

**Large herbivores promote habitat specialization and beta diversity of African
savanna trees**

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ABSTRACT

Edaphic variation in plant community composition is widespread, yet its underlying mechanisms are rarely understood and often assumed to be physiological. In East African savannas, *Acacia* tree species segregate sharply across soils of differing parent material: the ant-defended whistling thorn, *A. drepanolobium* (ACDR), is monodominant on clay vertisols that are nutrient rich but physically stressful, whereas poorly defended species such as *A. brevispica* (ACBR) dominate on nutrient-poor but otherwise benign sandy loams. Using a series of field experiments, we show that large-mammal herbivory interacts with soil properties to maintain this pattern. In the absence of large herbivores, transplanted saplings of both species established on both soil types. Browsers strongly suppressed survival and growth of ACDR saplings on sandy soil, where resource limitation constrained defensive investment. On clay soil, ACBR saplings established regardless of herbivory regime, but elephants prevented recruitment to maturity, apparently because trees could not tolerate the combination of physical and biotic stressors. Hence, both tree species were filtered out of one habitat by browsing in conjunction with different edaphic factors and at different ontogenetic stages. Browser abundance was greater on sandy soil, where trees were less defended, consistent with predicted feedbacks between plant community assembly and herbivore distributions. By exploring two inversely related axes of soil “quality” (physical stress and nutrient content), our study extends the range of mechanisms by which herbivores are known to promote edaphic specialization; illustrates how the high cost of a protection mutualism can constrain the realized niche of host trees; and shows that large-scale properties of savannas are shaped by species interactions in cryptic ways that may easily be mistaken for simple abiotic determinism. These results suggest that ongoing declines in large-herbivore populations may relax spatial heterogeneity in plant assemblages and reduce the beta diversity of communities.

INTRODUCTION

Differences in plant community structure across edaphic gradients are common worldwide, enhancing spatial turnover in species composition (beta diversity) and regional species richness. Although community assembly is known to involve both biotic and abiotic filters, edaphic variation in species distributions is frequently attributed to soil properties alone, irrespective of biotic interactions. Although there is much evidence that herbivores can delimit the ranges and local richness of plant species (Olf and Ritchie 1998, Maron and Crone 2006), little is known about the abiotic context dependence of these interactions or the extent to which they enforce (or reinforce) edaphic differences in community composition (Maron et al. 2014).

The idea that soil fertility and herbivory may interact in species- and habitat-specific ways to govern community assembly was proposed by Janzen (1974) to explain distinctive tropical forests on infertile white-sands soils. Janzen argued that poor soils increased the cost of replacing lost tissue such that only well-defended (and hence slow-growing) species could occur there; on richer soils, these species would be disadvantaged relative to fast-growing, poorly defended ones (cf. Coley et al. 1985). Later, Fine et al. (2004, 2006) experimentally confirmed this hypothesis in the Amazon: tree species from nutrient-rich clay soils outperformed congeneric white-sands specialists on both soil types when protected from insects, but did poorly on white-sands when exposed to herbivory. Thus, habitat specialization and beta diversity was not solely a product of plant physiological adaptations, but rather of interactions among soil properties, plant defenses, and herbivory.

There has been little effort to establish whether similar processes operate in other biomes with different edaphic gradients, plant lineages, and herbivore types (Maron et al. 2014). This gap is particularly conspicuous for tropical savannas, where ecologists have focused more on tree

cover and tree-grass coexistence (Belsky 1990, Scholes and Archer 1997, Sankaran et al. 2008, Bond 2008, Holdo 2013) than on species-level patterns of diversity and distribution. Yet the functional importance of plant species composition in savannas is increasingly clear (Anderson et al. 2015, Kartzinel et al. 2015), suggesting the need to identify its mechanistic drivers.

Strong associations between edaphic properties, plant communities, and herbivore assemblages are common in edaphically heterogeneous savannas (McNaughton 1983, Scholes 1990, Scholes and Walker 1993, Venter et al. 2003). A one-way influence of geology on biotic communities is often assumed to account for these associations (e.g., poor soils support low-quality forage, which limits herbivore biomass: Venter et al. 2003), and savanna ecologists have historically focused on nutrient availability as the primary determinant of soil quality (Bell 1982, Scholes and Walker 1993). However, a nutrient-centric view may often be misleading: various soil properties (e.g., depth, texture, pH, physical stability/dynamics) may influence “quality” in different contexts, and these may or may not be correlated with nutrient content. Moreover, mammalian herbivory is a potent top-down force in these systems (Augustine and McNaughton 1998, Skarpe and Hester 2008) and interacts with bottom-up forces to structure savanna vegetation (Scholes and Archer 1997, Bond 2008). Thus, soil×herbivory interactions may be a potent and widespread force in savanna plant community assembly, and to understand them, we may need to account for other soil attributes in addition to nutrient availability.

We investigated the causes of a striking pattern of edaphic specialization in the semi-arid savannas of Laikipia, Kenya (Fig. 1). There and elsewhere in East Africa, poorly drained, clay- and nutrient-rich vertisols (“black-cotton”) are mono-dominated by whistling-thorn trees (*Acacia drepanolobium*, “ACDR”), which are well defended via spines and symbiotic ants. Nearby well-drained, nutrient-poor sandy loams (“red-sands”) are co-dominated by *Acacia brevispica*

90 (“ACBR”), *A. etbaica*, and *A. mellifera*, which are lightly defended relative to ACDR and exhibit
91 traits associated with herbivory tolerance, such as cage-like architectures and basal resprouting
92 (Marquis 1996, Bond and Midgley 2001, Staver et al. 2012). Although black-cotton and red-
93 sands habitats are often separated by < 1 km, there is almost no overlap in tree community
94 composition (Fig. 1).

95 This sharp disjunction is unexplained and inverts the predictions of resource-availability
96 theory (Coley et al. 1985), because the better-defended trees occur on the richer soils and *vice*
97 *versa*. However, black-cotton soils also challenge plants physically via seasonal cycles of
98 cracking, water-logging, and shrink-swell dynamics. It has been suggested that most tree species
99 are physiologically unable to cope with such physically stressful conditions (Belsky 1990), and
100 that black-cotton trees such as ACDR “may be uniquely adapted to these specialized soils”
101 (Okello and Young 2000) in ways that prevent them from colonizing other soil types. Yet the
102 only prior study to address this question found no effect of soil type on ACDR germination or
103 seedling survival (Okello and Young 2000).

104 We propose that this pattern of edaphic niche separation arises from the interaction of soil
105 properties and herbivory (Fig. 2). The physical properties of black-cotton imposes severe stress
106 that can be withstood in isolation but necessitates effective defense, because the “multiple
107 stressors” (*sensu* Folt et al. 1999) of soil and herbivory are lethal; on these soils, herbivory
108 cannot be tolerated and must be resisted, which explains the success of ACDR and the absence
109 of poorly defended, tolerance-oriented species such as ACBR. On red-sands (which despite
110 being nutrient poor is the more benign of the two soil types in this view due to its physical
111 stability), tolerance and energetically cheap defenses such as spinescence are viable coping
112 mechanisms; however, resource limitation precludes costly strategies such as ACDR’s obligate

ant-plant symbiosis (Stanton and Palmer 2011), leaving these trees defenseless against herbivory. This hypothesis yields a series of specific predictions (Table S1), which we tested using manipulative field experiments and observations at the Mpala Research Centre (MRC).

METHODS

Study area and species

Rainfall at MRC (0°17' N, 36°52' E, 1600-1800 m elevation) averages ~600 mm yr⁻¹ in a weakly tri-modal annual pattern, with a short dry season from December-March. Fires are infrequent and localized (Kimuyu et al. 2014). The mammal fauna includes 25 species of large herbivores (≥ 5 kg) and an intact large-carnivore guild. Species that commonly eat *Acacia* (“browsers”) include elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), eland (*Taurotragus oryx*), impala (*Aepyceros melampus*), Grant’s gazelle (*Nanger granti*), steenbok (*Raphicerus campestris*), and dik-dik (*Madoqua guentheri*). Common grazers, which rarely if ever eat *Acacia* (Kartzinel et al. 2015), include plains and Grevy’s zebra (*Equus quagga* and *E. grevyi*), buffalo (*Syncerus caffer*), and domestic cattle (*Bos indicus*).

The two principal soil types (Fig. 1a) and their characteristic floras are well characterized (Ahn and Geiger 1987, Taiti 1992, Young et al. 1998). Approximately 43% of Laikipia (4200 of 9700 km²) and 10% of MRC (20 of 2000 km²) is underlain by black-cotton (pellic vertisols with impeded drainage, clay content $\geq 50\%$). The high clay content of these soils impedes root growth, aeration, and infiltration, while shrink-swell cycles and the “deep, wide cracks” (Ahn and Geiger 1987) that form during the dry season can break roots (Dexter 2004, Whitmore and Whalley 2009). The black-cotton plant community (Fig. 1b), characterized as “*Acacia drepanolobium* wooded grassland” (Taiti 1992), is productive but species-poor: five grasses constitute >85% of

understory cover (Porensky et al. 2013), and ACDR represents >95% of tree cover (Young et al. 1998). Similar vegetation occurs on black-cotton soils across East Africa, including large parts of Nairobi and Serengeti national parks. ACDR is defended by ~2-cm long stipular spines, some of which are swollen at the base (“domatia”) to house symbiotic ants that patrol trees and attack herbivores, fueled by extrafloral nectar from the trees (Fig. 1c). This combination of direct and indirect defenses strongly inhibits browsing by goats (Stapley 1998), giraffes (Madden and Young 1992), rhino (Martins 2010), and elephants (Goheen and Palmer 2010), and ants enhance lifetime fitness of their host trees (Palmer et al. 2010). But these highly effective defenses are costly to maintain: experimental ant removal over five years increased tree growth and reproduction (Stanton and Palmer 2011), and trees protected from browsers relaxed both spine length (Young et al. 2003) and their investment in supporting symbiotic ants (Palmer et al. 2008).

