

# The Effects of Mega-Herbivore Extinctions on Seed Dispersal and Community Structure in An East African Savanna

Miranda Bernard

Department of Ecology and Evolutionary Biology  
Princeton University, Princeton, New Jersey  
[mirandab@princeton.edu](mailto:mirandab@princeton.edu)

Laura Booth

Department of Ecology, Evolution and Environmental Biology  
Columbia University, New York City, New York  
[lsb2137@columbia.edu](mailto:lsb2137@columbia.edu)

Abraham Kiejar

Department of Ecology and Evolutionary Biology  
Princeton University, Princeton, New Jersey  
[akielar@princeton.edu](mailto:akielar@princeton.edu)

## Abstract

Herbivory is a prominent top-down force shaping the landscape of semi-arid savannas in East Africa. Herbivores participate in seed dispersal both by ingesting and defecating the seeds of endozoochorously-dispersed plants and by translocating the seeds of exozoochorously-dispersed plants. In this study, we sought to determine how the extinction of large mammalian herbivores would affect the abundance of five focal species of plants that use fruiting as their primary dispersal mechanism. We also examined how the absence of large mammalian herbivores affected seed predation by small mammals. We counted the number of individual plants for each of the five species in three short-term (5 year old) exclusion blocks and one long-term (15 year old) exclusion block. We found that total abundance of fleshy-fruited species increased as successive levels of large mammalian herbivores were excluded and as the duration of herbivore exclusion increased. Within species, we found that *C. orthacantha* and *S. campylacanthum* increased in the absence of herbivores, while *O. stricta* decreased in the absence of herbivores. *B. aegyptiaca* and *B. albitrunca* did not exhibit differences in abundance between different levels of herbivore exclusion. We found that small mammals demonstrated a preference for *B. albitrunca* and *O. stricta* seeds, which were consumed primarily by the fringe-tailed gerbil, *Gerbilliscus robustus*. Understanding the interactions between herbivores and vegetation is vital to conserving plant communities as well as understanding how they may change in the future.

## Author's Note

We thank and acknowledge R.M. Pringle, T.C. Coverdale, S. Kurukura, Mpala Research Centre, and the Tropical Biology and Sustainability program of Columbia and Princeton Universities for facilitating this research.

**Keywords:** Seed dispersal mechanisms, herbivore exclusion, seed bank, seed predation pressure, cafeteria trial

## 1. Introduction

Herbivory is a prominent top-down force that shapes the landscape of semi-arid savannas in East Africa by influencing seed dispersal and plant establishment, recruitment, and mortality (Augustine and McNaughton 2004, Sankaran et al. 2013). Large mammalian herbivores (> 5 kg) consume different components of the same plant; for example, mega-herbivores (e.g. elephants) typically consume plants of the understory and small woody plants whole, whereas meso-herbivores (e.g. impala) may consume only the fruits, thereby acting as seed dispersers (Pringle et al. 2014). Extinction of large mammalian herbivore species that selectively consume seeds and fruits may reduce the overall abundance of fleshy-fruited plant species by limiting the dispersal of seeds and, in turn, lowering rates of recruitment and establishment (Pringle et al. 2014, Janzen et al. 1984). Reduction in the abundance of fleshy-fruited species could have impacts across trophic levels, since smaller herbivores forage on the leaves and seeds of fleshy-fruited plants (Keesing 2000, Goheen et al. 2004). However, reductions in abundance may not be immediately apparent because of delayed plant responses to diminishing browsing pressure by large herbivores (Pringle et al. 2014).

