

# Elephants in the understory: opposing direct and indirect effects of consumption and ecosystem engineering by megaherbivores

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**Abstract.** Positive indirect effects of consumers on their resources can stabilize food webs by preventing overexploitation, but the coupling of trophic and non-trophic interactions remains poorly integrated into our understanding of community dynamics. Elephants engineer African savanna ecosystems by toppling trees and breaking branches, and although their negative effects on trees are well documented, their effects on small-statured plants remain poorly understood. Using data on 117 understory plant taxa collected over 7 yr within 36 1-ha experimental plots in a semi-arid Kenyan savanna, we measured the strength and direction of elephant impacts on understory vegetation. We found that elephants had neutral effects on most (83–89%) species, with a similar frequency of positive and negative responses among the remainder. Overall, estimated understory biomass was 5–14% greater in the presence of elephants across a range of rainfall levels. Whereas direct consumption likely accounts for the negative effects, positive effects are presumably indirect. We hypothesized that elephants create associational refuges for understory plants by damaging tree canopies in ways that physically inhibit feeding by other large herbivores. As predicted, understory biomass and species richness beneath elephant-damaged trees were 55% and 21% greater, respectively, than under undamaged trees. Experimentally simulated elephant damage increased understory biomass by 37% and species richness by 49% after 1 yr. Conversely, experimentally removing elephant damaged branches decreased understory biomass by 39% and richness by 30% relative to sham-manipulated trees. Camera-trap surveys revealed that elephant damage reduced the frequency of herbivory by 71%, whereas we detected no significant effect of damage on temperature, light, or soil moisture. We conclude that elephants locally facilitate understory plants by creating refuges from herbivory, which countervails the direct negative effects of consumption and enhances larger-scale biomass and diversity by promoting the persistence of rare and palatable species. Our results offer a counterpoint to concerns about the deleterious impacts of elephant “overpopulation” that should be considered in debates over wildlife management in African protected areas: understory species comprise the bulk of savanna plant biodiversity, and their responses to elephants are buffered by the interplay of opposing consumptive and non-consumptive interactions.

**Key words:** African savannas; associational defenses; disturbance; elephant damage; extinction; facilitation; herbivory; ivory poaching; *Loxodonta africana*; megafauna; plant diversity; wildlife management.

## INTRODUCTION

Elephants (*Loxodonta africana*) exert powerful influences on the structure and function of African savanna ecosystems due to their ability to uproot and consume entire plants and topple or otherwise alter the physical structure of trees (Laws 1970, Dublin et al. 1990, Asner and Levick 2012, Fig. 1A). In particular, the negative effects of elephant browsing on tree survivorship and cover, and their interactions with fire and climate, have received intensive study (e.g., Buss 1961, Laws 1970, Holdo 2007, Daskin et al. 2016). These effects have led

to concern about the effects of elephants on plant diversity and the conservation of native plant species and have fueled debates over whether and how to control elephant population density (Fayer-Hosken et al. 2000, Pimm and van Aarde 2001, Guldemon and Van Aarde 2008). Between 1967 and 1994, for example, more than 16,000 elephants were culled in the Kruger National Park, South Africa, due to “concern about the effects that these animals were having on vegetation” and other wildlife (Owen-Smith et al. 2006).

Elephants do not have uniformly negative ecological impacts, however, and have been shown to benefit other animal species. Damage to tree canopies, in particular, increases local and landscape-scale habitat heterogeneity, and elephants can enhance the availability of food and

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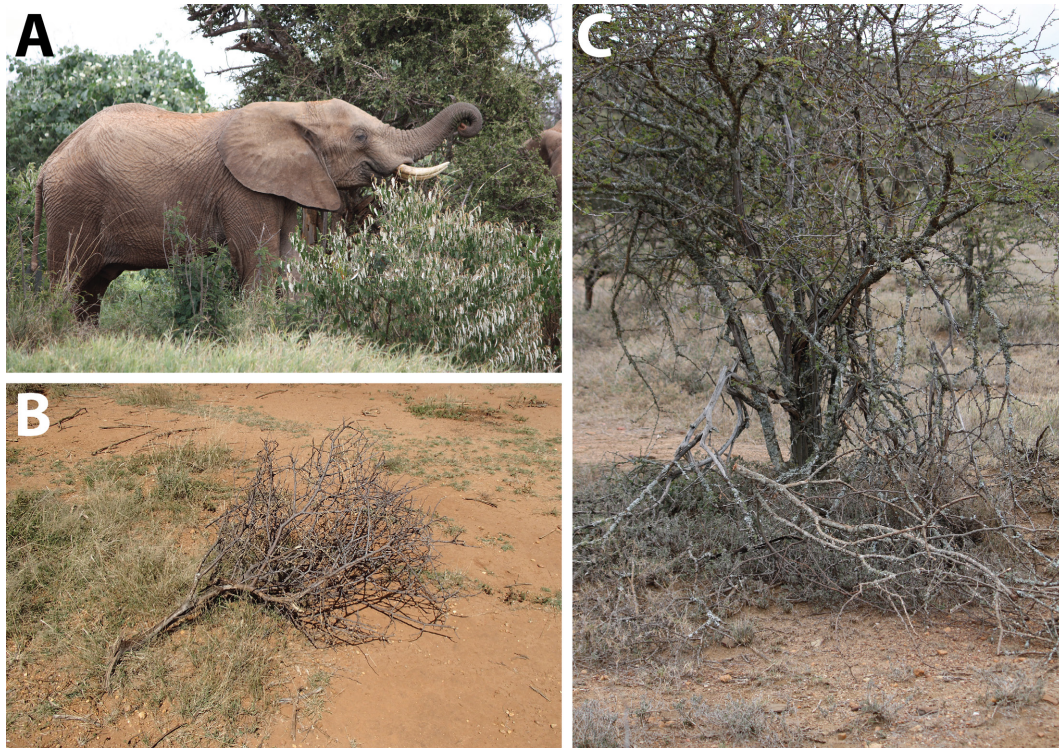


FIG. 1. Elephant damage and its consequences. (A) An adult elephant feeds on a *Balanites glabra* at Mpala Research Centre, Kenya. (B) An *Acacia mellifera* branch fully detached by elephants lies in open habitat. (C) Damaged branches that have remained attached to the tree canopy following elephant browsing.

shelter for co-occurring species by acting as disturbance agents (“habitat facilitation” sensu Menge 1995, see also Sousa 1984). For example, the breaking of tree trunks and toppling of adult trees (Fig. 1B, C) benefits smaller mammalian herbivores by increasing access to high-canopy browse (Midgley et al. 2005, Kohi et al. 2011, Valeix et al. 2011) and by maintaining open habitat with high grass productivity and reduced predation risk (Laws 1970, Dublin et al. 1990). Similarly, bark peeling and branch splitting can increase microhabitat heterogeneity and create refuges for small vertebrates and insects (Pringle 2008, Nasser et al. 2011, Pringle et al. 2015, Daskin and Pringle 2016). For these reasons, elephants are among the most important ecosystem engineers in savannas (Laws 1970, Jones et al. 1994), though other megaherbivores such as rhino (Waldram et al. 2008, Croomsigt and te Beest 2014) and hippo (Moore 2006) affect habitat structure and resource availability in analogous ways.

Perhaps surprisingly given the attention to their effects on trees and other animals, elephants’ interactions with understory plants—which can account for >70% of plant diversity in semi-arid savannas (Seibert and Scogings 2015)—remain little studied (but see, e.g., Augustine 2003, Veldman et al. 2013, Pringle et al. 2014, Louthan et al. 2013). Moreover, although elephants are often cited as a threat to the conservation of endemic plants and the maintenance of pastoral lands (Glover 1963, Johnson et al.

1999, Landman et al. 2014), many such reports only consider the direct (i.e., consumptive) effects of elephant herbivory. When feeding, however, elephants both consume plant material (hereafter “browsing”) and modify the physical structure of vegetation (hereafter “elephant damage”; Fig. 1). Elephants may thus have neutral or even positive net effects on understory plants if the indirect effects of habitat modification (over)compensate for the direct effects of consumption (Veldhuis 2016).

One likely mechanism by which elephant damage may facilitate understory plants is the creation of associational refuges against other mammalian herbivores (Kéfi et al. 2012). We follow Milchunas and Noy-Meir (2002) in using the term “associational refuge” to describe facilitative plant-plant interactions in which focal individuals experience reduced herbivory damage by growing in close proximity to neighbors that physically impede herbivore access. As ecosystem engineers capable of modifying canopy architecture, elephants may modulate the strength or prevalence of associational refuges, thereby locally enhancing understory biomass and diversity (Fig. 1; see also Callaway et al. 2005). If sufficiently frequent and strong, these local interactions may scale up: associational refuges are critical for the persistence of palatable species in various ecosystems and have been shown to increase plant-community robustness (sensu Levin and Lubchenco 2008) to drought and overgrazing (Hay 1986, Milchunas



and Noy-Meir 2002, Rebollo et al. 2002, Soliveres et al. 2015). Given the high large-herbivore biomass in many African savannas, the creation of associational refuges composed of damaged branches—many of which are defended by thorns or spines that further impede herbivore access—may reduce the risk of local extinction from overgrazing and help to maintain diverse plant communities by enhancing habitat heterogeneity (Horn 1975, Connell 1978). Furthermore, non-trophic facilitation via the creation of such associational refuges may stabilize the effect of elephants on understory food plants by reducing the likelihood of runaway consumption (Veldhuis 2016). Alternatively, elephant damage might adversely affect understory plant communities by, for example, decreasing light or water availability beneath tree canopies (Belsky 1994, Caylor et al. 2005), thereby exacerbating the negative direct effects of consumption. Evaluating these alternatives requires focused investigation of how elephants affect understory plant communities via both direct and indirect mechanistic pathways (Jonsson et al. 2010, van Coller et al. 2013).

We used a network of 1-ha herbivore-exclosure and control plots to evaluate the net effects of elephants on understory communities in a region where elephant densities (and the prevalence of elephant damage) have increased in recent decades. We further used manipulative field experiments and surveys at smaller scales to ascertain the extent to which elephants indirectly shape understory plant communities by damaging tree canopies. Specifically, we hypothesized that understory plant biomass and diversity would be greater beneath canopies of elephant-damaged trees (Fig. 1C) due to physical inhibition of foraging by large mammalian herbivores, and that the removal of elephant-damaged branches would reverse this effect by restoring access to foraging ungulates.

## METHODS

### *Study site*

The Mpala Research Centre and Conservancy (MRC), in Laikipia, Kenya encompasses 20,000 ha of savanna with a mean annual rainfall of ~600 mm. Most of MRC is underlain by infertile red alfisols that support a tree community dominated by three *Acacia* species (*A. brevispica*, *A. etbaica*, and *A. mellifera*), along with a discontinuous understory of grasses and forbs (Augustine 2003). More than 20 species of large mammalian herbivores (>5 kg, hereafter “LMH”) occur at MRC (Goheen et al. 2013). Elephant densities have increased in Laikipia over the past 25 yrs, reaching up to 2 individuals/km<sup>2</sup> (Augustine and McNaughton 2004, Litoroh et al. 2010).

### *Understory responses to elephant exclusion*

To quantify the net effects of elephants on the abundance of understory plant species, we assessed the response of 117 species of grasses, forbs, and subshrubs to the

presence of elephants using 7 yr (2008–2014) of data on understory composition from the UHURU large-herbivore exclosure experiment (Pringle 2012, Goheen et al. 2013, Kartzin et al. 2014). UHURU comprises 36 size-selective 1-ha LMH-exclosure and control plots in three locations along a 22-km transect from north to south within MRC (Goheen et al. 2013). At each location, there are three replicate blocks of four treatments: full exclosure (–all ungulate herbivores), mesoherbivore exclosure (–species ≥ 10 kg), megaherbivore exclosure (–giraffes and elephants) and unfenced controls.

We used data from 13 biannual surveys of plant biomass and community composition to assess impacts of elephant browsing and rainfall on understory plant assemblages with hierarchical Bayesian joint species distribution models (JSDM; see Clark et al. 2014, Pollock et al. 2014). In the first JSDM, we compared plant responses between megaherbivore exclosures ( $n = 9$ ) and unfenced plots ( $n = 9$ ); although this analysis potentially reflects impacts of both elephants and giraffes, the former should dominate the effect because giraffes rarely forage (<10% of feeding time) on understory plants (du Toit and Olf 2014, O'Connor et al. 2015). In a second, complementary JSDM analysis, we included data from all plots ( $n = 36$  total) and used elephant-dung counts rather than exclosure treatment as a proxy for relative elephant abundance, which accounts more finely for both natural and experimentally induced variation in elephant activity levels among UHURU treatments, blocks, and years. Dung counts are a reliable index of relative elephant abundance, and are typically no less accurate or precise than direct counts (Barnes 2001).

For both JSDMs, understory plant composition was monitored using a 10-pin frame placed at 49 evenly spaced, permanently marked points within a central 60 × 60 m grid in each 1-ha plot. Understory biomass at MRC is highly correlated ( $r^2 > 0.87$ ) with measurements of cover based on pin hits (Augustine 2003), and we use the latter as a nondestructive proxy for the former. Rainfall was monitored continuously using a network of tipping-bucket gauges, and dung surveys have been conducted quarterly since 2008, with observers identifying, counting, and crushing all LMH dung piles within three parallel 60 × 5 m belt transects within the plant-sampling grid (Goheen et al. 2013, Kartzin et al. 2014). Elephant dung density was averaged across the dung surveys immediately before and after each biannual vegetation survey.

The JSDMs were constructed as follows. Using a Markov chain Monte Carlo (Gibbs sampling) approach, we first fit a plot-specific rate of occurrence (i.e., number of pin hits/frame) for each plant species in each survey, using a Poisson likelihood. Then, treating the log-transformed species-occurrence rates as a multivariate normal response variable (to account for covariance among species in our subsequent estimates of total plant biomass; see Clark et al. 2014), we regressed understory species occurrence in each plot × survey combination against (1) total rainfall during the previous 6 months,

(2) herbivore-exclusion treatment (a categorical variable), and (3) the interaction of these variables. We then performed the same analysis using elephant dung density (a continuous variable) in lieu of experimental exclosure treatment. Regression parameters were given noninformative priors to allow data to inform parameter estimates (Clark et al. 2014). Regressions for both JSDMs included random effects of the three UHURU sites (north, central, south), block (nested within site), and year to account for potential spatial and temporal autocorrelation. Regressions between elephant presence (exclosure treatment) or abundance (dung density) and the log-transformed occurrence rate for each plant species at average rainfall were fit in R (v. 3.2.1, R Core Development Team 2015) using a Gibbs sampler run for 30,000 iterations. The median value of the resulting distribution of the slope parameters was used as our measure of each plant species' response to elephants. Credible intervals around each estimate (95%) were calculated directly from the modeled posterior distribution for each plant species. In keeping with the conventions of Bayesian inference, we did not subject individual species' responses to null-hypothesis significance testing; instead, each species was considered to have responded "positively" or "negatively" to elephants if its 95% CI was entirely above or below zero, respectively, or "neutrally" if the 95% CI overlapped zero. We also note that the joint Bayesian approach reduces the risk of false positives (Type I error) usually associated with multiple comparisons by utilizing information from the entire pool of species to shift individual estimates with high uncertainty towards the overall mean response (see Gelman et al. 2012 for a more extended technical description). Using the JSDMs, we estimated the mean predicted total plant biomass across (1) herbivore exclosure treatments and (2) the range of observed elephant dung densities at each of three levels of rainfall (the 25th, median, and 75th percentiles of recorded rainfall across all plots and years). Additional details about the JSDM models are provided in Appendix S1.

#### *Understory responses to elephant damaged trees*

Despite the expected negative effects of elephants on plants via direct consumption, our JSDM analyses suggested (see *Results*) that the majority of understory species in UHURU responded neutrally or positively to elephants, and that elephants tended to increase understory biomass across rainfall levels. In light of these results, along with (1) the high frequency of elephant-damaged trees at our study site and in protected areas throughout Africa and (2) recent work demonstrating the strong ecological impact of such ecosystem engineering (Pringle 2008, Nasseri et al. 2011, Pringle et al. 2015), we conducted a series of surveys and smaller-scale experiments between July 2013 and August 2014 to evaluate the effects of elephant damage on understory biomass and species richness (Appendix S1: Fig. S1).

*Experimental design and statistical analysis.*—All experiments described below were conducted in and around the southern and central UHURU plots; locations of surveys are provided in the *Methods* and Appendix S1: Fig. S1. Experimental replicates and treatments were evenly distributed between south and central MRC, and across the three UHURU blocks within each site. For all experiments, we used linear mixed-effects models to compare changes in understory biomass and species richness over 1 yr, with damage-addition or -removal treatment (and UHURU treatment for damage-addition experiment; see below) as fixed effects and site (south vs. central) as a random effect (JMP v. 11.1.1). All surveys included two levels of the primary fixed effect (damaged and undamaged trees) and were analyzed with matched-pairs *t* tests when data were collected from the damaged and undamaged portions of the same tree canopy, or with two-sample *t* tests when samples were collected from separate damaged and undamaged trees (see Appendix S1: Fig. S1). Error terms for all reported means are  $\pm 1$  SEM, with the exception of the results of the previously described JSDMs, which are  $\pm 95\%$  CI.

