**Received Date: 08 -FEB- 2016**
**Revised Date: 20 -MAY- 2016**
**Accepted Date: 13 –JUN- 2016**
**Article Type: Articles**

Final version received date : 27 July 2016

**RUNNING HEAD:** Elephants create associational refuges

**TITLE:** Elephants in the understory: opposing direct and indirect effects of consumption and ecosystem engineering

**AUTHORS:** Tyler C. Coverdale[1]*, Tyler R. Kartzinel[1], Kathryn L. Grabowski[1], Robert K. Shriver[2], Abdikadir A. Hassan[3], Jacob R. Goheen[4], Todd M. Palmer[5], and Robert M. Pringle[1]

1. Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA
2. University Program in Ecology, Duke University, Durham, NC 27708, USA
3. Mpala Research Centre, PO Box 555, Nanyuki, Kenya
4. Department of Zoology & Physiology, University of Wyoming, Laramie, WY 82071, USA
5. Department of Biology, University of Florida, Gainesville, FL 32611, USA

*Address for correspondence: tylerc@princeton.edu

**SUBMISSION TYPE:** Article

**KEYWORDS.** African savannas, associational defenses, disturbance, elephant damage, extinction, facilitation, herbivory, *Loxodonta africana,* plant diversity, megafauna, ivory poaching, wildlife management

**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 seven years within 36 one-hectare 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, understory biomass was 5-14% greater in the presence of elephants across a range of rainfall levels. Whereas direct consumption presumably accounts for the negative effects, positive effects are likely 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. Indeed, 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 one year. 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 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.

**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 & Levick 2012; Figure 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). 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 (Fayrer-Hosken et al. 2000, Pimm and van Aarde 2001, Guldemond 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 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 (Figure 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, Nasseri et al. 2011, Pringle et al. 2015). 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. 2009, Cromsigt & 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 fauna, elephant interactions with understory plants—which can account for >70% of plant diversity in semi-arid savannas (Seibert and Scogings 2015)—remain poorly understood (Augustine 2003, Veldman et al. 2013, Pringle et al. 2014). 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"; Figure 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 (Figure 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 and spines that further impede herbivore access—may reduce the risk of local extinction from overgrazing and help to maintain diverse 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). Conversely, elephant damage may adversely affect understory plant communities by, for example, decreasing light or water availability (Belsky 1994, Caylor et al. 2005), thereby amplifying 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 one-hectare 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 (Figure 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 hectares of savanna with a mean annual rainfall of ~600mm. 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 years, reaching up to 2 individuals km$^{-2}$ (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 seven years (2008-2014) of data on understory composition from the UHURU large-herbivore exclosure experiment (Pringle 2012, Goheen et al. 2013, Kartzinel et al. 2014). UHURU comprises 36 size-selective one-hectare 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 Olff 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 ten-pin frame placed at 49 evenly spaced, permanently marked points within a central 60m x 60m 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 non-destructive 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 60m x 5m belt transects within the plant-sampling grid (Goheen et al. 2013, Kartzinel 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 cover; see Clark et al. 2014), we regressed understory species occurrence in each plot*survey combination against (a) total rainfall during the previous six months, (b) herbivore-exclusion treatment (a categorical variable), and (c) the interaction of these variables. We then performed the same analysis using elephant dung frequency (a continuous variable) in lieu of experimental exclosure treatment. Regression parameters were given non-informative 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 cover (our proxy for biomass, as noted above) across (a) herbivore exclosure treatments and (b) the range of observed elephant dung densities at each of three levels of rainfall (the $25^{th}$, median, and $75^{th}$ 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 (a) the high frequency of elephant-damaged trees at our study site and in protected areas throughout Africa and (b) recent work demonstrating the ecological importance of such ecosystem engineering (Pringle 2008, Nasseri et al. 2011, Pringle et al. 2015) we conducted a series of surveys and experiments between July 2013 and August 2014 to evaluate the effects of elephant damage on understory biomass and species richness (Figure 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 Figure 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-effect models to compare changes in understory biomass and species richness over one year, 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 Figure S1). Error terms for all reported means are ± 1 SEM, with the exception of the results of the previously described joint species model, which are ± 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 one year, with changes in biomass and species richness between time points compared as described above.

*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 ≥2m height within ten 200m x 10m transects. For the purposes of this study, trees were classified as "damaged" if they met two criteria: (i) at least one branch ≥2cm diameter was damaged by elephants (which is readily distinguishable from other types of damage: Augustine and McNaughton 2004), and (ii) an area ≥1m$^2$ 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. Figure 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 $m^2$, damaged: 5 $m^2$). 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/$m^2$), 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 (Figure 1B). Using a handsaw, we removed live *A. etbaica* branches and moved them 10m from the nearest tree canopy (*n*=20 branches). Paired control areas without detached branches were established 5m 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; Figure 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 one year. We compared the independent and interactive effects of damage-addition and exclosure treatments on changes in understory species richness and biomass using a mixed-effects model, as described above.