In this study, we explored whether the abundance of five fleshy-fruited species decreases in the absence of large mammalian herbivores, the amount of time it takes for this effect to manifest, and whether the loss of large herbivores alters how smaller herbivores feed on the reproductive structures of fruited plant species by focusing on three primary questions: 1) Does exclusion of large mammalian herbivores reduce the abundance of fleshy-fruited plant species? We hypothesize that the abundance of fleshy-fruited plants experiencing reduced browsing pressure will either increase because the net effect of herbivore presence is negative (browsing pressure is more deleterious than animal dispersal is beneficial) or decrease because the net effect of herbivore presence is positive (browsing pressure is less deleterious than animal dispersal is beneficial). 2) Do differences in the abundance of fleshy-fruited species depend on the duration of the exclusion of large mammalian herbivores? We expect one of three scenarios to emerge over time: abundance will increase uniformly over time because the net effect of herbivore presence is negative, abundance will decrease uniformly over time because the net effect of herbivore presence is positive, or abundance will increase on short time scales (due to reduction in browsing pressure) and decrease on long time scales (due to diminished reproductive resources in the seed bank). We do not see a biologically viable explanation for the fourth scenario of an initial decrease in abundance followed by an increase on long time scales. 3) Does seed predation pressure by small mammals increase when large mammalian herbivores are excluded from the study system? Because rodent densities are known to increase in the absence of large mammalian herbivores and because rodents are known seed predators (Keesing 2000, Goheen et al. 2004), we expect the proportion of seeds taken by small mammals to be highest where all large mammalian herbivores are excluded.

Knowing the answers to these questions will increase our understanding of how herbivore diversity and foraging strategies structure plant communities. Our findings can be applied to future management of plant communities in the context of widespread declines in the populations of large mammalian herbivores, both in East Africa and in other tropical savanna ecosystems. (Wiitemeyer 2011, Craigie et al. 2010, Parker et al. 1989, Hoare et al. 1999, Barnes 1996).

## 2. Methods

### 2.1 Study Sites and System

Our study sites were located on red soil in the southern region of the Mpala Research Center (MRC) (0°17'N, 37°52'E) which receives approximately 650-700mm of rainfall annually. We used the three southernmost blocks of herbivore exclosures in the Ungulate Herbivory Under Rainfall Uncertainty (UHURU) experiment, which was established in 2008 (for details on the experimental design of UHURU, see Goheen et. al 2013), and exclosures established by D.J. Augustine in 1999 (for details see Augustine and McNaughton 2004). In UHURU, each block of exclosures includes four 100m x 100m plots. These include one control (no herbivores excluded) and three treatment plots: one mega-herbivore exclusion (elephants and giraffes excluded), one meso-herbivore exclusion (elephants, giraffes, and impala excluded), and one total exclusion (elephants, giraffes, impala, and dik-diks excluded). All plots in UHURU are accessible to rodents and hares (Pringle et al. 2014). In the Augustine exclosures, each block includes one 70m x 70m herbivore exclusion treatment adjacent to a 70m x 70m control plot. The treatment in Augustine is comparable to the meso-herbivore exclusion in UHURU because both exclude herbivores approximately the size of impala and above.

Our study focused on five species of fleshy-fruited plants: *Cyatbula orthacantha*, *Solanum campylacanthum*, *Opuntia stricta*, *Boscia albitrunca* and *Balanites aegyptiaca*. These species were chosen as representatives of several different categories of plants within the umbrella of fruiting species. *C. orthacantha*, *S. campylacanthum*, and *O. stricta* are understory species, whereas *B. albitrunca* and *B. aegyptiaca* are trees. *C. orthacantha* is a forb, *S. campylacanthum* is a woody shrub, and *O. stricta* is an invasive cactus originally from North America. Finally, *C. orthacantha* is dispersed exo-zoochorously via its “burr” fruiting structure, whereas each of the other four focal species is dispersed endo-zoochorously.

### 2.2 Data Collection

To assess the effects of large herbivore exclosure treatments on plant abundance, we sampled three blocks (three types of herbivore exclosure treatment and one control each) in the UHURU sites, yielding three replicates for each treatment and for the control. Within each treatment, we performed plant surveys along two transects 60m long and spaced 20m apart. Along each transect, we counted the number of *C. orthacantha*, *S. campylacanthum*, *O. stricta*, *B. albitrunca*, and *B. aegyptiaca* within 2m on either side of the transect.

To assess effects of the duration of large herbivore exclusion on plant abundance, we sampled one of the Augustine blocks containing the herbivore exclusion treatment and the control plot, yielding one data point each for the Augustine treatment and control. In both the treatment and the control, we conducted transects using the same procedure as described for the UHURU plots.