Red-sands are friable sandy loams (ferric and chromic luvisols, < 20% clay) derived from metamorphic basement rock. These well-drained soils are physically more stable, but have lower extractable nutrient concentrations, than black-cotton (Augustine 2002). In the red-sands plant community (Fig. 1d), characterized as “open *Acacia brevispica* thicket” (Taiti 1992), ACBR, *A. etbaica*, and *A. mellifera* collectively account for 80% of tree cover over a discontinuous understory (Young et al. 1995, Augustine 2002). ACBR has only short (< 1 cm) prickles (Fig. 1e); it is preferred forage for impala (Ford et al. 2014) and is the single most frequently consumed tree species at MRC by all large herbivores combined (Kartzinel et al. 2015). ACBR tolerates consumption in part via basal resprouting (Bond and Midgley 2001), with individuals exposed to browsers growing in dense multi-stemmed clumps (Fig. 1d).

Experiment 1: Soil×Herbivory×Resource effects on reciprocally transplanted saplings

To study the effects of soil type, herbivory, resource limitation, and their interactions on young trees, we reciprocally transplanted garden-grown ACDR and ACBR saplings in each soil type under factorial combinations of browser exclusion and resource (water and nutrients) addition.

Saplings were grown from locally collected seeds, which we planted in plastic bags with potting mix and kept in a common environment at MRC, where they were watered regularly and protected from large herbivores. In March 2007, when saplings were ~50-cm tall, we planted 320 individuals (160 per species) into the field (cutting away bags to leave root balls intact) under factorial combinations of +/- herbivory (caged *vs.* uncaged) and +/- resources (fertilizer and water added *vs.* not added) in each soil type. Transplants were conducted at 10 sites, five per soil type; each site contained four randomized blocks with one replicate of each herbivory×resource combination (20 total replicates per species per soil type: Fig. S1). We selected sites near unpaved dirt tracks (to facilitate weekly water addition) that we judged broadly representative of each soil type. All sites were within a 10-km radius, and the mean distance within soil types was ~1 km. The four blocks within each site were evenly spaced along a 200-m transect.

Exclosure cages were built from 2.5-cm wire mesh on metal frames around individual plants. Each +resources sapling was watered weekly (2.5 L) and received 50 g of granular NPK fertilizer (17:17:17) during transplanting. This treatment was designed in consultation with an agroforestry expert familiar with local soils and conditions (J. Vernon, Kiwi Consultants) to test whether resource limitation excluded ACDR from red-sands. We combined water and nutrients in one treatment because we did not know which resource was limiting, and because separating them would have entailed additional factorial treatments and a prohibitively complex design. Likewise, we followed Fine et al. (2004) in planting trees directly into the earth at each site rather than trying to nest soil types within each other (i.e., sand-pits in clay soils); the latter

approach would be misleading if it did not reproduce the relevant biotic, chemical, and physical properties of each soil type, which we considered unlikely and had no way of ascertaining.

Over 15 monthly surveys (through June 2008), we recorded survivorship, height (nearest cm) and basal diameter (nearest mm, using calipers). To quantify herbivore damage, we used a “browse score” on a 0-4 scale, based on the percentage of shoot tips browsed (0 = 0%, 1 = 1-25%, etc.). For ACDR only, we measured three defensive traits: spine length (nearest mm, averaged across three thorns on each of three branches), total number of swollen-thorn ant domatia, and the presence of symbiotic ants. After 17 months (August 2008), we conducted a final survey in which we recorded mortality only.

Each tree species was analyzed separately. To assess treatment effects on 17-month survival, we used mixed-effects Cox proportional-hazards (coxme) models in the ‘coxme’ package (Therneau 2015) of R (Development Core Team 2013). For all saplings that survived through June 2008, we analyzed net (final – initial) change in plant height and diameter; for browse scores and defensive traits, which were measured by subsampling within each sapling, we averaged values across surveys (except the first) to reduce noise in the data. Treatment effects on growth and traits were analyzed using linear mixed-effects models (lme) fit using maximum likelihood in the R package ‘nlme’ (Pinheiro et al. 2014). These models were initially specified with soil type, browser exclusion, and resource addition as fixed effects, and site and block (nested within site) as random effects. We used an information-theoretic approach to select the best model specification(s) for each response. We fit a set of 18 candidate models comprising all possible combinations of the three main effects and their interactions, plus a null model containing only the intercept, and compared model(s) using AIC_c (Burnham and Anderson 2002). In each case, the best-fitting model had far more explanatory power than the null ($\Delta_i > 2$, often

>> 2). In Table 1, we report all models with substantial support ($\Delta_i < 2$) and the relative variable importance (RVI) of fixed effects; the single best-fitting model for each response is also shown in the corresponding figure panel. A full list of all models and AIC_c values is given in Table S2.

To gauge sensitivity of performance to browsing pressure for +herbivory saplings, we analyzed mortality (0, 1) as a function of mean browse score using univariate logistic regression (binomial glm, plotted using logi.hist.plot in R package ‘popbio’: Stubben et al. 2015) and net height change using linear mixed-effects models (lme). For the latter analysis, which provides a measure of relative herbivory tolerance among treatments, we first specified a full model comprising all interactions of browse score, soil type, and resource treatment (with random effects of site and block-within-site), then sequentially dropped the least-significant terms until doing so no longer reduced AIC_c (Crawley 2007). Finally, we evaluated symbiotic ant occupancy of ACDR (number of months occupied) as a function of domatium number, using a negative-binomial generalized linear mixed model data (glmmPQL in R package ‘MASS’: Ripley et al. 2014). Fixed effects included domatium number, soil type, and their interaction, with site and block-within-site as random effects (too few red-sands saplings were colonized to enable inclusion of all factorial fixed effects). Values of the theta parameter in these models were determined by first running the model without random effects using glm.nb.

Experiment 2: Densities of adult ACBR within long-term exclosures

Prior work has addressed seed and seedling survival (Okello et al. 2000) and Experiment 1 focused on saplings, but biotic filters on tree recruitment may occur at later ontogenetic stages if larger plants are more apparent to lethal herbivores such as elephants. We tested this possibility for black-cotton ACBR using the Kenya Long-term Exclosure Experiment (KLEE), established in 1995 (Young et al. 1998). KLEE manipulates three guilds of large mammalian herbivores in

18 four-hectare plots. Megaherbivores (elephants and giraffes only) are excluded using electrified wires at 2-m height, while both mega- and mesoherbivores (15-1000 kg, including eland and Grant's gazelle) are excluded using 11 wires from 0.5–2 m. Both types of exclosure, along with unfenced plots, are replicated with and without cattle for a total of six treatments, each replicated three times in randomized blocks. In 2011, we exhaustively searched each plot and counted all individuals >50-cm tall ("post-sapling" stage; smaller seedlings and saplings are often concealed within the herbaceous layer and thus difficult to quantify). We compared ACBR densities (square-root transformed for normality) using mixed-effects models (lme) with presence/absence of (a) megaherbivores, (b) mesoherbivores, and (c) cattle as fixed effects, and block as a random effect. On red-sands, we tested for similar trends in ACBR abundance in the UHURU experiment, which has used similar fence configurations to exclude megaherbivores and mesoherbivores from one-hectare plots since 2008 (Goheen et al. 2013). In 2014, we searched the central 3600-m² portion of each plot, counting all post-sapling ACBR.

An equivalent analysis was not possible for ACDR, as it is entirely absent from red-sands on MRC, aside from a few small stands near the southern property boundary.

Experiment 3: Ant×Herbivory effects on transplanted ACDR saplings in red-sands

As noted above, few red-sands ACDR saplings were colonized by ants in Experiment 1 (see *Results*). In a follow-up experiment, we manipulated the presence/absence of (a) ants and (b) browsers in red-sands to test whether ant colonies were capable of establishing and protecting trees. Saplings were grown at MRC to ~50-cm height and periodically pruned to promote the growth of ant domatia. We established 15 blocks (~10-m apart) in a red-sands site ~5 km from the nearest black-cotton soil, transplanted four saplings (each with ≥ 5 domatia) into each block, and randomly assigned them to factorial combinations of +/- ants and +/- herbivory.

On +ants saplings, we simulated natural aerial colonization events by transferring entire nanitic colonies of the ant *Crematogaster nigriceps*. Nanitic colonies comprise a foundress queen and initial brood of workers and are identifiable by the small size of workers. Donor saplings with nanitic colonies were cut, bagged, transported to the red-sands site, and tied to recipient saplings in the +ants treatment. As a procedural control, we cut sapling-sized *ACDR* branches and opened all domatia to remove ants before tying them to–ants saplings. To facilitate colony establishment, we bored small holes in the domatia of recipient saplings using a needle. Because treatments were established at the onset of the dry season in December 2014, we watered all saplings (3 L every third day) through March to prevent mortality from drought stress.

At two-week intervals through July 2015 (duration = 228 d), we checked saplings for mortality (and apparent cause of death) and ant-colony establishment (measured as persistence since the preceding survey). Colonies that failed to establish were promptly replaced with new ones. Every 6-8 weeks, we measured sapling size (summed length of all aboveground stems), number of new domatia produced, and number of active extrafloral nectaries (the primary food source for these ants) on 15 haphazardly chosen leaves; browse score (0-4, per Experiment 1) was assessed through May, 2015. We observed no non-experimental colonization by ants.

We analyzed survival using Cox proportional-hazards model (coxph). For all surviving saplings, we analyzed net change in size, as well as means across surveys for browse score, domatia, and extrafloral nectaries, using linear models (lm) in R. Browse score and proportion of active nectaries were log- and arcsine-transformed, respectively, for normality. This experiment used a single site with no within-block replication, and random block effects did not substantially improve model fits; hence, we used simple 2x2 factorial fixed-effects models for all responses.

Quantifying large-herbivore abundance on each soil type

We used distance sampling to quantify large-herbivore biomass (Buckland et al. 2001). Two fixed transects in each soil type were driven twice monthly (0600-0900 h) from May 2007 to May 2008. Transects (low-traffic dirt tracks) varied from 1.4 to 2.4 km, totaling 3.4 km on black-cotton and 3.8 km on red-sands. Surveys were conducted in a Land Rover at 10 km hr⁻¹ with a driver, one seated observer, and two standing observers. We recorded species, number of individuals, distance to transect (using a laser rangefinder), and azimuth (using a compass). We used Distance 6.0 (Thomas et al. 2010) to estimate densities of five browsing antelope species (dik-dik, steenbok, impala, Grant's gazelle, eland) and one grazing species (plains zebra); other species, notably giraffe and elephant, were too infrequently sighted for density estimation. We estimated densities separately for each species in each transect in each month (averaging the two observations from each transect) using a constant detection function (hazard-rate with a second-order cosine adjustment), multiplied densities by species-specific body masses to obtain mean monthly biomass densities for each species, and calculated energetic demand using mass-specific metabolic rates (Nagy 2005). We averaged the two transects in each soil type within each month to reduce data dispersion, giving 11 monthly measurements per soil type, and compared total biomass and energy densities of the browsing and grazing guilds using *t*-tests.

