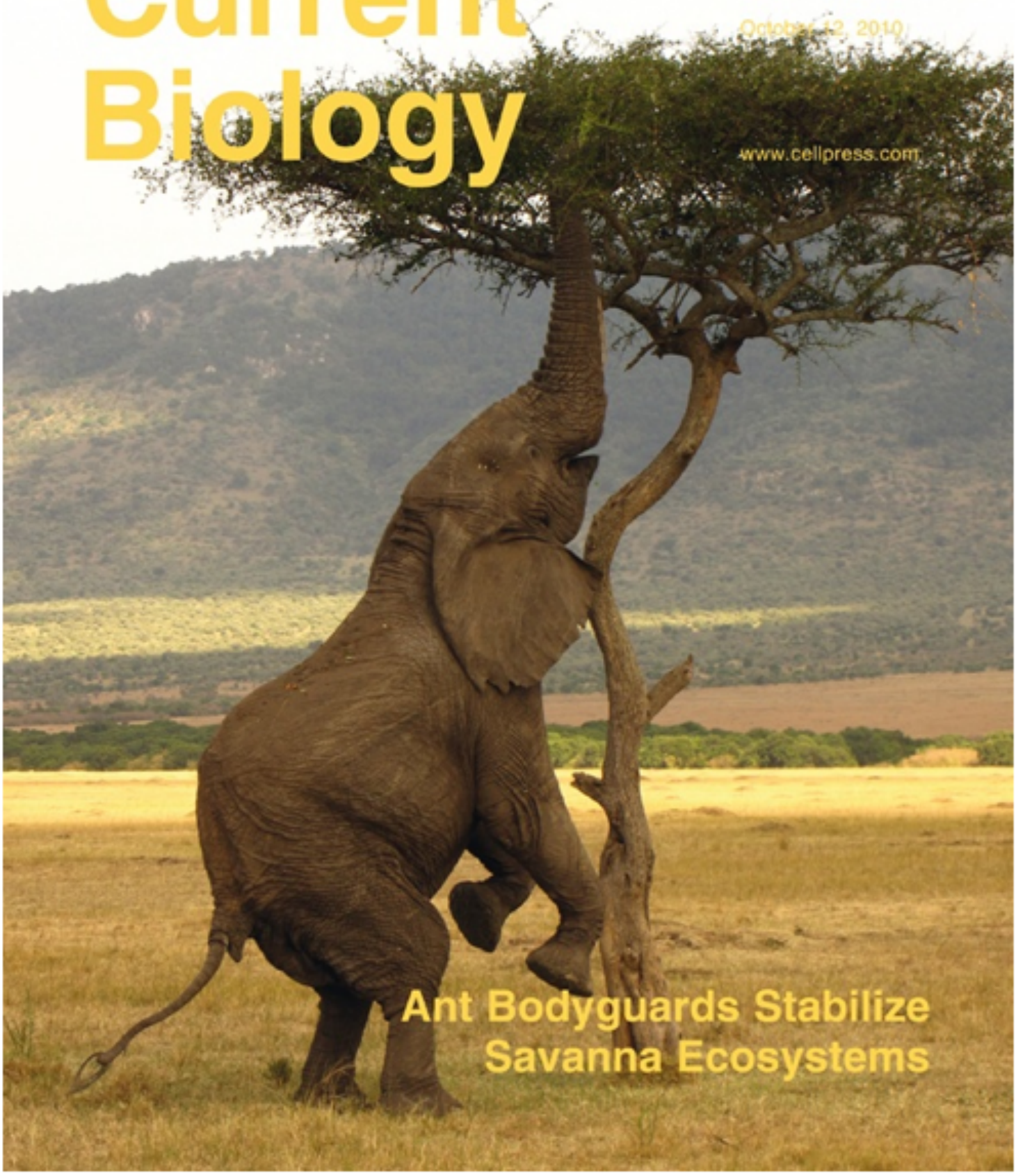
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Ant Bodyguards Stabilize Savanna Ecosystems

