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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 cracking clay vertisols that are nutrient rich but physically stressful, whereas poorly defended species such as *A. brevispica* (ACBR) dominate on nutrient-poor but otherwise less-stressful 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 biotic and abiotic stressors. Hence, each tree species was 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" (abiotic 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 savanna ecosystems are shaped by species interactions in cryptic ways that mimic 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.

Key words: community assembly; edaphic specialization; fundamental niche; habitat filtering; megafauna; multiple stressor synergy; plant defenses; positive feedbacks; savannah tree cover; tolerance and apparency; wildlife declines; ungulate herbivory.

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. And although there is much evidence that herbivores can delimit the ranges and local richness of plant species (Olff and Ritchie 1998, Maron and Crone 2006), little is known about the abiotic context dependence of these interactions or the extent to which herbivory creates (or amplifies) 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 were not solely the products 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

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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, Bond 2008, Sankaran et al. 2008, Holdo 2013) than on species-level patterns of diversity and distribution. Yet the ecological significance 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 soil 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 soil quality is often interpreted in terms of nutrient availability (Bell 1982, Scholes and Walker 1993). However, various soil properties (e.g., depth, texture, pH, physical stability/dynamics) influence "quality" in different contexts, and these may or may not be correlated with nutrient content. In water-limited savannas, for example, soil effects on plant-available moisture may trump or modulate the effects of nutrient availability on productivity. Moreover, mammalian herbivory is a potent top-down force in these systems (Augustine and McNaughton 1998, Skarpe and Hester 2008, Pringle et al. 2011) 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 dimensions of soil quality than nutrient availability alone.

We investigated the causes of edaphic specialization in the semiarid savannas of Laikipia, Kenya (Fig. 1). There and elsewhere in East Africa, poorly drained, clay- and nutrient-rich vertisols (black-cotton) are monospecifically dominated by whistling-thorn trees (*Acacia drepanolobium*, ACDR), which are well defended via long spines and symbiotic ants. Nearby well-drained, nutrient-poor sandy loams (red-sands) are codominated by *Acacia brevispica* (ACBR), *A. mellifera*, and *A. etbaica*, which are lightly defended relative to ACDR (prickles or spines, no ants) and exhibit traits associated with herbivory tolerance, such as cage-like architectures and basal resprouting (Marquis 1996, Bond and Midgley 2001, Staver et al. 2012). Although black-cotton and red-sands habitats are often separated by <1 km, there is almost no overlap in tree community composition (Fig. 1).

This sharp disjunction is unexplained and seemingly at odds with the predictions of resource-availability theory (Coley et al. 1985), because the better-defended trees occur on the richer soils and vice versa. However, the high clay content of nutrient-rich black-cotton vertisols also challenges plants physically via seasonal shrink–swell cycles and cracking, with impeded infiltration and low water potentials during the dry season. It has been suggested that most tree species are physiologically unable to cope with such physically stressful conditions (Belsky 1990), and that black-cotton trees such as ACDR "may be uniquely adapted to these specialized soils" (Okello and Young 2000) in ways that prevent them from colonizing other soil types. Yet the only prior test of this idea found that "soil type did not influence germination or seedling survival" after 19 weeks (Okello and Young 2000). Although it remains possible that soil-specific effects on seedling survival not tested by Okello and Young (2000) contribute to edaphic specialization (e.g., by modulating dry-season seedling survival of species that are more vs. less robust to desiccation), it is also possible that context-dependent effects of herbivory filter the recruitment of tree species across soil types. Here, we evaluate this latter possibility.

Specifically, we propose that the observed pattern of edaphic niche separation (Fig. 1) is not abiotically deterministic, but instead arises at least in part from interactive effects of soil properties and herbivory on tree species that differ in defensive traits and tolerance ability (Table 1). We hypothesize that the physical and hydrological stress imposed by black-cotton soils can be withstood in isolation by many species, but that the "combined stressors" (sensu Folt et al. 1999) of clay soil and herbivory together are lethal; hence, herbivory cannot be tolerated and must be resisted, which helps explain the success of heavily defended ACDR and the absence of poorly defended, tolerance-oriented species such as ACBR. On red-sands (which are relatively nutrient poor but less stressful than black-cotton vertisols), we hypothesize that tolerance and energetically cheap defenses such as spinescence are viable coping mechanisms, which permits ACBR and other tree species to thrive; however, resource limitation precludes extremely costly defense strategies, such as ACDR's ant–plant symbiosis (Stanton and Palmer 2011), leaving individuals of that species defenseless against herbivory and inhibiting population establishment. This hypothesis yields a series of specific predictions (Table 1), 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°53′ E, 1600–1800 m elevation) averages ~600 mm/yr in a weakly tri-modal annual pattern, with a short dry season from December to March. Fires are infrequent and localized (Kimuyu et al. 2014, Pringle et al. 2015). The mammal fauna includes 25 species of large herbivores (≥5 kg) and an intact large-carnivore guild. Browsing species that commonly eat *Acacia* 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 eat *Acacia* (Kartzinel et al.

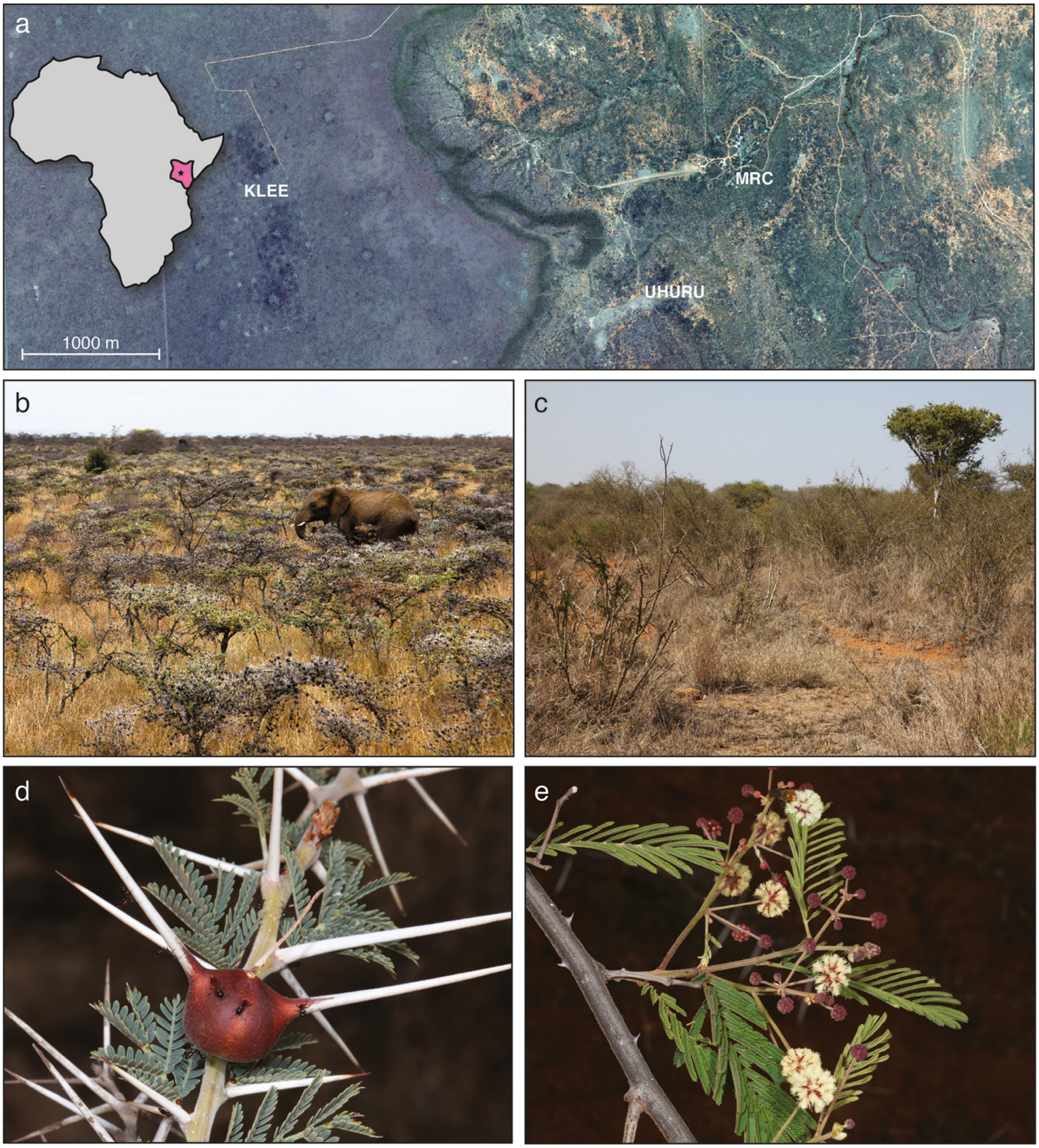

FIG. 1. Study system. (a) Satellite image of black-cotton (left) and red-sands (right) habitats at Mpala Research Centre (MRC), Laikipia, Kenya, showing locations of KLEE and southern UHURU exclosures on black-cotton and red-sands, respectively. (b) Black-cotton soil habitat, showing *Acacia drepanolobium* (ACDR) monoculture (see elephant for scale). (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 and large leaves. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

2015), include plains and Grevy's zebra (*Equus quagga* and *E. grevyi*), buffalo (*Syncerus caffer*), domestic cattle (*Bos indicus*), warthog (*Phacochoerus africanus*), hartebeest (*Alcelaphus buselaphus*), and oryx (Oryx beisa).