To obtain an index of relative abundance for megaherbivores, we identified, counted, and crushed (to avoid subsequently re-counting) all giraffe and elephant dung piles within each block of Experiment 1 during monthly surveys from August 2007 through June 2008. We summed dung piles of each species within each block ($n = 20$ per soil type) across the 11 surveys and analyzed each species separately using negative-binomial generalized linear mixed models with soil type as a fixed effect and block as a random effect (using glmmPQL as described above).

RESULTS

Experiment 1: Sapling reciprocal transplant with herbivore and resource manipulation

Saplings of both *Acacia* species exhibited the capacity to survive and grow on both soil types. Both species also exhibited strong responses to herbivore exclusion and resource addition, but differed in their responses across soil types.

As predicted, browsers dramatically reduced ACDR survival on red-sands, and resource addition mitigated this effect: 15% of +herbivory –resources saplings and 40% of +herbivory +resources saplings on red-sands survived the experiment, compared with 85–95% in all other treatment combinations (Fig. 3a). The single best coxme model for this response included additive effects of soil and herbivory ($w_i = 0.22$); four additional models received substantial empirical support (combined $w_i = 0.55$), of which two included soil×herbivory (RVI = 0.44), and one included soil×resources (RVI = 0.22; Table 1). Our predictions were even more clearly supported for ACDR net height growth, which was disproportionately negative for red-sands +herbivory –resources, greatest for red-sands –herbivory +resources, and intermediate with little effect of herbivory×resource treatments on black-cotton (Fig. 3c). The best-fitting model for height ($w_i = 0.38$) included all main effects and interactions, and RVI of both soil×herbivory and soil×resources was ≥ 0.75 (Table 1). The soil×herbivory interaction was likewise important (RVI = 0.55) for diameter growth, which was negligible in all +herbivory scenarios and enhanced considerably by herbivore exclusion on red-sands only (Fig. 3e).

ACBR saplings responded strongly to both herbivory and resource addition, but contrary to our prediction, these effects were similar in magnitude across soil types. Overall survival was high: 100% of –herbivory ACBR saplings in all soil×resource combinations survived the experiment, vs. 80% of all +herbivory saplings; resource addition (RVI = 0.83) increased

survival of +herbivory saplings by 29% (Fig. 3b, Table 1). Growth was heavily suppressed by herbivory (RVI = 1.0 for both height and diameter) in all soil×resource combinations, and diameter growth increased with resource addition (RVI = 0.93) on both soil types (Fig. 3d,f), but none of the substantially supported models contained interaction terms (all RVI ≤ 0.25; Table 1).

Browse damage was negligible in all –herbivory saplings (i.e., exclosures were effective and insects/rodents had little impact; Fig. 4a,b) and among +herbivory saplings was greater on red-sands (soil RVI = 0.80 for ACDR, 0.90 for ACBR; Table 1). Saplings with higher browse scores exhibited increased mortality (binomial glm: ACDR est. = 1.13, $z = 1.97$, $P = 0.05$; ACBR est. = 0.067, $z = 1.94$, $P = 0.05$; Fig. 4c,d) and decreased height growth (Fig. 4e,f). For ACDR, the negative effect of browsing on growth was strongest for red-sands –resources saplings (browse score×soil×resources: $F_{1,13} = 7.88$, $P = 0.015$), suggesting that herbivory tolerance on red-sands is resource limited and restored by resource addition, whereas for ACBR slopes were similar among treatments; these results broadly parallel those for survival and growth (Fig. 3).

Mean spine length and domatium number, key defense traits of ACDR, were both (a) greater on average in black-cotton than red-sands and (b) lowest in red-sands +herbivory –resources saplings (Fig. 5a,b), as predicted if defensive investment is resource limited in red-sands. Although prior work has shown that these traits are induced by herbivory (Young et al. 2003, Palmer et al. 2008), we found no consistent main effect of herbivore exclusion on either defensive trait (Table 1). Saplings with more domatia were more frequently occupied by ants (Fig. 5c) on both soil types, but overall colonization rates were much greater on black-cotton soil dominated by conspecifics (78% were ever colonized, with 26% occupied on average in each survey) than on red-sands (15% and 2%, all of which were inside herbivore exclosures).

Experiment 2: Effects of long-term exclosures on post-sapling ACBR densities

In black-cotton, post-sapling ACBR densities were >20-fold higher (1.67 ± 0.31 vs. 0.08 ± 0.05 ha⁻¹) in KLEE plots that excluded megaherbivores (est. = -2.49, $F_{1,12} = 41.75$, $P < 0.0001$), whereas mesoherbivores (est. = +0.74, $F_{1,12} = 3.83$, $P = 0.074$) and cattle had non-significant effects (est. = -0.37, $F_{1,12} = 1.45$, $P = 0.25$; Fig. S2). By contrast, ACDR densities in KLEE were reduced just 29% by megaherbivores (Kimuyu et al. 2014). We found flowering and fruiting ACBR inside KLEE exclosures (Fig. S3), showing that ACBR can recruit and reproduce on black-cotton in the absence of megaherbivores. In red-sands, ACBR densities did not differ significantly in UHURU plots with vs. without megaherbivores after 6 years (338 ± 79 vs. 386 ± 70 ha⁻¹; est. = -0.36, $F_{1,26} = 0.05$, $P = 0.83$; Fig. S2).

Experiment 3: Transplant of *ACDR* saplings and symbiotic ants in red-sands

Ant-colony establishment rates in the 30 +ant ACDR saplings were initially low (~46%) during the dry season, but increased to 88% by mid-April. In the final survey, 58% of the surviving +ant trees had active colonies, all of which had persisted >2.5 months. Colony establishment success was similar in both herbivory treatments.

Only 27% of +herbivory saplings in each ant treatment survived the experiment, vs. 63% for -herbivory saplings (herbivory: $\chi^2 = 9.20$, $P = 0.002$; Fig. 6a). Ants reduced the proportion of shoot tips browsed by >66% (ants×herbivory: $F_{1,23} = 9.84$, $P = 0.005$; Fig. 6b), but did not enhance survival (ants: $\chi^2 = 0.20$, $P = 0.67$; ants×herbivory: $\chi^2 = 1.18$, $P = 0.28$), 70% of which was due to catastrophic herbivory (top-browsing or uprooting: Fig. S4). Net change in size (herbivory: $F_{1,23} = 21.85$, $P = 0.0001$) and domatia (herbivory: $F_{1,23} = 27.46$; $P < 0.0001$) were negative in +herbivory and positive in -herbivory saplings, regardless of ants (Fig. 6c,d). Proportion of active extrafloral nectaries was significantly greater when ants were present and herbivores absent ($F_{1,23} = 4.36$; $P = 0.02$ and $F_{1,23} = 50.92$, respectively; $P < 0.0001$; Fig. 6e).

Large-herbivore activity on each soil type

Mean monthly biomass density of all browsing antelopes combined was 70% greater ($t_{20} = -2.74$, $P = 0.013$), and energetic demand 120% greater ($t_{20} = -3.20$, $P < 0.001$) on red-sands than black-cotton, whereas the reverse held for the grazer, plains zebra (biomass: $t_{1,20} = 4.04$, $P < 0.001$; energy: $t_{1,20} = 3.47$, $P < 0.001$; Fig. 7a,b). The overall discrepancy in browsers was driven by dik-dik and impala, which we never observed on black-cotton. Similarly, for the two megaherbivore browsers, dung density was 370% greater for giraffe ($t_8 = 2.71$, $P = 0.027$) and 1200% greater for elephant (est. = 2.59, $t_8 = 3.88$, $P = 0.0047$) on red-sands than black-cotton (Fig. 7c).

DISCUSSION

Large herbivores enforce edaphic specialization of African savanna trees

Collectively, our results provide strong experimental evidence that browsers constrain the realized edaphic niches of two dominant savanna tree species. In the absence of browsers, saplings of these apparent “habitat specialists” established and grew in soils where they do not occur as adults, sometimes even performing slightly better than in their “preferred” habitats (Fig. 3e,f). Similarly, prior experiments found that ACDR germination and seedling survival rates were indistinguishable on red-sands vs. black-cotton (Okello and Young 2000), suggesting that soil type poses no barrier to recruitment at earlier ontogenetic stages. Hence, edaphic segregation of tree species is not due entirely to soil properties and the intrinsic physiological traits of trees; instead, it is an emergent, context-dependent effect of herbivory, which differentially filters community assembly in each soil type (Fig. 2). Because our two focal species are among the four *Acacia* that comprise >80% of tree cover at MRC (Young et al. 1995) and differ markedly in

their traits and utilization by animals, this biotic filter substantially increases the taxonomic, structural, and functional beta diversity of the landscape (compare Figs. 1b,c).

We argue that such “edaphic niche enforcement” by large herbivores is likely to be an important unappreciated factor shaping savanna plant community assembly throughout Africa. The theoretical prediction that soil properties and herbivory interact to govern the distribution of plant species and traits (Janzen 1974, Coley et al. 1985) has been shown to drive the origin and maintenance of beta diversity in edaphically heterogeneous tropical forests, where insects are the most important herbivore guild (Fine et al. 2004, 2006, 2013). However, examples from savannas dominated by large mammalian herbivores are lacking. Most of the diagrammatic conceptual models that have been proposed to explain salient features of savanna vegetation (e.g., Cumming 1982, Walker 1987, Belsky 1990, Scholes and Walker 1993, Venter et al. 2003, Riginos and Grace 2008, Anderson et al. 2015) include soil properties and/or herbivory, but should be expanded to include possibility that these factors are strongly contingent upon one another. Abiotic context-dependence of herbivory on savanna plants has been studied with respect to rainfall gradients (Wigley et al. 2015), but rainfall and soil type are often either confounded or amalgamated into a single productivity metric (Pringle et al. 2007, Young et al. 2013), making it impossible to disentangle the independent and interactive effects of different bottom-up drivers. Replicated manipulations of herbivory across edaphic gradients in other African savanna systems are needed to establish the continent-wide prevalence and significance of soil×herbivory interactions on plant community assembly.