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 (Figure S1). Branches in damage-removal replicates were detached with a handsaw and discarded >25m 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 common grass species in each location (*Cynodon plechtostachyus* and *Aristida kenyensis* in south and central MRC, respectively) beneath 24 damaged and undamaged *A. etbaica* ($n$=8 grass stems/tree and 12 trees/type/site) and compared the proportion of blades damaged for each grass species (separately) across damaged and undamaged trees. We also used camera traps (Bushnell TrophyCam, model #119435(c), Bushnell Corporation) to quantify the incidence of ungulate herbivory beneath 5 pairs of damaged and undamaged *A. etbaica* trees (3 pairs in south, 2 in central). Cameras were mounted 15m from each focal tree and recorded 3-photo bursts when triggered by an infrared motion sensor. Each camera trap was deployed for ~430 hours, yielding >4700 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.). 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 thermochrons (model DS1923, iButtonLink Technologies) 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 50cm above ground level. Temperatures were recorded hourly for 10 days 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 (2014). All measurements were taken within one hour 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 (Figure 2A, 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 (Figure S2A, Table S3), of which six were graminoids. No species responded negatively to rainfall. Across rainfall levels, understory plant cover was 8.3–9.4% greater in the presence of elephants than in their absence (Figure 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 (Figure 2B, 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 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 (Figure S2B, Table S4), of which just one was a grass. Finally, total understory cover increased by 5.4–14.0% as a function of elephant-dung density across rainfall levels (Figure S3B).

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

*Surveys of naturally elephant-damaged trees*. Elephant damage was common, affecting 84.8 ± 4.7% of *A. brevispica*, 83.1 ± 3.2% of *A. mellifera*, and 61.6 ± 3.2% of *A. etbaica* (Figure S4). *Acacia etbaica* comprised 48.1% of all trees surveyed. Of *A. etbaica* classified as damaged, an average of 33.8 ± 2.6% of the understory habitat beneath the canopy was directly overlain by damaged branches (Figure 1C). Approximately 6% of all elephant damage encountered (i.e., 10 branches per ha) was in the form of branches fully detached from trees. Taken together, partially and fully detached damaged branches covered 2,340 ± 280$m^2$ of the two hectares surveyed. Understory plant biomass was 55% greater ($t_{17}$=7.43, $P$<0.0001) beneath elephant-damaged canopies than beneath undamaged canopies (Figure 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 ± 19.1% ($F_{1,29}$=13.17, $P$=0.001) and species richness by 71.0 ± 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; Figure 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; Figure 4B). However, there was no significant 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; Figure 4C) and species richness ($F_{1,33}$=12.32, $P$=0.001; Figure 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; Figure 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 relative water content ($t_{22.0}$=1.45, $P$=0.16) did not differ significantly between damaged and undamaged tree canopies (Figure S5).

**DISCUSSION.** Our results indicate that elephants have surprisingly mild net effects on understory vegetation. Using two complementary approaches that characterized elephant presence/absence and relative abundance in our JSDM 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 had neutral effects on the remaining 83-89% (Figure 2). Elephants had mild positive effects on total understory plant cover (5.4-8.7%) at median rainfall, suggesting that responses of positively affected understory species outweighed those of negatively affected species (Figure 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 disparities) 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 one year, paralleling patterns beneath naturally damaged trees (Figures 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 enhancement) of associational refuges that inhibit ungulate foraging. Herbivore utilization and grazing damage were significantly reduced beneath damaged trees, whereas we 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 (Figure 4C,D).

In our view, the unexpected finding that simulated damage enhanced understory species richness within full herbivore exclosures (Figure 4B) is 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 is nonetheless 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 invasive and heavily defended forbs and promoting native 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 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. 2007, Pringle et al. 2014). The historical view of elephants as destructive to vegetation and a threat to plant biodiversity is based largely on assessment 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). Taken together, these benefits to understory plants often, but not always, outweigh the cost of growing in close proximity to overstory competitors. In this sense, our results suggest that elephant damage may often enhance pre-existing 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 will strengthen competitive effects 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, Nasseri 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.

**ACKNOWLEDGMENTS.** We thank the government of Kenya (NACOSTI/P/14/8746/1626) and Mpala Research Centre and Conservancy for permission to conduct this study. B. Culver, I. Adan, R. Diaz, T. Pearson, M. Mohamed, S. Kurukura, and R. Hohbein assisted with field work. P. Chen, J. Daskin, J. Guyton, A. Pellegrini, C. Clements, R. Long, D. Morris, and two anonymous reviewers provided insightful comments on the manuscript, and we thank M. Veldhuis and H. Olff for thought-provoking conversations about the importance of non-trophic interactions in food webs. This work was supported by awards from the US National Science Foundation (NSF Graduate Research Fellowship to TCC; Doctoral Dissertation Improvement Grant DEB-1601538 to TCC and RMP; DEB-1355122 to RMP and CE Tarnita; and DEB-1547679 to JRG) and National Geographic Society Young Explorers Grant #9503-14 to TCC. We thank the Thermodata Corporation for replacing lost thermochrons free of charge and A. Ngaina for logistical support. 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.