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 (4,200 of 9,700 km^2) and 10% of MRC (20 of 2,000 km^2) is underlain by black-cotton (pellic vertisols with impeded drainage, clay content ≥50%). The high clay content of these soils inhibits root growth, aeration, and infiltration, while shrink–swell cycles and the "deep, wide

TABLE 1. Hypotheses and predictions tested in this this study.

Hypotheses and predictions	Tests	Data	Strength of support
H1. Edaphic segregation of tree species is not abiotically deterministic and is maintained in part by browsers.			
P1. Saplings of tree species from each soil type survive and grow on both soil types if browsers are excluded.	Expt. 1	Fig. 2	high
H2. Well-defended ACDR thrives in stressful black-cotton vertisols due in part to costly defenses that can be sustained in resource-rich soils.			
P2a. ACDR saplings survive and grow on black-cotton in both presence and absence of browsers.	Expt. 1	Fig. 2	high
P2b. ACDR saplings have higher levels of defensive traits on black-cotton than red-sands.	Expt. 1	Fig. 4	high
H3. Poorly defended trees such as ACBR are excluded from black-cotton by "one-two punch" of biotic and abiotic stressors: soil physical stress can be tolerated alone, but not combined with herbivory.			
P3a. ACBR saplings do not survive/grow on black-cotton in the presence of browsers.	Expt. 1	Fig. 2	low
P3b. Effects of browsing on ACBR growth and survival are disproportionately negative on black-cotton.	Expt. 1	Fig. 3	low
P3c. ACBR saplings fail to recruit to maturity on black-cotton, but can recruit on red-sands.	Expt. 2	Appendix S1: Fig. S2	high
H4. ACDR is excluded from red-sands in part because the ant-protection mutualism that enables it to resist herbivory and persist in black-cotton is prohibitively costly on resource-poor sands, leaving trees vulnerable to herbivory.			
P4a. ACDR saplings do not survive/grow on red-sands in the presence of browsers.	Expts. 1, 3	Figs. 2, 5	high
P4b. Effects of browsing on ACDR growth and survival are disproportionately negative on red-sands.	Expt. 1	Fig. 3	high
P4c. Resource addition enhances ACDR performance and defense on red-sands, but not on black-cotton.	Expt. 1	Figs. 3, 4	high
P4d. Colonization by ant symbionts does not "rescue" ACDR saplings from browsers on red-sands.	Expt. 3	Fig. 5	high
H5. ACBR persists on red-sands in part via mechanisms for tolerating herbivory.			
P5a. ACBR saplings survive, grow, and recruit on red-sands in both presence and absence of browsers.	Expts. 1, 2	Fig. 2; Appendix S1: Fig. S2	high
P5b. Resource addition enhances ACBR's tolerance ability, increasing survival/growth in presence of browsers.	Expt. 1	Figs. 2, 3	mixed
H6. Assembly of differently defended plant communities feeds back to influence browser abundance across soil types.			
P6a. Abundance of browsers, but not necessarily grazers, is greater on red-sands than on black-cotton.	Surveys	Appendix S1: Fig. S5	correlative
P6b. Both tree species sustain greater herbivore damage on red-sands than on black cotton.	Expt. 1	Fig. 3	high

Notes: ACDR, *Acacia drepanolobium*; ACBR, *Acacia brevispica*; Expt., experiment.

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. 1d). 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, than black-cotton vertisols but have lower extractable nutrient concentrations (Augustine 2002). In the red-sands plant community (Fig. 1c), 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 Coverdale et al. 2016).

Multiple lines of evidence indicate that ACBR is lightly defended relative to ACDR and other trees at MRC. In addition to lacking symbiotic ants, ACBR is browsed preferentially by impala due to its small prickles (~0.6-cm) and comparatively large leaves (compare Fig. 1d and e; Ford et al. 2014). Indeed, ACBR is the single most commonly eaten woody species by large herbivores at MRC, occurring more frequently in fecal samples than ACDR and other long-spined *Acacia* species combined (Kartzinel et al. 2015). ACBR's condensed-tannin concentrations (Ford et al. 2014) are similar to those of ACDR (Ward and Young 2002) and other *Acacia* at MRC; although ACBR's other secondary compounds have not been quantified, the frequency with which it is consumed by diverse large-herbivore species, together with the ability of browsers such as elephants and impala to consume large quantities of even famously toxic taxa such as *Solanum* (Pringle et al. 2014), suggest that any deterrent effects of foliar chemistry are limited. In lieu of strong defense, ACBR appears to tolerate consumption, in part via basal resprouting (Bond and Midgley 2001), with individuals exposed to browsers growing in dense, multi-stemmed clumps (Fig. 1c).

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 into each soil type under factorial combinations of browser exclusion and resource (water + nutrients) addition.

Saplings were grown from locally collected seeds, which were 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 approximately one year old and ~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. (Our decision to leave the root balls of fertile potting soil intact means that all saplings in the study likely received a slight nutrient boost relative to baseline.) 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; Appendix S1: 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 inter-site 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 initial transplanting. This treatment was designed in consultation with an agroforestry expert familiar with local soils and conditions (J. Vernon) 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 (future studies should disaggregate water and nutrient treatments to identify the relative contribution of each). 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 and vice versa); the latter approach would be misleading if it did not reproduce the relevant biotic, chemical, and physical properties of each soil type, which we had no way of testing.

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 spines on each of three branches), total number of swollen-thorn ant domatia, and 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 (R 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 models using AIC_c (Burnham and Anderson 2002). In each case, the best-fitting model had far more explanatory power than the null (Δ_i >2, often >>2). In Table 2, we report all models with substantial support (Δ_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 Appendix S1: Table S1.

To gauge sensitivity of performance to browsing pressure for +herbivory saplings, we used mean browse score as a predictor to analyze mortality (0, 1), using univariate logistic regression (binomial glm, plotted using logi.hist.plot in R package popbio; Stubben et al. 2015), and net height change (a measure of relative herbivory tolerance) using linear mixed-effects models (lme). For simplicity in the latter analysis, in lieu of a full model-selection approach, we instead 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 (per 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 to account for overdispersion in the zero-heavy 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 and Young 2000) and Experiment 1 focused on saplings, but biotic filters on tree recruitment may occur at even later ontogenetic stages if larger plants are more apparent to potentially lethal herbivores such as elephants (Louthan et al. 2014). 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 4-ha plots. Megaherbivores (elephants and giraffes only) are excluded using electrified wires at 2-m height, while both mega- and mesoherbivores (15–1,000 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 (1) megaherbivores, (2) mesoherbivores, and (3) 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 1-ha plots since 2008 (Pringle 2012, Goheen et al. 2013, Louthan et al. 2013, Kartzinel et al. 2014). In 2014, we searched the central 3,600-m^2 portion of each plot, counting all post-sapling ACBR.

Equivalent comparisons were not possible for ACDR, because 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 transplants were colonized by ants in Experiment 1 (see *Results*). In a follow-up experiment, we manipulated the presence/absence of (1) ants and (2) 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), the number of new domatia produced, and the 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 a 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 2 × 2 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 (06:00–09:00) 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/h 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 recounting) 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).

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 (Fig. 2).

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. 2a). 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 2). 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. 2c). 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 were ≥0.75 (Table 2). The soil × herbivory interaction was likewise important (RVI = 0.55) for diameter growth, which was negligible in all +herbivory scenarios and was enhanced considerably by herbivore exclusion on red-sands only (Fig. 2e).

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. 2b, Table 2). 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. 2d, f), but none of the substantially supported models contained interaction terms (all RVI ≤ 0.25; Table 2).