For all experiments and surveys, understory biomass was measured using three 10-pin frames per replicate (except beneath detached branches, where two 10-pin frames were used), and the number of pin hits per frame was averaged for each replicate prior to analysis. Understory species richness was quantified by visual survey within the damaged and undamaged portions of canopies and beneath detached branches, which were size-matched between damage-addition and -removal and control replicates for all experiments. Seedlings of overstory species were excluded from understory species-richness surveys. For all experiments, data were collected prior to manipulation and again after 1 yr, with changes in biomass and species richness between time points compared as described earlier.

*Observational surveys of elephant damaged trees.*—To quantify the frequency of elephant damage on tree canopies, and hence its potential to indirectly affect understory community composition, we surveyed all trees  $\geq 2$  m height within ten  $200 \times 10$  m transects. For the purposes of this study, trees were classified as "damaged" if they met two criteria: (1) at least one branch  $\geq 2$  cm diameter was damaged by elephants (which is readily distinguishable from other types of damage: Augustine and McNaughton 2004), and (2) an area  $\geq 1$  m<sup>2</sup> beneath the canopy was overlain by damaged branches. All other trees were classified as "undamaged." We also recorded the species, number, and area of branches that had been fully detached from trees by elephants (cf. Fig. 1B).

We quantified the proportion of individual trees of each species damaged by elephants and the mean area of understory habitat beneath damaged trees and detached branches. The most abundant tree species in these transects, *A. etbaica*, was selected as a focal species for additional surveys and experiments. We quantified understory

plant biomass and species richness directly beneath the damaged and undamaged portions of 18 damaged trees (thereby controlling for spatial heterogeneity) and compared estimates using matched-pairs *t* tests. The undamaged area of each canopy was consistently larger than the damaged area (undamaged: 10 m<sup>2</sup>, damaged: 5 m<sup>2</sup>). This difference in area should not influence the biomass estimate but might affect the species-richness estimate; we therefore also compared species richness scaled by area (species/m<sup>2</sup>), although this comparison should be interpreted cautiously because species richness does not scale linearly with area.

**Damage-addition and -removal experiments.**—To test the hypothesized causal relationship between elephant damage and understory plant biomass and species richness, we conducted three manipulative experiments. First, we simulated the common scenario in which elephants completely detach branches from trees and drag them some distance away from the canopy; this also allowed us to test the effect of elephant damage on understory plants in open habitat, away from the influence of trees on factors such as light, soil nutrients, and water availability (Fig. 1B). Using a handsaw, we removed live *A. etbaica* branches and moved them 10 m from the nearest tree canopy ( $n = 20$  branches). Paired control areas without detached branches were established 5 m north of each detached branch. Four experimental replicates were displaced during the experiment and were excluded from analyses along with their corresponding control areas. Due to the smaller size of detached branches relative to tree canopies, we used measurements from just two pin frames to assess biomass in this experiment.

We then simulated elephant damage beneath tree canopies within both unfenced UHURU control plots (“+LMH”,  $n = 6$  plots) and total-exclosure plots that excluded all large mammalian herbivores (“-LMH”,  $n = 6$  plots) to test the prediction that simulated elephant damage would increase biomass and species richness to a greater extent in the presence of large herbivores than in their absence. Within each plot, we randomly selected and assigned four undamaged *A. etbaica* to damage-addition or procedural-control treatments (total  $n = 12$  trees per treatment; Appendix S1: Fig. S1). For each damage-addition tree, a single large branch was cut at the trunk and lowered to the ground beneath the canopy to simulate elephant damage. For each procedural-control tree, a single branch was partially sawed (~25% of branch diameter) and left attached to the tree. Understory biomass and species richness were quantified immediately beneath the treated areas at the onset of the experiment and again after 1 yr. We compared the independent and interactive effects of damage-addition and exclosure treatment on changes in understory species richness and biomass using a mixed-effects model, as described earlier.

Finally, we experimentally removed elephant-damaged branches beneath damaged tree canopies to test whether understory biomass and species richness would decrease

in the absence of associational refuges. We identified 36 damaged *A. etbaica* near but outside the UHURU plots and randomly assigned each to damage-removal or procedural-control treatments (Appendix S1: Fig. S1). Branches in damage-removal replicates were detached with a handsaw and discarded >25 m from the nearest experimental tree. For procedural-control replicates, damaged branches were cut from the tree and immediately returned to their initial position. Biomass and species richness were quantified directly beneath the manipulated areas.

**Mechanisms of facilitation.**—Changes in understory plant communities associated with elephant-damaged trees might arise from any of several non-exclusive mechanisms, including herbivory, light, temperature, and soil moisture. We therefore quantified the effect of canopy damage on each of these attributes to determine which one(s) best explained the observed variation in understory plant biomass and species richness.

To assess herbivory, we quantified grazing scars on two of the most abundant grass species in each location (*Cynodon plechtostachyus* and *Aristida kenyanensis* in south and central MRC, respectively) beneath 24 damaged and 24 undamaged *A. etbaica* ( $n = 8$  grass stems/tree and 12 trees/type/site) and compared the proportion of stems damaged for each grass species (separately) across damaged and undamaged trees. We also used camera traps (Bushnell TrophyCam, model #119435(c); Bushnell Corporation, Overland Park, Missouri, USA) to quantify the incidence of ungulate herbivory beneath five pairs of damaged and undamaged *A. etbaica* trees (three pairs in south, two in central). Cameras were mounted 15 m from each focal tree and recorded three-photo bursts when triggered by an infrared motion sensor. Each camera trap was deployed for ~430 h, yielding >4,700 total photos. We compared the number of LMH feeding beneath damaged and undamaged trees over the duration of the trial.

To assess light transmission to the understory, we measured photosynthetically active radiation (PAR) beneath the canopies of damaged and undamaged *A. etbaica* in south MRC ( $n = 8$  trees/type) with a portable light meter (LightScout Quantum Meter, model #3415F; Spectrum Technologies, Inc., Aurora, Illinois, USA). We recorded four measurements of PAR immediately below each tree canopy to estimate mean light availability and compared the PAR levels in the understory beneath damaged and undamaged tree canopies.

We further quantified ground and air temperatures using iButton hygrochrons (model DS1923; iButtonLink Technologies, Whitewater, Wisconsin, USA) encased in thermally inert housings (following Compagnoni and Adler 2014). We placed two thermochrons beneath five pairs of damaged and undamaged *A. etbaica* in south MRC, one at ground level and one suspended 50 cm above ground level. Temperatures were recorded hourly for 10 d and the mean daily maximum and minimum air and ground temperatures were calculated for each tree.

Finally, we attempted to directly quantify soil moisture using both probe sensors and pre- and post-drying sample weights, but the compacted soils typical of our study site did not allow probe penetration and soil moisture was sufficiently low that all soil samples collected in the field gained weight when dried in a solar oven. Thus, we assessed the effect of elephant damage on soil hydrologic conditions by measuring the relative water content (RWC) of a common understory subshrub (*Barleria eranthemoides*) beneath 12 pairs of damaged and undamaged *A. etbaica* canopies in central MRC (1 leaf/shrub). The RWC is a proxy for water stress in plants and was calculated as the realized water content of a leaf relative to the fully hydrated potential of the same leaf, following Munns (2010). All measurements were taken within 1 h on the same day to control for temporal variability.

## RESULTS

### *Understory responses to elephant exclusion and relative abundance*

The JSDM analysis based on categorical treatment effects indicated that six of 117 species responded

positively to the presence of elephants, five of which were graminoids (four Poaceae and one Cyperaceae), along with one Asteraceae (Fig. 2A, Appendix S1: Table S1). Seven other species responded negatively to elephants, of which only two were grasses (plus one each from the families Amaranthaceae, Caryophyllaceae, Commelinaceae, Lamiaceae, and Solanaceae). The individual abundances of the remaining 104 species (89%) responded neutrally. Ten species responded positively to rainfall (Appendix S1: Fig. S2A, Table S3), of which six were graminoids. No species responded negatively to rainfall. Across rainfall levels, modeled understory plant biomass was 8.3–9.4% greater in the presence of elephants than in their absence (Appendix S1: Fig. S3A).

Similarly, using elephant dung as a proxy for elephant activity in lieu of exclosure treatments, we found that 10 of 117 understory species responded positively to elephants; of these, eight were graminoids (seven Poaceae, one Cyperaceae), along with one species each from the families Acanthaceae and Asteraceae (Fig. 2B, Appendix S1: Table S2). Ten other species responded negatively to elephants, of which only two were grasses (plus one each from Acanthaceae, Amaranthaceae, Asparagaceae, Euphorbiaceae, Lamiaceae, and Solanaceae, and two

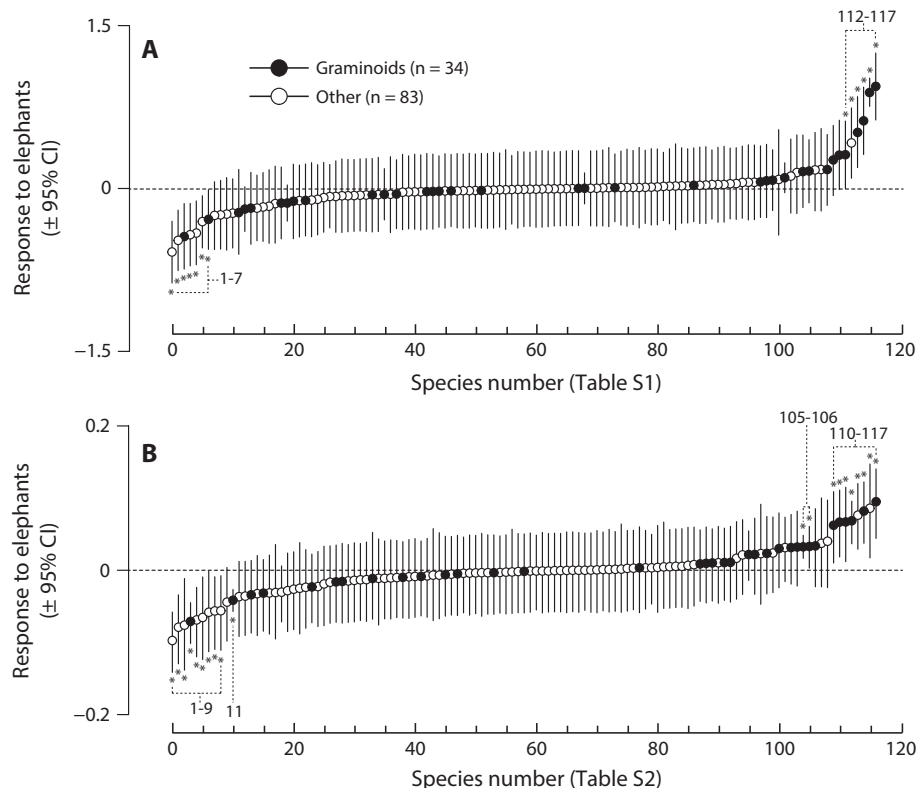


FIG. 2. Joint species distribution model results for elephant effects on 117 understory plant species, showing that many grasses in particular responded positively to elephants. The effect of elephants was modeled in two ways: as presence-absence using herbivore-exclosure treatment (A) and relative abundance using dung counts (B). Data are means  $\pm$  95% CI, denoted with \* when CI does not overlap zero. Darkened circles are graminoids (families Poaceae and Cyperaceae). Numbers correspond to those in Appendix S1: Tables S1 and S2, which contain detailed lists of all plant taxa assessed.



from Malvaceae). The abundance of the remaining 97 species (83%) responded neutrally. Fourteen species responded positively to rainfall, of which ten were graminoids, while four species responded negatively to rainfall (Appendix S1: Fig. S2B, Table S4), of which just one was a grass. Finally, total understory biomass increased by 5.4–14.0% as a function of elephant-dung density across rainfall levels (Appendix S1: Fig. S3B).

#### *Understory responses to elephant ecosystem engineering of canopy architecture*

**Surveys of naturally elephant-damaged trees.**—Elephant damage was frequent, affecting  $84.8\% \pm 4.7\%$  of *Acacia brevispica*,  $83.1\% \pm 3.2\%$  of *Acacia mellifera*, and  $61.6\% \pm 3.2\%$  of *Acacia etbaica* (Appendix S1: Figure S4). *Acacia etbaica* comprised 48.1% of all trees surveyed. Of *A. etbaica* classified as damaged, an average of  $33.8\% \pm 2.6\%$  of the understory habitat beneath the canopy was directly overlain by damaged branches (Fig. 1C). Approximately 6% of all elephant damage encountered (i.e., 10 branches/ha) was in the form of branches fully detached from trees. Taken together, partially and fully detached damaged branches covered  $2,340 \pm 280 \text{ m}^2$  of the 2 ha surveyed. Understory plant biomass was 55% greater ( $t_{17} = 7.43$ ,  $P < 0.0001$ ) beneath elephant-damaged canopies than beneath undamaged canopies (Fig. 3A). Likewise, total species richness was 21% greater ( $t_{17} = 2.34$ ,  $P = 0.025$ ) under damaged than undamaged canopies, despite the latter covering approximately twice the area (Fig. 3B;  $t_{17} = 5.09$ ,  $P < 0.0001$ ); thus, this result conservatively characterizes the positive effect of elephant damage on species richness. Per-area species richness was 155% greater beneath damaged canopies (Fig. 3C;  $t_{17} = 5.04$ ,  $P < 0.0001$ ).

**Damage-addition and -removal experiments.**—Experimental addition of detached branches outside tree canopies increased understory biomass by  $37.3\% \pm 19.1\%$  ( $F_{1,29} = 13.17$ ,  $P = 0.001$ ) and species richness by  $71.0\% \pm 30.1\%$  ( $F_{1,29} = 8.53$ ,  $P = 0.007$ ). Similarly, simulated elephant damage beneath canopies increased

understory biomass ( $F_{1,43} = 4.66$ ,  $P = 0.03$ ) and species richness ( $F_{1,43} = 9.23$ ,  $P = 0.004$ ). There was no main effect of UHURU exclosure treatment on biomass change ( $F_{1,43} = 0.03$ ,  $P = 0.87$ ; Fig. 4A), whereas species richness increased to a greater extent within -LMH exclosures than in unfenced control plots, irrespective of damage-addition treatment ( $F_{1,43} = 9.08$ ,  $P = 0.004$ ; Fig. 4B). However, we did not observe the predicted interaction between damage-addition and exclosure treatments on understory biomass or species richness ( $F_{1,43} = 1.84$ ,  $P = 0.18$ , and  $F_{1,43} = 0.002$ ,  $P = 0.97$ , respectively).

Conversely, removing naturally occurring elephant-damaged branches significantly reduced understory biomass ( $F_{1,33} = 28.98$ ,  $P < 0.0001$ ; Fig. 4C) and species richness ( $F_{1,33} = 12.32$ ,  $P = 0.001$ ; Fig. 4D) relative to sham-manipulated control treatments.

**Mechanism of facilitation.**—Elephant damage reduced the incidence of grazing scars on both grass species by 44–68% (*C. plechtostachyus*:  $t_{22,0} = 13.99$ ,  $P < 0.0001$ ; *A. kenyensis*:  $t_{21,5} = 3.16$ ,  $P = 0.005$ ) and reduced the number of herbivores feeding on understory plants by >70% ( $t_{5,24} = 3.04$ ,  $P = 0.03$ ; Fig. 5). Available PAR ( $t_{13,1} = 1.30$ ,  $P = 0.21$ ), mean maximum and minimum soil and air temperature (all  $t < 0.54$ ,  $P > 0.34$ ) and RWC ( $t_{22,0} = 1.45$ ,  $P = 0.16$ ) did not differ significantly between damaged and undamaged canopies (Appendix S1: Fig. S5).

#### DISCUSSION

Our results indicate that elephants have surprisingly mild net effects on understory vegetation. Using two complementary approaches to characterize elephant presence/absence and relative abundance in our JSMD models, we found that roughly as many species responded positively as negatively to elephants, with the vast majority responding neutrally. These trends were largely consistent across the two models: both approaches indicated that elephants positively affected 5–9% of all species (among which graminoids were disproportionately represented), negatively affected 6–9% (predominantly  $C_3$  forbs and subshrubs) and

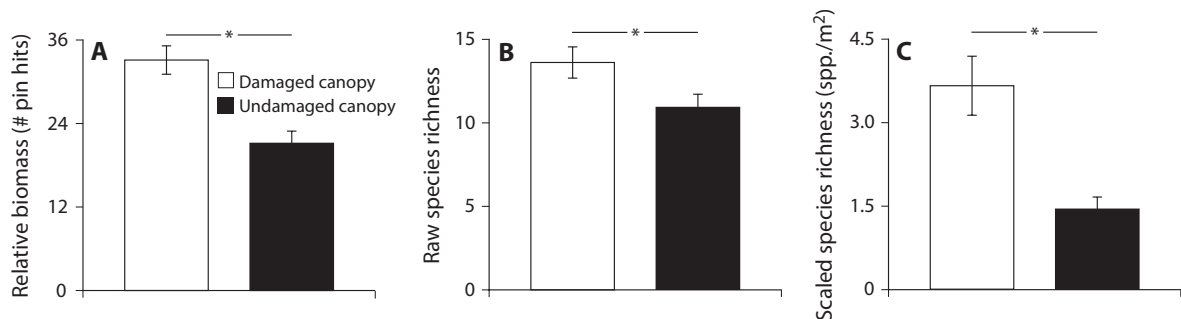


FIG. 3. Results of biomass and species richness surveys beneath *Acacia etbaica* canopies. Elephant damaged branches (white bars) enhanced understory plant biomass (A) and species richness (B, unscaled; C, scaled by area) relative to undamaged portions of the same tree canopy (black bars). Values are means  $\pm$  SE.