**LITERATURE CITED.**

Asner, G. P., and S. R. Levick. 2012. Landscape-scale effects of herbivores on treefall in African savannas. Ecology Letters 15:1211–1217.

Augustine, D. J. 2003. Spatial heterogeneity in the herbaceous layer of a semi-arid savanna ecosystem. Plant Ecology 167:319–332.

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

Barnes, R. F. W. 2001. How reliable are dung counts for estimating elephant numbers? African Journal of Ecology 39:1–9.

Belsky, A. 1994. Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. Ecology 75:922–932.

Buss, I. O. 1961. Some observations of food habits and behavior of the African elephant. The Journal of Wildlife Management 25:131–148.

Callaway, R., D. Kikodze, M. Chiboshvili, and L. Khetsuriani. 2005. Unpalatable plants protect neighbors from grazing and increase plant community diversity. Ecology 86:1856–1862.

Caylor, K. K., H. H. Shugart, and I. Rodriguez-Iturbe. 2005. Tree canopy effects on simulated water stress in Southern African savannas. Ecosystems 8:17–32.

Clark, J. S., A. E. Gelfand, C. W. Woodall, and K. Zhu. 2014. More than the sum of the parts: Forest climate response from joint species distribution models. Ecological Applications 24:990–999.

Compagnoni, A., and P. Adler. 2014. Warming, competition, and *Bromus tectorum* population growth across an elevation gradient. Ecosphere 5:1–34.

Connell, J. 1978. Diversity in Tropical Rain Forests and Coral Reefs. Science 199:1302–1310.

Cromsigt, J. P. G. M., and M. te Beest. 2014. Restoration of a megaherbivore: landscape-level impacts of white rhinoceros in Kruger National Park, South Africa. Journal of Ecology 102:566–575.

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

du Toit, J. T. and H. Olff. 2014. Generalities in grazing and browsing ecology: using across-guild comparisons to control contingencies. Oecologia 174:1075–1083.

Fayrer-Hosken, R., D. Grobler, J. Van Altena, H. Bertschinger, and J. Kirkpatrick. 2000. Immunocontraception of African elephants. Nature 407:149.

Foxcroft, L. C., D. M. Richardson, and J. R. U. Wilson. 2008. Ornamental plants as invasive aliens: problems and solutions in Kruger National Park, South Africa. Environmental Management 41:32–51.

Gelman, A., J. Hill, and M. Yajima. 2012. Why we (usually) don't have to worry about multiple comparisons. Journal of Research on Educational Effectiveness 5:189–211.

Glover, J. 1963. The elephant problem at Tsavo. African Journal of Ecology 1:30–39.

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

Goheen, J. R., T. M. Palmer, G. K. Charles, K. M. Helgen, S. N. Kinyua, J. E. Maclean, B. L. Turner, H. S. Young, and R. M. Pringle. 2013. Piecewise disassembly of a large-herbivore community across a rainfall gradient: the UHURU experiment. PloS One 8:e55192.

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

Hay, M. 1986. Associational plant defenses and the maintenance of species diversity: turning competitors into accomplices. American Naturalist 128:617–641.

Holdo, R. 2007. Elephants, fire, and frost can determine community structure and composition in Kalahari Woodlands. Ecological Applications 17:558–568.

Horn, H. S. 1975. Markovian properties of forest succession. Pages 196-211 in M. L. Cody and J. M. Diamond, editors. Ecology and Evolution of Communities, Belknap, Cambridge, MA.

Johnson, C. F., R. M. Cowling, and P. B. Phillipson. 1999. The flora of the Addo Elephant National Park , South Africa: are threatened species vulnerable to elephant damage? Biodiversity and Conservation 8:1447–1456.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos 69:373–386.

Jonsson, M., D. Bell, J. Hjältén, T. Rooke, and P. F. Scogings. 2010. Do mammalian herbivores influence invertebrate communities via changes in the vegetation? Results from a preliminary survey in Kruger National Park, South Africa. African Journal of Range and Forage Science 27:39–44.

Kartzinel, T., P. Chen, T. Coverdale, D. Erickson, W. Kress, M. Kuzmina, D. Rubenstein, W. Wang, and R. Pringle. 2015. DNA metabarcoding illuminates dietary niche partitioning by large African herbivores. Proceedings of the National Academy of Sciences 112:8019–8024.