Browse damage was negligible in all –herbivory saplings (i.e., exclosures were effective and insects/rodents had little impact; Fig. 3a, b) and among +herbivory saplings was greater on red-sands (soil RVI = 0.80 for ACDR and 0.90 for ACBR; Table 2). Saplings with higher browse scores exhibited increased mortality (binomial glm: ACDR estimate = 1.13, z = 1.97, P = 0.05; ACBR estimate = 0.067, z = 1.94, P = 0.05; Fig. 3c, d) and

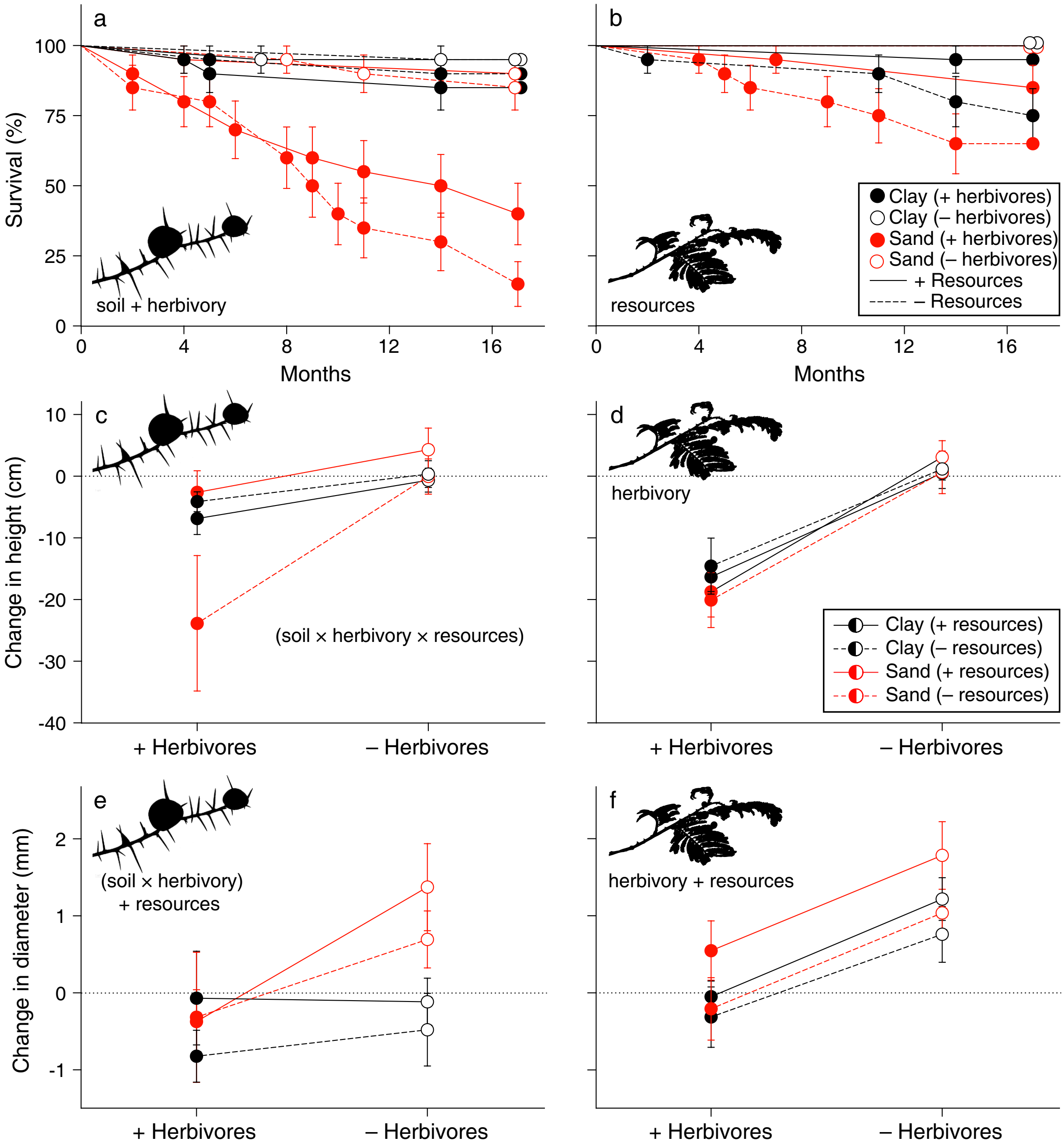

FIG. 2. Growth and survival of ACDR (left) and ACBR (right) saplings in Experiment 1. (a, b) Sapling survival over 17 months (legend in panel b). (c, d) Net change in height and (e, f) basal stem diameter for saplings that survived at least 16 months (legend in panel d). Specification of the best-fitting coxme or lme model is shown for each response (per Table 2), where parentheses indicate inclusion of all main effects and interactions between the enclosed terms. Values are mean ± SE. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

decreased height growth (Fig. 3e, 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 tolerance on red-sands was limited by resources and restored by resource addition, whereas for ACBR slopes were similar among treatments; these results broadly parallel those for survival and growth (see Fig. 2).

Mean spine length and domatium number, key defense traits of ACDR, were both (1) greater on average in black-cotton than red-sands and (2) lowest in red-sands +herbivory –resources saplings (Fig. 4a, 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

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

				Relative variable importance (Σw_i)					
Response and model	AIC$_c$	Δ_i	w_i	S	H	R	S × H	S × R	H × R
Acacia drepanolobium (ACDR)									
Survival, Fig. 2a				1.00	1.00	0.59	0.44	0.22	0.15
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						
S + H + R + (S × H)	355.38	1.21	0.12						
S + H + R + (S × R)	356.00	1.83	0.09						
Height, Fig. 2c				0.90	1.00	0.90	0.75	0.81	0.56
All main effects and interactions	996.20	0	0.38						
S + H + R + (S × H) + (S × R)	997.48	1.28	0.20						
Diameter, Fig. 2e				0.88	0.88	0.66	0.55	0.16	0.16
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						
S + H	529.03	1.89	0.08						
Browse, Fig. 3a				0.80	1.00	0.76	0.66	0.29	0.49
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						
H	152.81	1.49	0.08						
All main effects and interactions	153.08	1.76	0.07						
Spine length, Fig. 4a				0.99	0.38	0.65	0.10	0.45	0.08
S + R + (S × R)	529.31	0	0.27						
S	529.61	0.30	0.23						
S + R	531.01	1.70	0.12						
Domatium number, Fig. 4b				0.82	0.71	0.69	0.20	0.22	0.51
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						
S + H + R + (S × H) + (H × R)	862.30	1.62	0.08						
Acacia brevispica (ACBR)									
Survival†, Fig. 2b				0.43	n/a	0.83	n/a	0.11	n/a
R	159.58	0	0.46						
S + R	160.72	1.13	0.26						
Height, Fig. 2d				0.43	1.00	0.36	0.17	0.05	0.10
H	1202.9	0	0.38						
S + H	1204.7	1.80	0.16						
Diameter, Fig. 2f				0.58	1.00	0.93	0.15	0.18	0.25
H + R	534.43	0	0.28						
S + H + R	535.06	0.63	0.21						
Browse, Fig. 3b				0.90	1.00	0.60	0.78	0.19	0.29
S + H + (S × H)	186.43	0	0.30						
S + H + R + (S × H)	187.55	1.12	0.17						
S + H + R + (S × H) + (H × R)	187.85	1.42	0.15						

Notes: S, soil type; H, herbivore exclusion; R, resource addition. Notation per Burnham and Anderson (2002). Akaike weight (w_i) is the likelihood that model *i* is the best in the set. Relative variable importance (RVI) is the sum of w_i for all models containing that variable; main effects cannot be compared with interactions, as the latter occurred in only six of the 14 models.

†We could not statistically evaluate effects of H on ACBR survival (because all caged saplings survived), but the data (Fig. 2b) indicate that herbivory was a biologically significant driver of reduced survival.

exclusion on either defensive trait (Table 2). Saplings with more domatia were more frequently occupied by ants on both soil types (Fig. 4c), but overall colonization rates were much greater on black-cotton soil dominated by conspecifics (78% were ever colonized, and 26% on average were occupied during each survey) than on red-sands dominated by heterospecifics (15% and 2%, all of which were inside herbivore exclosures).