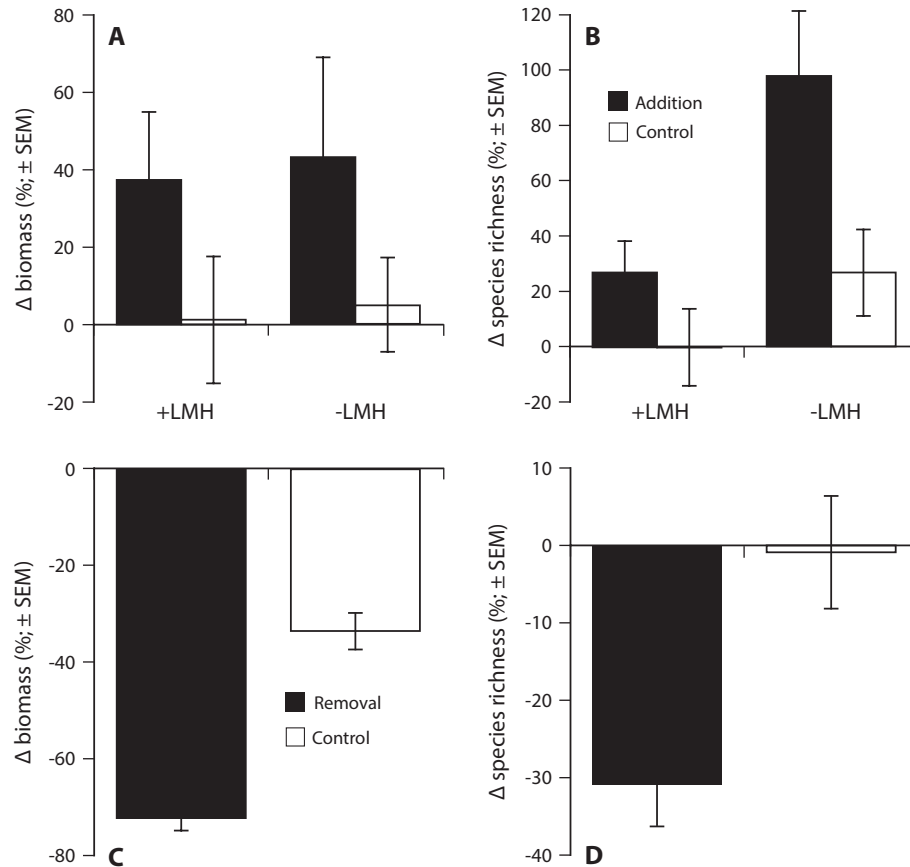


FIG. 4. Results of damage-addition (top) and -removal (bottom) experiments beneath *Acacia etbaica* canopies. Changes in understory biomass (A) and species richness (B) were measured over 1 yr after tree canopies in the full enclosure (-LMH) and control (+LMH) UHURU plots were experimentally damaged to simulate destructive elephant browsing. Similarly, changes in biomass (C) and species richness (D) were monitored following the removal of naturally damaged branches from tree canopies outside the UHURU plots.

had neutral effects on the remaining 83–89% (Fig. 2). Elephants had mild positive effects on total understory plant biomass (5.4–8.7%) at median rainfall, suggesting that responses of positively affected understory species outweighed those of negatively affected species (Appendix S1: Fig. S3). Importantly, the largely neutral net effect of elephants on understory vegetation is not because elephants feed predominantly on overstory plants; although we are currently unable (due to unresolved taxonomic discrepancies) to match all of the plant taxa in the UHURU surveys to those detected in elephant diets via DNA metabarcoding of feces (Kartzinel et al. 2015), we know that at least 33 of the 46 plant taxa (71.7%) detected in elephant diets at MRC are understory species (20 of them graminoids), and that understory plants account for >65% of species detected on average in individual elephant diets. Qualitative comparison of these published dietary data with our tree-scale experimental results indicates that many of the understory taxa most commonly consumed by elephants were among those that benefited most from elephant browsing and canopy damage.

Comprehensively elucidating the suite of positive and negative pathways that collectively define elephants' net effects on any given plant species (e.g., Goheen et al. 2010, Pringle et al. 2014) is beyond the scope of our community-level study. However, we found clear evidence for strong and widespread effects of a local-scale facilitative mechanism that has been largely overlooked in the literature: namely that elephants increase understory richness and biomass by damaging tree canopies. Simulated elephant damage beneath and outside tree canopies increased both metrics over 1 yr, paralleling patterns beneath naturally damaged trees (Figs. 3, 4), while removal of damaged branches significantly reduced understory biomass and species richness relative to sham-manipulated control areas over the same time period.

We suggest that the observed local facilitation of understory communities following elephant damage is explained in large part by the creation (and/or enhancement) of associational refuges that inhibit ungulate foraging. Herbivore utilization and grazing damage were significantly reduced beneath damaged trees, whereas we



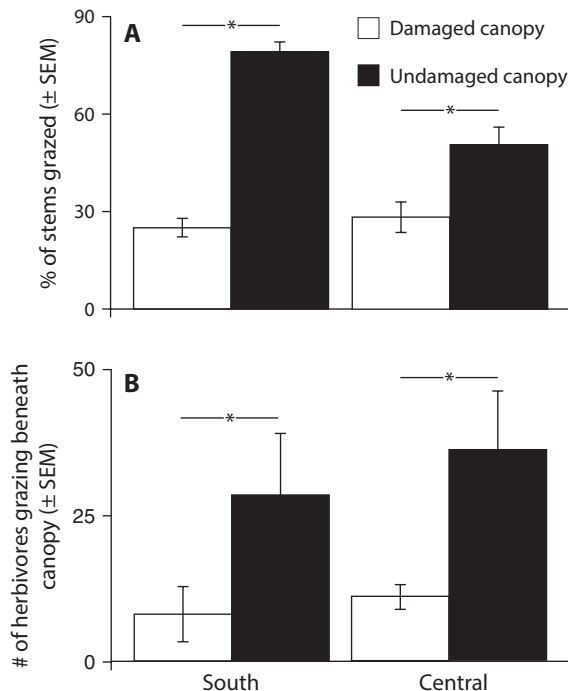


FIG. 5. Effects of elephant damage on ungulate grazing intensity. (A) The proportion of stems of two common grass species grazed by ungulates beneath damaged and undamaged *Acacia etbaica* canopies in south (*C. plectostachyus*) and central (*A. kenyaensis*) MRC. (B) The number of ungulates photographed with camera traps feeding beneath damaged and undamaged tree canopies in south and central MRC.

did not detect significant differences in temperature, light transmission, or water stress beneath damaged and undamaged canopies. In this regard, our findings are in agreement with another recent study from our site (Louthan et al. 2014), which found that understory plants growing among neighbors benefit less from the amelioration of abiotic stress than from reduced apparency to large mammalian herbivores. Although severe damage to trees could conceivably benefit nearby understory plants by reducing competition for water or nutrients, our damage-addition treatment simulated moderate-to-severe elephant damage, and yet all manipulated trees survived for the duration of the study, suggesting that competitive effects were not severely diminished. Moreover, reduced competition for resources cannot explain the positive effects of adding isolated branches away from tree canopies or the negative effects of removing naturally damaged branches (Fig. 4C, D).

The unexpected finding that simulated damage enhanced understory species richness within full herbivore exclosures (Fig. 4B) is perhaps most likely explained by the effects of small herbivores such as hares (*Lepus* spp.) and rodents that are not excluded by the exclosure fences (Goheen et al. 2013), but whose foraging may nonetheless be inhibited by damaged branches. However, it is also possible that subtle abiotic effects of

our manipulations on local light and moisture conditions contributed to these effects, even though we failed to detect such effects in our surveys; more fully investigating the indirect biotic and abiotic effects of elephant damage on understory plants is a promising avenue for future research.

Collectively, our results suggest that indirect positive effects of associational refuges at the scale of individual trees may largely offset the negative direct effects of consumption at the landscape scale, and therefore moderate the net impact of elephants on understory communities. Furthermore, while elephant browsing has long been known to benefit grazing wildlife and cattle by maintaining relatively open habitat (Laws 1970, Dublin et al. 1990), our results indicate that they may also alter understory species composition in ways that further benefit grazers (cf. Young et al. 2005): by reducing the abundance of forbs and promoting grasses, elephants may increase forage quality and availability for grazing wildlife and livestock. Graminoids were disproportionately represented among species that responded positively to elephants, comprising 80–83% of positively responding species despite accounting for less than a third of the understory species pool in the UHURU plots. Conversely, forbs and subshrubs were most common among negatively responding species, and several of the most strongly responding taxa (e.g., *Solanum campylacanthum* and *Sansevieria* spp.) are opportunistic “encroachers” that are considered a major threat to rangeland health and sustainability (Foxcroft et al. 2008, Pringle et al. 2014). The historical view of elephants as destructive to vegetation and a threat to plant biodiversity is based largely on assessments of canopy tree species (Laws 1970), but our results indicate that their net effects on understory plant assemblages may be largely neutral overall, and patchily positive at local scales.

Positive plant-plant interactions, like the associational refuges we document here, are common across ecosystems and can help maintain robust vegetation communities by modifying biotic and/or abiotic conditions (Hay 1986, Milchunas and Noy-Meir 2002). For example, intact *Acacia* canopies provide a variety of potential benefits to understory plants by ameliorating the harsh abiotic conditions found in open savanna habitat, including increasing soil nutrients, reducing water stress, and increasing regrowth capacity (Belsky 1994, Caylor et al. 2005). In this sense, our results suggest that elephant damage may often enhance preexisting facilitative relationships between overstory trees and understory plants by inhibiting large herbivores; however, we also show that elephants can create associational refuges de novo by depositing broken branches some distance from trees. This facilitative relationship is likely unidirectional, particularly in savannas with frequent fires: the accumulation of dense understory biomass beneath canopies will strengthen competitive effects of understory plants on trees (Riginos 2009) and may also create hot-spots of fire

intensity due to higher fuel loads, with the potential to increase tree mortality (Scholes and Archer 1997, Thaxton and Platt 2006). Future work should investigate the longer-term temporal dynamics of these associational refuges, particularly in fire-prone landscapes.

Our study contributes to a growing body of evidence that elephants, as ecosystem engineers, locally and indirectly benefit various species through the creation of associational refuges against natural enemies (e.g., Pringle 2008, Nasser et al. 2011, Pringle et al. 2015); however, there remain few data about the extent to which such refuges influence larger-scale ecosystem properties. Our results suggest that such multi-scale dynamics may occur in savanna systems occupied by megaherbivores, and that the neutral-to-positive effects of elephants on understory plants at the hectare scale can be explained, in part, by the countervailing effects of consumption across the landscape and ecosystem engineering at the scale of individual trees. Similarly, it is likely that such refuges also enhance population persistence and stability, and hence community diversity, by acting as sources in a metapopulation context (e.g., Milchunas and Noy-Meir 2002, Rebollo et al. 2002). Future work should explicitly address this possibility, and how it depends on the density, distribution, and efficacy of associational refuges.

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#### AUTHOR CONTRIBUTIONS

TCC and RMP conceived the study and designed experiments; TCC coordinated the study and implemented experiments; TCC, TRK, KLG, and AAH collected data; JRG, RMP, and TMP designed and maintain the UHURU experiment; RKS conducted the JSDM analyses; TCC wrote the manuscript with input from RMP and RKS; all authors contributed revisions.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.1557/supinfo>



## Appendix S1

Elephants in the understory: opposing direct and indirect effects of consumption and ecosystem engineering by megaherbivores. Tyler C. Coverdale, Tyler R. Kartzinel, Kathryn L. Grabowski, Robert K. Shriver, Abdikadir A. Hassan, Jacob R. Goheen, Todd M. Palmer, and Robert M. Pringle. *Ecology*

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### Technical Description of Joint Species Distribution Model

The Bayesian joint species distribution modeling approach begins with an observation model of the rate of occurrence (total pinhits/total pinframe area) of each species ( $S$ ) in the sampled area ( $a$ , not all plots had all 49 locations surveyed all years) of each plot for each survey ( $i$ ). Data are available at [<http://www.esapubs.org/archive/ecol/E095/064/>]. The data was fit as:

$$y_{i,s} \sim \text{Poisson}(\gamma_{i,s} * a_{i,s})$$

where  $y_{i,s}$  is the measured number of pinhits of a species in the whole plot in each survey, and  $\gamma_{i,s}$  is the inferred rate of occurrence for each species in each survey (Clark et al. 2014).

To connect covariates (elephant abundance or presence/absence and rainfall) to species occurrence rate, a multivariate normal regression, with  $S$  dimensions ( $S$  being the number of

species), was used to explain how elephants and rainfall altered the rate of occurrence of each species. Multivariate regression allows us to account for covariance among species' occurrences that are not explained by covariates alone when making predictions of changes in species cover or diversity (Clark et al. 2014, Pollock et al. 2014). The rate of occurrence for each species, which is continuous and positive, was log transformed:

$$\ln(\gamma_{it, jks}) \sim N_S(x_{i,s}\mathbf{B} + \boldsymbol{\varepsilon}_t + \boldsymbol{\omega}_j + \boldsymbol{\tau}_k, \mathbf{A})$$

where  $x_{i,s}$  is a  $Q$  length vector of all covariates for each plot in each survey,  $\mathbf{B}$  is a  $Q \times S$  matrix of regression coefficients,  $\mathbf{A}$  is an  $S \times S$  covariance matrix (which includes all correlations among species not accounted for by covariates),  $S$  is the number of species,  $\boldsymbol{\varepsilon}$  is a random effect for year,  $\boldsymbol{\omega}$  is a random effect for block, and  $\boldsymbol{\tau}$  is a random effect for site (North, Central, South). Random effects were defined as multivariate normal with mean zero.

Covariates included in the regression were: 1) Rainfall six months prior to each survey, 2) herbivore enclosure treatment (total enclosure vs. megaherbivore enclosure; categorical) and 3) the interaction of herbivore enclosure treatment and rainfall. Because control treatments are not necessarily visited by elephants during each time period and because megaherbivore enclosures also exclude giraffes we used elephant dung counts as a continuous approximation of elephant activity to explain variation in plant cover in a second, complementary JSDM. In this analysis, elephant dung was included as a continuous variable.

Regression coefficients,  $\mathbf{B}$ , were given flat, non-informative, Jeffreys priors. The covariance matrix was given an inverse-wishart prior,  $IW(diag(\boldsymbol{\sigma}_1^2, \dots, \boldsymbol{\sigma}_S^2), S + 1)$  where the

diagonal values are variances from individual regressions of each species (Clark et al. 2014). Because we had no specific information on the strength of the random effects, random effects were given less specific priors  $\mathbf{IW}(\text{diag}0.001), S + 1$ .

In cases where there was no measurement of a species abundance in a plot (missing values in all 49 pinframes), missing values were imputed based on the relationship between the species abundance, covariates, and the covariance among species (Clark 2007).

$$p(\ln(\gamma_{it,jk,s}) \mid \mathbf{x}_{i,s}\mathbf{B}, \boldsymbol{\varepsilon}_t, \boldsymbol{\omega}_j, \boldsymbol{\tau}_k, \mathbf{A}) \propto N_S(\ln(\gamma_{it,jk,s}) \mid \mathbf{x}_{i,s}\mathbf{B} + \boldsymbol{\varepsilon}_t + \boldsymbol{\omega}_j + \boldsymbol{\tau}_k, \mathbf{A})$$

The model was fit using a Gibbs sampler run for 40,000 iterations, with a burn-in period of 10,000 iterations. Conditional distributions for regression parameters, random effects, and covariance matrix were sampled directly. The Poisson rate parameter and missing values were determined using a Metropolis-Hastings algorithm.