Kartzinel, T., J. Goheen, G. Charles, E. DeFranco, J. Maclean, T. Otieno, T. Palmer, and R. Pringle. 2014. Plant and small-mammal responses to large-herbivore exclusion in an African savanna: five years of the UHURU experiment. Ecology 95:787.

Kéfi, S., E. L. Berlow, E. Wieters, S. Navarrete, O. L. Petchey, S. Wood, A. Boit, L. N. Joppa, K. D. Lafferty, R. J. Williams, N. D. Martinez, B. Menge, C. Blanchette, A. C. Iles, and U. Brose. 2012. More than a meal…integrating non-feeding interactions into food webs. Ecology Letters 15:291–300.

Kohi, E. M., W. F. De Boer, M. J. S. Peel, R. Slotow, C. Van Der Waal, A. Skidmore, and H. H. T. Prins. 2011. African elephants *Loxodonta africana* amplify browse heterogeneity in African savanna. Biotropica 43:711–721.

Landman, M., D. Schoeman, A. Hall-Martin, and G. Kerley. 2014. Long-term monitoring reveals differing impacts of elephants on elements of a canopy shrub community. Ecological Applications 24:2002–2012.

Laws, R. 1970. Elephants as agents of habitat and landscape change in East Africa. Oikos 21:1–15.

Levin, S., and J. Lubchenco. 2008. Resilience, robustness, and marine ecosystem-based management. Bioscience 58:27–32.

Litoroh, M., F. W. Ihwagi, R. Mayienda, J. Bernard, and I. Douglas-Hamilton. 2010. Total aerial count of elephants in Laikipia-Samburu ecosystem in November 2008. Pages 1–42.

Louthan, A., D. Doak, J. Goheen, T. Palmer, and R. Pringle. 2014. Mechanisms of plant–plant interactions: concealment from herbivores is more important than abiotic-stress mediation in an African savannah. Proceedings of the Royal Society B 281:1–7.

Menge, B. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. Ecological Monographs 65:21–74.

Midgley, J. J., D. Balfour, and G. I. Kerley. 2005. Why do elephants damage savanna trees?

South African Journal of Science 101:213–216.

Milchunas, D. G., and I. Noy-Meir. 2002. Grazing refuges, external avoidance of herbivory and plant diversity. Oikos 99:113–130.

Moore, J. 2006. Animal ecosystem engineers in streams. BioScience 56:237–246.

Munns, R. 2010. Plant water content and relative water content. Version 6. [Online URL: {http://www.publish.csiro.au/prometheuswiki/tiki-pagehistory.php?page=Plant water content and relative water content&preview=6}.]

Nasseri, N., L. McBrayer, and B. Schulte. 2011. The impact of tree modification by African elephant (*Loxodonta africana*) on herpetofaunal species richness in northern Tanzania. African Journal of Ecology 49:1–8.

O'Connor, D. A. O., B. Butt, and J. B. Foufopoulos. 2015. Foraging ecologies of giraffe (*Giraffa camelopardalis reticulata*) and camels (*Camelus dromedarius*) in northern Kenya: effects of habitat structure and possibilities for competition? African Journal of Ecology 53:183–193.

Owen-Smith, N., G. Kerley, B. Page, R. Slotow, and R. J. van Aarde. 2006. A scientific perspective on the management of elephants in the Kruger National Park and elsewhere. South African Journal of Science 102:389–394.

Pimm, S., and R. van Aarde. 2001. African elephants and contraception. Nature 411:766.

Pollock, L. J., R. Tingley, W. K. Morris, N. Golding, R. B. O'Hara, K. M. Parris, P. A. Vesk, and M. A. McCarthy. 2014. Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). Methods in Ecology and Evolution 5:397–406.

Pringle, R. M. 2008. Elephants as agents of habitat creation for small vertebrates at the patch scale. Ecology 89:26–33.

Pringle, R. M. 2012. How to be manipulative: intelligent tinkering is key to understanding ecology and rehabilitating ecosystems. American Scientist 100:30–37.

Pringle, R., J. Goheen, T. Palmer, G. Charles, E. DeFranco, R. Hohbein, A. Ford, and C. Tarnita. 2014. Low functional redundancy among mammalian browsers in regulating an encroaching shrub (*Solanum campylacanthum*) in African savannah. Proceedings of the Royal Society B 281:1–9.

Pringle, R. M., D. M. Kimuyu, R. L. Sensenig, T. M. Palmer, C. Riginos, K. E. Veblen, and T. P.

Young. 2015. Synergistic effects of fire and elephants on arboreal animals in an African savanna. Journal of Animal Ecology 84:1637–1645.

R Core Development Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Rebollo, S., D. G. Milchunas, and P. L. Chapman. 2002. The role of a spiny plant refuge in structuring grazed shortgrass steppe plant communities. Oikos 98:53–64.