To assess seed predation pressure under different herbivore exclusion treatments, we conducted a cafeteria trial experiment in each of the four plot types in two blocks of UHURU. We placed 3, 3, 10, and 20 *B. aegyptiaca*, *B. albitrunca*, *O. stricta*, and *S. campylacanthum* seeds, respectively, and 3 whole fruits of each species in petri dishes at the center of each 100m x 100m plot. The number of seeds was chosen based on seed size, where *S. campylacanthum* seeds were ~1mm x 1mm, *O. stricta* were ~3mm x 3mm, and both *B. aegyptiaca* and *B. albitrunca* seeds were approximately the same size as their fruits (See Table 1). We standardized the microhabitat of the cafeteria trial by choosing an area with open ground on which to place the seeds and fruits, shielded by moderate grassy cover nearby. We avoided densely wooded areas, which could obscure the trial from view, as well as large patches of bare ground, which could deter small mammals based on increased risk of predation. Our trial ran for 48 hours total, and we checked each location after 24 hours. We collected data on the number of seeds removed over the course of each day. We collected video footage of seed predators using Bushnell infrared camera traps placed on the ground in front of the seeds and fruits and used the videos to identify seed predator species.

## 2.3 Statistical Analyses

We analyzed data using JMP Pro 10 and R statistical software. We used an ANOVA in JMP to test for effects of herbivore exclusion treatment on total abundance of fleshy-fruited species in the UHURU and Augustine plots. We used post-hoc Tukey HSD analyses to compare specific treatments. In R, we used negative binomial generalized linear models, which are appropriate for non-normally distributed data that is over-dispersed, to assess species-level differences in abundance across treatments in UHURU. We used single-sample tests in JMP to look for effects of duration of herbivore exclusion on species-level differences in abundance. In these tests, we specified the mean to be the value obtained by averaging the two transects in the Augustine plot and the standard deviation to be the standard deviation obtained from that average.

## 3. Results

### 3.1 Total Abundance

We found that the abundance of fleshy-fruited species in UHURU varied across different levels of herbivore exclusion. To normalize the data, we used a square root transformation and found a general trend of increased plant abundance as additional species are excluded (one-way ANOVA,  $F_{5,22}=3.60$ ,  $N=28$ ,  $P=0.02$ ). Average abundance was significantly higher in the total exclusion than in the control (Tukey HSD,  $P=0.04$ ) and was higher in the meso- and mega-herbivore exclusions than in the control (See Figure 1).

### 3.2 Species-Level Abundance

For species-level statistics, please refer to the respective panels in Figure 2. As with total abundance, both *C. orthacantha* and *S. campylacanthum* were significantly more abundant in the total herbivore exclusion treatment than in the control plot and had higher abundance in the mega- and meso-exlosures (See Figures 2C and 2E, respectively). *S. campylacanthum* was also significantly more abundant in the mega-herbivore and meso-herbivore exclosures than in the control (See Figure 2E). *O. stricta* was significantly more abundant in the control than in the mega-, meso-, and total exclusion treatments (See Figure 2D). We found no statistically significant differences in abundance across treatment types for either *B. aegyptiaca* or *B. albitrunca* (See Figure 2A and 2B, respectively). We found significant effects of block for both *C. orthacantha* (negative binomial GLM,  $N=3$ ,  $DF=2$ ,  $P=0.01$ ) and *S. campylacanthum*, (negative binomial GLM,  $N=3$ ,  $DF=2$ ,  $P=0.02$ ), indicating that abundances of these species were not the same across the three blocks that we sampled. However, because we are interested in variance in abundance driven by the type of treatment rather than by sampling block, these differences did not prohibit analyses at the treatment level.

### 3.3 Abundance Over Time

We found that the duration of exclosures did not affect the overall abundance of fleshy-fruited plant species. There were no statistically significant differences between abundance in the Augustine treatment and the UHURU meso-herbivore exclosure (See Figure 1). At the species level, we found that overall abundances of *O. stricta* and *S. campylacanthum* were higher in the UHURU meso-herbivore exclosure than in the Augustine treatment (Single sample tests,  $N=3$ ,  $DF=2$ ,  $P_{O. stricta}=0.02$ ,  $P_{S. campylacanthum}<0.0001$ ; (See Figure 3D and 3E, respectively). For *O. stricta*, this difference was likely driven by the complete absence of *O. stricta* in the Augustine treatment. We found no statistically significant differences between the Augustine and UHURU plots for *B. aegyptiaca* and *B. albitrunca* (See Figure 3A, 3E).