Broadly speaking, our results were consistent with the mechanistic hypotheses in Table S1, although the strength of support for different specific predictions was variable. Below, we present our interpretation of the results for each tree species in turn.

Mechanisms confining ACDR to black-cotton soils

We hypothesized that ACDR's ant-plant protection mutualism helps to explain both its dominance on black-cotton (where the severe physical stress is lethal when combined with herbivory) and also its absence from red-sands (where resource availability is insufficient to sustain such a costly strategy). This hypothesis predicted that herbivore exclusion and resource addition would enhance ACDR performance in red-sands but not in black-cotton, and that resource addition would neutralize the negative effects of herbivores in red-sands (Table S1).

These predictions were supported by Experiment 1. Browsers reduced survival and growth weakly in black-cotton but strongly in red-sands (Fig. 3), where herbivory tolerance was disproportionately low (Fig. 4e). In red-sands, herbivore exclusion restored responses to levels commensurate with or greater than those on black-cotton (Fig. 3), and resource addition buffered the impacts of browsing (Fig. 4a); this ameliorative effect was moderate for survival (Fig. 3a), but was fully compensatory for height (Fig. 3c).

The results of Experiments 1 and 3 on ACDR antiherbivore defenses, taken together with prior work demonstrating both the efficacy (Stapley 1998, Goheen and Palmer 2010) and costliness (Goheen et al. 2007, Stanton and Palmer 2011, Tarnita et al. 2014) of nectar, domatia, and spine production support the hypothesized mechanism of resource-limited defense on red-sands. In +herbivory saplings, spine length and domatium number were greater on black-cotton than red-sands, but resource addition eliminated this difference (Fig. 5a,b). Ant colonization in Experiment 1 increased with domatium number and was frequent in black-cotton, but was rare in red-sands and observed only in –herbivory trees (Fig. 5c). Thus, lack of protective symbionts inhibited defense in red-sands, but this might reflect either (or both) an inability of (a) resource-limited hosts to support effective ant colonies or (b) dispersing ant queens to colonize trees far

from the nearest source population. By forcibly “colonizing” red-sands saplings in Experiment 3, we removed dispersal limitation to test whether saplings could support nascent ant colonies capable of protecting saplings. And although ant colonies eventually established on most trees and reduced the incidence of browsing, they did not enhance growth or survival (Fig. 6).

The most parsimonious interpretation of these results is that both ant dispersal limitation and host resource limitation contributed to ACDR’s vulnerability to herbivores in red-sands. In Experiment 1, isolation-by-distance surely diminished colonization rates for red-sands saplings, while black-cotton saplings likely gained symbionts from conspecific neighbors via both *de novo* aerial colonization and ground-based expansion of mature colonies (Palmer et al. 2013); the latter may be more effective than nastic colonies in host protection and only occurs for saplings close to large conspecifics. Yet dispersal limitation cannot explain the results of Experiment 3, and domatium number (which was tied to colonization rates) was enhanced by resource addition in red-sands +herbivory saplings (Fig. 5b,c), suggesting resource limitation. Red-sands ACDR face a Catch-22: resource shortage and browsing pressure combine to prevent trees from acquiring the symbionts they need to resist browsing pressure!

Future experiments should attempt to (a) isolate the relative importance of dispersal and resource limitation in disrupting the ant-plant mutualism in red-sands (e.g., by combining ant transplants with resource addition and herbivore exclusion on both soil types simultaneously); and (b) investigate whether “outsourcing” defense to symbiotic ants creates an Allee effect that reinforces ACDR monodominance on black-cotton soils (where symbiont sources are plentiful) while inhibiting its colonization of nearby sink habitats dominated by heterospecifics (where ant dispersal and host-finding limitation leaves trees unprotected). Theory predicts such Allee effects in metacommunities of mobile mutualists and non-mobile hosts (Amarasekare 2004), and this

might help explain the tendency of obligate ant-plants to occur at high local densities or in monodominant stands (Janzen 1966, Frederickson et al. 2005).

Mechanisms confining ACBR to red-sands soils

Browsers reduced survival and growth of ACBR saplings, but contrary to our initial prediction, these effects were similar in magnitude across soil types (Fig. 3). However, we found strong support for an alternative explanation for the absence of ACBR from black-cotton: young trees could establish, but only recruited to reproductive maturity in the sustained absence of megaherbivores (Fig. S2), consistent with our hypothesis that the “one-two punch” of soil and herbivory stress knocks out this poorly defended species. Absolute ACBR densities within KLEE exclosures remained low even after 16 years, however, perhaps due to absence of nearby seed sources, and perhaps also reflecting edaphic stress independent of herbivory. That ACBR densities in KLEE did not increase further following the exclusion of mesoherbivores suggests that chronic browsing by antelope is less important than lethal browsing of newly “apparent” individuals emerging from the understory (especially by elephants, as giraffes rarely forage on plants <2-m tall: (Toit and Olf 2014). We expect apparency effects to be particularly pronounced on black-cotton, because monodominance by well-defended ACDR should increase both the visual contrast and relative attractiveness of other tree species to browsers. Although +herbivory ACBR saplings shrunk in height while maintaining high survival, suggestive of chronic herbivory (the “browse trap”: Staver and Bond 2014), this effect did not differ across soil types and therefore cannot explain why ACBR is only absent from black-cotton.

Prior work has shown that browsers can suppress ACBR in red-sands (Goheen et al. 2013, Ford et al. 2014), but we found no megaherbivore effect even remotely comparable to the order-of-magnitude decrease observed on black-cotton (Fig. S2), as predicted if relative

tolerance ability is greater on red-sands than black-cotton. However, we note that Experiment 1 offers little support for this mechanism, as sapling performance was essentially equivalent across soil types (Fig. 3, 4; Table 1). Moreover, while there is an intuitive reason why tolerance should be low on black-cotton due to severe abiotic stress (per the literature on multi-stressor synergy: Folt et al. 1999), our prediction of greater tolerance on red-sands hinges on our supposition that physical stress is more potent than resource stress, which to our knowledge has not been tested. Controlled defoliation experiments on both soil types would be useful.

Feedbacks between plant-community development and large-herbivore distribution

We found greater antelope biomass and megaherbivore dung density on red-sands (Fig. 7), along with greater mean browse scores (Fig. 4a,b), consistent with our hypothesis that herbivore-mediated development of a better-defended tree community on black-cotton soils feeds back negatively on browser abundance (Fig. 2). This putative feedback might help explain the stronger suppression of red-sands ACDR relative to black-cotton ACBR in Experiment 1: high browser density on red-sands due to better forage would amplify the vulnerability of ACDR deprived of protective ants; low browser density in black-cotton would increase ACBR's odds of avoiding detection as inconspicuous saplings, which would diminish as apparency increases with size. This scenario resembles refuge-mediated apparent competition (Orrock et al. 2010).

Conclusions

We show that browsers enforce the segregation of savanna tree species across soil types and outline a conceptual model to explain this finding in terms the context-dependent costs and benefits of plant strategies for coping with herbivory in different edaphic environments (Fig. 2, Table S1). This framework differs from prior work on herbivore-driven habitat specialization (Fine et al. 2004) by considering two independent axes of soil quality, physical stress and

resource availability; in short, we suggest there is no “good” soil type in this system, but rather two that are challenging in different ways. This outlook diverges from a narrow interpretation of the resource-availability hypothesis (Coley et al. 1985) while simultaneously reaffirming its central premise that harsh environments require stringent antiherbivore resistance.

Canonical understanding of savanna vegetation places primary importance on abiotic variables: rainfall, fire, and soil composition (Sankaran et al. 2008). Our results show that large herbivores filter plant communities in ways that superficially appear to be abiotically determined, adding to the growing body of evidence that herbivory interacts with abiotic forces to generate emergent properties of savannas. Such interactions may often be cryptic and hence overlooked in continental-scale studies, underscoring the importance of manipulative field experiments as a complement observational, modeling, and remote-sensing approaches.

We consider it likely that our findings are generalizable to other plant species. For example, *Acacia mellifera*, another poorly defended red-soil co-dominant, occurs at low densities on black-cotton soils, where it is heavily utilized and suppressed by elephants (Goheen and Palmer 2010). If elephants and other large herbivores disappear from this system, we predict that many of the dominant plant species on each soil type will invade the other, leading to spatial homogenization of plant communities and a reduction in niche space for consumer populations. Indeed, the ongoing decline of mammalian browsers throughout Africa (Ripple et al. 2015) may already be diminishing the beta diversity of its savanna ecosystems.

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LITERATURE CITED

- Ahn, P., and L. Geiger. 1987. Soils of Laikipia District. Kenya Soil Survey. National Agricultural Laboratories, Kabete, Kenya.
- Amarasekare, P. 2004. Spatial dynamics of mutualistic interactions. *Journal of Animal Ecology* 73:128–142.
- Anderson, T. M., J. Bukombe, and K. L. Metzger. 2015. Spatial and temporal drivers of plant structure and diversity in Serengeti savannas. Pages 105–124 *in* A. R. E. Sinclair, K. L. Metzger, S. A. R. Mduma, and J. M. Fryxell, editors. *Serengeti IV: sustaining biodiversity in a coupled human-natural system*. University of Chicago Press, Chicago.
- Augustine, D. J. 2002, November 25. Large herbivores and process dynamics in a managed savanna ecosystem. Ph.D. Thesis, Syracuse University, Syracuse, New York.
- Augustine, D. J., and S. J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *Journal of Wildlife Management* 62:1165–1183.

548 Bell, R. 1982. The effect of soil nutrient availability on community structure in African
 549 ecosystems. Pages 193–216 *in* B. J. Huntley and B. H. Walker, editors. Ecology of tropical
 550 savannas. Springer, Berlin.

551 Belsky, A. J. 1990. Tree/grass ratios in East African savannas: a comparison of existing models.
 552 *Journal of Biogeography* 17:483–489.

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

555 Bond, W. J., and J. J. Midgley. 2001. Ecology of sprouting in woody plants: the persistence
 556 niche. *Trends in Ecology & Evolution*.

557 Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas.
 558 2001. Introduction to distance sampling: estimating abundance of biological populations.
 559 Oxford University Press, Oxford, U.K.