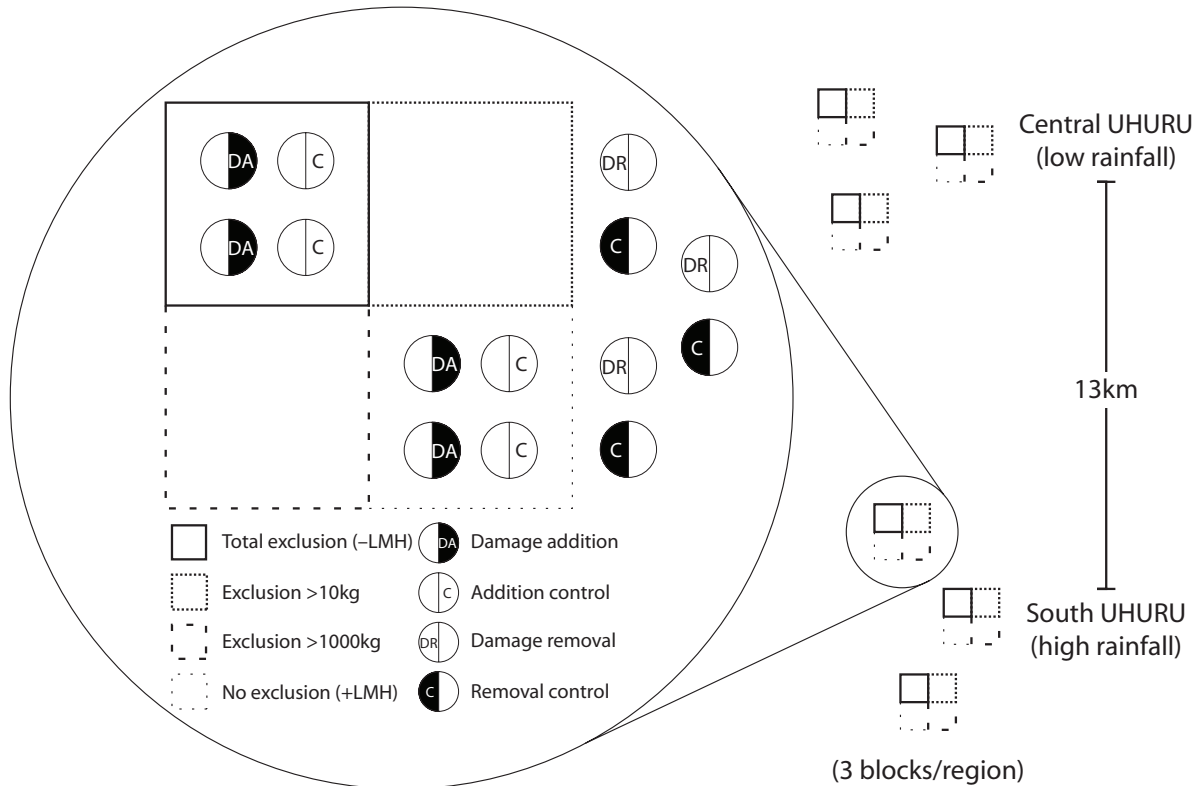
The sensitivity (or response) of each species to elephants is the posterior distribution of the elephant regression coefficient, assuming average rainfall (i.e., the reported sensitivity is the slope of the relationship between elephant dung or exclosure treatment and a plant species  $\ln(\gamma)$ ).

## Figure Legends

**Figure S1.** Schematic diagram of damage-removal and -addition experiments. (Top) The south and central UHURU plots are separated by approximately 13km, with the southern sites receiving modestly greater rainfall in an average year. Each block (3 blocks/region) contains four treatments: unfenced control, megaherbivore exclusion (elephants and giraffes only), mesoherbivore exclusion (species >10 kg), and total exclusion (all species >5 kg) (Goheen et al. 2013). Within each total exclusion (–LMH) and control (+LMH) plot, we randomly selected four undamaged *A. etbaica* and assigned them to a damage addition (black) or control (white) treatment. The damage-removal experiment was conducted outside the UHURU plots, where naturally damaged trees were either left intact as controls (black) or had all damaged branches removed (white). (Bottom) List of experiments and surveys with description of locations and scale of replication.



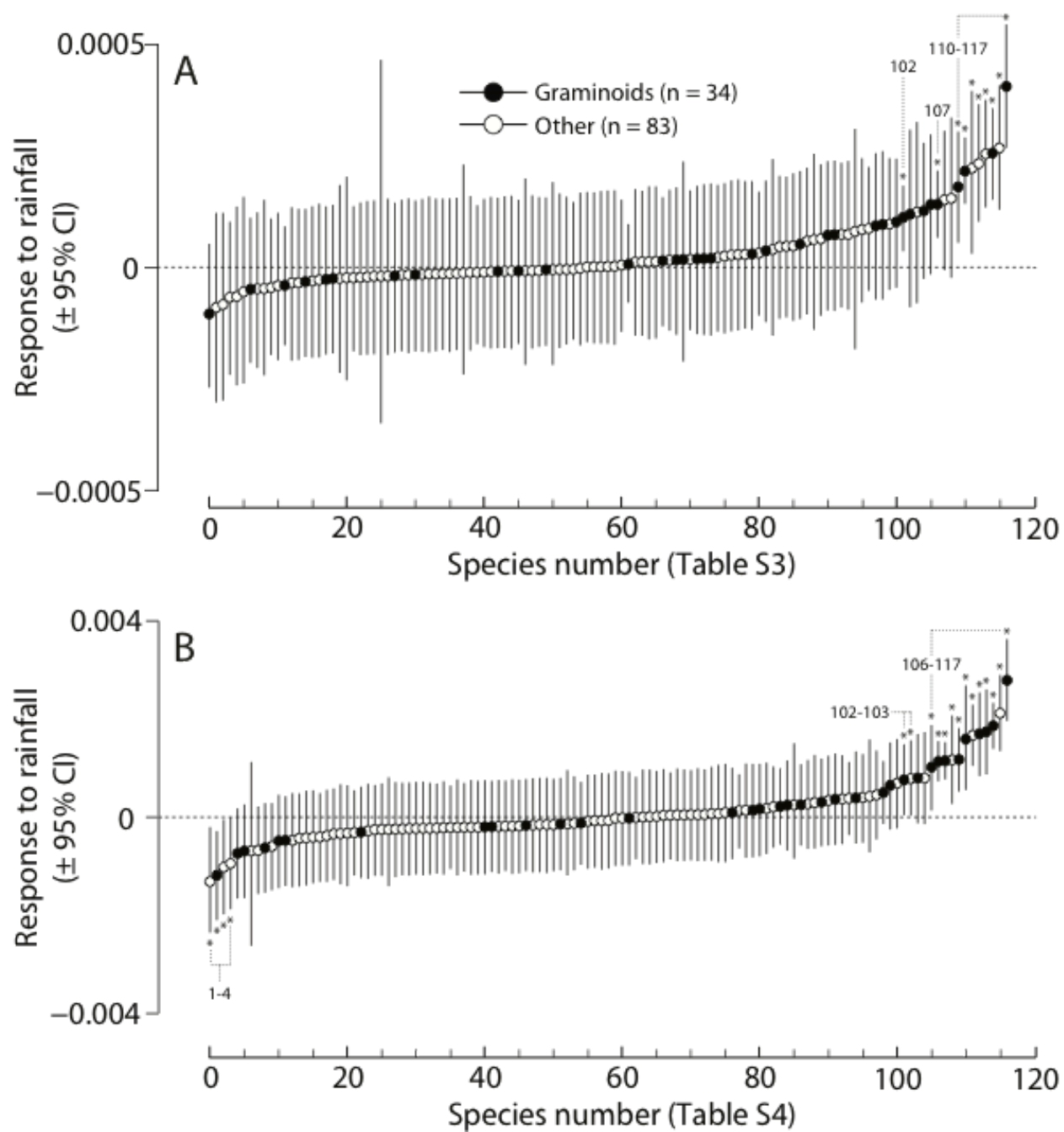
Figure S1



Experiment/Survey	Location(s)	Type of Replicate
Damage transect survey	S, C	Whole tree canopy, detached branch
Understory biomass and species richness survey	S, C	Partial tree canopy (2 replicates /tree)
Damage-addition experiment (beneath tree canopies)	S, C	Partial tree canopy (1 replicate/tree)
Damage-addition experiment (outside tree canopies)	S, C	Detached branch (1 replicate/branch)
Damage-removal experiment	S, C	Partial tree canopy (1 replicate/tree)
Grazing damage survey	S, C	Partial tree canopy (1 replicate/tree)
Camera trap survey	S, C	Whole tree canopy
PAR survey	S	Partial tree canopy (1 replicate/tree)
Temperature survey	S	Partial tree canopy (1 replicate/tree)
RWC survey	C	Whole plant ( <i>B. eranthemoides</i> )

**Figure S2.** Effects of rainfall on the relative abundance of 117 understory plants. The independent effect of elephants (Figure 2A,B) and rainfall were determined using separate Bayesian joint species distribution models that modeled elephant presence and abundance using herbivore exclosure type (A) and elephant dung count (B), respectively. Data are means  $\pm$  95% CI, which are derived from the modeled posterior distribution of each species. Species whose 95% CI lies entirely above or below zero are considered to respond positively or negatively, respectively. Black circles denote graminoids (Families Poaceae and Cyperaceae). Identifying species information provided in Tables S3 and S4.

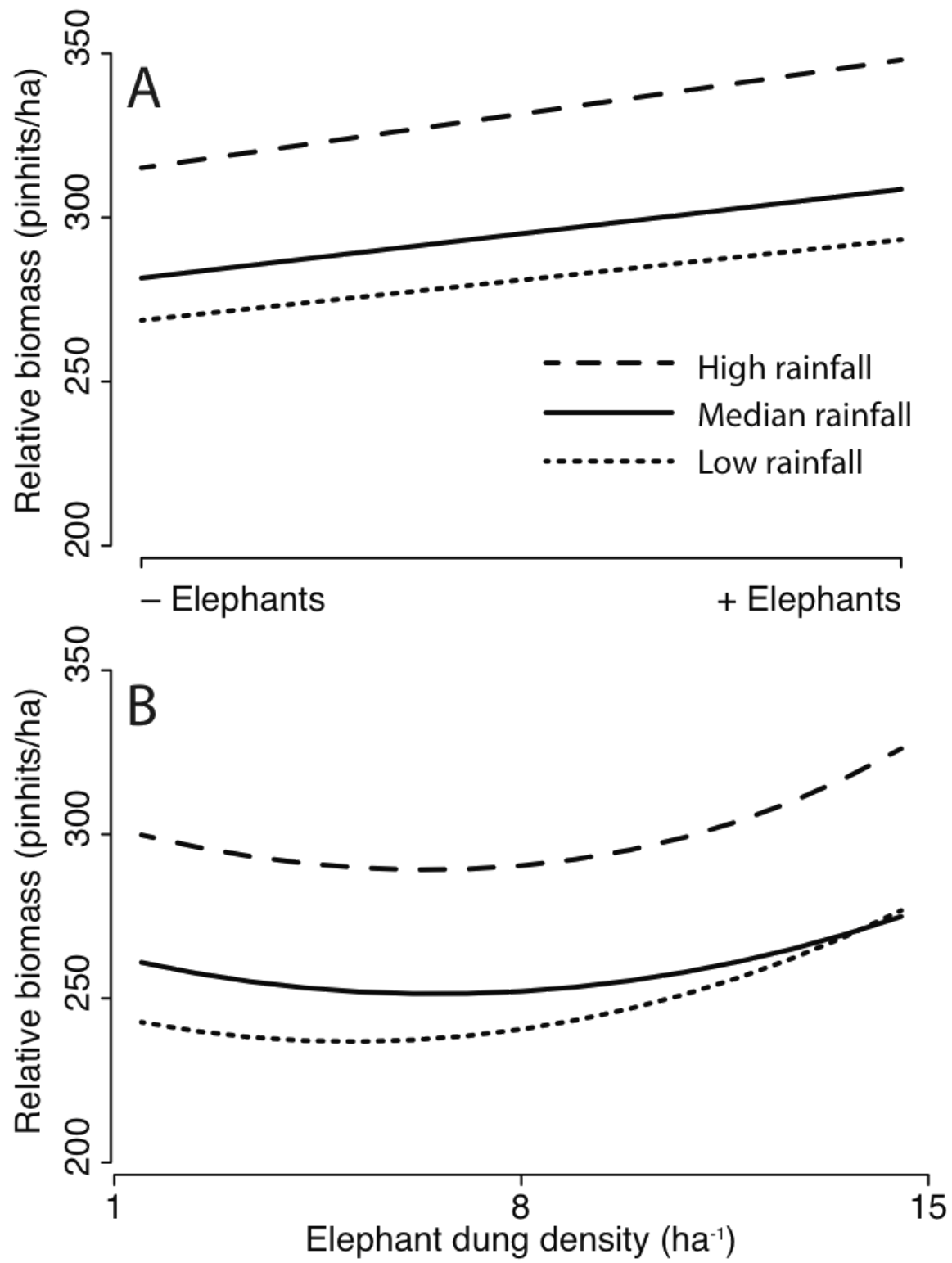
Figure S2



**Figure S3.** Predicted changes in total understory biomass (pinhits/ha) as a result of elephant activity at 25<sup>th</sup> percentile (low), median, and 75<sup>th</sup> percentile (high) rainfall levels. (A) Estimates derived from JSDM using herbivore exclosure treatment as a proxy for elephant abundance. – Elephants corresponds to megaherbivore exclosure treatment; +Elephants corresponds to control exclosure treatment. (B) Results derived from JSDM using elephant dung count as a proxy for elephant abundance. Regardless of the proxy of elephant abundance selected, greater elephant density increases understory biomass across rainfall levels.