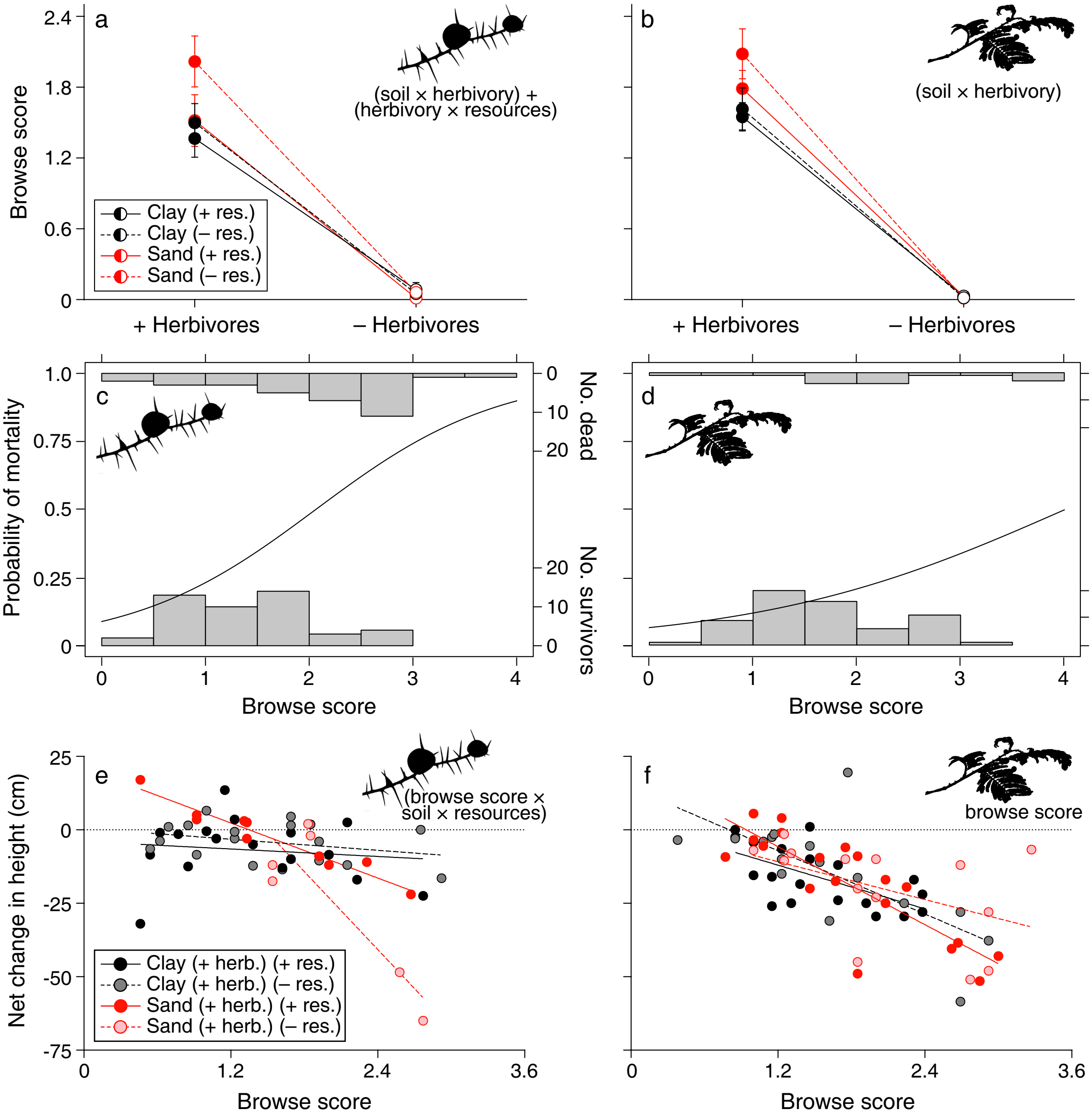

FIG. 3. Effects of browsing on ACDR (left) and ACBR (right) saplings in Experiment 1. (a, b) Browse score (mean ± SE) for surviving saplings over 16 months (legend in panel a), with best-fitting lme model specifications (per Table 2). (c, d) Fitted logistic-regression curves (left *y*-axes) showing probability 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). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

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 trees/ha vs. 0.08 ± 0.05 trees/ha) in KLEE plots that excluded megaherbivores (estimate = −2.49, $F_{1,12}$ = 41.75, $P < 0.0001$), whereas mesoherbivores (Effects of browsing. = +0.74, $F_{1,12}$ = 3.83, $P = 0.074$) and cattle (estimate = −0.37, $F_{1,12}$ = 1.45, $P = 0.25$) had nonsignificant effects (Appendix S1: 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 (Appendix S1: Fig. S3), showing that ACBR can recruit to maturity and reproduce on black-cotton in the absence of megaherbivores. In red-sands, ACBR

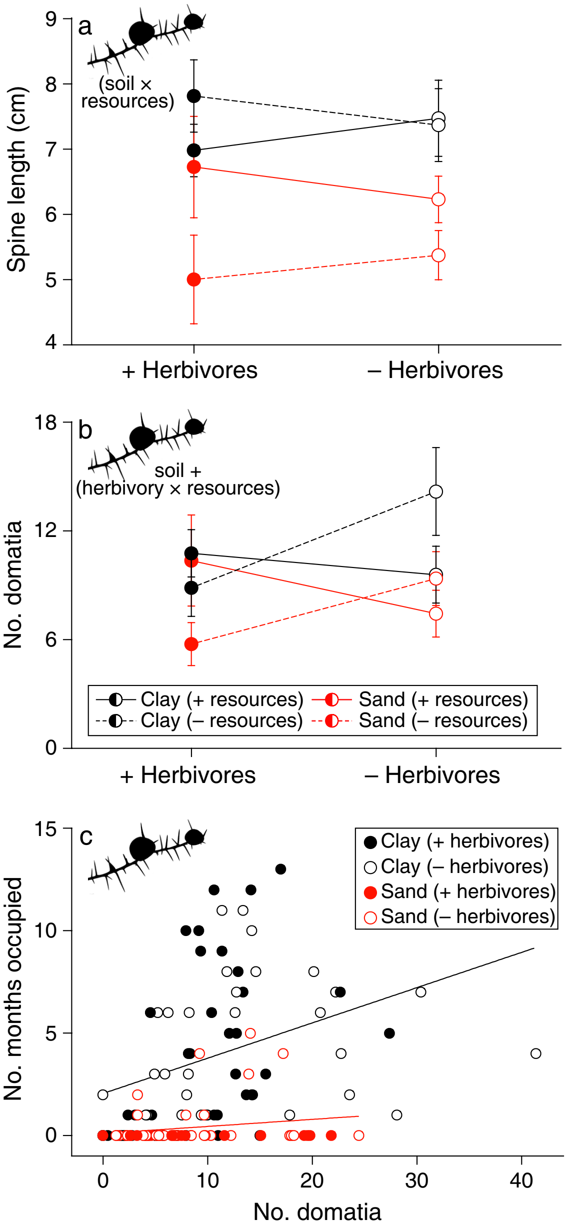

FIG. 4. Defense traits of ACDR saplings in Experiment 1. (a, b) Spine length and ant-domatium number for surviving saplings over 16 months, with best-fitting model specifications (legend in panel a; values are mean ± SE). (c) Cumulative months of ant occupation as a function of domatium number; lines are OLS regressions for each soil type, pooling herbivory and resource treatments. Effects of soil ($t_{1,8} = -4.28$, $P = 0.003$), domatium number ($t_{1,84} = 4.74$, $P < 0.0001$), and their interaction ($t_{1,84} = 1.02$, $P = 0.31$) were tested using a negative-binomial generalized linear mixed model. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

densities did not differ significantly in UHURU plots with vs. without megaherbivores after six years (338 ± 79 vs. 386 ± 70 trees/ha; estimate = −0.36, $F_{1,26} = 0.05$, $P = 0.83$; Appendix S1: 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. 5a). Ants reduced the proportion of shoot tips browsed by >66% (ants × herbivory, $F_{1,23} = 9.84$, $P = 0.005$; Fig. 5b), but did not reduce mortality (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; Appendix S1: Fig. S4). Net change in size (herbivory, $F_{1,23} = 21.85$, $P = 0.0001$) and domatium number (herbivory, $F_{1,23} = 27.46$; $P < 0.0001$) were negative in +herbivory and positive in –herbivory saplings, regardless of ants (Fig. 5c, 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 $F_{1,23} = 50.92$ $P < 0.0001$, respectively; Fig. 5e).

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, $t_{1,20} = 3.47$, $P < 0.001$; Appendix S1: Fig. S5). The overall discrepancy in browsers was driven by dik-dik and impala, which were 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 1,200% greater for elephant (estimate = 2.59, $t_8 = 3.88$, $P = 0.0047$) on red-sands than black-cotton (Appendix S1: Fig. S5).