560 Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: a
 561 Practical Information-Theoretic Approach. Springer, New York.

562 Coley, P. D., J. P. Bryant, and F. S. Chapin. 1985. Resource availability and plant antiherbivore
 563 defense. *Science* 230:895–899.

564 Crawley, M. J. 2007. The R Book. John Wiley & Sons, Chichester, UK.

565 Cumming, D. H. M. 1982. The influence of large herbivores on savanna structure in Africa. *in* B.
 566 J. Huntley and B. H. Walker, editors. Ecology of tropical savannas. Springer, Berlin.

567 Dexter, A. R. 2004. Soil physical quality: Part I. Theory, effects of soil texture, density, and
 568 organic matter, and effects on root growth. *Geoderma* 120:201–214.

569 Fine, P. V. A., I. Mesones, and P. D. Coley. 2004. Herbivores promote habitat specialization by
 570 trees in Amazonian forests. *Science* 305:663–665.

571 Fine, P. V. A., Z. J. Miller, I. Mesones, S. Irazuzta, H. M. Appel, M. H. H. Stevens, I. Sääksjärvi,
 572 J. C. Schultz, and P. D. Coley. 2006. The growth-defense trade-off and habitat specialization
 573 by plants in Amazonian forests. *Ecology* 87:S150–62.

574 Fine, P., M. R. Metz, J. Lokvam, and I. Mesones. 2013. Insect herbivores, chemical innovation,
 575 and the evolution of habitat specialization in Amazonian trees. *Ecology* 94:1764–1775.

576 Folt, C. L., C. Y. Chen, M. V. Moore, and J. Burnaford. 1999. Synergism and antagonism among
 577 multiple stressors. *Limnology and Oceanography* 44:864–877.

578 Ford, A. T., J. R. Goheen, T. O. Otieno, L. Bidner, L. A. Isbell, T. M. Palmer, D. Ward, R.
 579 Woodroffe, and R. M. Pringle. 2014. Large carnivores make savanna tree communities less
 580 thorny. *Science* 346:346–349.

581 Frederickson, M. E., M. J. Greene, and D. M. Gordon. 2005. “Devil's gardens” bedevilled by
 582 ants. *Nature* 437:495–496.

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

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

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

590 Holdo, R. M. 2013. Revisiting the two-layer hypothesis: coexistence of alternative functional
 591 rooting strategies in savannas. *PLoS ONE* 8:e69625.

592 Janzen, D. H. 1966. Coevolution of mutualism between ants and acacias in Central America.
 593 *Evolution* 20:249–275.

594 Janzen, D. H. 1974. Tropical blackwater rivers, animals, and mast fruiting by the
 595 Dipterocarpaceae. *Biotropica* 6:69–103.

596 Kartzinel, T. R., P. A. Chen, T. C. Coverdale, E. D. L. W. J. Kress, M. L. Kuzmina, D. I.
 597 Rubenstein, W. Wang, and R. M. Pringle. 2015. DNA metabarcoding illuminates dietary
 598 niche partitioning by African large herbivores. *Proceedings of the National Academy of*
 599 *Sciences* 112:8019–8024.

600 Kimuyu, D. M., R. L. Sensenig, C. Riginos, K. E. Veblen, and T. P. Young. 2014. Native and
 601 domestic browsers and grazers reduce fuels, fire temperatures, and acacia-ant mortality in an
 602 African savanna. *Ecological Applications* 24:741–749.

603 Madden, D., and T. P. Young. 1992. Symbiotic ants as an alternative defense against giraffe
 604 herbivory in spinescent *Acacia drepanolobium*. *Oecologia* 91:235–238.

605 Maron, J. L., and E. Crone. 2006. Herbivory: effects on plant abundance, distribution and
 606 population growth. *Proceedings of the Royal Society B: Biological Sciences* 273:2575–2584.

607 Maron, J. L., K. C. Baer, and A. L. Angert. 2014. Disentangling the drivers of context-dependent
 608 plant-animal interactions. *Journal of Ecology* 102:1485–1496.

609 Marquis, R. J. 1996. Plant architecture, sectoriality and plant tolerance to herbivores. *Vegetatio*
 610 127:85–97.

611 Martins, D. J. 2010. Not all ants are equal: obligate acacia ants provide different levels of
 612 protection against mega-herbivores. *African Journal of Ecology* 48:1115–1122.

613 McNaughton, S. J. 1983. Serengeti grassland ecology: the role of composite environmental
 614 factors and contingency in community organization. *Ecological Monographs* 53:291–320.

615 Nagy, K. A. 2005. Field metabolic rate and body size. *Journal of Experimental Biology*
 616 208:1621–1625.

617 Okello, B. D., and T. P. Young. 2000. Effects of fire, bruchid beetles and soil type on
 618 germination and seedling establishment of *Acacia drepanolobium*. African Journal of Range
 619 & Forage Science 17:46–51.

620 Olff, H., and M. E. Ritchie. 1998. Effects of herbivores on grassland plant diversity. Trends in
 621 Ecology & Evolution 13:261–265.

622 Orrock, J. L., R. D. Holt, and M. L. Baskett. 2010. Refuge-mediated apparent competition in
 623 plant-consumer interactions. Ecology Letters 13:11–20.

624 Palmer, T. M., D. F. Doak, M. L. Stanton, J. L. Bronstein, E. T. Kiers, T. P. Young, J. R.
 625 Goheen, and R. M. Pringle. 2010. Synergy of multiple partners, including freeloaders,
 626 increases host fitness in a multispecies mutualism. Proceedings of the National Academy of
 627 Sciences 107:17234–17239.

628 Palmer, T. M., M. L. Stanton, T. P. Young, J. R. Goheen, R. M. Pringle, and R. Karban. 2008.
 629 Breakdown of an ant-plant mutualism follows the loss of large herbivores from an African
 630 savanna. Science 319:192–195.

631 Palmer, T. M., M. L. Stanton, T. P. Young, J. S. Lemboi, J. R. Goheen, and R. M. Pringle. 2013.
 632 A role for indirect facilitation in maintaining diversity in a guild of African acacia ants.
 633 Ecology 94:1531–1539.

634 Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R. Core Team. 2014. nlme: Linear and
 635 nonlinear mixed effects models. R package version 3.1-117.

636 Porensky, L. M., S. E. Wittman, C. Riginos, and T. P. Young. 2013. Herbivory and drought
 637 interact to enhance spatial patterning and diversity in a savanna understory. Oecologia
 638 173:591–602.

639 Pringle, R. M., T. P. Young, D. I. Rubenstein, and D. J. McCauley. 2007. Herbivore-initiated

640 interaction cascades and their modulation by productivity in an African savanna.

641 Proceedings of the National Academy of Sciences 104:193–197.

642 R Core Team. 2013. R: a language and environment for statistical computing. R Foundation for
643 Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.

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

646 Ripley, B., B. Venables, D. M. Bates, K. Hornik, A. Gebhardt, and D. Firth. 2014. MASS:
647 Support functions and datasets for Venables and Ripley's MASS. R package version 7.3-35.

648 Ripple, W. J., et al.. 2015. Collapse of the world's largest herbivores. *Science Advances*
649 1:e1400103.

650 Sankaran, M., J. Ratnam, and N. Hanan. 2008. Woody cover in African savannas: the role of
651 resources, fire and herbivory. *Global Ecology and Biogeography* 17:236–245.

652 Scholes, R. J. 1990. The influence of soil fertility on the ecology of southern African dry
653 savannas. *Journal of Biogeography* 17:415–419.

654 Scholes, R. J., and B. H. Walker. 1993. An African savanna: synthesis of the Nylsvley study.
655 Cambridge University Press, Cambridge.

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

658 Skarpe, C., and A. Hester. 2008. Plant traits, browsing and grazing herbivores, and vegetation
659 dynamics. Pages 217–274 *in* I. J. Gordon and H. H. T. Prins, editors. *The ecology of*
660 *browsing and grazing*. Springer, Berlin.

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

663 Stapley, L. 1998. The interaction of thorns and symbiotic ants as an effective defence mechanism
 664 of swollen-thorn acacias. *Oecologia* 115:401–405.

665 Staver, A. C., and W. J. Bond. 2014. Is there a “browse trap?” Dynamics of herbivore impacts on
 666 trees and grasses in an African savanna. *Journal of Ecology* 102:595–602.

667 Staver, A. C., W. J. Bond, M. D. Cramer, and J. L. Wakeling. 2012. Top-down determinants of
 668 niche structure and adaptation among African Acacias. *Ecology Letters* 15:673–679.

669 Stubben, C., B. Milligan, and P. Nantel. 2015. popbio: Construction and analysis of matrix
 670 population models. R package version 2.4.2.

671 Taiti, S. W. 1992. The Vegetation of Laikipia District, Kenya. Laikipia Research Programme,
 672 Universities of Nairobi and Bern, Bern, Switzerland.

673 Tarnita, C. E., T. M. Palmer, and R. M. Pringle. 2014. Colonisation and competition dynamics
 674 can explain incomplete sterilisation parasitism in ant-plant symbioses. *Ecology Letters*
 675 17:1290–1298.

676 Therneau, T. M. 2015. coxme: Mixed effects Cox models. R package version 2.2-5.

677 Thomas, L., et al. 2010. Distance software: design and analysis of distance sampling surveys for
 678 estimating population size. *Journal of Applied Ecology* 47:5–14.

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

681 Venter, F. J., R. J. Scholes, and H. C. Eckhardt. 2003. The abiotic template and its associated
 682 vegetation pattern. Pages 83–129 in J. T. du Toit, K. H. Rogers, and H. C. Biggs, editors.
 683 The Kruger experience. Island Press, Washington, DC.

684 Walker, B. H. 1987. A general model of savanna structure and function. Pages 1–12 in B. H.
 685 Walker, editors. Determinants of tropical savannas. IUBS Monograph Series No. 3, IRL

686 Press, Oxford.

687 Whitmore, A. P., and W. R. Whalley. 2009. Physical effects of soil drying on roots and crop
688 growth. *Journal of Experimental Botany* 60:2845–2857.

689 Wigley, B. J., W. J. Bond, H. Fritz, and C. Coetsee. 2015. Mammal browsers and rainfall affect
690 *Acacia* leaf nutrient content, defense, and growth in South African savannas. *Biotropica*
691 47:190–200.