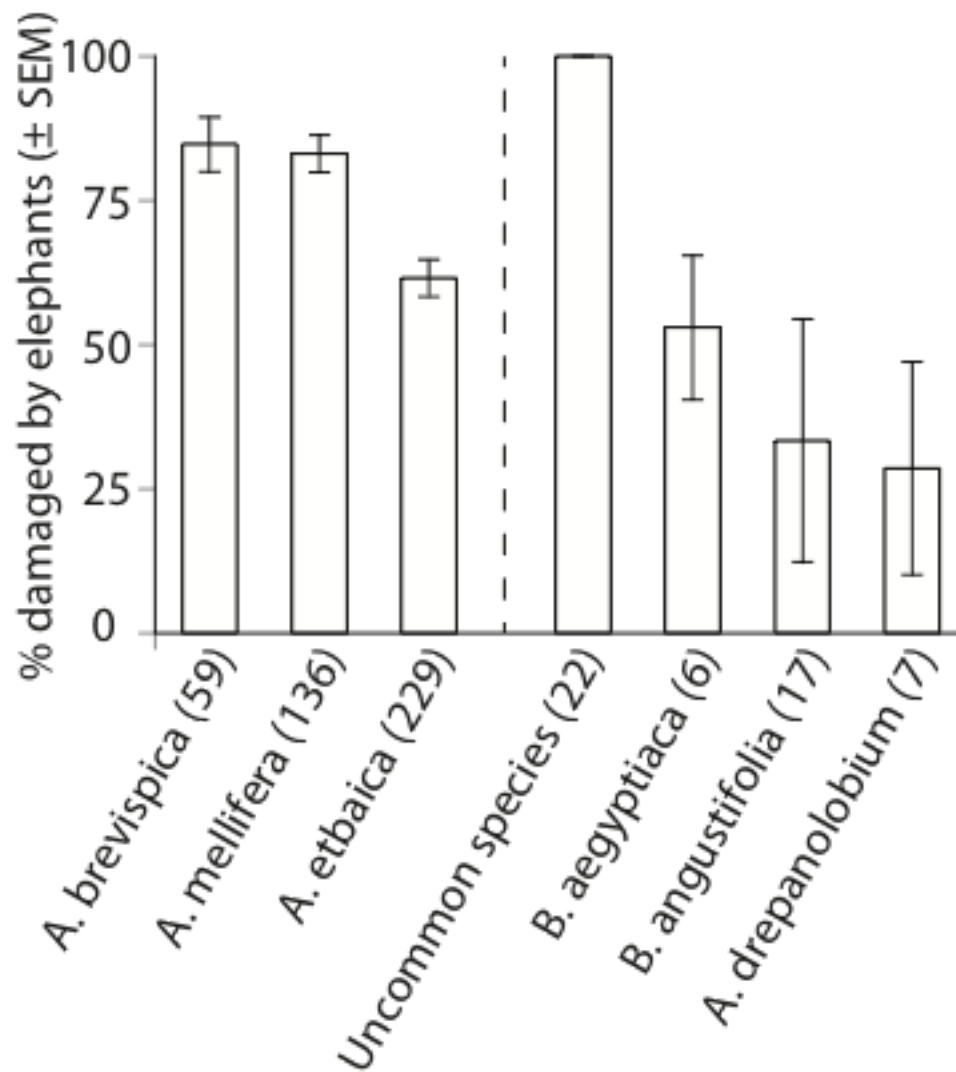


Figure S3



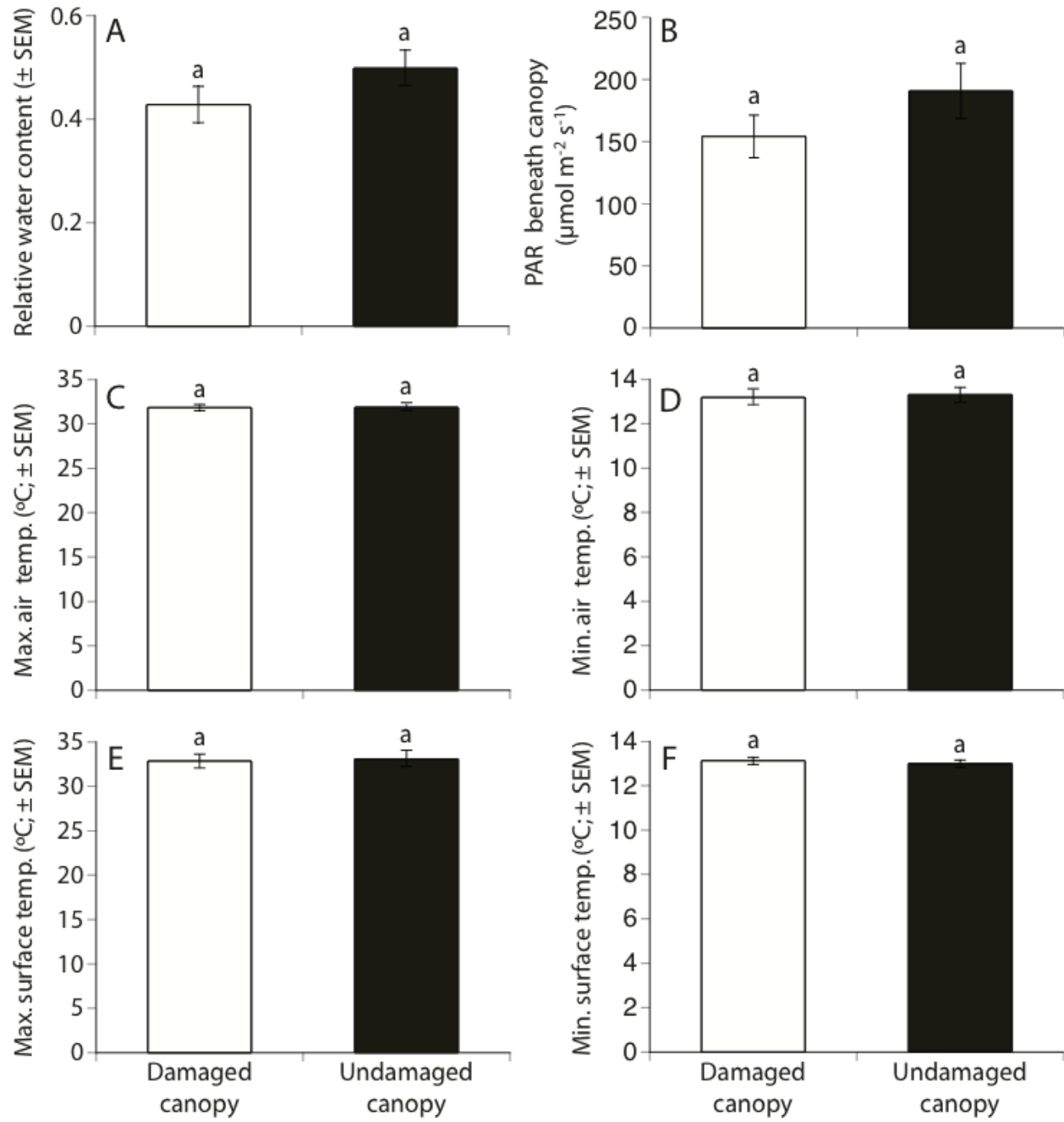
**Figure S4.** Prevalence of elephant damage on trees at Mpala Research Centre, Kenya. Trees were considered damaged if elephant browsing had occurred on branches >2cm diameter and if these covered an area of >1m<sup>2</sup> beneath the canopy. Numbers associated with each species correspond to the total number of trees encountered along ten 10m x 200m transects. Data were pooled for five uncommon species of which 100% of individuals were damaged.

Figure S4



**Figure S5.** Abiotic conditions in the understory beneath damaged (white) and undamaged (black) *A. etbaica*. The presence of elephant damage did not detectably affect (A) relative water content of understory plants, (B) availability of photosynthetically active radiation (PAR), (C) maximum air temperature, (D) minimum air temperature, (E) maximum ground-surface temperature, or (F) minimum ground-surface temperature.

Figure S5



## Tables.

**Table S1.** List of taxa included in our Bayesian joint species distribution model of plant responses to elephants (herbivore exclosure treatment; Figure 2A). Species number corresponds to rank order in Figure 2A. Species identity corresponds to UHURU large quadrat survey data (“UNDERSTORY\_LGQUAD.TXT” in Kartzin et al. 2014). Graminoids (families Cyperus and Poaceae) are shaded and correspond to darkened circles in Figure 2A. Species denoted with an asterisk (\*) are those whose 95% CI did not overlap zero. All others overlapped zero (neutral). All data files are available in Ecological Archives #E095-064 (<http://www.esapubs.org/archive/ecol/E095/064/>).

Species Number	Response	Species Identity (Kartzin et al. 2014)	Family	Mean Response	Lower 95% CI	Upper 95% CI
1	*	Plectranthus_small	Lamiaceae	-0.579	-0.867	-0.296
2	*	Cyathula	Amaranthaceae	-0.473	-0.752	-0.193
3	*	Chloris_roxburghiana	Poaceae	-0.438	-0.738	-0.133
4	*	Solanum_big	Solanaceae	-0.421	-0.708	-0.131
5	*	Pollichia	Caryophyllaceae	-0.405	-0.699	-0.109
6	*	Commelina	Commelinaceae	-0.300	-0.543	-0.061
7	*	Brachiaria_leersoides	Poaceae	-0.279	-0.556	-0.004
8	neutral	Hibiscus_calyphyllus	Malvaceae	-0.243	-0.557	0.069
9	neutral	Osteospermum	Asteraceae	-0.238	-0.554	0.081
10	neutral	Sansevieria	Asparagaceae	-0.230	-0.563	0.107
11	neutral	Achyranthes_aspera	Amaranthaceae	-0.222	-0.544	0.096
12	neutral	Eragrostis_rigidior	Poaceae	-0.217	-0.601	0.182
13	neutral	Microchloa_kunthii	Poaceae	-0.183	-0.390	0.022
14	neutral	Digitaria_milanjiana	Poaceae	-0.175	-0.509	0.156
15	neutral	Portulaca_quadrifida	Portulacaceae	-0.174	-0.476	0.130
16	neutral	Phyllanthus	Phyllanthaceae	-0.164	-0.483	0.154
17	neutral	Plectranthus_big	Lamiaceae	-0.157	-0.500	0.180
18	neutral	Hibiscus_meyeri	Malvaceae	-0.134	-0.499	0.212
19	neutral	Eragrostis_papposa	Poaceae	-0.128	-0.459	0.205
20	neutral	Eragrostis_tenuifolia	Poaceae	-0.128	-0.295	0.039
21	neutral	Setaria	Poaceae	-0.111	-0.458	0.231

22	neutral	Barleria_ramulosa_white	Acanthaceae	-0.106	-0.442	0.223
23	neutral	Panicum_maximum	Poaceae	-0.103	-0.432	0.233
24	neutral	Euphorbia_sp_small	Euphorbiaceae	-0.101	-0.439	0.245
25	neutral	Hibiscus_2	Malvaceae	-0.094	-0.423	0.227
26	neutral	Sida	Malvaceae	-0.077	-0.398	0.247
27	neutral	Gutenbergia	Asteraceae	-0.068	-0.358	0.229
28	neutral	Abutilon	Malvaceae	-0.067	-0.398	0.262
29	neutral	Kalanchoe	Crassulaceae	-0.061	-0.400	0.279
30	neutral	Monechma	Acanthaceae	-0.060	-0.393	0.276
31	neutral	Lippia	Verbenaceae	-0.058	-0.390	0.274
32	neutral	Blepharis	Acanthaceae	-0.055	-0.386	0.281
33	neutral	Pavonia	Malvaceae	-0.054	-0.391	0.282
34	neutral	Sporobolus_africanus	Poaceae	-0.052	-0.395	0.283
35	neutral	Justicia_odora	Acanthaceae	-0.050	-0.391	0.294
36	neutral	Enteropogon	Poaceae	-0.049	-0.284	0.190
37	neutral	Euphorbia_crotonoides	Euphorbiaceae	-0.047	-0.401	0.301
38	neutral	Dactyloctenium	Poaceae	-0.045	-0.364	0.272
39	neutral	Amaranthus	Amaranthaceae	-0.027	-0.374	0.322
40	neutral	Chenopodium	Aizoaceae	-0.026	-0.366	0.308
41	neutral	Sarcostemma	Apocynaceae	-0.025	-0.369	0.323
42	neutral	Euphorbia_inaequilatera	Euphorbiaceae	-0.024	-0.377	0.318
43	neutral	Enneapogon	Poaceae	-0.022	-0.369	0.330
44	neutral	Sporobolus_spp	Poaceae	-0.020	-0.369	0.324
45	neutral	Aristida_spp.	Poaceae	-0.020	-0.351	0.308
46	neutral	Pelargonium	Geraniaceae	-0.016	-0.360	0.328
47	neutral	Dinebra	Poaceae	-0.015	-0.345	0.321
48	neutral	Oxygonum	Polygonaceae	-0.015	-0.358	0.329
49	neutral	Ipomoea_2	Convolvulaceae	-0.015	-0.361	0.325
50	neutral	Hibiscus_flavifolius	Malvaceae	-0.015	-0.360	0.332
51	neutral	Barleria_2	Acanthaceae	-0.013	-0.349	0.326
52	neutral	Rhynchelytrum_repens	Poaceae	-0.012	-0.360	0.331
53	neutral	Portulaca_oleracea	Portulacaceae	-0.008	-0.362	0.330
54	neutral	Solanum_nigrum	Solanaceae	-0.008	-0.359	0.341
55	neutral	Opuntia	Cactaceae	-0.006	-0.351	0.334
56	neutral	Portulaca_kermisina	Portulacaceae	-0.005	-0.372	0.365



57	neutral	Melhania spp.	Malvaceae	-0.004	-0.323	0.312
58	neutral	Barleria_3	Acanthaceae	-0.003	-0.360	0.348
59	neutral	Phyllanthus_sp	Phyllanthaceae	-0.001	-0.346	0.345
60	neutral	Cissus	Vitaceae	-0.001	-0.344	0.342
61	neutral	Aerva	Amaranthaceae	-0.001	-0.352	0.353
62	neutral	Caralluma_sp	Apocynaceae	0.001	-0.351	0.356
63	neutral	Monsonia	Geraniaceae	0.003	-0.347	0.353
64	neutral	Lily	Liliaceae	0.003	-0.340	0.344
65	neutral	Euphorbia_big	Euphorbiaceae	0.004	-0.340	0.348
66	neutral	Craterostigma	Linderniaceae	0.005	-0.337	0.354
67	neutral	Priva	Verbenaceae	0.005	-0.338	0.357
68	neutral	Chloris_2	Poaceae	0.007	-0.336	0.356
69	neutral	Cynodon_pleachtostachyus	Poaceae	0.008	-0.136	0.151
70	neutral	Portulaca_spp	Portulacaceae	0.008	-0.340	0.354
71	neutral	Polygala	Polygalaceae	0.009	-0.341	0.356
72	neutral	Kleinia spp.	Asteraceae	0.012	-0.340	0.363
73	neutral	Hypoestes	Acanthaceae	0.013	-0.346	0.385
74	neutral	Chloris_gayana	Poaceae	0.014	-0.301	0.325
75	neutral	Hibiscus_aponeurus	Malvaceae	0.015	-0.333	0.352
76	neutral	Evolvulus	Convolvulaceae	0.015	-0.343	0.370
77	neutral	Pentania	Rubiaceae	0.016	-0.327	0.358
78	neutral	Cordia	Boraginaceae	0.016	-0.358	0.386
79	neutral	Euphorbia_rare	Euphorbiaceae	0.017	-0.316	0.360
80	neutral	Leonitis_sp	Lamiaceae	0.019	-0.331	0.374
81	neutral	Ipomoea_kituensis	Convolvulaceae	0.020	-0.329	0.372
82	neutral	Ocimum	Lamiaceae	0.027	-0.290	0.341
83	neutral	Tagetes	Asteraceae	0.028	-0.320	0.373
84	neutral	Cleome_sp	Cleomaceae	0.029	-0.375	0.419
85	neutral	Felicia_muricata	Asteraceae	0.032	-0.316	0.382
86	neutral	Trubulus	Zygophyllaceae	0.032	-0.313	0.374
87	neutral	Eragrostis_spp	Poaceae	0.036	-0.300	0.382
88	neutral	Cyphostemma_orodo	Vitaceae	0.036	-0.317	0.389
89	neutral	Ipomoea_3	Convolvulaceae	0.038	-0.317	0.393
90	neutral	Barleria_spinisepala	Acanthaceae	0.043	-0.276	0.363

91	neutral	Cassia	Fabaceae	0.043	-0.306	0.387
92	neutral	Cucumis	Cucurbitaceae	0.044	-0.304	0.396
93	neutral	Ipomoea_sinensis	Convolvulaceae	0.051	-0.274	0.380
94	neutral	Leucas	Lamiaceae	0.053	-0.279	0.383
95	neutral	Indigofera spp.	Fabaceae	0.062	-0.268	0.398
96	neutral	Crabbea	Acanthaceae	0.064	-0.284	0.410
97	neutral	Justicia spp.	Acanthaceae	0.065	-0.282	0.408
98	neutral	Sporobolus_ioclados	Poaceae	0.068	-0.261	0.400
99	neutral	Eragrostis_racemosa	Poaceae	0.078	-0.262	0.415
100	neutral	Themeda_triandra	Poaceae	0.082	-0.197	0.364
101	neutral	Solanum_coagulens	Solanaceae	0.090	-0.425	0.550
102	neutral	Pennisetum_stramineum	Poaceae	0.106	-0.033	0.244
103	neutral	Emilia	Asteraceae	0.121	-0.221	0.463
104	neutral	Hibiscus_micranthus	Malvaceae	0.154	-0.225	0.501
105	neutral	Bothriochloa_insculpta	Poaceae	0.163	-0.170	0.500
106	neutral	Tragus	Poaceae	0.167	-0.126	0.458
107	neutral	Barleria_eranthemoides	Acanthaceae	0.177	-0.200	0.524
108	neutral	Barleria_acanthoides_tan	Acanthaceae	0.181	-0.202	0.560
109	neutral	Heteropogon_contortus	Poaceae	0.181	-0.149	0.505
110	neutral	Cenchrus_ciliaris	Poaceae	0.271	-0.059	0.589
111	neutral	Harpachne_schimperi	Poaceae	0.315	-0.003	0.637
112	*	Cyperus	Cyperaceae	0.318	0.005	0.629
113	*	Helichrysum_glumaceum	Compositae	0.427	0.101	0.751
114	*	Pennisetum_mezianum	Poaceae	0.525	0.199	0.855
115	*	Eragrostis_superba	Poaceae	0.632	0.320	0.943
116	*	Cynodon_dactylon	Poaceae	0.892	0.765	1.026
117	*	Cymbopogon	Poaceae	0.950	0.639	1.258

**Table S2.** List of taxa included in our Bayesian joint species distribution model of plant responses to elephants (dung count surveys; Figure 2B). Species number corresponds to rank order in Figure 2B. Species identity corresponds to UHURU large quadrat survey data (“UNDERSTORY\_LGQUAD.TXT” in Kartzin et al. 2014). Graminoids (families Cyperus and Poaceae) are shaded and correspond to darkened circles in Figure 2B. Species denoted with an asterisk (\*) are those whose 95% CI did not overlap zero. All others overlapped zero (neutral). All data files are available in Ecological Archives #E095-064 (<http://www.esapubs.org/archive/ecol/E095/064/>).

Species Number	Response	Species Identity (Kartzinel et al. 2014)	Family	Mean Response	Lower 95% CI	Upper 95% CI
1	*	Plectranthus_small	Lamiaceae	-0.097	-0.142	-0.058
2	*	Solanum_big	Solanaceae	-0.079	-0.130	-0.034
3	*	Sansevieria	Asparagaceae	-0.076	-0.138	-0.012
4	*	Cynodon_plehtostachyus	Poaceae	-0.071	-0.101	-0.045
5	*	Cyathula	Amaranthaceae	-0.069	-0.120	-0.024
6	*	Blepharis	Acanthaceae	-0.065	-0.124	-0.009
7	*	Euphorbia_crotonoides	Euphorbiaceae	-0.058	-0.113	-0.001
8	*	Hibiscus_2	Malvaceae	-0.056	-0.110	-0.009
9	*	Hibiscus_calyphyllus	Malvaceae	-0.056	-0.111	-0.008
10	neutral	Pollichia	Caryophyllaceae	-0.044	-0.098	0.004
11	*	Pennisetum_stramineum	Poaceae	-0.041	-0.057	-0.027
12	neutral	Portulaca_quadridida	Portulacaceae	-0.037	-0.092	0.012
13	neutral	Ocimum	Lamiaceae	-0.036	-0.090	0.012
14	neutral	Chloris_roxburghiana	Poaceae	-0.034	-0.087	0.014
15	neutral	Pavonia	Malvaceae	-0.033	-0.091	0.020
16	neutral	Brachiaria_leersoides	Poaceae	-0.032	-0.084	0.015
17	neutral	Plectranthus_big	Lamiaceae	-0.031	-0.088	0.021
18	neutral	Barleria_eranthemoides	Acanthaceae	-0.031	-0.095	0.036
19	neutral	Commelina	Commelinaceae	-0.030	-0.072	0.006
20	neutral	Justicia_odora	Acanthaceae	-0.028	-0.085	0.024
21	neutral	Abutilon	Malvaceae	-0.026	-0.082	0.026
22	neutral	Portulaca_oleracea	Portulacaceae	-0.025	-0.088	0.038
23	neutral	Barleria_2	Acanthaceae	-0.024	-0.080	0.029
24	neutral	Dinebra	Poaceae	-0.023	-0.073	0.022
25	neutral	Ipomoea_sinensis	Convolvulaceae	-0.022	-0.078	0.026
26	neutral	Kalanchoe	Crassulaceae	-0.019	-0.077	0.033
27	neutral	Phyllanthus	Phyllanthaceae	-0.017	-0.074	0.034
28	neutral	Digitaria_milanjiana	Poaceae	-0.016	-0.072	0.035
29	neutral	Rhynchelytrum_repens	Poaceae	-0.015	-0.073	0.037
30	neutral	Barleria_spinisepala	Acanthaceae	-0.015	-0.072	0.036
31	neutral	Euphorbia_sp_small	Euphorbiaceae	-0.014	-0.072	0.038
32	neutral	Osteospermum	Asteraceae	-0.013	-0.070	0.037
33	neutral	Pentanisia	Rubiaceae	-0.013	-0.071	0.039
34	neutral	Eragrostis_rigidior	Poaceae	-0.011	-0.068	0.052
35	neutral	Hypoestes	Acanthaceae	-0.011	-0.076	0.043
36	neutral	Polygala	Polygalaceae	-0.011	-0.067	0.041
37	neutral	Hibiscus_flavifolius	Malvaceae	-0.011	-0.068	0.042
38	neutral	Lippia	Verbenaceae	-0.010	-0.066	0.041
39	neutral	Pennisetum_mezianum	Poaceae	-0.010	-0.066	0.040
40	neutral	Chenopodium	Aizoaceae	-0.009	-0.067	0.043
41	neutral	Cassia	Fabaceae	-0.008	-0.065	0.044
42	neutral	Cenchrus_ciliaris	Poaceae	-0.008	-0.063	0.041
43	neutral	Oxygonum	Polygonaceae	-0.008	-0.065	0.044