### 3.4 Seed Predation

*B. albitrunca* and *O. stricta* had the highest proportion of seeds taken (See Figure 4). *B. albitrunca* seeds were removed in the control, mega-, and total exclusion treatments, and *O. stricta* seeds were removed in all four treatments. seeds taken. Only in the total exclosure treatment were seeds of all five focal species removed. Seed predators included yellow-necked spur fowl (*Francolinus leucoscepus*), common bulbul (*Pycnonotus barbatus*), fringe-tailed gerbil (*Gerbilliscus robustus*), spotted morning thrush (*Chichladusa g. guttata*), and northern pouched mouse (*Saccostomus mearnsi*) (See Table 1). *G. robustus* was the only species sighted more than once (See Table 1).

## 4. Discussion

We found that over the course of both five and fifteen years, plants producing fleshy fruits increase in overall abundance as successive levels of large mammalian herbivores are excluded (See Figure 1). Because this trend appears to remain constant over time, we find that these results support the hypothesis that consumption by herbivores is more detrimental to parent plants than animal dispersal is beneficial, implying that fleshy-fruited plant species will increase in the absence of large herbivores. A major limitation to these conclusions was our inability to replicate the Augustine treatments; our conclusions about abundance trends over time would be strengthened by additional samples in the 15-year old exclosures, and future studies should not only increase replicates but sample more than two different ages of plots to better understand the effects of duration of herbivore exclusion on fruiting plant abundance.

At the species level, certain fruiting species were affected more by large mammalian herbivores than others. *C. orthacantha* and *S. campylacanthum*—both understory species—were significantly more abundant when all herbivores were excluded in comparison to the control. For *C. orthacantha*, this difference appears to be driven by the absence of browsing pressure by dik-diks, since a significant increase occurs only in the total herbivore exclusion. For *S. campylacanthum*, abundance was significantly increased at each level of treatment and does not appear to be related to the exclusion of a particular herbivore. Conversely, *B. albitrunca* and *B. aegyptiaca*—the two tree species—showed no differences in abundance across the different treatments; it is possible that any differences driven by treatment were obscured by the generally low abundance of these species. Future studies could index each species' relative abundance against the background woody cover in each treatment to ameliorate this problem.

The only species that had higher abundance in the control than in any of the UHURU treatments was *O. stricta* (See Figure 2D), which suggests that *O. stricta*, unlike the other understory species, is benefitted more by endozoochorous dispersal than it is damaged by herbivore consumption. This result agrees with the observation that *O. stricta* is also the most heavily physically defended species in the subset of plants that we studied. It is worth noting that the behavior of *O. stricta*—an invasive species from North America—is opposite from our other focal species, which are all native to Kenya. While *O. stricta* is extraordinarily well-adapted to the harsh abiotic conditions and intense herbivory of Africa, its high investment in physical defense and fruiting structures may not prove advantageous in a future where large mammalian herbivores are scarce.

We found that small mammals preferred *B. albitrunca* and *O. stricta* seeds over all other species (See Figure 4, Table 1). This suggests that, in a scenario where small mammal populations increase in the absence of large mammals, *O. stricta* populations may be further reduced due to heavy predation of seeds by increasing populations of small mammals (Keesing 2000, Goheen et. al 2004). *B. albitrunca*, which was not affected by the exclusion of large mammalian herbivores, represents a more stable seed source. Because of the indirect effects of large mammalian herbivores on seed predation, the loss of large mammalian herbivores has implications for food stability across trophic levels. Furthermore, extinction of large mammalian herbivores could cause permanent changes to the mosaic of plant and animal species characterizing savanna bushland by altering the species that consume and disperse the seeds. Maintaining the current balance of *C. orthacantha*, *S. campylacanthum*, and *O. stricta* may

be particularly difficult because their populations are driven in opposite directions by the removal of large mammalian herbivores. Despite the various negative consequences of large mammalian herbivore extinctions, our study indicates that there may be one benefit: diminishing populations of the now-prolific invasive species, *O. stricta*.