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Report

Defensive Plant-Ants Stabilize Megaherbivore-Driven Landscape Change in an African Savanna

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Summary

Tree cover in savanna ecosystems is usually regarded as unstable, varying with rainfall, fire, and herbivory [1–4]. In sub-Saharan Africa, elephants (*Loxodonta africana*) suppress tree cover, thereby maintaining landscape heterogeneity by promoting tree-grass coexistence. In the absence of elephants, tree encroachment may convert savannas into closed-canopy woodlands [5, 6]; when elephants increase in abundance, intensified browsing pressure can transform savannas into open grasslands [5–8]. We show that symbiotic ants stabilize tree cover across landscapes in Kenya by protecting a dominant tree from elephants. In feeding trials, elephants avoided plants with ants and did not distinguish between a myrmecophyte (the whistling-thorn tree [*Acacia drepanolobium*]) from which ants had been removed and a highly palatable, nonmyrmecophytic congener. In field experiments, elephants inflicted severe damage on whistling-thorn trees from which ants had been removed. Across two properties on which elephants increased between 2003 and 2008, cover of whistling-thorn did not change significantly inside versus outside large-scale elephant exclusion fences; over the same period of time, cover of nonmyrmecophytes differed profoundly inside versus outside exclusion fences. These results highlight the powerful role that symbioses and plant defense play in driving tree growth and survival in savannas, ecosystems of global economic and ecological importance.

Results and Discussion

Within African savannas, elephants are powerful drivers of landscape-level habitat heterogeneity, capable of inflicting intensive and extensive damage to woody plants [4–8]. Trees and shrubs employ various mechanisms to reduce such catastrophic herbivory, including vigorous resprouting of broken stems, the development of heavy buttresses, growth to large sizes, and the production of a variety of chemical and spinescent defenses that may reduce palatability [9]. In African savanna ecosystems, including the Laikipia plateau in central Kenya, many trees in the widespread genus *Acacia* are defended with spines and digestibility-reducing secondary compounds (tannins). Despite such defenses, these plants often suffer intense bouts of elephant herbivory that may severely damage or kill mature trees (Figure 1). In striking contrast, a co-occurring congener defended by ant bodyguards (*Acacia drepanolobium*) is seldom browsed by elephants and occurs in dense near-monocultures (800–1100 individuals/hectare) throughout many portions of its range [10–13]. We hypothesized that the protective ant symbionts of *A. drepanolobium* serve as an effective defense against elephant herbivory and thus play a strong role in buffering this species from fluctuations in abundance in the face of variation in elephant numbers.

We investigated the role of symbiotic ants in determining levels of tree cover following manipulated and natural changes in numbers of large mammalian herbivores in central Kenya. Our study sites in Laikipia, Kenya (see Figure S1 available online) are underlain by one of two well-defined soil types: black clayey vertisols of volcanic origin (hereafter "clayey soils"), comprising ~35% of Laikipia, and red sandy aridosols derived from quartzite (hereafter "sandy soils"), comprising the remaining 65% of Laikipia [14]. Although elephant abundances are similar between clayey and sandy soils [15], each soil type harbors a distinctive community of woody plants. On clayey soils, *A. drepanolobium* occurs in virtual monoculture, typically accounting for $\geq$95% of the overstory vegetation [16]. *Acacia drepanolobium* is a myrmecophyte (ant-plant), providing both housing (swollen thorn domatia) and food (extrafloral nectar) for symbiotic ants. Four species of ants (*Crematogaster mimosae*, *C. nigriceps*, *C. sjostedti*, and *Tetraponera penzigi*) compete for exclusive access to host plants and protect host trees (to varying degrees) by swarming, biting, and stinging intruders [17]. Tree communities occurring on sandy soils are more diverse, with the 3–5 most common woody plant species typically accounting for no more than 80% of the canopy in a given locale. *Acacia drepanolobium* is virtually absent from sandy soils, constituting <0.1% of the overstory.