DISCUSSION

Large herbivores enforce edaphic specialization of African savanna trees

Our results provide 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. 2e, f). Similarly, prior experiments found that ACDR germination and initial seedling survival rates were comparable on red-sands vs. black-cotton (Okello and Young 2000), suggesting that soil type alone does not prevent

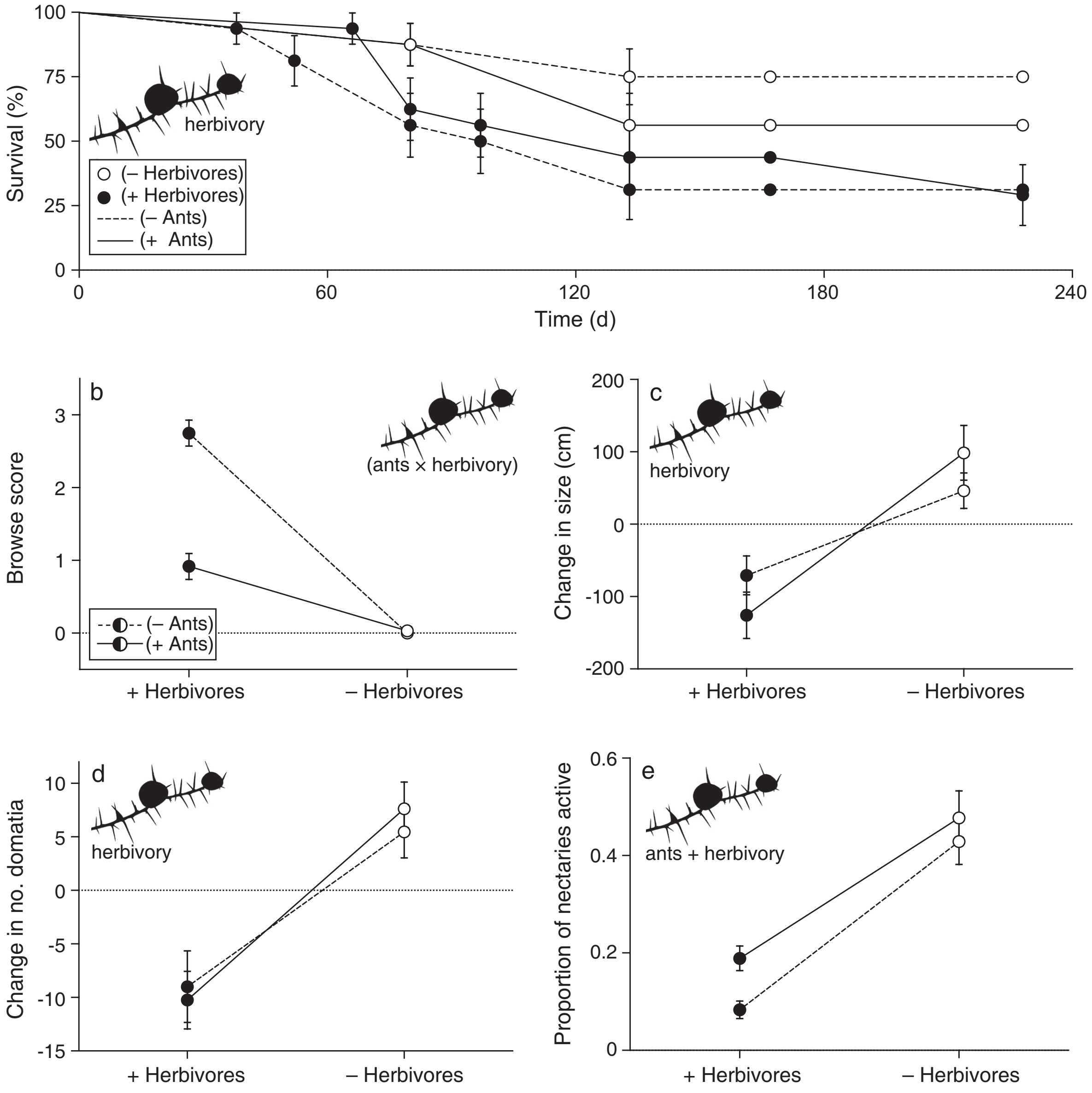

FIG. 5. Herbivore and ant effects on red-sands ACDR saplings in Experiment 3. (a) Sapling survival. (b) Browse score across surveys, net change in (c) sapling size (total branch length), and (d) number of ant domatia after 228 d, and (e) proportion of active extrafloral nectaries after 167 d. Panels b–d pertain only to saplings surviving >228 d (legend in panel b). Values are mean ± SE; statistically significant model effects are shown in each panel.

recruitment at earlier ontogenetic stages. Hence, edaphic segregation of tree species is not determined entirely by soil properties and intrinsic physiological traits of trees; instead, it emerges as a context-dependent effect of herbivory, which differentially filters community assembly in each soil type. Collectively, these results are consistent with the general conceptual model presented in Fig. 6. Because our two focal species are among the four *Acacia* spp. that comprise >80% of total tree cover at MRC (Young et al. 1995) and differ markedly in their traits, architectures, and utilization by animals, this biotic filter substantially increases the taxonomic, structural, and functional beta diversity of the landscape (compare Fig. 1b, c).

We argue that such "edaphic niche enforcement" by large herbivores is likely to shape 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

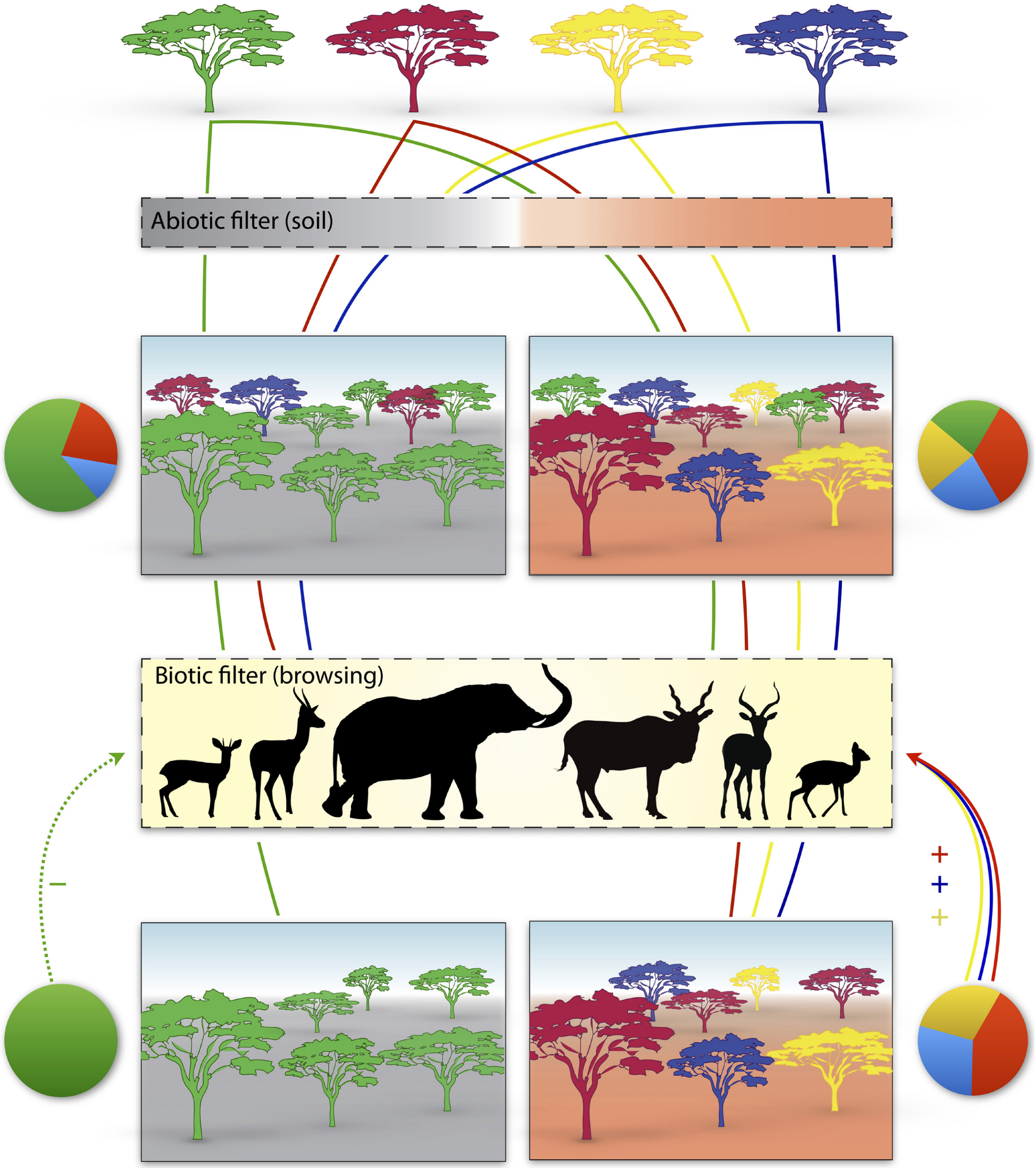

FIG. 6. Conceptual model of herbivore-enforced edaphic specialization in African savanna trees. From top, the regional pool of tree species is initially filtered by soil (left, nutrient-rich but stressful black-cotton vertisols; right, nutrient-poor but benign red-sands). Pie charts illustrate local community composition, with colors corresponding to tree species in the regional pool. Species exhibit differential success across soil types (e.g., due to local adaptation), but the majority of species are not completely excluded by this abiotic filter alone. However, the added biotic filter of herbivory excludes the most heavily defended (green) species from red-sands (where costly resistance traits cannot be sustained) and excludes poorly defended species (red, yellow, blue) from black-cotton vertisols (where herbivory cannot be tolerated in combination with physical stress). The assembly of a less-defended tree community on red-sands is predicted to feed back positively onto browser density, whereas the development of a well-defended monoculture on black-cotton feeds back negatively (consistent with the data in Appendix S1: Fig. S5). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

large mammalian herbivores are lacking. 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) typically include soil properties and/

or herbivory, but should be expanded to include the possibility that these factors are 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, Young et al. 2015, Daskin and Pringle 2016), 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 presented in Table 1, 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 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 1).