44	neutral	Barleria_ramulosa_white	Acanthaceae	-0.007	-0.070	0.058
45	neutral	Portulaca_kermisina	Portulacaceae	-0.007	-0.067	0.052
46	neutral	Eragrostis_spp	Poaceae	-0.006	-0.064	0.047
47	neutral	Sarcostemma	Apocynaceae	-0.005	-0.062	0.047
48	neutral	Enneapogon	Poaceae	-0.005	-0.063	0.048
49	neutral	Monechma	Acanthaceae	-0.004	-0.059	0.046
50	neutral	Pelargonium	Geraniaceae	-0.004	-0.062	0.049
51	neutral	Lily	Liliaceae	-0.004	-0.060	0.048
52	neutral	Hibiscus_meyeri	Malvaceae	-0.003	-0.064	0.051
53	neutral	Portulaca_spp	Portulacaceae	-0.003	-0.061	0.049
54	neutral	Setaria	Poaceae	-0.003	-0.061	0.049
55	neutral	Melhaniania spp.	Malvaceae	-0.003	-0.059	0.048
56	neutral	Tagetes	Asteraceae	-0.003	-0.061	0.049
57	neutral	Cordia	Boraginaceae	-0.002	-0.060	0.057
58	neutral	Cucumis	Cucurbitaceae	-0.002	-0.059	0.051
59	neutral	Sporobolus_spp	Poaceae	-0.002	-0.059	0.050
60	neutral	Caralluma_sp	Apocynaceae	-0.001	-0.058	0.052
61	neutral	Achyranthes_aspera	Amaranthaceae	-0.001	-0.055	0.049
62	neutral	Solanum_nigrum	Solanaceae	-0.001	-0.059	0.052
63	neutral	Kleinia spp.	Asteraceae	-0.001	-0.058	0.051
64	neutral	Phyllanthus_sp	Phyllanthaceae	0.000	-0.058	0.051
65	neutral	Monsonia	Geraniaceae	0.000	-0.058	0.051
66	neutral	Cissus	Vitaceae	0.000	-0.059	0.053
67	neutral	Craterostigma	Linderniaceae	0.000	-0.058	0.053
68	neutral	Priva	Verbenaceae	0.000	-0.058	0.052
69	neutral	Ipomoea_2	Convolvulaceae	0.000	-0.056	0.052
70	neutral	Aerva	Amaranthaceae	0.000	-0.058	0.052
71	neutral	Euphorbia_rare	Euphorbiaceae	0.001	-0.059	0.055
72	neutral	Trubulus	Zygophyllaceae	0.001	-0.056	0.053
73	neutral	Opuntia	Cactaceae	0.001	-0.058	0.057
74	neutral	Cyphostemma_orodo	Vitaceae	0.001	-0.057	0.054
75	neutral	Euphorbia_inaequilatera	Euphorbiaceae	0.002	-0.058	0.064
76	neutral	Ipomoea_kituensis	Convolvulaceae	0.003	-0.057	0.055
77	neutral	Hibiscus_aponeurus	Malvaceae	0.003	-0.055	0.056
78	neutral	Chloris_2	Poaceae	0.003	-0.059	0.060
79	neutral	Amaranthus	Amaranthaceae	0.003	-0.054	0.055
80	neutral	Indigofera spp.	Fabaceae	0.003	-0.047	0.050
81	neutral	Cleome_sp	Cleomaceae	0.004	-0.058	0.062
82	neutral	Barleria_3	Acanthaceae	0.005	-0.053	0.067
83	neutral	Ipomoea_3	Convolvulaceae	0.005	-0.053	0.056
84	neutral	Crabbea	Acanthaceae	0.005	-0.052	0.057
85	neutral	Euphorbia_big	Euphorbiaceae	0.006	-0.051	0.058
86	neutral	Leonitis_sp	Lamiaceae	0.007	-0.053	0.059
87	neutral	Felicia_muricata	Asteraceae	0.008	-0.050	0.060
88	neutral	Dactyloctenium	Poaceae	0.009	-0.043	0.056

89	neutral	Sporobolus_africanus	Poaceae	0.010	-0.045	0.060
90	neutral	Aristida spp.	Poaceae	0.010	-0.043	0.057
91	neutral	Justicia spp.	Acanthaceae	0.010	-0.046	0.061
92	neutral	Eragrostis_papposa	Poaceae	0.011	-0.042	0.058
93	neutral	Panicum_maximum	Poaceae	0.011	-0.044	0.061
94	neutral	Leucas	Lamiaceae	0.017	-0.040	0.067
95	neutral	Sida	Malvaceae	0.021	-0.033	0.070
96	neutral	Enteropogon	Poaceae	0.022	-0.014	0.055
97	neutral	Sporobolus_ioclados	Poaceae	0.022	-0.033	0.072
98	neutral	Solanum_coagulens	Solanaceae	0.023	-0.047	0.091
99	neutral	Bothriochloa_insculpta	Poaceae	0.023	-0.033	0.075
100	neutral	Emilia	Asteraceae	0.024	-0.031	0.074
101	neutral	Eragrostis_racemosa	Poaceae	0.030	-0.024	0.079
102	neutral	Gutenbergia	Asteraceae	0.031	-0.016	0.074
103	neutral	Chloris_gayana	Poaceae	0.031	-0.019	0.077
104	neutral	Harpachne_schimperii	Poaceae	0.032	-0.022	0.082
105	*	Cynodon_dactylon	Poaceae	0.033	0.017	0.048
106	*	Microchloa_kunthii	Poaceae	0.033	0.003	0.061
107	neutral	Heteropogon_contortus	Poaceae	0.034	-0.023	0.085
108	neutral	Evolvulus	Convolvulaceae	0.037	-0.023	0.100
109	neutral	Hibiscus_micranthus	Malvaceae	0.040	-0.024	0.097
110	*	Cyperus	Cyperaceae	0.062	0.010	0.109
111	*	Tragus	Poaceae	0.067	0.018	0.111
112	*	Eragrostis_superba	Poaceae	0.067	0.012	0.115
113	*	Eragrostis_tenuifolia	Poaceae	0.069	0.037	0.096
114	*	Helichrysum_glumaceum	Compositae	0.076	0.029	0.120
115	*	Themeda_triandra	Poaceae	0.082	0.037	0.122
116	*	Barleria_acanthoides_tan	Acanthaceae	0.086	0.017	0.147
117	*	Cymbopogon	Poaceae	0.095	0.044	0.140

**Table S3.** Species responses to rainfall for JSDM using herbivore exclosure treatment as a proxy for relative elephant abundance (Figure 2A). Species number corresponds to rank order in Figure S2A. Species identity corresponds to UHURU large quadrat survey data (“UNDERSTORY\_LGQUAD.TXT” in Kartzin et al. 2014). Graminoids (families Cyperus and Poaceae) are shaded and correspond to darkened circles in Figure S2A. Species denoted with an asterisk (\*) are those whose 95% CI did not overlap zero. All others overlapped zero (neutral).

Species Number	Response	Species Identity (Kartzin et al. 2014)	Family	Mean Response	Lower 95% CI	Upper 95% CI
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1	neutral	Heteropogon_contortus	Poaceae	-0.00104	-0.0027	0.0005
2	neutral	Euphorbia_crotonoides	Euphorbiac	-0.00090	-0.0030	0.0012
3	neutral	Evolvulus	Convolvula	-0.00083	-0.0030	0.0012
4	neutral	Hibiscus_aponeurus	Malvaceae	-0.00067	-0.0024	0.0010
5	neutral	Blepharis	Acanthace	-0.00065	-0.0026	0.0014
6	neutral	Cordia	Boraginace	-0.00054	-0.0026	0.0016
7	neutral	Harpachne_schimper	Poaceae	-0.00049	-0.0021	0.0011
8	neutral	Barleria_ramulosa_white	Acanthace	-0.00047	-0.0023	0.0012
9	neutral	Barleria_acanthoides_tan	Acanthace	-0.00047	-0.0024	0.0015
10	neutral	Sida	Malvaceae	-0.00045	-0.0020	0.0011
11	neutral	Pavonia	Malvaceae	-0.00041	-0.0021	0.0012
12	neutral	Brachiaria_leersoides	Poaceae	-0.00040	-0.0017	0.0009
13	neutral	Opuntia	Cactaceae	-0.00034	-0.0021	0.0014
14	neutral	Amaranthus	Amarantha	-0.00034	-0.0021	0.0013
15	neutral	Panicum_maximum	Poaceae	-0.00031	-0.0020	0.0013
16	neutral	Oxygonum	Polygonac	-0.00030	-0.0020	0.0014
17	neutral	Cassia	Fabaceae	-0.00028	-0.0020	0.0014
18	neutral	Sporobolus_africanus	Poaceae	-0.00027	-0.0020	0.0014
19	neutral	Cymbopogon	Poaceae	-0.00024	-0.0019	0.0014
20	neutral	Euphorbia_inaequilatera	Euphorbiac	-0.00024	-0.0024	0.0019
21	neutral	Barleria_eranthemoides	Acanthace	-0.00023	-0.0025	0.0020
22	neutral	Chenopodium	Aizoaceae	-0.00023	-0.0019	0.0014
23	neutral	Phyllanthus_sp	Phyllantha	-0.00022	-0.0020	0.0015
24	neutral	Craterostigma	Linderniac	-0.00021	-0.0020	0.0015
25	neutral	Kleinia spp.	Asteraceae	-0.00020	-0.0019	0.0015
26	neutral	Solanum_coagulens	Solanacea	-0.00020	-0.0035	0.0047
27	neutral	Portulaca_spp	Portulacac	-0.00019	-0.0020	0.0015
28	neutral	Eragrostis_superba	Poaceae	-0.00018	-0.0019	0.0015
29	neutral	Caralluma_sp	Apocynace	-0.00016	-0.0019	0.0015
30	neutral	Cyphostemma_orodo	Vitaceae	-0.00016	-0.0019	0.0016
31	neutral	Rhynchelytrum_repens	Poaceae	-0.00016	-0.0019	0.0015
32	neutral	Lily	Liliaceae	-0.00015	-0.0019	0.0015
33	neutral	Cucumis	Cucurbitac	-0.00014	-0.0019	0.0016
34	neutral	Euphorbia_big	Euphorbiac	-0.00014	-0.0019	0.0015
35	neutral	Ipomoea_3	Convolvula	-0.00014	-0.0018	0.0015
36	neutral	Monsonia	Geraniace	-0.00014	-0.0019	0.0016
37	neutral	Justicia_odora	Acanthace	-0.00013	-0.0019	0.0016
38	neutral	Hibiscus_micranthus	Malvaceae	-0.00012	-0.0024	0.0023
39	neutral	Solanum_nigrum	Solanacea	-0.00011	-0.0019	0.0016
40	neutral	Phyllanthus	Phyllantha	-0.00011	-0.0017	0.0014
41	neutral	Barleria_2	Acanthace	-0.00011	-0.0018	0.0015
42	neutral	Felicia_muricata	Asteraceae	-0.00009	-0.0018	0.0016
43	neutral	Eragrostis_spp	Poaceae	-0.00009	-0.0018	0.0016
44	neutral	Indigofera spp.	Fabaceae	-0.00008	-0.0018	0.0016
45	neutral	Ipomoea_kitensis	Convolvula	-0.00008	-0.0018	0.0016
46	neutral	Cyperus	Cyperacea	-0.00008	-0.0017	0.0015
47	neutral	Cleome_sp	Cleomacea	-0.00007	-0.0022	0.0020

48	neutral	Tagetes	Asteraceae	-0.00007	-0.0018	0.0016
49	neutral	Polygala	Polygalace	-0.00007	-0.0018	0.0016
50	neutral	Bothriochloa_insculpta	Poaceae		-0.0018	0.0016
51	neutral	Portulaca_kermisina	Portulacac	-0.00005	-0.0022	0.0019
52	neutral	Hibiscus_flavifolius	Malvaceae	-0.00004	-0.0018	0.0017
53	neutral	Barleria_spinisepala	Acanthace	-0.00004	-0.0017	0.0016
54	neutral	Ocimum	Lamiaceae	-0.00004	-0.0016	0.0015
55	neutral	Leonitis_sp	Lamiaceae	-0.00001	-0.0017	0.0017
56	neutral	Ipomoea_2	Convolvula	0.00002	-0.0017	0.0017
57	neutral	Pelargonium	Geraniace	0.00002	-0.0017	0.0017
58	neutral	Aerva	Amarantha	0.00002	-0.0017	0.0017
59	neutral	Cissus	Vitaceae	0.00002	-0.0017	0.0017
60	neutral	Pentanisia	Rubiaceae	0.00003	-0.0017	0.0017
61	neutral	Pollichia	Caryophyll	0.00006	-0.0014	0.0015
62	neutral	Eragrostis_tenuifolia	Poaceae	0.00008	-0.0008	0.0010
63	neutral	Sarcostemma	Apocynace	0.00012	-0.0015	0.0018
64	neutral	Melhania spp.	Malvaceae	0.00013	-0.0015	0.0017
65	neutral	Justicia spp.	Acanthace	0.00013	-0.0016	0.0018
66	neutral	Priva	Verbenace	0.00014	-0.0016	0.0018
67	neutral	Chloris_roxburghiana	Poaceae	0.00015	-0.0013	0.0016
68	neutral	Sansevieria	Asparagac	0.00017	-0.0014	0.0017
69	neutral	Cenchrus_ciliaris	Poaceae	0.00017	-0.0015	0.0018
70	neutral	Chloris_2	Poaceae	0.00018	-0.0021	0.0024
71	neutral	Osteospermum	Asteraceae	0.00019	-0.0014	0.0017
72	neutral	Enneapogon	Poaceae	0.00019	-0.0015	0.0018
73	neutral	Setaria	Poaceae	0.00020	-0.0015	0.0019
74	neutral	Sporobolus_spp	Poaceae	0.00021	-0.0015	0.0019
75	neutral	Euphorbia_sp_small	Euphorbiac	0.00023	-0.0014	0.0019
76	neutral	Crabbea	Acanthace	0.00026	-0.0015	0.0019
77	neutral	Helichrysum_glumaceum	Composita	0.00028	-0.0014	0.0020
78	neutral	Emilia	Asteraceae	0.00029	-0.0014	0.0020
79	neutral	Kalanchoe	Crassulace	0.00030	-0.0014	0.0019
80	neutral	Digitaria_milanjiana	Poaceae	0.00030	-0.0014	0.0019
81	neutral	Cyathula	Amarantha	0.00032	-0.0011	0.0017
82	neutral	Dinebra	Poaceae	0.00038	-0.0012	0.0020
83	neutral	Hypoestes	Acanthace	0.00041	-0.0015	0.0024
84	neutral	Monechma	Acanthace	0.00047	-0.0011	0.0021
85	neutral	Portulaca_quadrifida	Portulacac	0.00047	-0.0011	0.0020
86	neutral	Ipomoea_sinensis	Convolvula	0.00049	-0.0012	0.0021
87	neutral	Sporobolus_ioclados	Poaceae	0.00052	-0.0012	0.0022
88	neutral	Leucas	Lamiaceae	0.00059	-0.0011	0.0022
89	neutral	Barleria_3	Acanthace	0.00063	-0.0014	0.0026
90	neutral	Trubulus	Zygophylla	0.00064	-0.0011	0.0023
91	neutral	Aristida spp.	Poaceae	0.00072	-0.0010	0.0024
92	neutral	Pennisetum_mezianum	Poaceae	0.00074	-0.0010	0.0024
93	neutral	Plectranthus_big	Lamiaceae	0.00074	-0.0009	0.0024
94	neutral	Lippia	Verbenace	0.00074	-0.0009	0.0024

95	neutral	Euphorbia_rare	Euphorbiac	0.00081	-0.0018	0.0031
96	neutral	Abutilon	Malvaceae	0.00085	-0.0008	0.0025
97	neutral	Plectranthus_small	Lamiaceae	0.00088	-0.0005	0.0023
98	neutral	Eragrostis_racemosa	Poaceae	0.00094	-0.0007	0.0026
99	neutral	Eragrostis_papposa	Poaceae	0.00097	-0.0007	0.0026
100	neutral	Hibiscus_calyphyllus	Malvaceae	0.00098	-0.0005	0.0025
101	neutral	Themeda_triandra	Poaceae	0.00102	-0.0005	0.0024
102	*	Pennisetum_stramineum	Poaceae	0.00112	0.0004	0.0018
103	neutral	Eragrostis_rigidior	Poaceae	0.00120	-0.0009	0.0031
104	neutral	Portulaca_oleracea	Portulacac	0.00124	-0.0008	0.0033
105	neutral	Chloris_gayana	Poaceae	0.00127	-0.0003	0.0028
106	neutral	Dactyloctenium	Poaceae	0.00142	-0.0002	0.0030
107	*	Cynodon_plehtostachyus	Poaceae	0.00142	0.0007	0.0022
108	neutral	Achyranthes_aspera	Amarantha	0.00152	-0.0001	0.0031
109	neutral	Hibiscus_2	Malvaceae	0.00155	-0.0002	0.0034
110	*	Enteropogon	Poaceae	0.00181	0.0006	0.0031
111	*	Cynodon_dactylon	Poaceae	0.00216	0.0014	0.0029
112	*	Hibiscus_meyeri	Malvaceae	0.00223	0.0003	0.0040
113	*	Solanum_big	Solanacea	0.00233	0.0010	0.0037
114	*	Commelina	Commelin	0.00255	0.0013	0.0038
115	*	Microchloa_kunthii	Poaceae	0.00257	0.0015	0.0036
116	*	Gutenbergia	Asteraceae	0.00268	0.0013	0.0041
117	*	Tragus	Poaceae	0.00406	0.0027	0.0055

**Table S4.** Species responses to rainfall for JSDM using dung count as a proxy for relative elephant abundance (Figure 2B). Species number corresponds to rank order in Figure S2B.