692 Young, H. S., D. J. McCauley, K. M. Helgen, J. R. Goheen, E. Otárola-Castillo, T. M. Palmer, R.
693 M. Pringle, T. P. Young, and R. Dirzo. 2013. Effects of mammalian herbivore declines on
694 plant communities: observations and experiments in an African savanna. *Journal of Ecology*
695 101:1030–1041.

696 Young, T. P., B. D. Okello, D. Kinyua, and T. M. Palmer. 1998. KLEE: A long-term multi-
697 species herbivore exclusion experiment in Laikipia, Kenya. *African Journal of Range &*
698 *Forage Science* 14:94–102.

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

701 Young, T. P., N. Patridge, and A. Macrae. 1995. Long-term glades in *Acacia* bushland and their
702 edge effects in Laikipia, Kenya. *Ecological Applications* 5:97–108.

703 **TABLE 1.** Mixed-effects models with substantial empirical support ($\Delta_i < 2$) for Experiment 1.

	response	model	AIC _c	Δ_i	w_i	relative variable importance (Σw_i)					
						S	H	R	S×H	S×R	H×R
Acacia drepanolobium (ACDR)	survival fig. 3a	S + H	354.17	0	0.22						
		S + H + (S×H)	354.66	0.48	0.18						
		S + H + R	354.91	0.74	0.16	1.00	1.00	0.59	0.44	0.22	0.15
		S + H + R + (S×H)	355.38	1.21	0.12						
		S + H + R + (S×R)	356.00	1.83	0.09						
	height fig. 3c	(All main effects and interactions)	996.20	0	0.38						
		S + H + R + (S×H) + (S×R)	997.48	1.28	0.20	0.90	1.00	0.90	0.75	0.81	0.56
	diameter fig. 3e	S + H + R + (S×H)	527.14	0	0.21						
		S + H + (S×H)	527.67	0.53	0.08						
		S + H + R	528.98	1.84	0.16	0.88	0.88	0.66	0.55	0.16	0.16
		S + H	529.03	1.89	0.08						
	browse fig. 4a	S + H + R + (S×H) + (H×R)	151.32	0	0.17						
		S + H + R + (S×H) + (S×R) + (H×R)	151.90	0.58	0.13						
		S + H + (S×H)	152.04	0.72	0.12						
		S + H + R + (S×H)	152.26	0.94	0.11	0.80	1.00	0.76	0.66	0.29	0.49
		H	152.81	1.49	0.08						
		(All main effects and interactions)	153.08	1.76	0.07						
	spine fig. 5a	S + R + (S×R)	529.31	0	0.27						
		S	529.61	0.30	0.23	0.99	0.38	0.65	0.10	0.45	0.08
		S + R	531.01	1.70	0.12						
	domatia fig. 5b	S + H + R + (H×R)	860.68	0	0.19						
		S	861.48	0.80	0.13						
		S + H + R + (S×R) + (H×R)	861.62	0.94	0.12	0.82	0.71	0.69	0.20	0.22	0.51
		S + H + R + (S×H) + (H×R)	862.30	1.62	0.08						
Acacia brevispica (ACBR)	survival* fig. 3b	R	159.58	0	0.46						
		S + R	160.72	1.13	0.26	0.43	n/a	0.83	n/a	0.11	n/a
	height fig. 3d	H	1202.9	0	0.38						
		S + H	1204.7	1.80	0.16	0.43	1.00	0.36	0.17	0.05	0.10
	diameter fig. 3f	H + R	534.43	0	0.28						
		S + H + R	535.06	0.63	0.21	0.58	1.00	0.93	0.15	0.18	0.25
	browse fig. 4b	S + H + (S×H)	186.43	0	0.30						
		S + H + R + (S×H)	187.55	1.12	0.17	0.90	1.00	0.60	0.78	0.19	0.29
		S + H + R + (S×H) + (H×R)	187.85	1.42	0.15						

704

705 *Notes.* S = Soil type, H = Herbivore exclusion, R = Resource addition. Notation per Burnham and

706 Anderson 2002). Akaike weight (w_i) is the likelihood that model i is the best in the set. Relative

707 variable importance is the sum of w_i for all models containing that variable; main effects cannot

708 be compared with interactions, as the latter occurred in only 6 of the 14 models. *We could not

709 evaluate effects of H on ACBR survival (because all caged saplings survived), but the data (Fig.

710 2) indicate that herbivory was a biologically significant driver.

FIGURE LEGENDS

Fig. 1. Study system. **(a)** Satellite image of black-cotton (left) and red-sands (right) habitats at Mpala Research Centre (MRC), Laikipia, Kenya, showing locations of KLEE and UHURU exclosures on black-cotton and red-sands, respectively. **(b)** Black-cotton soil habitat, showing *Acacia drepanolobium* (ACDR) monoculture. **(c)** Red-sands soil habitat dominated by *Acacia brevispica* (ACBR, left foreground and elsewhere). **(d)** Close-up of the well defended ACDR on black-cotton, showing long stipular spines, swollen-thorn ant domatium, extrafloral nectaries (visible on petioles of two leaves beneath the domatium) and *Crematogaster nigriceps* ant symbionts. **(e)** Close-up of the poorly defended ACBR, showing small prickles.

Figure 2. Conceptual model of plant community assembly at MRC. From top: the regional pool of tree species is initially filtered by soil (left: rich-but-stressful black-cotton; right: poor-but-benign red-sands). Pie charts illustrate local community composition. Species exhibit differential success across soil types (e.g., due to local adaptation), but most are not excluded by this abiotic filter alone. However, the added biotic filter of herbivory excludes ACDR from red-sands (where it cannot sustain its costly defenses) and excludes ACBR and other species from black-cotton (where they cannot tolerate herbivory in combination with physical stress). The assembly of a less-defended tree community on red-sands feeds back positively onto browser density, whereas the development of a well-defended ACDR monoculture on black-cotton feeds back negatively.

Fig. 3. Growth and survival of ACDR (left) and ACBR (right) saplings in Experiment 1. **(a, b)** Sapling survival over 17 months (legend in panel b). **(c, d)** Net change in height and **(e, f)** basal stem diameter for saplings that survived at least 16 months (legend in panel d). Specification of the best-fitting coxme or lme model is shown for each response (per Table 1), where parentheses indicate inclusion of all main effects and interactions between the enclosed terms.

Fig. 4. Browser effects on ACDR (left) and ACBR (right) saplings in Experiment 1. **(a, b)** Mean browse score for surviving saplings over 16 months (legend in panel a), with best-fitting lme model specifications (per Table 1). **(c, d)** Fitted logistic-regression curves (left y-axes) showing probability of mortality for +herbivory saplings (only) as a function of browse score, pooling soil and resource treatments; histograms (right y-axes) show observed survival and mortality in 0.5-wide bins. **(e, f)** Growth as function of browse score in +herbivory saplings; lines are OLS regressions for each soil-resource treatment combination; best-fitting linear mixed-effects model specifications are shown (legend in panel e).

Fig. 5. Defense traits of ACDR saplings in Experiment 1. **(a, b)** Mean spine length and ant-domatium number for surviving saplings over 16 months, with best-fitting model specifications (legend in panel a). **(c)** Cumulative months of ant occupation as a function of domatium number; lines are OLS regressions for each soil type, pooling herbivory and resource treatments. Effects of soil ($t_{1,8} = -4.28$, $P = 0.003$), domatia ($t_{1,84} = 4.74$, $P < 0.0001$), and their interaction ($t_{1,84} = 1.02$, $P = 0.31$) were tested using a negative-binomial generalized linear mixed model.

Fig. 6. Herbivore and ant effects on red-sands ACDR saplings in Experiment 3. **(a)** Sapling survival. **(b)** Mean browse score across surveys, net change in **(c)** sapling size (total branch length) and **(d)** number of ant domatia after 228 d, and **(e)** mean proportion of active extrafloral nectaries after 167 d. Panels b-d pertain only to saplings surviving >228 d (legend in panel b).

Fig. 7. **(a)** Mean biomass densities of five browsing antelope (individually and combined) and a grazer, plains zebra, across 11 monthly distance-sampling surveys. **(b)** Total energetic demand for browsers and grazers, calculated from the distance-sampling data. **(c)** Mean dung densities of browsing megaherbivores across 11 surveys of transects spanning each block of Experiment 1.