These predictions were supported by Experiment 1. Browsers reduced survival and growth weakly in black-cotton but strongly in red-sands (Fig. 2), where herbivory tolerance was disproportionately low (Fig. 3e). In red-sands, herbivore exclusion restored responses to levels commensurate with, or greater than, those on black-cotton (Fig. 2), and resource addition buffered the negative impacts of browsing (Fig. 3a); this ameliorative effect was moderate for survival (Fig. 2a) but fully compensatory for height (Fig. 2c).

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. 4a, 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. 4c). Thus, lack of protective symbionts inhibited defense in red-sands, but this might reflect either (or both) an inability of (1) resource-limited hosts to support effective ant colonies or (2) 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. 5).

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 aerial colonization and ground-based expansion of mature colonies (Palmer et al. 2013); the latter may be more effective than nanitic colonies in host protection and is only possible for saplings growing 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. 4b, c), suggesting resource limitation. Red-sands ACDR may face a Catch-22, wherein resource shortage and browsing pressure combine to prevent trees from acquiring the symbionts they need to resist browsing pressure.

There is considerable scope for work to further illuminate these processes. One worthwhile experiment would be to isolate the relative importance of ant dispersal limitation and host resource limitation in disrupting the ant–plant mutualism in red-sands. This could be done by combining ant transplants (as in our Experiment 3) with herbivore exclusion and resource addition (as in our Experiment 1) on both soil types simultaneously, ideally devolving our +resources treatment into separate water- and nutrient-addition treatments to assess the relative importance of each. It would also be interesting to determine 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), which might help explain the apparent tendency of obligate ant-plants to occur at high local densities or in monodominant stands (Janzen 1966, Frederickson et al. 2005). This could be evaluated by monitoring ant colonization and performance of saplings planted at varying distances from ant source populations across the transition from black-cotton to red-sands, one prediction being that colonization rates and sapling performance should both decline with distance from monospecific ACDR stands.

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. 2). However, we found strong support for an alternative explanation for the absence of ACBR from black-cotton: saplings could establish, but could only recruit to reproductive maturity in the sustained absence of megaherbivores (Appendix S1: Fig. S2), consistent with our hypothesis (Table 1) that the "one-two punch" of soil and herbivory stressors 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 or hydrological stresses 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 by megaherbivores (especially elephants, as giraffes rarely forage on plants <2 m tall; du Toit and Olff 2014). We expect apparency effects to be especially pronounced on black-cotton, because monodominance by well-defended ACDR should increase the visual contrast and relative attractiveness of other tree species to browsers. Uncaged ACBR saplings shrunk in height while maintaining high survival, suggestive of chronic herbivory (the "browse trap"; Staver and Bond 2014), but this effect did not differ across soil types and thus cannot explain why ACBR is absent from black-cotton only.

Although prior work has shown that browsers suppress ACBR on red-sands (Goheen et al. 2013, Ford et al. 2014), we found no megaherbivore effect even remotely comparable to the order-of-magnitude decrease observed on black-cotton (Appendix S1: Fig. S2), consistent with our prediction that tolerance ability is greater on red-sands than black-cotton. However, we caution that Experiment 1 offers little support for this mechanism, as sapling performance was essentially equivalent across soil types (Figs. 2, 3, Table 2). Moreover, while there is an intuitive reason why tolerance should be low on black-cotton due to 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 distributions

We found greater antelope biomass and megaherbivore dung density on red-sands (Appendix S1: Fig. S5), along with greater mean browse scores (Fig. 3a, 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. 6). Such a 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), but our data are only correlative and this "feedback" hypothesis awaits rigorous testing in future work.

CONCLUSIONS

We show that browsers enforce the segregation of savanna tree species across soil types, and we 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 (Table 1, Fig. 6). 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 that there is no "good" soil type in this system, but rather two that challenge plants 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 can 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 large-scale properties of savannas. Such interactions may often be cryptic and hence overlooked or misinterpreted in continental-scale studies, underscoring the importance of manipulative field experiments as a complement to observational, modeling, and remote-sensing approaches. It would be profitable to revisit potential filters on seedling survival that might contribute to the observed pattern of edaphic specialization: Although Okello and Young (2000) found no effect of soil type on initial survival of ACDR seedlings in a greenhouse study, repeating these experiments with multiple tree species under water-limited field conditions would help establish the importance of soil-type-specific filters at all ontogenetic stages. Also informative would be to survey ACDR and ACBR seedlings in the soil types where they do not occur as adults—if they are common, it may be fair to conclude that soil × herbivory interactions on saplings and post-saplings is the principal mechanism of edaphic specialization, whereas their rarity would underscore the need to search for additional seed- and seedling-stage filters.

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 (Kartzinel et al. 2015) and suppressed by large herbivores (Goheen and Palmer 2010, Ford et al. 2015). If elephants and other large herbivores disappear from this system, we predict that many of the dominant plant species on each soil type will eventually 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.

Acknowledgments

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.1522/suppinfo

Appendix S1

Supporting information for

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

Robert M. Pringle, Kirsten M. Prior, Todd M. Palmer, Truman P. Young, Jacob R. Goheen

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Table S1 – Complete list of models and AIC_c values for sapling reciprocal transplant experiment (Experiment 1)

Figure S1 – Schematic of experimental design for sapling reciprocal-transplant study (Experiment 1)

Figure S2 – Densities of *Acacia brevispica* (ACBR) within long-term large-herbivore exclosures ~~on both soil types~~

Figure S3 – Photograph of a reproductive adult *Acacia brevispica* (ACBR) inside the KLEE exclosures on black-cotton soil

Figure S4 – Photographs of ant-transplant experiment with *Acacia drepanolobium* (ACDR) saplings on red-sands

Figure S5 – Large-herbivore abundance across soil types~~.~~

Table S1. Full list of models, their AIC_c and ΔAIC_c values, and rank within the candidate set for each response in Experiment 1.