## Bibliography

- Augustine, D.J. and McNaughton, S.J. (2004). Regulation of shrub dynamics by native browsing ungulates on East African rangeland. *Journal of Applied Ecology*. 41:45-58.
- Barnes, R. F. W. (1996). The conflict between humans and elephants in the central African forests. *Mammal Review*, 26(2-3), 67-80.
- Craigie, I. D., Baillie, J. E., Balmford, A., Carbone, C., Collen, B., Green, R. E., & Hutton, J. M. (2010). Large mammal population declines in Africa's protected areas. *Biological Conservation*, 143(9), 2221-2228.
- Goheen, J. R., Keesing, F., Allan, B. F., Ogada, D., & Ostfeld, R. S. (2004). Net effects of large mammals on Acacia seedling survival in an African savanna. *Ecology*. 85(6), 1555-1561.
- Goheen, J. R., Palmer, T. M., Charles, G. K., Helgen, K. M., Kinyua, S. N., Maclean, J. E., ... & Pringle, R. M. (2013). Piecewise disassembly of a large-herbivore community across a rainfall gradient: the UHURU experiment. *PloS one*, 8(2), e55192.
- Hoare, R. E., & Du Toit, J. T. (1999). Coexistence between people and elephants in African savannas. *Conservation Biology*. 13(3), 633-639.
- Keesing, F. (2000). Cryptic consumers and the ecology of an African savanna. *BioScience*, 50(3), 205-215.
- Parker, I. S., & Graham, A. D. (1989). Elephant decline (Part I) downward trends in African elephant distribution and numbers. *International Journal of Environmental Studies*. 34(4), 287-305.
- Parker, I. S., & Graham, A. D. (1989). Elephant decline: downward trends in African elephant distribution and numbers (Part II). *International Journal of Environmental Studies*, 35(1-2), 13-26.
- Pringle, R. M., J.R. Goheen, T.M. Palmer, G.K. Charles, E. DeFranco, R. Hohbein, A.T. Ford, and C.E. Tarnita. (2014). Low functional redundancy among sympatric large herbivores in regulating an encroaching shrub (*Solanum campylacanthum*) in African savanna. *Proceedings of the Royal Society B*. In press.
- Sankaran, M., Augustine, D. J., & Ratnam, J. (2013). Native ungulates of diverse body sizes collectively regulate long-term woody plant demography and structure of a semi-arid savanna. *Journal of Ecology*, 101(6), 1389-1399.
- Weltzin, J. F., Archer, S., & Heitschmidt, R. K. (1997). Small-mammal regulation of vegetation structure in a temperate savanna. *Ecology*. 78(3), 751-763.



Wittemyer, G. (2011). Effects of economic downturns on mortality of wild African Elephants. *Conservation Biology*, 25(5), 1002-1009.