FIGURE 1

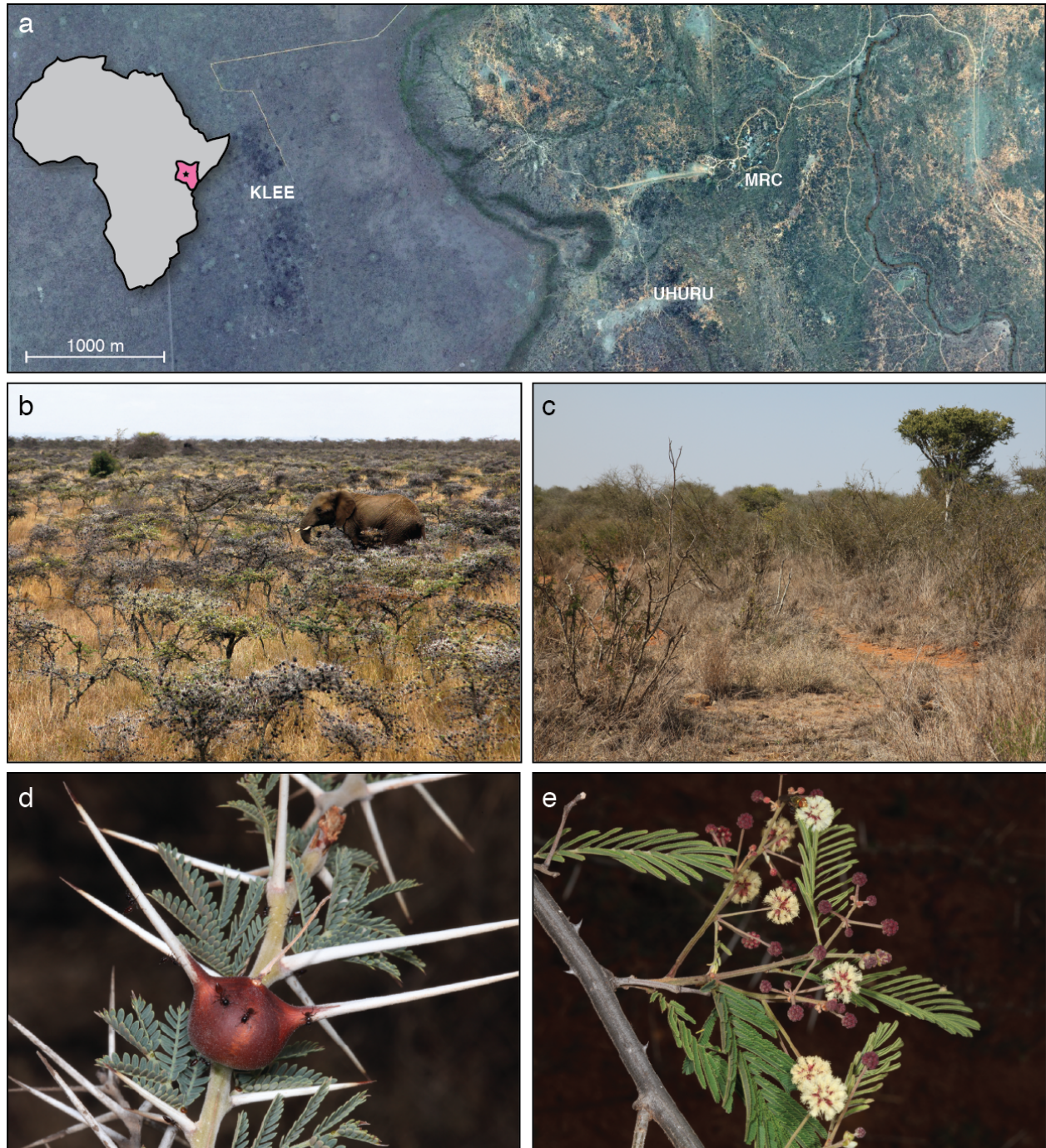


FIGURE 2

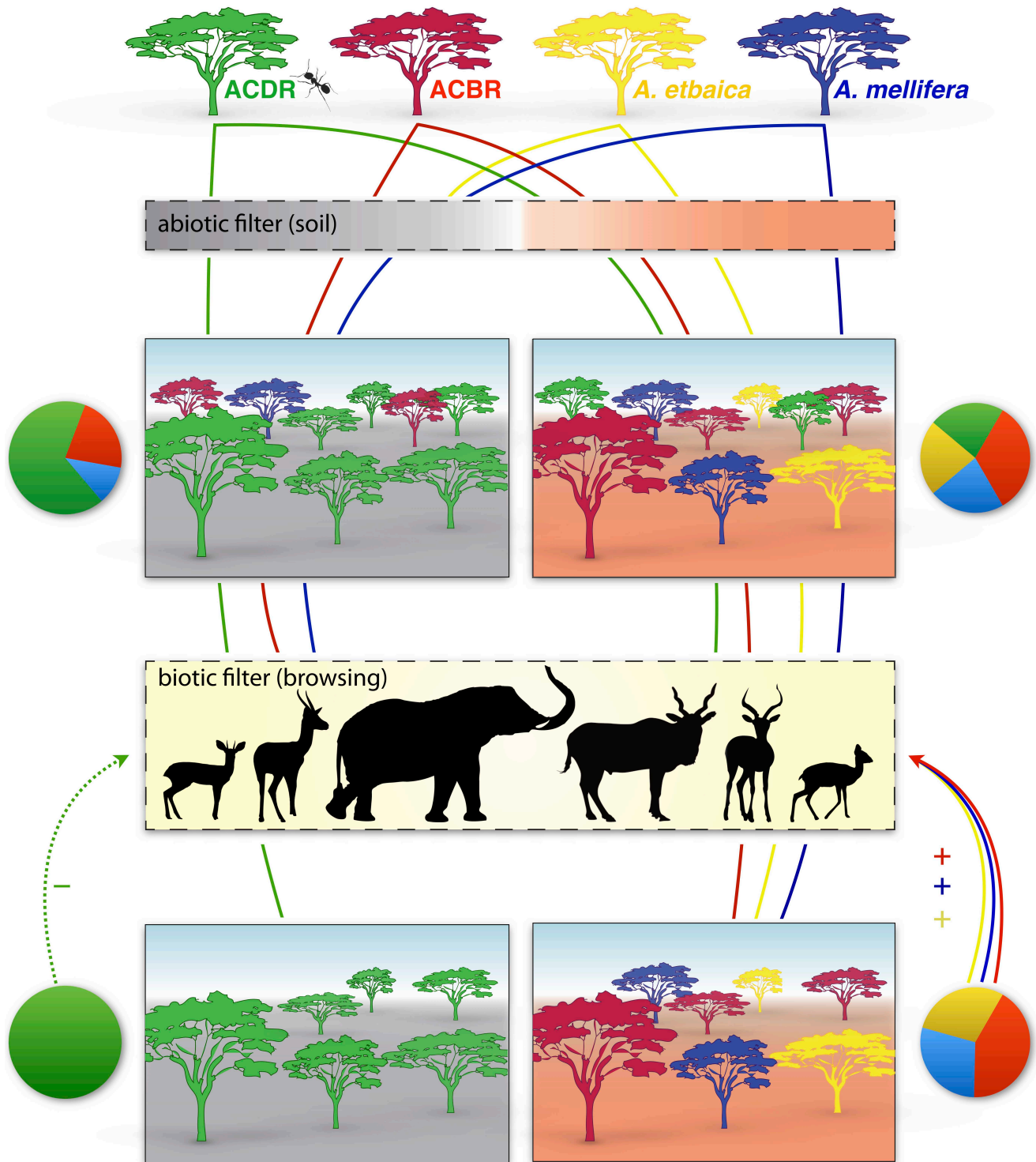


FIGURE 3

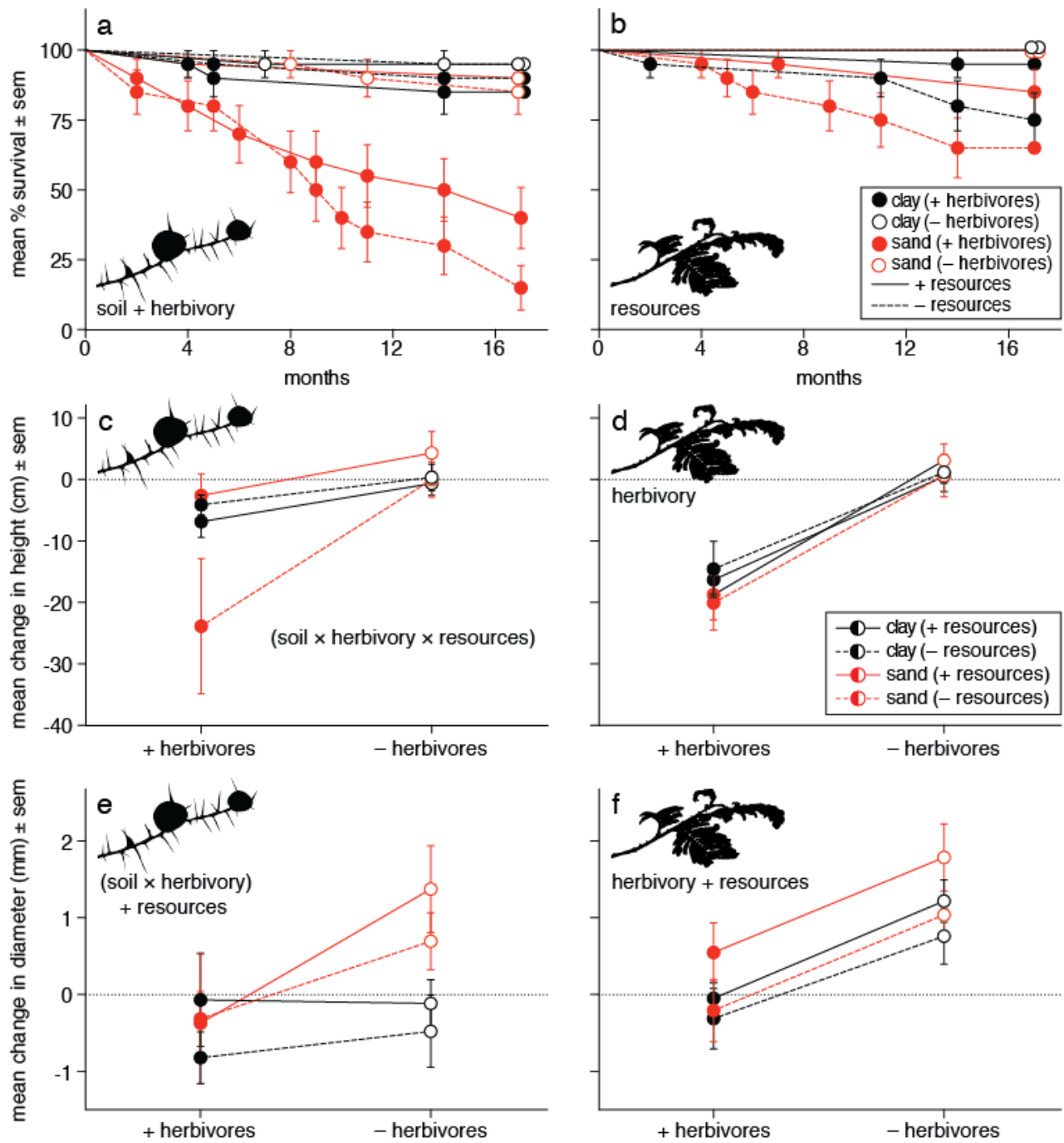