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

Scholes, R., S. Archer. 1997. Tree-grass interactions in savannas. Annual Review of Ecology and Systematics 28:517–544.

Seibert, F. and P. Scogings. 2015. Browsing intensity of herbaceous forbs across a semi-arid savanna catenal sequence. South African Journal of Botany 100:69–74.

Soliveres, S., F. T. Maestre, M. Berdugo, and E. Allan. 2015. A missing link between facilitation and plant species coexistence: nurses benefit generally rare species more than common ones. Journal of Ecology 103:1183-1189.

Sousa, W. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15:353–391.

Thaxton, J. M., W. J. Platt. 2006. Small-scale fuel variation alters fire intensity and shrub abundance in a pine savanna. Ecology 87:1331–1337.

van Coller, H., F. Siebert, S. J. Siebert. 2013. Herbaceous species diversity patterns across various treatments of herbivory and fire along the sodic zone of the Nkuhlu exclosures, Kruger National Park. Koedoe 55:1–6.

Valeix, M., H. Fritz, R. Sabatier, F. Murindagomo, D. Cumming, and P. Duncan. 2011. Elephant-induced structural changes in the vegetation and habitat selection by large herbivores in an African savanna. Biological Conservation 144:902–912.

Veldhuis, Michiel P. 2016. On the organization of ecosystems: ecological autocatalysis in African savannas. PhD thesis, University of Groningen, Netherlands.

Veldman, J., W. Mattingly, and L. Brudvig. 2013. Understory plant communities and the functional distinction between savanna trees, forest trees, and pines. Ecology 94:424–434.

Waldram, M. S., W. J. Bond, and W. D. Stock. 2007. Ecological engineering by a mega-grazer: white rhino impacts on a South African savanna. Ecosystems 11:101–112.

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

**FIGURE LEGENDS.**

**Figure 1.** Elephant damage and its consequences. (A) An adult elephant damages 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.

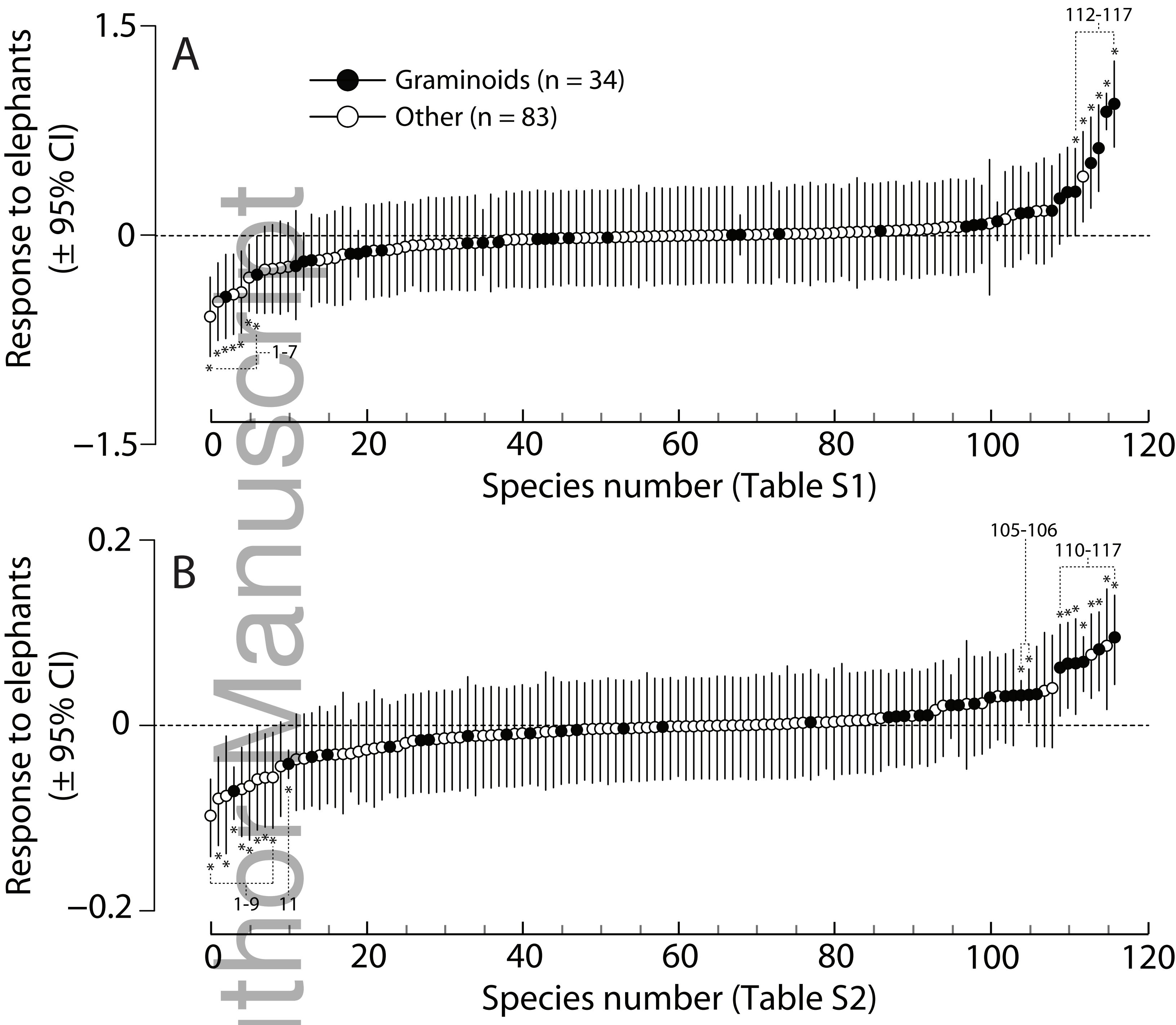
**Figure 2.** Joint species distribution model results for elephant effects on 117 understory plant species. The effect of elephants was modeled in two ways: as presence-abence using herbivore exclosure treatment (A) and relative abundance using dung counts (B). Data are means ± 95% CI, denoted with * when CI does not overlap zero. Darkened circles are graminoids (families Poaceae and Cyperaceae). Species numbers correspond to those in Tables S1 and S2, which contain detailed lists of all plant taxa assessed.