## Figures

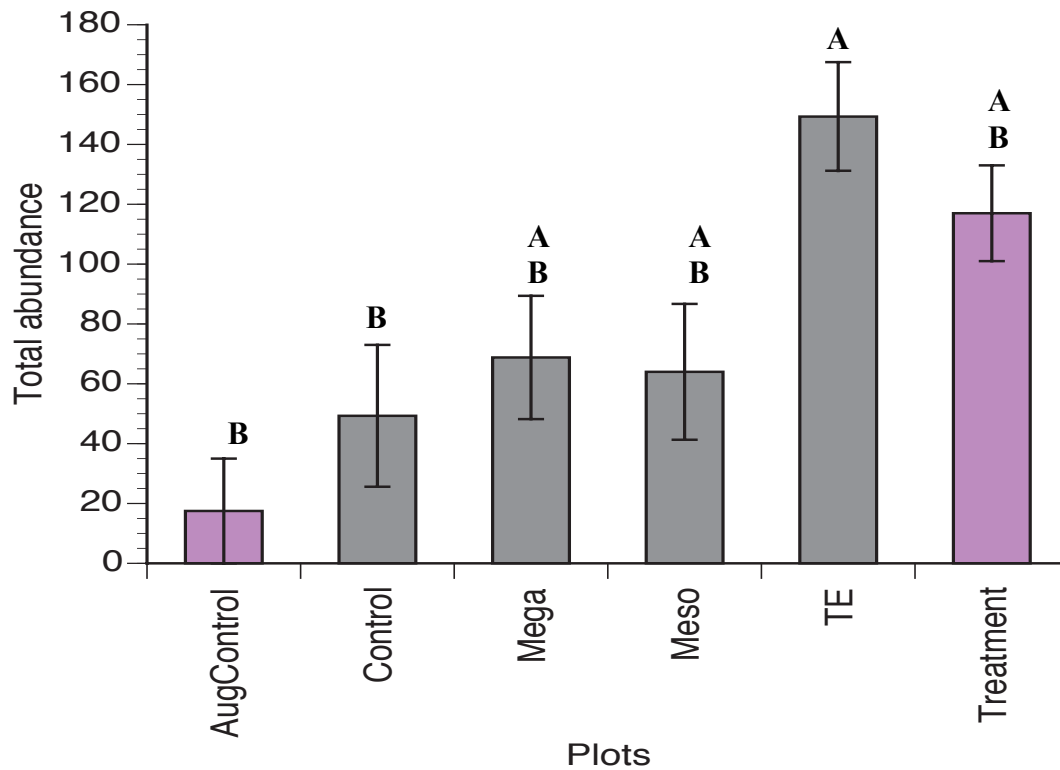


Figure 1: Total abundance of all plant species in the Augustine control and treatment plots (shown in purple) and the UHURU control, mega-, meso- and total exclusion plots (shown in gray). Different letters indicate that the categories were significantly different. Error bars represent one standard error from the mean. (N=28; P=0.0157).

