison in the LTRE causes a dramatic change in the transition rates underlying that matrix element (Caswell 2001). Both of these scenarios are demonstrated in our results. Wild ungulates have only a small negative effect on survival (i.e., they kill only a very few adult trees each year), but this equates to a large contribution to $\Delta\lambda$ because λ is highly sensitive to changes in rates of adult survival. Conversely, rodents influence tree fecundity by dramatically reducing recruitment; although $\Delta\lambda$ is relatively insensitive to this demographic event, fecundity makes a large contribution to $\Delta\lambda$ because the differences between matrix fecundities in the presence versus absence of rodents are very large.
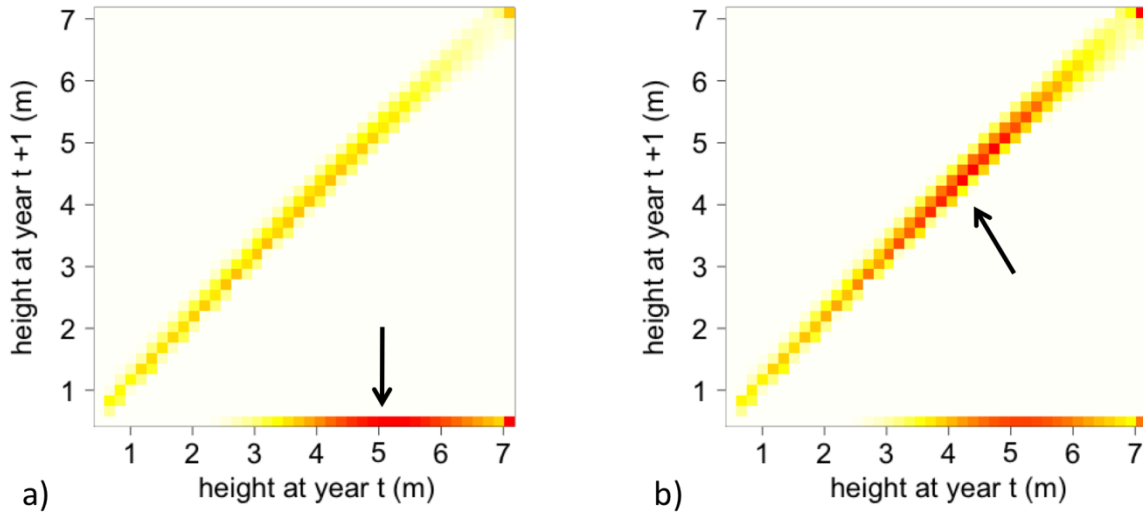
Figure D1: Positive contributions of each matrix element to the impact of wild ungulates on stochastic population growth (λ_s) in a) the absence and b) the presence of rodents. Colours range from white through yellow to red as value increases. The bottom row displays the fecundity of trees of increasing size; the colored diagonal displays adult growth and survival. Wild ungulates impact λ_s primarily through tree fecundities in the absence of rodents (black arrow in panel a) and primarily through adult tree survival and growth in the presence of rodents (black arrow in panel b).

Appendix E. Stable stage distribution and stage-specific reproductive value for tree populations growing in the presence and absence of rodents
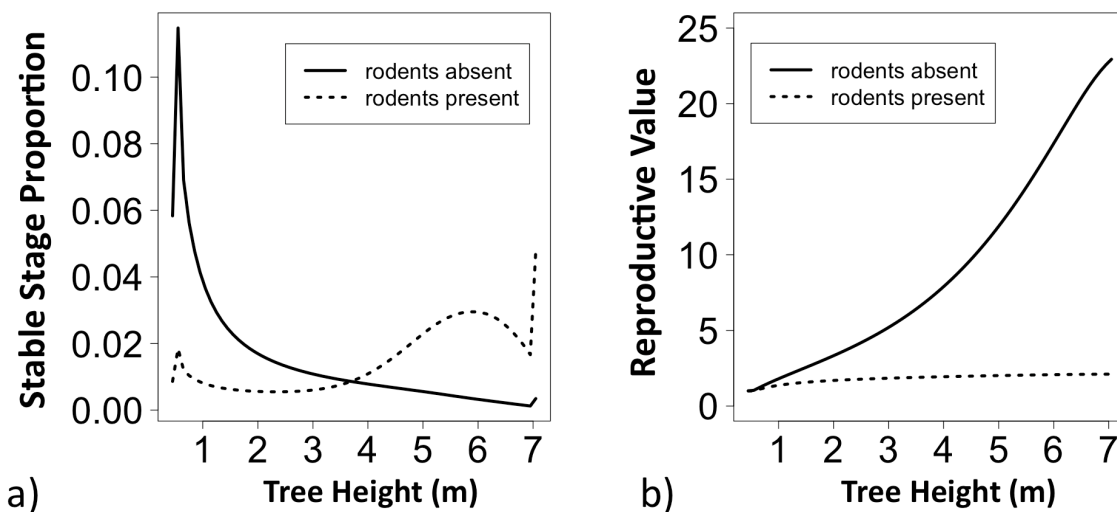

Figure E1: a) Stable stage distribution and b) stage-specific reproductive value in the presence and absence of rodents. In the presence of rodents, juvenille stages constitute a lower proportion of the population, and adult trees of all heights have a lower lifetime reproductive value.