Species identity corresponds to UHURU large quadrat survey data

(“UNDERSTORY\_LGQUAD.TXT” in Kartzin et al. 2014). Graminoids (families Cyperus and Poaceae) are shaded and correspond to darkened circles in Figure S2B. Species denoted with an asterisk (\*) are those whose 95% CI did not overlap zero. All others overlapped zero (neutral).

Species Number	Response	Species Identity (Kartzin et al. 2014)	Family	Mean Response	Lower 95% CI	Upper 95% CI
1	*	Euphorbia_crotonoides	Euphorbiaceae	-0.00131	-0.00235	-0.00020
2	*	Harpachne_schimperi	Poaceae	-0.00118	-0.00210	-0.00028
3	*	Hibiscus_aponeurus	Malvaceae	-0.00102	-0.00198	-0.00005
4	*	Melhanian spp.	Malvaceae	-0.00094	-0.00188	0.00000
5	neutral	Eragrostis_superba	Poaceae	-0.00074	-0.00166	0.00018

6	neutral	Heteropogon_contortus	Poaceae	-0.00069	-0.00165	0.00026
7	neutral	Solanum_coagulens	Solanaceae	-0.00068	-0.00262	0.00113
8	neutral	Sida	Malvaceae	-0.00067	-0.00156	0.00022
9	neutral	Cymbopogon	Poaceae	-0.00062	-0.00154	0.00029
10	neutral	Phyllanthus	Phyllanthaceae	-0.00059	-0.00149	0.00029
11	neutral	Bothriochloa_insculpta	Poaceae	-0.00048	-0.00145	0.00046
12	neutral	Cyperus	Cyperaceae	-0.00047	-0.00140	0.00043
13	neutral	Evolvulus	Convolvulaceae	-0.00047	-0.00143	0.00049
14	neutral	Barleria_eranthemoides	Acanthaceae	-0.00043	-0.00141	0.00049
15	neutral	Tagetes	Asteraceae	-0.00042	-0.00139	0.00054
16	neutral	Euphorbia_rare	Euphorbiaceae	-0.00041	-0.00135	0.00055
17	neutral	Osteospermum	Asteraceae	-0.00040	-0.00132	0.00049
18	neutral	Polygala	Polygalaceae	-0.00038	-0.00132	0.00056
19	neutral	Sarcostemma	Apocynaceae	-0.00034	-0.00128	0.00059
20	neutral	Portulaca_oleracea	Portulacaceae	-0.00033	-0.00137	0.00067
21	neutral	Blepharis	Acanthaceae	-0.00032	-0.00141	0.00065
22	neutral	Portulaca_quadrifida	Portulacaceae	-0.00031	-0.00119	0.00055
23	neutral	Sporobolus_ioclados	Poaceae	-0.00030	-0.00124	0.00062
24	neutral	Lily	Liliaceae	-0.00028	-0.00126	0.00068
25	neutral	Barleria_ramulosa_white	Acanthaceae	-0.00025	-0.00120	0.00066
26	neutral	Euphorbia_sp_small	Euphorbiaceae	-0.00025	-0.00120	0.00069
27	neutral	Hypoestes	Acanthaceae	-0.00024	-0.00141	0.00082
28	neutral	Cucumis	Cucurbitaceae	-0.00024	-0.00122	0.00072
29	neutral	Caralluma_sp	Apocynaceae	-0.00024	-0.00118	0.00071
31	neutral	Ipomoea_2	Convolvulaceae	-0.00023	-0.00117	0.00072
30	neutral	Hibiscus_flavifolius	Malvaceae	-0.00023	-0.00119	0.00071
32	neutral	Euphorbia_big	Euphorbiaceae	-0.00023	-0.00118	0.00073
33	neutral	Indigofera spp.	Fabaceae	-0.00022	-0.00117	0.00070
34	neutral	Lippia	Verbenaceae	-0.00022	-0.00115	0.00069
35	neutral	Ipomoea_kituensis	Convolvulaceae	-0.00021	-0.00117	0.00074
36	neutral	Ocimum	Lamiaceae	-0.00021	-0.00106	0.00065
37	neutral	Craterostigma	Linderniaceae	-0.00021	-0.00119	0.00077
38	neutral	Sansevieria	Asparagaceae	-0.00020	-0.00111	0.00070
39	neutral	Amaranthus	Amaranthaceae	-0.00020	-0.00117	0.00076
40	neutral	Ipomoea_3	Convolvulaceae	-0.00020	-0.00117	0.00075
41	neutral	Rhynchelytrum_repens	Poaceae	-0.00020	-0.00117	0.00076
42	neutral	Digitaria_milanjiana	Poaceae	-0.00019	-0.00112	0.00074
43	neutral	Justicia spp.	Acanthaceae	-0.00019	-0.00115	0.00076
44	neutral	Opuntia	Cactaceae	-0.00018	-0.00110	0.00075
45	neutral	Monsonia	Geraniaceae	-0.00018	-0.00116	0.00078
46	neutral	Phyllanthus_sp	Phyllanthaceae	-0.00018	-0.00114	0.00077
47	neutral	Eragrostis_papposa	Poaceae	-0.00016	-0.00110	0.00078
48	neutral	Kleinia spp.	Asteraceae	-0.00016	-0.00113	0.00080
49	neutral	Solanum_nigrum	Solanaceae	-0.00015	-0.00112	0.00081
50	neutral	Cyphostemma_orodo	Vitaceae	-0.00015	-0.00114	0.00081
51	neutral	Cassia	Fabaceae	-0.00015	-0.00110	0.00078
52	neutral	Sporobolus_spp	Poaceae	-0.00014	-0.00108	0.00081

53	neutral	Barleria_3	Acanthaceae	-0.00013	-0.00119	0.00096
54	neutral	Portulaca_spp	Portulacaceae	-0.00012	-0.00108	0.00084
55	neutral	Themeda_triandra	Poaceae	-0.00012	-0.00097	0.00072
56	neutral	Priva	Verbenaceae	-0.00008	-0.00105	0.00087
57	neutral	Pelargonium	Geraniaceae	-0.00007	-0.00103	0.00087
58	neutral	Portulaca_kermisina	Portulacaceae	-0.00007	-0.00107	0.00091
59	neutral	Felicia_muricata	Asteraceae	-0.00006	-0.00105	0.00089
60	neutral	Leonitis_sp	Lamiaceae	-0.00002	-0.00099	0.00095
61	neutral	Aerva	Amaranthaceae	-0.00002	-0.00099	0.00094
62	neutral	Setaria	Poaceae	-0.00002	-0.00099	0.00093
63	neutral	Hibiscus_calyphyllus	Malvaceae	0.00000	-0.00085	0.00083
64	neutral	Emilia	Asteraceae	0.00000	-0.00096	0.00097
65	neutral	Cissus	Vitaceae	0.00001	-0.00096	0.00097
66	neutral	Barleria_spinisepala	Acanthaceae	0.00002	-0.00093	0.00095
67	neutral	Kalanchoe	Crassulaceae	0.00004	-0.00092	0.00098
68	neutral	Barleria_2	Acanthaceae	0.00004	-0.00086	0.00092
69	neutral	Pavonia	Malvaceae	0.00005	-0.00090	0.00099
70	neutral	Justicia_odora	Acanthaceae	0.00005	-0.00089	0.00098
71	neutral	Monechma	Acanthaceae	0.00005	-0.00088	0.00096
72	neutral	Pentanisia	Rubiaceae	0.00005	-0.00090	0.00100
73	neutral	Helichrysum_glumaceum	Compositae	0.00006	-0.00089	0.00098
74	neutral	Trubulus	Zygophyllaceae	0.00007	-0.00089	0.00103
75	neutral	Cleome_sp	Cleomaceae	0.00007	-0.00092	0.00107
76	neutral	Euphorbia_inaequilatera	Euphorbiaceae	0.00009	-0.00092	0.00109
77	neutral	Panicum_maximum	Poaceae	0.00009	-0.00085	0.00101
78	neutral	Cyathula	Amaranthaceae	0.00013	-0.00064	0.00088
79	neutral	Crabbea	Acanthaceae	0.00014	-0.00083	0.00110
80	neutral	Enneapogon	Poaceae	0.00014	-0.00082	0.00109
81	neutral	Aristida_spp.	Poaceae	0.00017	-0.00080	0.00109
82	neutral	Oxygonum	Polygonaceae	0.00018	-0.00075	0.00111
83	neutral	Pollichia	Caryophyllacea	0.00021	-0.00062	0.00104
84	neutral	Brachiaria_leersoides	Poaceae	0.00022	-0.00056	0.00100
85	neutral	Chloris_2	Poaceae	0.00025	-0.00068	0.00116
86	neutral	Barleria_acanthoides_tan	Acanthaceae	0.00025	-0.00085	0.00151
87	neutral	Chloris_roxburghiana	Poaceae	0.00026	-0.00058	0.00108
88	neutral	Ipomoea_sinensis	Convolvulaceae	0.00027	-0.00065	0.00117
89	neutral	Hibiscus_meyeri	Malvaceae	0.00030	-0.00064	0.00127
90	neutral	Dinebra	Poaceae	0.00031	-0.00059	0.00120
91	neutral	Leucas	Lamiaceae	0.00034	-0.00058	0.00126
92	neutral	Eragrostis_spp	Poaceae	0.00037	-0.00056	0.00130
93	neutral	Abutilon	Malvaceae	0.00037	-0.00055	0.00127
94	neutral	Plectranthus_small	Lamiaceae	0.00038	-0.00036	0.00113
95	neutral	Sporobolus_africanus	Poaceae	0.00040	-0.00054	0.00134
96	neutral	Hibiscus_micranthus	Malvaceae	0.00040	-0.00052	0.00129
97	neutral	Cordia	Boraginaceae	0.00043	-0.00071	0.00159
98	neutral	Plectranthus_big	Lamiaceae	0.00045	-0.00045	0.00136
99	neutral	Eragrostis_tenuifolia	Poaceae	0.00050	-0.00014	0.00115

100	neutral	Pennisetum_mezianum	Poaceae	0.00065	-0.00025	0.00153
101	neutral	Chenopodium	Aizoaceae	0.00069	-0.00023	0.00160
102	*	Enteropogon	Poaceae	0.00076	0.00004	0.00149
103	*	Solanum_big	Solanaceae	0.00079	0.00003	0.00157
104	neutral	Eragrostis_racemosa	Poaceae	0.00080	-0.00013	0.00170
105	neutral	Hibiscus_2	Malvaceae	0.00080	-0.00014	0.00174
106	*	Cenchrus_ciliaris	Poaceae	0.00102	0.00014	0.00188
107	*	Cynodon_dactylon	Poaceae	0.00114	0.00073	0.00155
108	*	Pennisetum_stramineum	Poaceae	0.00115	0.00077	0.00153
109	*	Achyranthes_aspera	Amaranthaceae	0.00117	0.00027	0.00208
110	*	Microchloa_kunthii	Poaceae	0.00118	0.00052	0.00182
111	*	Eragrostis_rigidior	Poaceae	0.00159	0.00055	0.00269
112	*	Commelina	Commelinaceae	0.00167	0.00104	0.00230
113	*	Chloris_gayana	Poaceae	0.00170	0.00084	0.00254
114	*	Dactyloctenium	Poaceae	0.00174	0.00087	0.00261
115	*	Cynodon_pleachtostachyus	Poaceae	0.00187	0.00139	0.00233
116	*	Gutenbergia	Asteraceae	0.00212	0.00135	0.00290
117	*	Tragus	Poaceae	0.00279	0.00196	0.00363

**Table S5.** The interactive effects of rainfall and elephant abundance on understory species' abundance for JSDM using herbivore exclosure treatment as a proxy for relative elephant abundance (Figure 2A, S2A). Positive values of interaction slope denote increasing positive elephant effects at greater rainfall levels; negative values denote increasing negative effects of elephants at greater rainfall levels. Species identity corresponds to UHURU large quadrat survey data ("UNDERSTORY\_LGQUAD.TXT" in Kartzinel et al. 2014). Graminoids (families Cyperus and Poaceae) are shaded.

Species Number	Species Identity (Kartzinel et al. 2014)	Family	Interaction Slope	Lower 95% CI	Upper 95% CI
1	Solanum_big	Solanaceae	-0.002360	-0.004333	-0.000423



2	Hibiscus_meyeri	Malvaceae	-0.001569	-0.003894	0.000770
3	Chloris_roxburghiana	Poaceae	-0.001489	-0.003606	0.000614
4	Enteropogon	Poaceae	-0.001389	-0.003124	0.000335
5	Commelina	Commelinac	-0.000995	-0.002677	0.000688
6	Achyranthes_aspera	Amaranthac	-0.000965	-0.003149	0.001233
7	Portulaca_quadrifida	Portulacace	-0.000939	-0.003124	0.001259
8	Euphorbia_sp_small	Euphorbiac	-0.000868	-0.003295	0.001500
9	Plectranthus_big	Lamiaceae	-0.000811	-0.003190	0.001493
10	Abutilon	Malvaceae	-0.000787	-0.003072	0.001498
11	Cyathula	Amaranthac	-0.000778	-0.002732	0.001172
12	Barleria_eranthemoides	Acanthacea	-0.000705	-0.002969	0.001569
13	Osteospermum	Asteraceae	-0.000632	-0.002919	0.001584
14	Cynodon_dactylon	Poaceae	-0.000627	-0.001448	0.000164
15	Barleria_2	Acanthacea	-0.000595	-0.002929	0.001728
16	Enneapogon	Poaceae	-0.000562	-0.002884	0.001804
17	Digitaria_milanjiana	Poaceae	-0.000520	-0.002817	0.001793
18	Hibiscus_calyphyllus		-0.000516	-0.002666	0.001623
19	Dactyloctenium	Poaceae	-0.000503	-0.002710	0.001688
20	Eragrostis_papposa	Poaceae	-0.000496	-0.002789	0.001817
21	Sarcostemma	Apocynacea	-0.000480	-0.002809	0.001850
22	Lippia	Verbenacea	-0.000452	-0.002808	0.001902
23	Gutenbergia	Asteraceae	-0.000448	-0.002404	0.001500
24	Hibiscus_2	Malvaceae	-0.000427	-0.002722	0.001836
25	Sida	Malvaceae	-0.000412	-0.002668	0.001777
26	Crabbea	Acanthacea	-0.000408	-0.002743	0.001938
27	Helichrysum_glumaceum	Compositae	-0.000401	-0.002729	0.001918
28	Kalanchoe	Crassulacea	-0.000397	-0.002781	0.001967
29	Setaria	Poaceae	-0.000390	-0.002800	0.001984
30	Tagetes	Asteraceae	-0.000359	-0.002770	0.002035
31	Themeda_triandra	Poaceae	-0.000346	-0.002320	0.001648
32	Trubulus	Zygophyllac	-0.000343	-0.002773	0.002096
33	Polygala	Polygalacea	-0.000341	-0.002681	0.002047
34	Sporobolus_spp	Poaceae	-0.000328	-0.002712	0.002081
35	Dinebra	Poaceae	-0.000326	-0.002570	0.001911
36	Sansevieria	Asparagace	-0.000317	-0.002569	0.001923
37	Pennisetum_mezianum	Poaceae	-0.000294	-0.002596	0.002045
38	Chloris_gayana	Poaceae	-0.000293	-0.002364	0.001817
39	Sporobolus_ioclados	Poaceae	-0.000278	-0.002607	0.002032
40	Aristida spp.	Poaceae	-0.000259	-0.002615	0.002115
41	Melhanian spp.	Malvaceae	-0.000256	-0.002529	0.002023
42	Pelargonium	Geraniacea	-0.000245	-0.002644	0.002125
43	Priva	Verbenacea	-0.000229	-0.002643	0.002127
44	Cucumis	Cucurbitace	-0.000226	-0.002650	0.002166
45	Euphorbia_big	Euphorbiac	-0.000188	-0.002594	0.002203
46	Amaranthus	Amaranthac	-0.000186	-0.002583	0.002206
47	Harpachne_schimperi	Poaceae	-0.000156	-0.002382	0.002069
48	Justicia_odora	Acanthacea	-0.000156	-0.002555	0.002218