FIGURE 4

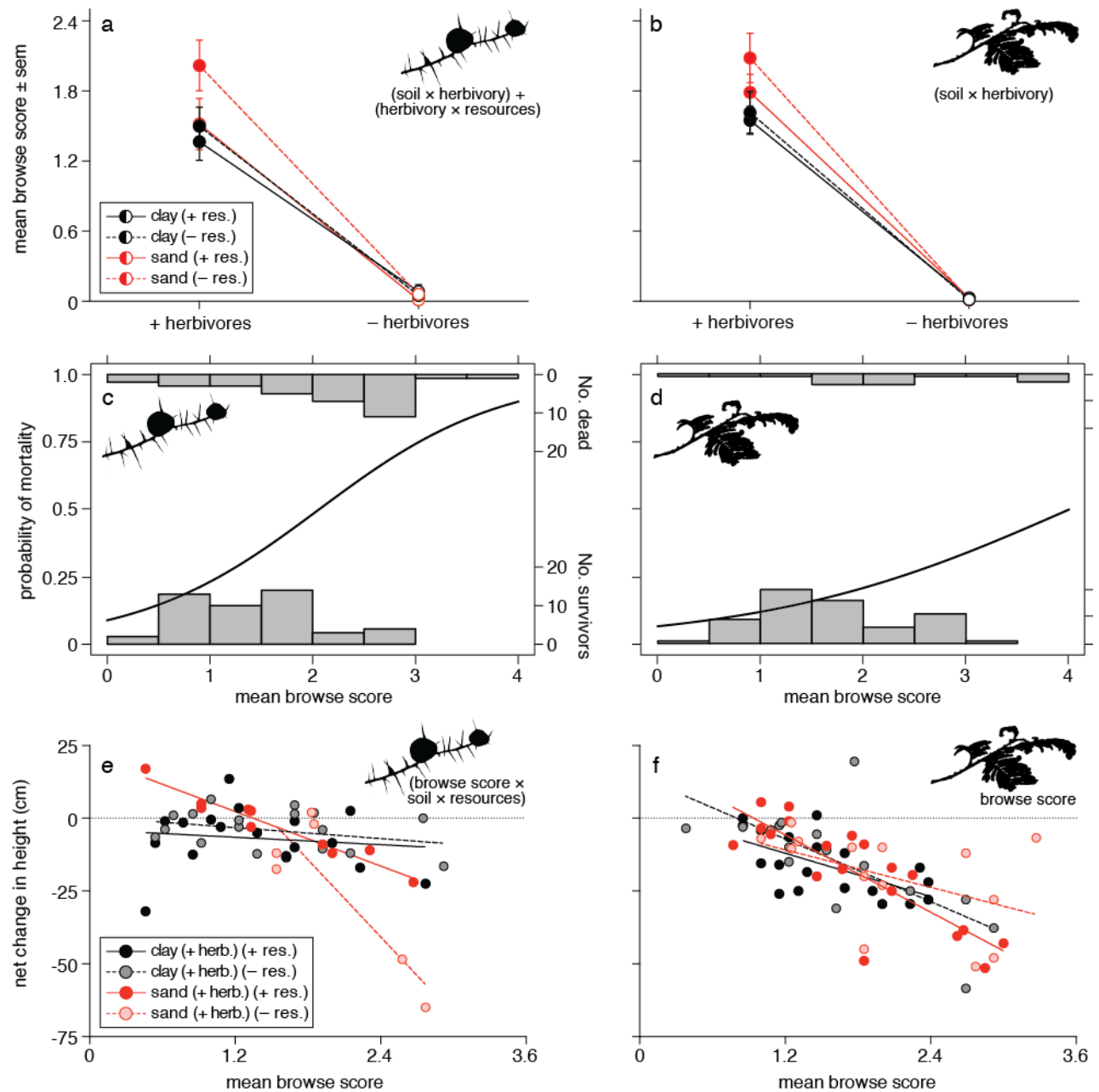


FIGURE 5

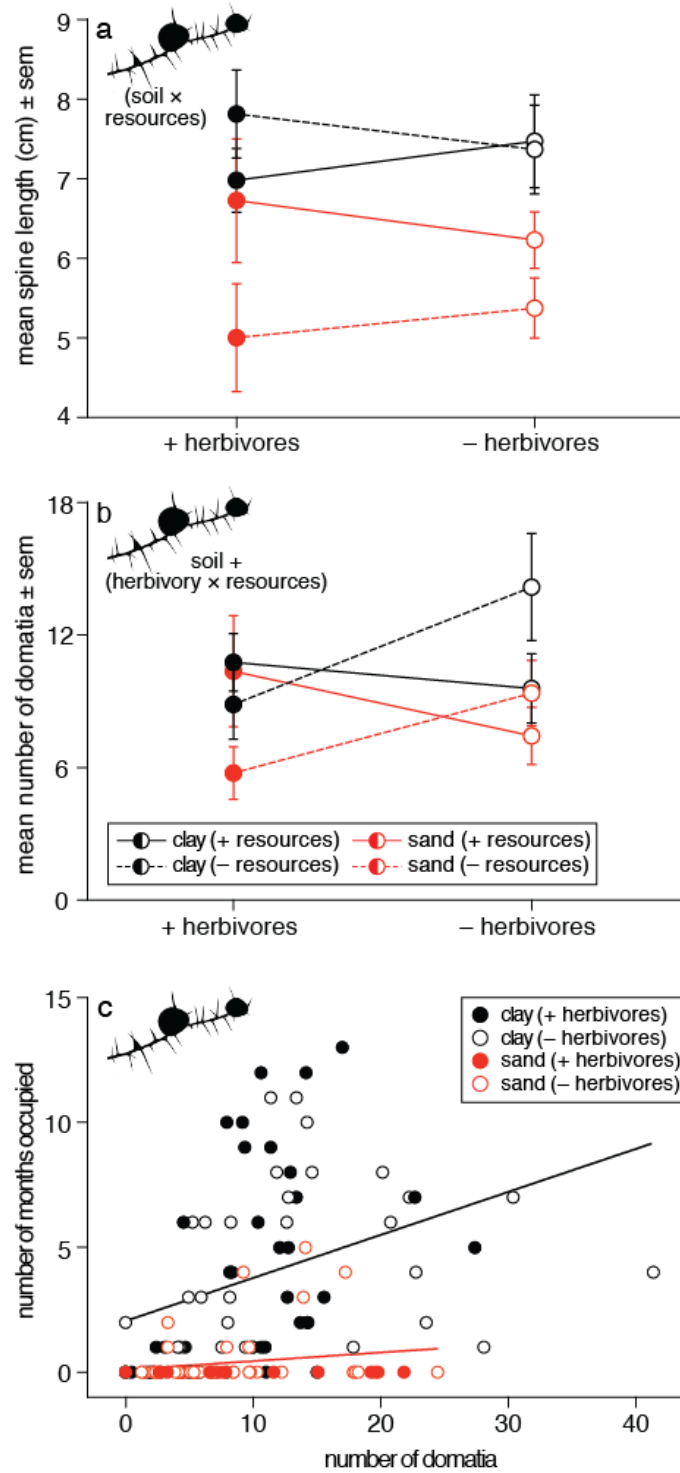


FIGURE 6

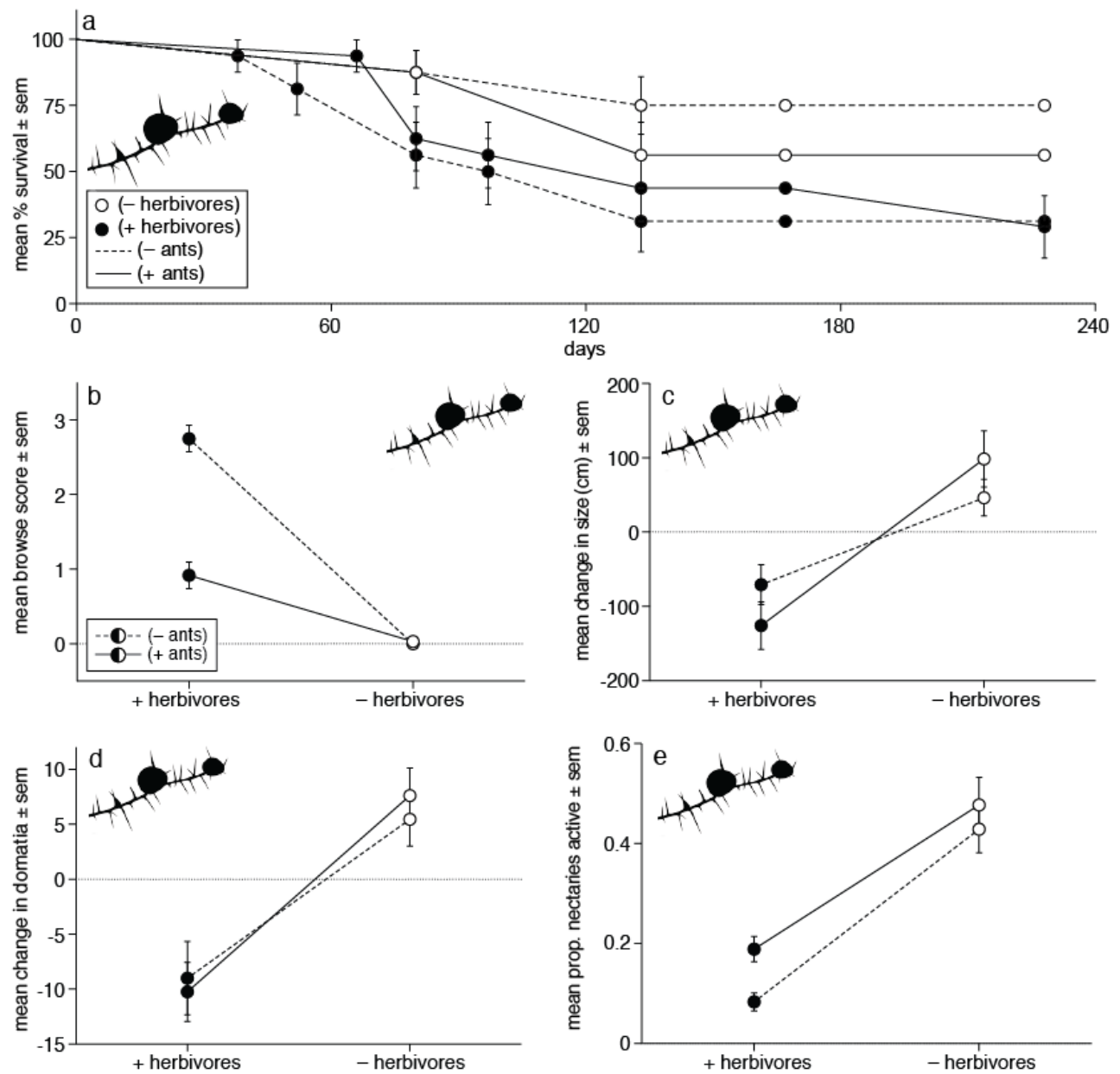


Figure 7