	survival			**height**			**basal diameter**			**browse score**			**spine length**			**domatium number**		
Acacia drepanolobium	**AIC_c**	**rank**	**Δ**	**AIC_c**	**rank**	**Δ**	**AIC_c**	**rank**	**Δ**	**AIC_c**	**rank**	**Δ**	**AIC_c**	**rank**	**Δ**	**AIC_c**	**rank**	**Δ**
(Soil × Herbivory × Resources)	360.82	11	6.64	**★996.20**	**1**	**0**	533.07	18	5.93	**153.08**	**6**	**1.76**	536.50	13	7.19	865.59	15	4.91
(Soil × Herbiv.)+ (Herbiv. × Resour.) + (Soil × Resour.)	358.68	10	4.51	998.48	3	2.28	531.47	13	4.33	**151.90**	**2**	**0.58**	535.63	12	6.32	863.38	9	2.70
(Soil × Herbivory) + (Herbivory × Resources)	357.53	8	3.36	1003.72	13	7.52	529.30	6	2.16	**★151.32**	**1**	**0**	536.86	14	7.55	**862.30**	**4**	**1.62**
(Soil × Herbivory) + (Soil × Resources)	356.49	6	2.32	**997.48**	**2**	**1.28**	529.28	5	2.14	153.67	9	2.35	533.54	8	4.23	867.54	19	6.86
(Soil×Resources) + (Herbivory×Resources)	358.13	9	3.96	1000.79	6	4.59	533.15	19	6.01	155.71	13	4.39	533.51	7	4.20	**861.62**	**3**	**0.94**
(Soil×Herbivory) + Resources	**355.38**	**4**	**1.21**	1001.86	9	5.66	**★527.14**	**1**	**0**	**152.26**	**4**	**0.94**	535.09	11	5.78	865.69	16	5.01
Soil + (Herbivory × Resources)	357.03	7	2.86	1005.04	14	8.84	531.09	12	3.95	154.64	11	3.32	534.86	10	5.55	**★860.68**	**1**	**0**
(Soil × Resources) + Herbivory	**356.00**	**5**	**1.83**	999.42	4	3.22	531.04	11	3.90	156.42	14	5.10	531.44	4	2.13	866.16	17	5.48
Soil + Herbivory + Resources	**354.91**	**3**	**0.74**	1003.07	12	6.87	**528.98**	**3**	**1.84**	154.80	12	3.48	533.09	6	3.78	864.41	11	3.73
(Soil × Herbivory)	**354.66**	**2**	**0.48**	1001.31	8	5.11	**527.67**	**2**	**0.53**	**152.04**	**3**	**0.72**	533.59	9	4.28	864.05	10	3.37
(Soil × Resources)	386.39	17	32.21	1011.98	16	15.78	532.49	15	5.35	327.39	19	176.07	**★529.31**	**1**	**0**	864.90	14	4.22
(Herbivory × Resources)	369.52	14	15.34	1002.97	11	6.77	532.41	14	5.27	153.41	7	2.09	542.86	19	13.55	863.18	8	2.50
Soil + Herbivory	**★354.17**	**1**	**0.00**	1002.27	10	6.07	**529.03**	**4**	**1.89**	154.20	10	2.88	531.64	5	2.33	862.72	5	2.04
Soil + Resources	385.08	16	30.91	1014.22	19	18.02	530.53	9	3.39	325.31	18	173.99	**531.01**	**3**	**1.70**	863.11	7	2.43
Herbivory + Resources	367.41	13	13.24	1001.02	7	4.82	530.32	7	3.18	153.48	8	2.16	540.97	18	11.66	866.22	18	5.54
Soil	383.90	15	29.73	1013.12	18	16.92	530.36	8	3.22	323.33	16	172.01	**529.61**	**2**	**0.30**	**861.48**	**2**	**0.80**
Herbivory	366.26	12	12.08	1000.22	5	4.02	530.54	10	3.40	**152.81**	**5**	**1.49**	539.61	17	10.30	864.71	13	4.03
Resources	396.78	19	42.61	1012.29	17	16.09	532.73	17	5.59	324.65	17	173.33	539.02	16	9.71	864.43	12	3.75
Intercept	395.48	18	41.31	1011.26	15	15.06	532.71	16	5.57	322.73	15	171.41	537.72	15	8.41	862.96	6	2.28
Acacia brevispica																		
(Soil × Herbivory × Resources)				1213.69	14	10.76	543.10	14	8.67	191.01	8	4.58						
(Soil × Herbiv.)+ (Herbiv. × Resour.) + (Soil × Resour.)				1211.48	13	8.55	540.90	12	6.47	189.48	5	3.06						
(Soil × Herbivory) + (Herbivory × Resources)				1209.81	11	6.88	539.30	11	4.88	**187.85**	**3**	**1.42**						
(Soil × Herbivory) + (Soil × Resources)				1209.37	10	6.44	538.75	9	4.32	189.21	4	2.78						
(Soil×Resources) + (Herbivory×Resources)				1210.60	12	7.67	538.71	8	4.29	193.61	14	7.18						
(Soil×Herbivory) + Resources				1207.74	7	4.80	537.19	6	2.76	**187.55**	**2**	**1.12**						
Soil + (Herbivory × Resources)				1208.86	9	5.93	537.15	5	2.72	191.76	12	5.33						
(Soil × Resources) + Herbivory				1208.52	8	5.59	536.59	4	2.16	193.12	13	6.69						
Soil + Herbivory + Resources				1206.82	5	3.89	**535.06**	**2**	**0.63**	191.27	10	4.84						
(Soil × Herbivory)				1205.62	4	2.69	541.31	13	6.89	**★186.43**	**1**	**0**						
(Soil × Resources)	162.51	4	2.93	1263.77	19	60.84	560.72	19	26.30	423.72	19	237.29						
(Herbivory × Resources)				1207.00	6	4.07	536.49	3	2.07	191.63	11	5.20						
Soil + Herbivory				**1204.73**	**2**	**1.80**	539.21	10	4.79	190.04	7	3.61						
Soil + Resources	**160.72**	**2**	**1.13**	1261.84	18	58.91	558.98	16	24.56	421.62	18	235.19						
Herbivory + Resources				1205.00	3	2.06	**★534.43**	**1**	**0**	191.14	9	4.71						
Soil	163.59	5	4.01	1259.85	16	56.91	560.59	18	26.17	419.60	16	233.17						
Herbivory				**★1202.93**	**1**	**0**	538.66	7	4.24	189.92	6	3.49						
Resources	**★159.58**	**1**	**0**	1259.87	17	56.94	558.47	15	24.04	420.13	17	233.70						
Intercept	162.48	3	2.90	1257.90	15	54.97	560.14	17	25.71	418.14	15	231.71						

Notes: Symbols and terminology follow Burnham & Anderson 2002. Models are listed in order of decreasing complexity; parentheses indicate all main effects and interactions of enclosed terms. For each response, ★ indicates the single best model; all models with $\Delta\text{AIC}_c < 2$ (per Table 2) are shaded gray. Caged ACBR had 100% survival, so we did not fit models including herbivore exclusion.

Figure S1

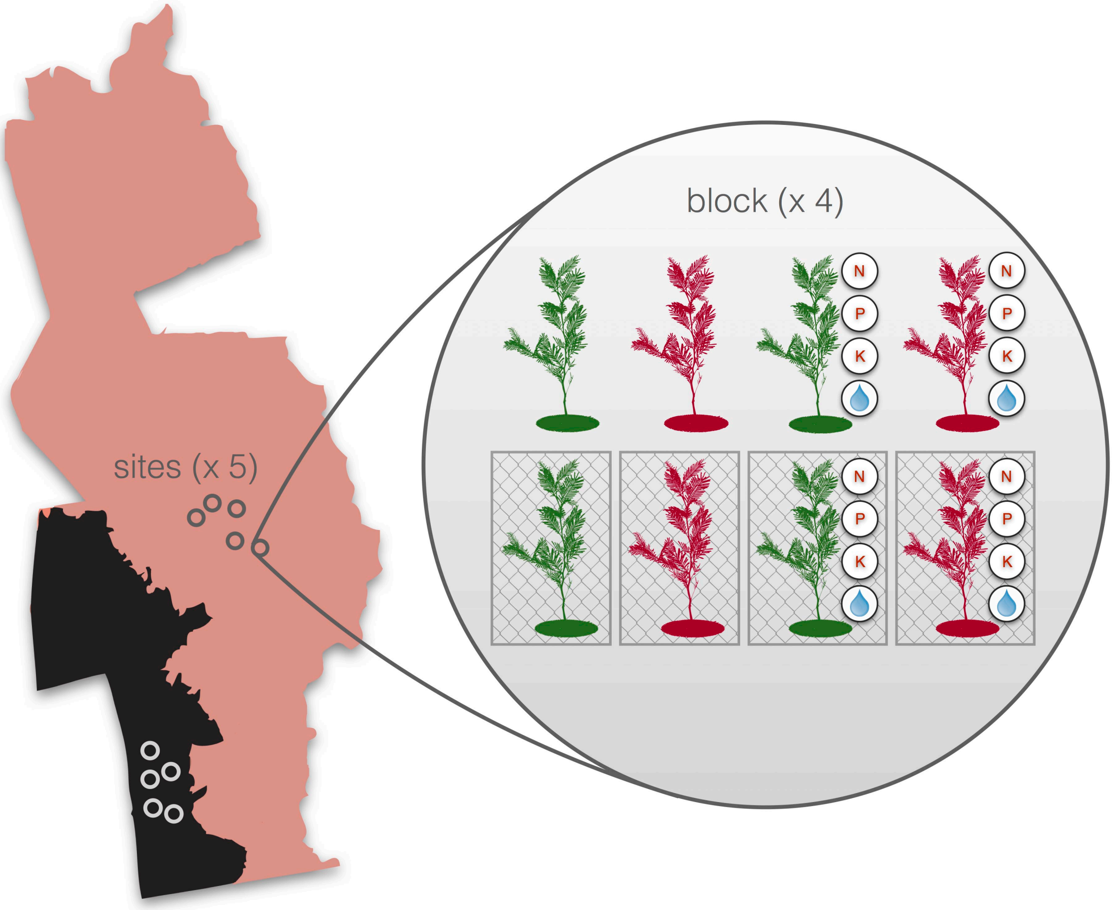

Fig. S1. Schematic of reciprocal-transplant design (Experiment 1). Five sites were situated haphazardly on both red-sands and black-cotton soils within the 20,000-ha Mpala Conservancy (see also Fig. 1). Each site contained four replicate blocks of saplings. Each block contained one sapling of each species (e.g., green = ACDR and red = ACBR) planted under all four factorial combinations of herbivore exclusion (bottom row) and resource addition (NPK fertilizer + water).