**Figure 3.** Results of biomass and species richness surveys beneath *Acacia etbaica* canopies. Elephant damaged branches (white bars) enhance understory plant biomass (A) and species richness (B, unscaled; C, scaled by area) relative to undamaged portions of the same tree canopy (black bars).

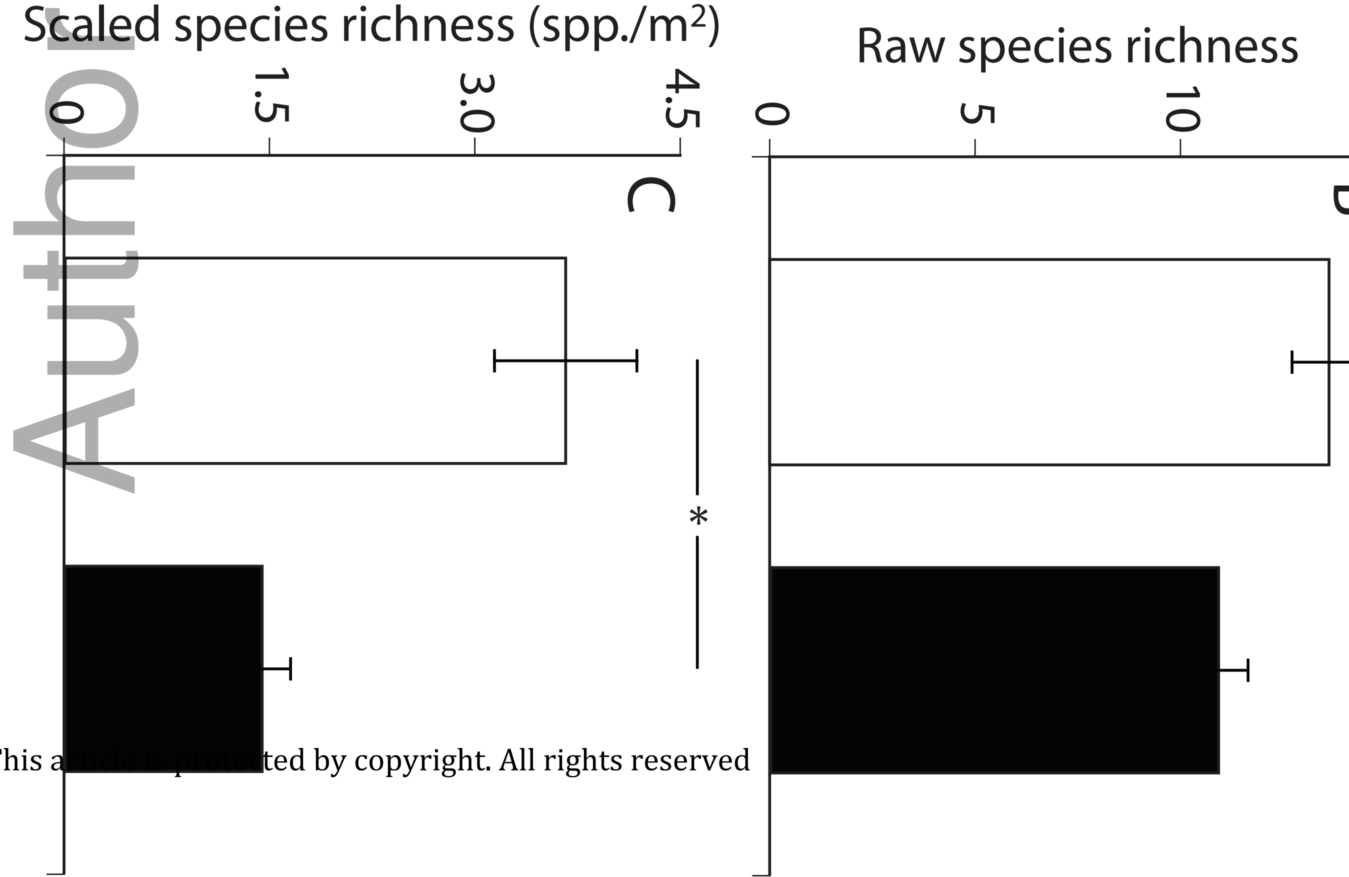
**Figure 4.** Results of damage-addition (top) and -removal (bottom) experiments beneath *Acacia etbaica* canopies. Changes in understory biomass (A) and species richness (B) were measured over one year after tree canopies in the full exclosure (–LMH) and control (+LMH) UHURU plots were experimentally 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.