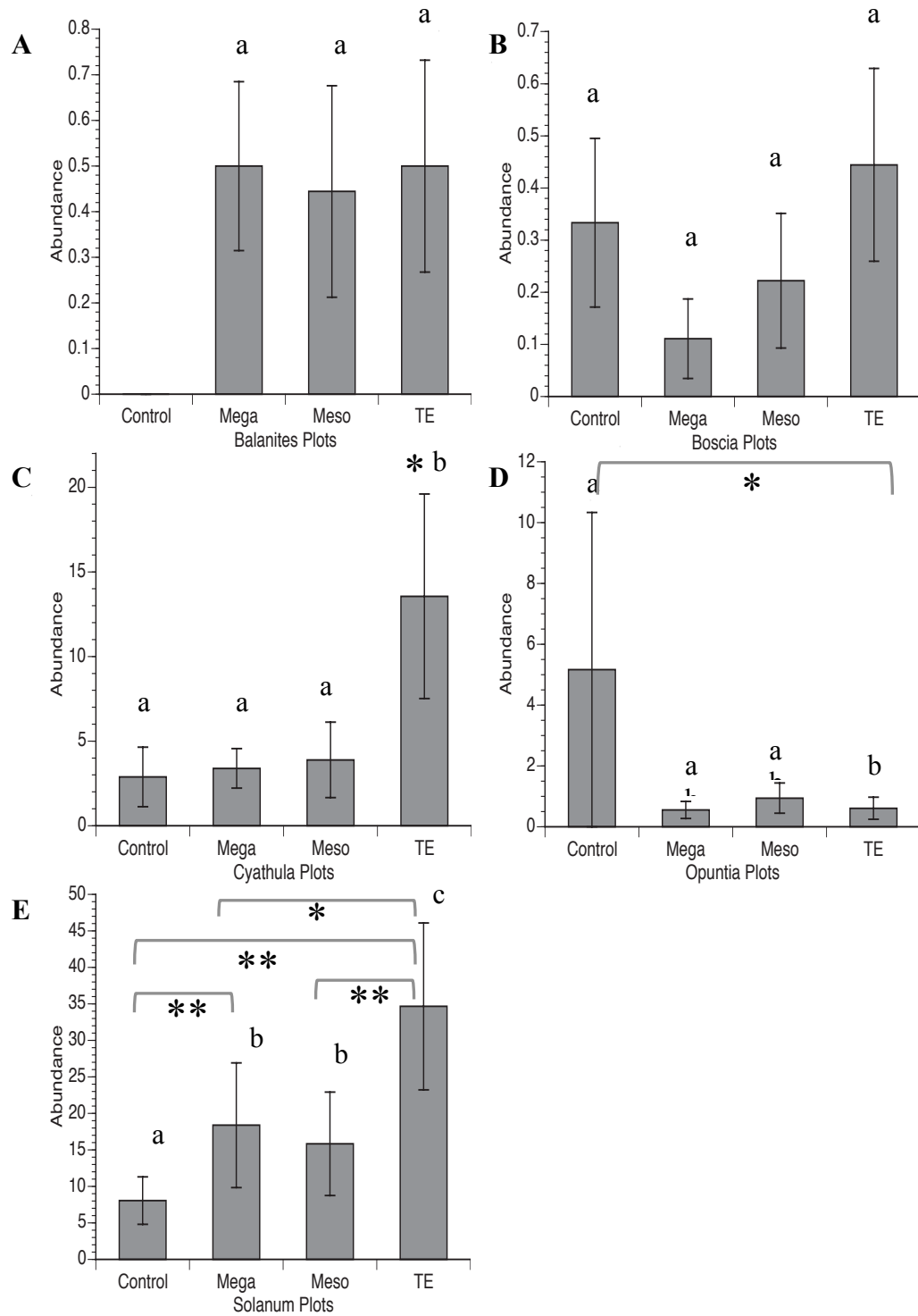


Figure 2: Abundance of plant species in the UHURU plots. Different letters indicate that the categories were significantly different. Error bars represent one standard error from the mean. \* P<0.05; \*\*P<0.01; \*\*\*P<0.0001.