49	Hypoestes	Acanthaceae	-0.000151	-0.002664	0.002132
50	Portulaca_oleracea	Portulacaceae	-0.000143	-0.002405	0.002142
51	Ipomoea_sinensis	Convolvulac	-0.000141	-0.002487	0.002121
52	Monsonia	Geraniaceae	-0.000125	-0.002487	0.002275
53	Ipomoea_3	Convolvulac	-0.000121	-0.002555	0.002293
54	Hibiscus_micranthus	Malvaceae	-0.000115	-0.002428	0.002138
55	Ipomoea_2	Convolvulac	-0.000115	-0.002463	0.002220
56	Cyphostemma_orodo	Vitaceae	-0.000107	-0.002489	0.002346
57	Cleome_sp	Cleomaceae	-0.000104	-0.002459	0.002278
58	Caralluma_sp	Apocynaceae	-0.000092	-0.002497	0.002291
59	Leucas	Lamiaceae	-0.000087	-0.002378	0.002193
60	Hibiscus_flavifolius	Malvaceae	-0.000082	-0.002533	0.002353
61	Kleinia spp.	Asteraceae	-0.000081	-0.002487	0.002327
62	Solanum_nigrum	Solanaceae	-0.000078	-0.002494	0.002328
63	Craterostigma	Linderniaceae	-0.000077	-0.002509	0.002332
64	Barleria_spinisepala	Acanthaceae	-0.000072	-0.002328	0.002227
65	Cordia	Boraginaceae	-0.000066	-0.002452	0.002357
66	Portulaca_spp	Portulacaceae	-0.000064	-0.002485	0.002343
67	Euphorbia_inaequilatera	Euphorbiac	-0.000055	-0.002548	0.002419
68	Justicia spp.	Acanthaceae	-0.000052	-0.002404	0.002309
69	Monechma	Acanthaceae	-0.000041	-0.002272	0.002200
70	Pennisetum_stramineum	Poaceae	-0.000013	-0.001035	0.000997
71	Cissus	Vitaceae	-0.000013	-0.002402	0.002368
72	Leonitis_sp	Lamiaceae	-0.000010	-0.002457	0.002428
73	Hibiscus_aponeurus	Malvaceae	-0.000009	-0.002408	0.002406
74	Euphorbia_rare	Euphorbiac	-0.000004	-0.002322	0.002399
75	Oxygonum	Polygonaceae	-0.000004	-0.002343	0.002343
76	Aerva	Amaranthac	0.000004	-0.002401	0.002435
77	Microchloa_kunthii	Poaceae	0.000037	-0.001283	0.001383
78	Opuntia	Cactaceae	0.000039	-0.002335	0.002370
79	Eragrostis_spp	Poaceae	0.000048	-0.002273	0.002402
80	Pentanisia	Rubiaceae	0.000062	-0.002346	0.002454
81	Phyllanthus_sp	Phyllanthac	0.000072	-0.002362	0.002471
82	Solanum_coagulens	Solanaceae	0.000084	-0.004926	0.005982
83	Portulaca_kermisina	Portulacaceae	0.000096	-0.002328	0.002494
84	Barleria_3	Acanthaceae	0.000118	-0.002335	0.002530
85	Pollichia	Caryophylla	0.000130	-0.001997	0.002233
86	Ipomoea_kituensis	Convolvulac	0.000131	-0.002271	0.002531
87	Bothriochloa_insculpta	Poaceae	0.000161	-0.002142	0.002480
88	Chloris_2	Poaceae	0.000185	-0.002290	0.002730
89	Pavonia	Malvaceae	0.000199	-0.002170	0.002550
90	Lily	Liliaceae	0.000205	-0.002171	0.002575
91	Rhynchelytrum_repens	Poaceae	0.000215	-0.002165	0.002592
92	Felicia_muricata	Asteraceae	0.000226	-0.002142	0.002607
93	Plectranthus_small	Lamiaceae	0.000258	-0.001725	0.002226
94	Cymbopogon	Poaceae	0.000271	-0.001907	0.002423
95	Heteropogon_contortus	Poaceae	0.000375	-0.001872	0.002644

96	Cyperus	Cyperaceae	0.000381	-0.001796	0.002568
97	Chenopodium	Aizoaceae	0.000382	-0.001925	0.002697
98	Euphorbia_crotonoides	Euphorbiac	0.000383	-0.001874	0.002653
99	Indigofera spp.	Fabaceae	0.000384	-0.001940	0.002707
100	Eragrostis_racemosa	Poaceae	0.000389	-0.001870	0.002627
101	Cenchrus_ciliaris	Poaceae	0.000392	-0.001883	0.002651
102	Sporobolus_africanus	Poaceae	0.000396	-0.001892	0.002686
103	Blepharis	Acanthacea	0.000414	-0.001976	0.002736
104	Cynodon_plechstachyus	Poaceae	0.000460	-0.000566	0.001461
105	Cassia	Fabaceae	0.000464	-0.001905	0.002853
106	Emilia	Asteraceae	0.000484	-0.001827	0.002776
107	Barleria_ramulosa_white	Acanthacea	0.000534	-0.001833	0.002868
108	Phyllanthus	Phyllanthac	0.000538	-0.001662	0.002774
109	Barleria_acanthoides_tan	Acanthacea	0.000627	-0.001724	0.003070
110	Brachiaria_leersoides	Poaceae	0.000700	-0.001186	0.002603
111	Eragrostis_rigidior	Poaceae	0.000882	-0.001483	0.003201
112	Ocimum	Lamiaceae	0.000910	-0.001233	0.003077
113	Panicum_maximum	Poaceae	0.000914	-0.001373	0.003226
114	Eragrostis_superba	Poaceae	0.000951	-0.001288	0.003184
115	Evolvulus	Convolvulac	0.001268	-0.001282	0.003776
116	Eragrostis_tenuifolia	Poaceae	0.001336	0.000257	0.002424
117	Tragus	Poaceae	0.001871	0.000006	0.003740

**Table S6.** The interactive effects of rainfall and elephant abundance on understory species' abundance for JSMD using dung count as a proxy for relative elephant abundance (Figure 2B, S2B). Positive values of interaction slope denote increasing positive elephant effects at greater rainfall levels; negative values denote increasing negative effects of elephants at greater rainfall levels. Species identity corresponds to UHURU large quadrat survey data ("UNDERSTORY\_LGQUAD.TXT" in Kartzin et al. 2014). Graminoids (families Cyperus and Poaceae) are shaded.

Species	Species Identity (Kartzin)	Family	Interaction	Lower	Upper
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Number	et al. 2014)		Slope	95% CI	95% CI
1	Enteropogon	Poaceae	-0.000300	-0.000042	-0.000614
2	Barleria_acanthoides_tan	Acanthaceae	-0.000286	0.000106	-0.000685
3	Cyathula	Amaranthac	-0.000224	0.000070	-0.000518
4	Dactyloctenium	Poaceae	-0.000210	0.000136	-0.000571
5	Sida	Malvaceae	-0.000204	0.000115	-0.000556
6	Brachiaria_leersoides	Poaceae	-0.000172	0.000118	-0.000465
7	Solanum_big	Solanaceae	-0.000159	0.000117	-0.000454
8	Pollichia	Caryophylla	-0.000154	0.000189	-0.000522
9	Cenchrus_ciliaris	Poaceae	-0.000152	0.000192	-0.000528
10	Abutilon	Malvaceae	-0.000145	0.000211	-0.000522
11	Barleria_2	Acanthaceae	-0.000135	0.000222	-0.000516
12	Plectranthus_big	Lamiaceae	-0.000133	0.000231	-0.000521
13	Chenopodium	Aizoaceae	-0.000133	0.000225	-0.000515
14	Sporobolus_africanus	Poaceae	-0.000124	0.000226	-0.000498
15	Dinebra	Poaceae	-0.000116	0.000228	-0.000490
16	Commelina	Commelinac	-0.000116	0.000127	-0.000340
17	Hibiscus_micranthus	Malvaceae	-0.000105	0.000214	-0.000450
18	Pennisetum_mezianum	Poaceae	-0.000103	0.000228	-0.000479
19	Cynodon_dactylon	Poaceae	-0.000101	0.000004	-0.000202
20	Hibiscus_meyeri	Malvaceae	-0.000099	0.000240	-0.000473
21	Plectranthus_small	Lamiaceae	-0.000097	0.000220	-0.000432
22	Euphorbia_sp_small	Euphorbiac	-0.000092	0.000266	-0.000480
23	Eragrostis_spp	Poaceae	-0.000092	0.000268	-0.000479
24	Oxygonum	Polygonace	-0.000089	0.000272	-0.000481
25	Enneapogon	Poaceae	-0.000089	0.000277	-0.000485
26	Trubulus	Zygophyllac	-0.000089	0.000265	-0.000470
27	Chloris_roxburghiana	Poaceae	-0.000088	0.000200	-0.000400
28	Portulaca_quadrifida	Portulacace	-0.000076	0.000266	-0.000449
29	Osteospermum	Asteraceae	-0.000072	0.000278	-0.000456
30	Gutenbergia	Asteraceae	-0.000067	0.000205	-0.000330
31	Ipomoea_sinensis	Convolvulac	-0.000063	0.000280	-0.000432
32	Hibiscus_calyphyllus	Malvaceae	-0.000059	0.000278	-0.000413
33	Crabbea	Acanthaceae	-0.000058	0.000302	-0.000436
34	Sporobolus_ioclados	Poaceae	-0.000052	0.000310	-0.000441
35	Leucas	Lamiaceae	-0.000047	0.000301	-0.000423
36	Chloris_2	Poaceae	-0.000047	0.000328	-0.000423
37	Barleria_3	Acanthaceae	-0.000044	0.000315	-0.000434
38	Cleome_sp	Cleomaceae	-0.000044	0.000304	-0.000416
39	Polygala	Polygalacea	-0.000043	0.000322	-0.000429
40	Ipomoea_3	Convolvulac	-0.000043	0.000324	-0.000435
41	Setaria	Poaceae	-0.000041	0.000319	-0.000429
42	Phyllanthus	Phyllanthac	-0.000039	0.000310	-0.000419
43	Amaranthus	Amaranthac	-0.000038	0.000327	-0.000427
44	Helichrysum_glumaceum	Compositae	-0.000036	0.000300	-0.000393
45	Justicia_odora	Acanthaceae	-0.000035	0.000322	-0.000418
46	Euphorbia_rare	Euphorbiac	-0.000032	0.000369	-0.000413

47	Euphorbia_big	Euphorbiac	-0.000031	0.000335	-0.000411
48	Pennisetum_stramineum	Poaceae	-0.000031	0.000068	-0.000135
49	Kalanchoe	Crassulacea	-0.000029	0.000336	-0.000426
50	Tagetes	Asteraceae	-0.000026	0.000336	-0.000407
51	Pelargonium	Geraniaceae	-0.000026	0.000341	-0.000418
52	Portulaca_spp	Portulacace	-0.000024	0.000345	-0.000420
53	Achyranthes_aspera	Amaranthac	-0.000024	0.000293	-0.000339
54	Cyphostemma_orodo	Vitaceae	-0.000022	0.000339	-0.000408
55	Cucumis	Cucurbitace	-0.000022	0.000333	-0.000402
56	Sporobolus_spp	Poaceae	-0.000020	0.000345	-0.000410
57	Pentania	Rubiaceae	-0.000019	0.000348	-0.000411
58	Kleinia_spp.	Asteraceae	-0.000017	0.000346	-0.000412
59	Euphorbia_inaequilatera	Euphorbiac	-0.000014	0.000345	-0.000409
60	Cassia	Fabaceae	-0.000014	0.000335	-0.000400
61	Hibiscus_aponeurus	Malvaceae	-0.000014	0.000347	-0.000406
62	Solanum_nigrum	Solanaceae	-0.000011	0.000355	-0.000399
63	Hibiscus_flavifolius	Malvaceae	-0.000010	0.000346	-0.000395
64	Opuntia	Cactaceae	-0.000007	0.000349	-0.000402
65	Leonitis_sp	Lamiaceae	-0.000006	0.000366	-0.000403
66	Eragrostis_rigidior	Poaceae	-0.000004	0.000343	-0.000395
67	Heteropogon_contortus	Poaceae	-0.000004	0.000361	-0.000395
68	Cissus	Vitaceae	-0.000004	0.000364	-0.000399
69	Caralluma_sp	Apocynacea	-0.000004	0.000358	-0.000394
70	Sarcostemma	Apocynacea	-0.000004	0.000358	-0.000385
71	Craterostigma	Linderniace	-0.000003	0.000357	-0.000394
72	Justicia_spp.	Acanthacea	-0.000001	0.000357	-0.000388
73	Aerva	Amaranthac	-0.000001	0.000363	-0.000394
74	Monsonia	Geraniaceae	0.000001	0.000356	-0.000380
75	Cordia	Boraginace	0.000003	0.000370	-0.000383
76	Digitaria_milanjiana	Poaceae	0.000004	0.000356	-0.000365
77	Lippia	Verbenacea	0.000017	0.000375	-0.000362
78	Ipomoea_kituensis	Convolvulac	0.000019	0.000378	-0.000365
79	Chloris_gayana	Poaceae	0.000022	0.000327	-0.000285
80	Rhynchelytrum_repens	Poaceae	0.000023	0.000389	-0.000376
81	Priva	Verbenacea	0.000023	0.000384	-0.000355
82	Barleria_ramulosa_white	Acanthacea	0.000023	0.000392	-0.000372
83	Pavonia	Malvaceae	0.000029	0.000397	-0.000357
84	Lily	Liliaceae	0.000029	0.000391	-0.000358
85	Portulaca_kermisina	Portulacace	0.000032	0.000397	-0.000357
86	Eragrostis_tenuifolia	Poaceae	0.000033	0.000181	-0.000105
87	Ipomoea_2	Convolvulac	0.000034	0.000389	-0.000333
88	Melhanian_spp.	Malvaceae	0.000038	0.000385	-0.000336
89	Barleria_eranthemoides	Acanthacea	0.000038	0.000408	-0.000355
90	Phyllanthus_sp	Phyllanthac	0.000038	0.000385	-0.000313
91	Hypoestes	Acanthacea	0.000044	0.000396	-0.000328
92	Microchloa_kunthii	Poaceae	0.000059	0.000218	-0.000105
93	Indigofera_spp.	Fabaceae	0.000061	0.000408	-0.000309

94	Eragrostis_racemosa	Poaceae	0.000063	0.000384	-0.000264
95	Felicia_muricata	Asteraceae	0.000074	0.000429	-0.000299
96	Evolvulus	Convolvulac	0.000078	0.000423	-0.000281
97	Harpachne_schimperi	Poaceae	0.000096	0.000442	-0.000277
98	Eragrostis_papposa	Poaceae	0.000098	0.000438	-0.000265
99	Barleria_spinisepala	Acanthacea	0.000103	0.000465	-0.000276
100	Ocimum	Lamiaceae	0.000116	0.000451	-0.000228
101	Hibiscus_2	Malvaceae	0.000118	0.000417	-0.000223
102	Bothriochloa_insculpta	Poaceae	0.000119	0.000471	-0.000266
103	Panicum_maximum	Poaceae	0.000122	0.000470	-0.000255
104	Aristida_spp.	Poaceae	0.000127	0.000474	-0.000247
105	Cyperus	Cyperaceae	0.000129	0.000433	-0.000175
106	Monechma	Acanthacea	0.000143	0.000465	-0.000192
107	Blepharis	Acanthacea	0.000145	0.000495	-0.000233
108	Portulaca_oleracea	Portulacace	0.000189	0.000552	-0.000203
109	Emilia	Asteraceae	0.000194	0.000533	-0.000166
110	Sansevieria	Asparagace	0.000197	0.000564	-0.000204
111	Cynodon_plehtostachyus	Poaceae		0.000374	0.000126
112	Eragrostis_superba	Poaceae	0.000253	0.000595	-0.000123
113	Themeda_triandra	Poaceae	0.000269	0.000580	-0.000069
114	Cymbopogon	Poaceae	0.000277	0.000609	-0.000074
115	Euphorbia_crotonoides	Euphorbiac	0.000282	0.000626	-0.000106
116	Solanum_coagulens	Solanaceae	0.000498	0.001231	-0.000667
117	Tragus	Poaceae	0.000615	0.000870	0.000385

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**Supplement**  
**Joint Species Distribution Model.**

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## File list in DataS1.zip

Joint Species Distribution Model.R

## Description

Annotated R code for joint species distribution models of UHURU herbivore exclosure vegetation survey data. UHURU survey data available in Kartzin et al. 2014 (*Ecology*, DOI: 10.1890/13-1023R.1). See Appendix for detailed description of JSDM.

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