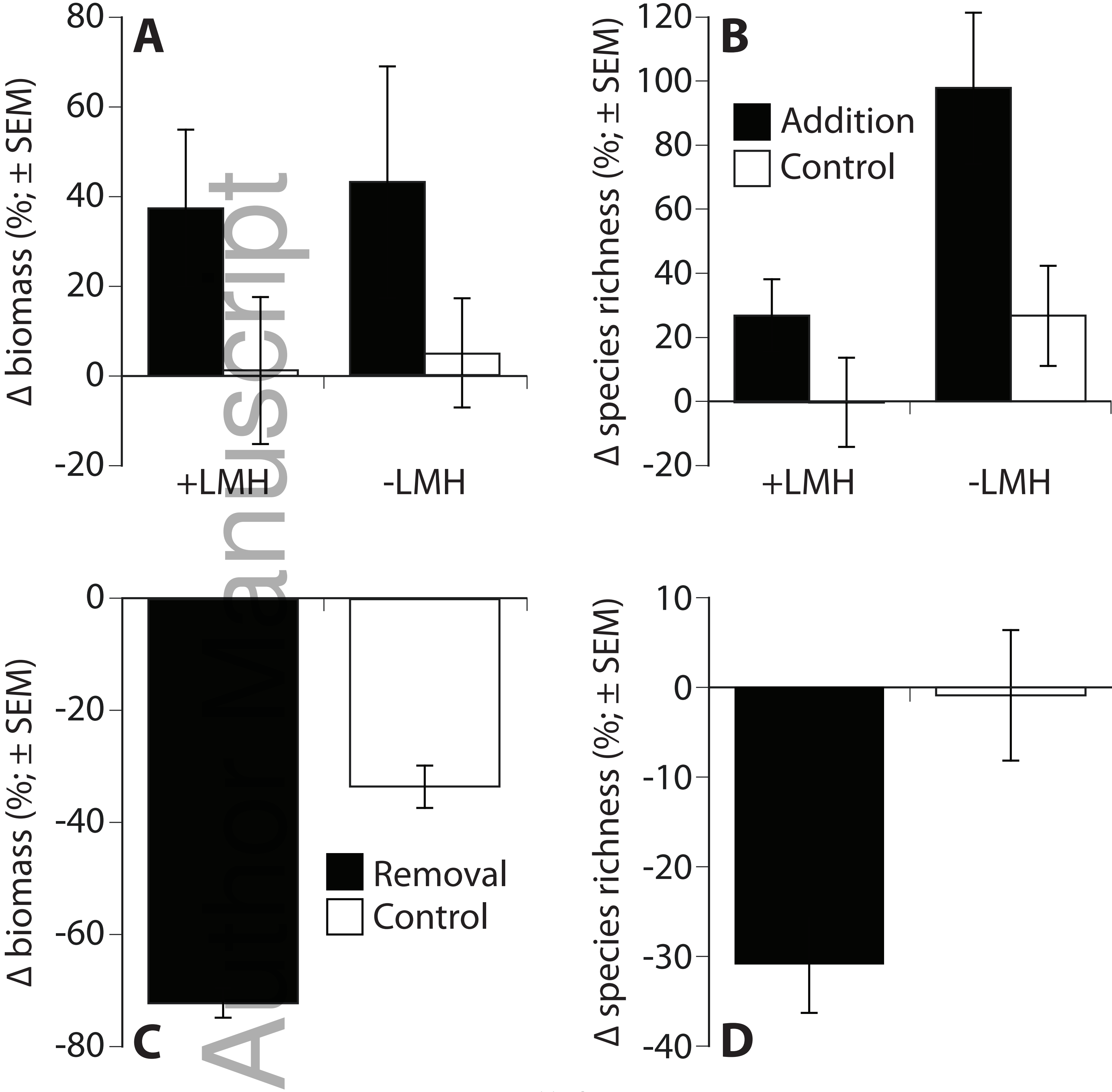
**Figure 5.** Effects of elephant damage on ungulate grazing intensity. (A) The proportion of stems of two common grass species grazed by ungulates beneath damaged and undamaged *Acacia etbaica* canopies in south (*C. plectostachyus*) and central (*A. kenyensis*) MRC. (B) The number of ungulates photographed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