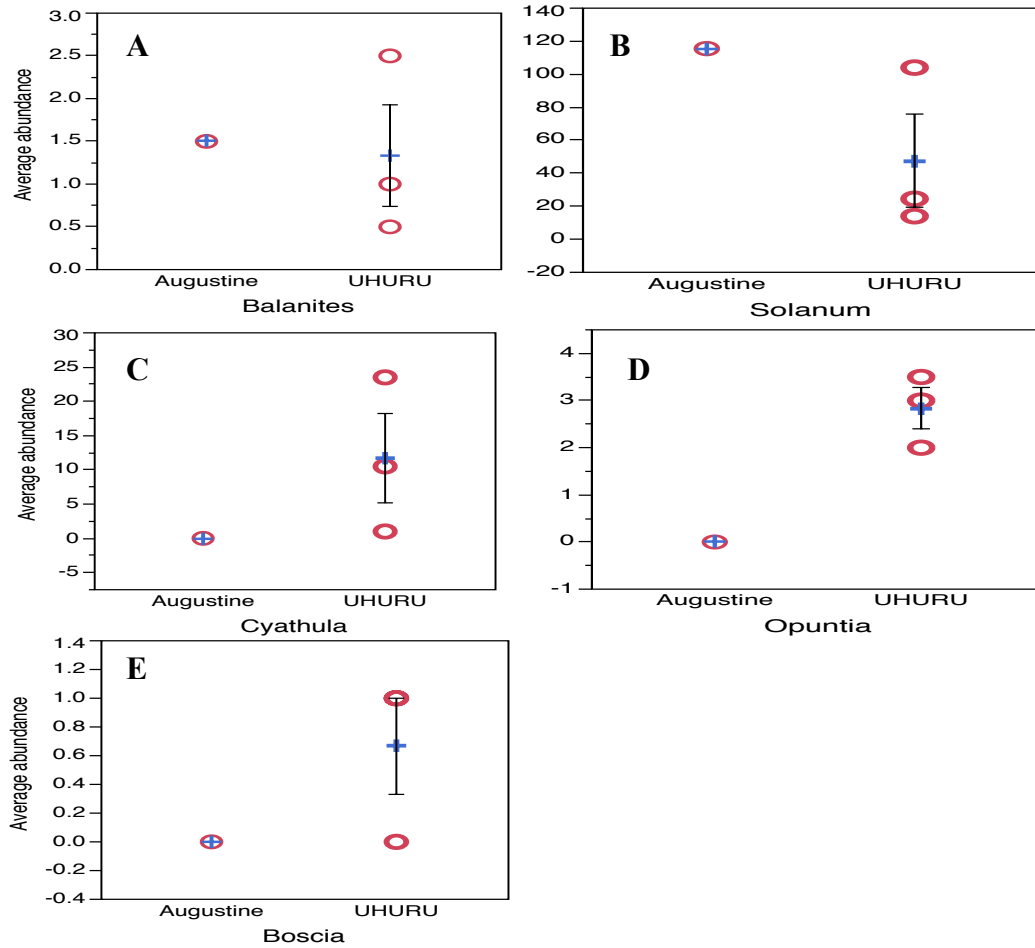


Figure 3: Average abundance of (A) *B. aegyptiaca*, (B) *S. campylacanthum*, (C) *C. orthacantha*, (D) *O. stricta* and (E) *B. albitrunca* in the Augustine treatment and UHURU meso-herbivore plot. The red circles represent the average of the two transects within each plot (UHURU) or the observed value for the plot (Augustine), while the blue crosses represent the mean of the plots sampled.

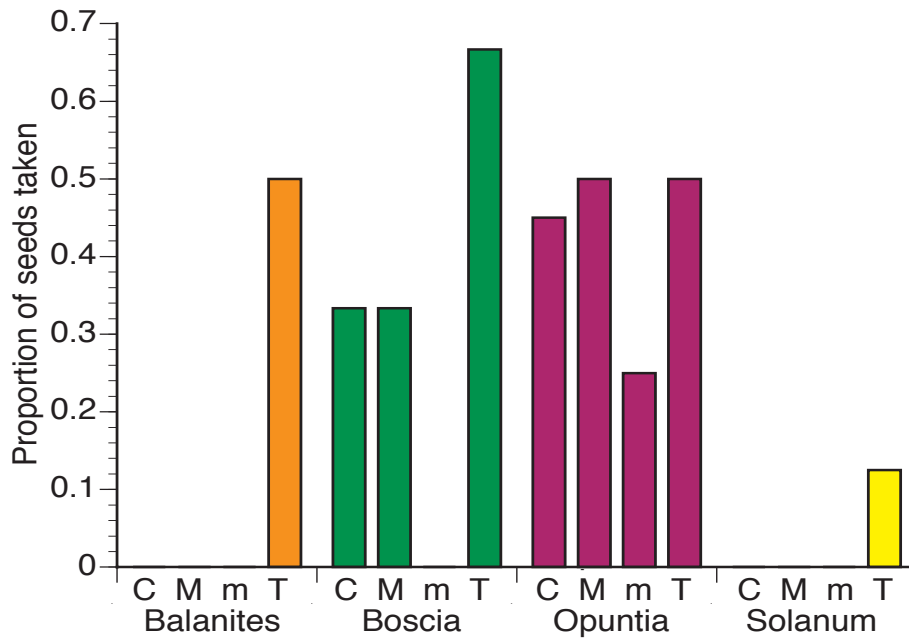


Figure 4: Proportion of *B. aegyptiaca*, *S. campylacanthum*, *C. orthacantha*, *O. stricta* and *B. albitrunca* seeds taken from the control (C), mega- (M), meso- (m), and total exclusion (T) plots.

## Tables

Table 1: Seed Predation in UHURU by small mammals

SPECIES OF PLANT	FRUIT DESCRIPTION	SEED PREDATOR	# OF SIGHTINGS
Common Prickly Pear, <i>Opuntia stricta</i>	Roughly cone-shaped, purple ~ 25mm wide at base, 10mm wide at tip, and 55mm tall	Fringe-tailed gerbil, <i>Gerbilliscus robustus</i>	2
		Yellow-necked Spur Fowl, <i>Francolinus leucoscepus</i>	1
<i>Boscia albitrunca</i>	Spherical, green ~ 12mm wide x 14mm tall	Northern pouched mouse, <i>Saccostomus mearnsi</i>	1
		Fringe-tailed gerbil, <i>Gerbilliscus robustus</i>	2
		Yellow-necked Spur Fowl, <i>Francolinus leucoscepus</i>	1
		Common bulbul, <i>Pycnonotus barbatus</i>	1
<i>Balanites aegyptiaca</i>	Oblong, orange when ripe ~15mm wide, 20mm tall	Fringe-tailed gerbil, <i>Gerbilliscus robustus</i>	1
<i>Solanum campylacanthum</i>	Spherical, yellow, ~ 24mm wide x 22m tall	Spotted Morning Thrush, <i>Chicbladusa g. guttata</i>	1