Figure S2

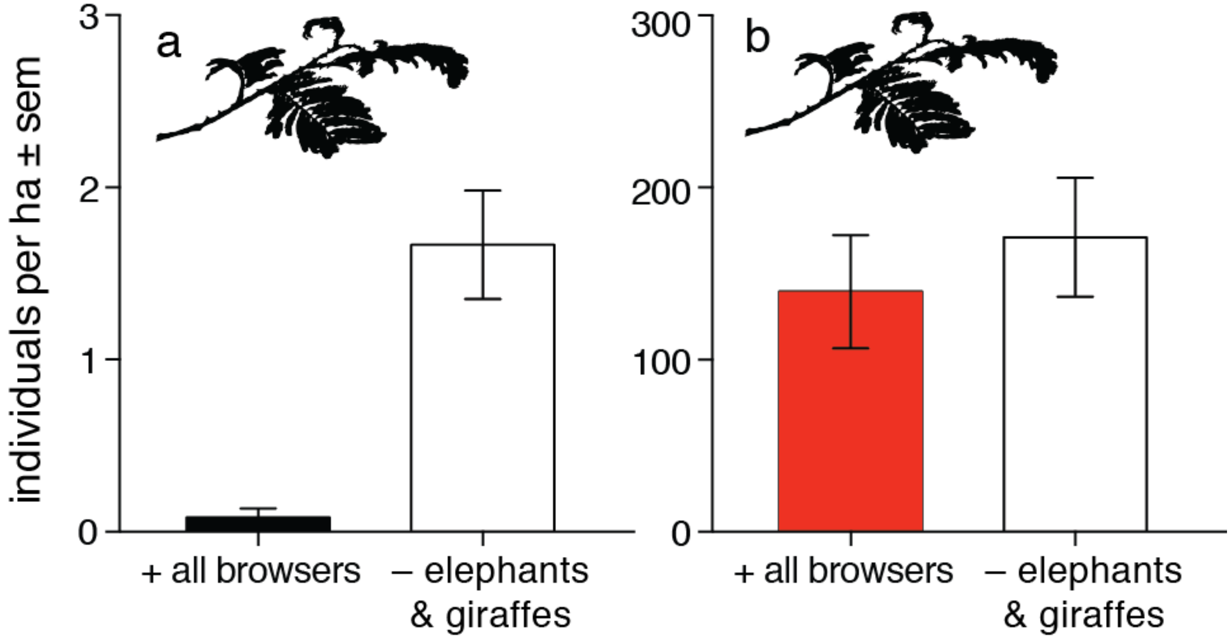

Fig. S2. Densities of *Acacia brevispica* (ACBR) within long-term exclosures on both soil types in Experiment 2. **(a)** Densities of ACBR on black-cotton soil in the presence of all browsing mammal species (black bar) and in four-hectare plots from which megaherbivores (i.e., only elephants and giraffes) had been excluded for 16 years (white bar) in the Kenya Long-term Exclosure Experiment (Young et al. 1998). **(b)** Densities of ACBR on red-sands soil in the presence of all browsing mammal species (red bar) and in one-hectare plots where had been excluded for 7 years (white bar) in the UHURU experiment (Goheen et al. 2013). The KLEE and UHURU experiments use nearly identical fencing configurations to exclude megaherbivores (electrified wires at 2-m above ground level). On black-cotton soil, ACBR densities were 20-fold greater in the absence of megaherbivores; on red-sands, ACBR densities are several orders of magnitude higher than on black-cotton in the presence of megaherbivores, but did not increase significantly following their exclusion.

Figure S3

Fig. S3. This robust adult *Acacia brevispica* (ACBR) in black-cotton soil, located within a fenced large-herbivore exclusion plot the Kenya Long-term Exclosure Experiment (KLEE), illustrates the ability of this species to recruit to adulthood and produce both flowers and seeds on black-cotton soil. Thriving mature plants like this one are not observed in black-cotton soil at the Mpala Conservancy in areas where browsers are present. This individual was photographed in 2014.

Figure S4

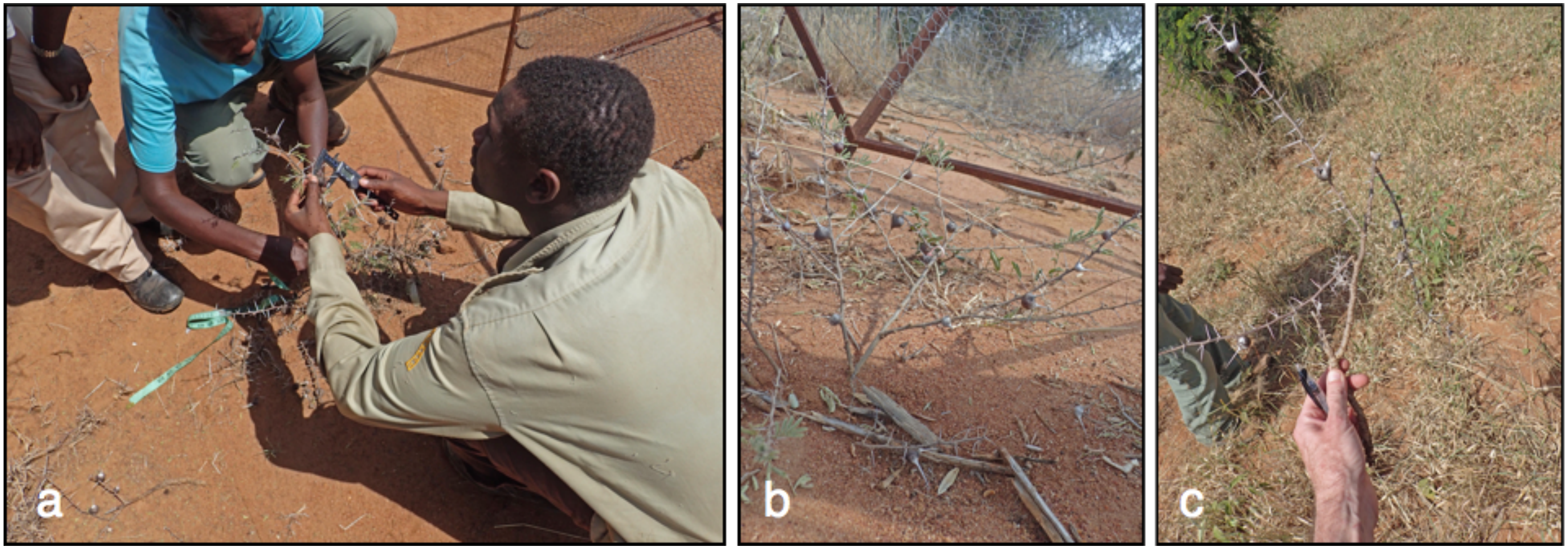

Figure S4. Ant-transplant experiment with *Acacia drepanolobium* (ACDR) saplings on red-sands (Experiment 3). **(a)** From left to right: Ali Hassan, John Lemboi, and Sam Kurukura measure one of the –herbivory +ants ACDR saplings on red-soil. Kurukura is measuring the dimensions of swollen-thorn ant domatiua; symbiotic *Crematogaster nigriceps* ants can be seen attacking his thumb. The herbivore-exclusion cage has been laid to one side to enable measurement. **(b)** One of the caged ACDR saplings in the treatment with no ants added. **(c)** Remains of an uncaged sapling that had been plucked and discarded several meters away by an elephant.

Figure S5

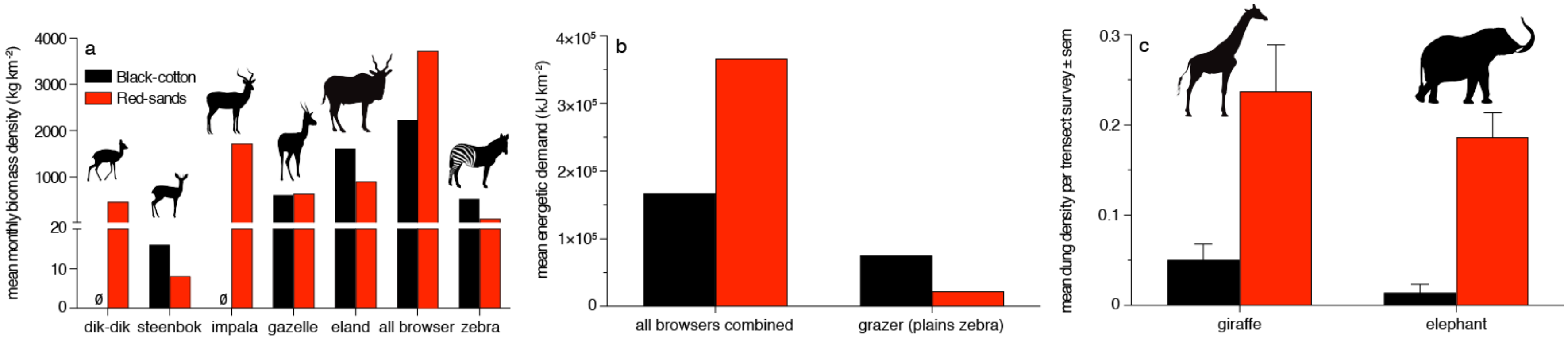

Fig. S5. (a) Mean biomass densities of five browsing antelope (individually and combined) and a grazer, plains zebra, across 11 monthly distance-sampling surveys. **(b)** Total energetic demand for browsers and grazers, calculated from the distance-sampling data. **(c)** Mean dung densities of browsing megaherbivores across 11 surveys of transects spanning each block of Experiment 1.

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