ecy_1557_f1.tif

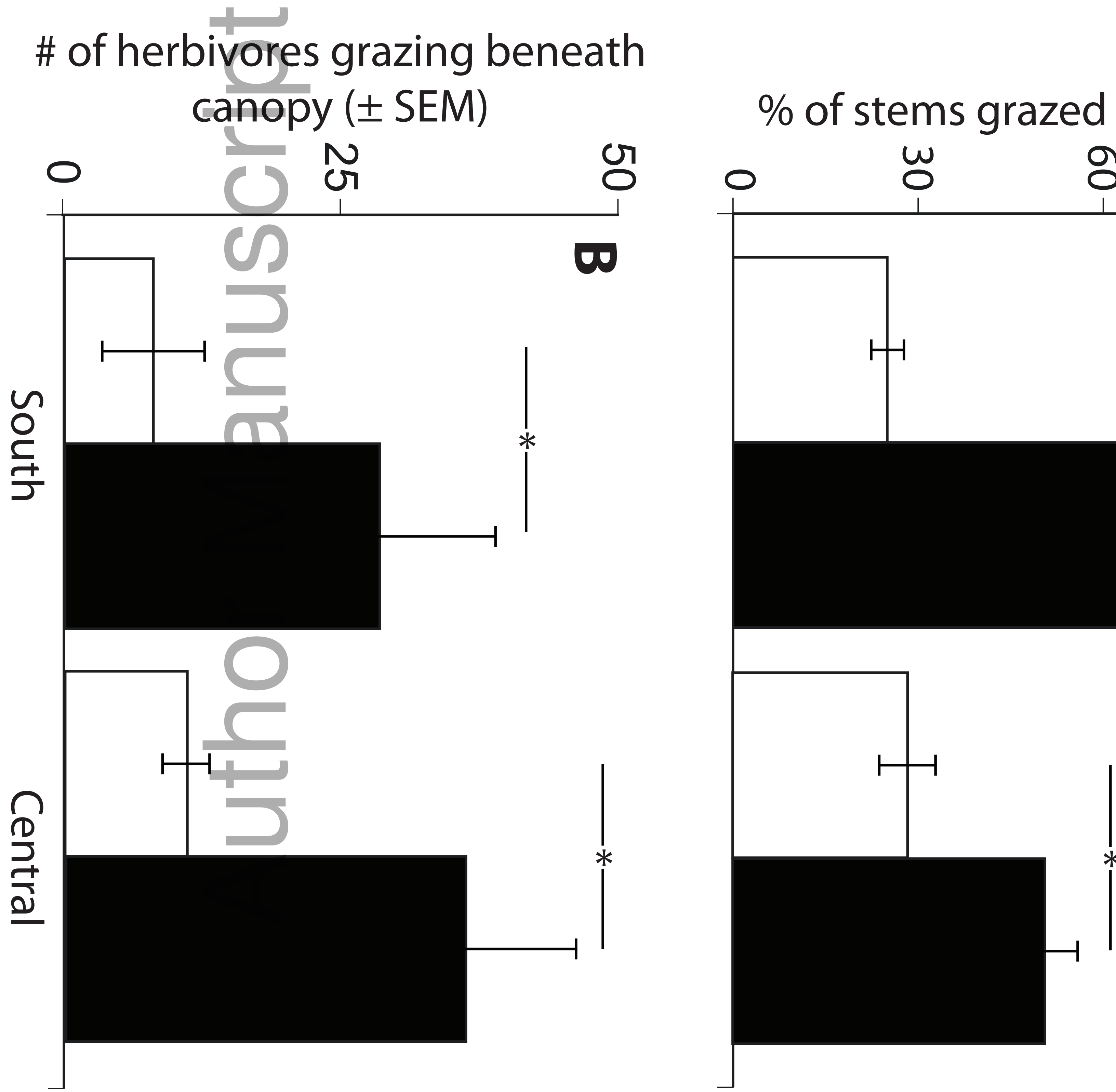



ecy_1557_f2.eps


Scaled species richness (spp./m2)
0
1.5
3.0
4.5
C
*
Raw species richness
0
5
10




ecy_1557_f4.eps






ecy_1557_f5.eps