Between 1992 and 2002, elephant abundances throughout the Laikipia ecosystem increased approximately 5-fold [18] (P. Omondi, personal communication) and continued to increase over the course of our study (unpublished data; W. Giesen, personal communication; Figure S2]. To assess the impact of increased elephant densities on tree assemblages, we quantified changes in tree cover both inside and outside of plots excluding megaherbivores (elephants and less-common giraffe [*Giraffa camelopardalis*]) on sandy and clayey soils at the Lewa Wildlife Conservancy in central Kenya (37°41′E, 0°2′N, Figure S1). Changes in tree cover were determined by comparing high-resolution (60 cm) Quickbird satellite images (Digital Globe) acquired in 2003 and 2008. Between 1992 and 2002, six double-strand, electrified fences were erected on Lewa to exclude megaherbivores from parcels of land while allowing other wildlife species to freely pass beneath the 2 m high fence strands. Four fences were established in sandy soil, and two fences were established in clayey soil (Table S1). Hereafter, we refer to megaherbivore exclosures as elephant exclosures, because elephants (and not giraffes) were responsible for the vast majority of differences arising from megaherbivore browsing on both clayey and sandy soils (Tables S2 and S3). Control plots paired with

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Figure 1. Elephant Herbivory on *Acacia* spp.

Recent catastrophic herbivory by elephants on the nonmyrmecophyte *Acacia mellifera* (foreground) surrounded by unbrowsed individuals of the myrmecophyte *A. drepanolobium*.

elephant exclosures were sampled from 200 m wide buffer strips around each exclosure (see "Satellite Imagery and Aerial Photos" in Experimental Procedures).

To increase our sample sizes within clayey soil habitats, we further quantified changes in tree cover at the Kenya Long-term Exclusion Experiment (KLEE) at the Mpala Research Centre in central Kenya (36°52′E, 0°17′N, Figure S1) using a single Quickbird satellite image from June 2003 (Digital Globe) and a high-resolution (30 cm) aerial photograph (Ramani Communications) from December 2007. Established in 1995, KLEE consists of three replicate blocks, each of which contains two plots accessible to all wildlife, two plots accessible to all wildlife except megaherbivores, and two plots from which all wildlife are excluded. KLEE occurs entirely on clayey soil.

Between 2003 and 2008, tree cover diverged significantly between elephant exclosures and control plots on sandy soil at Lewa ($F_{1,6}$ = 9.27, p = 0.02). Absolute tree cover increased by 6.0% in response to elephant exclusion (from 25.3% in 2003 to 31.3% in 2008; Figure 2) while simultaneously decreasing by 8.3% within control plots (from 24.7% in 2003 to 16.6% in 2008; Figure 2). The decline in tree cover in control plots coincided with an ~2.5-fold increase in elephant densities at Lewa (Figure S2). In 2003, tree cover within elephant exclosures and control plots on clayey soils did not differ between Lewa and KLEE, nor did change in tree cover between 2003 and 2008 differ significantly between Lewa and KLEE (see "Analysis of Remotely-Sensed Imagery" in Supplemental Experimental Procedures). Thus, we pooled sites in our analysis for tree cover within elephant exclosures on clayey soils. Between 2003 and 2008 (2007 at KLEE), tree cover did not change significantly between elephant exclosures and control plots on *A. drepanolobium*-dominated clayey soil at Lewa and KLEE (exclosures: 26.5%–23.9%; controls: 22.5%–22.8%; $F_{1,8}$ = 0.90, p = 0.37; Figure 2), nor did the change in tree cover inside versus outside elephant exclosures differ significantly from zero, despite increasing elephant numbers on both Lewa and Mpala (Figure S2).

To explore whether differential change in tree cover was due to ants or other factors associated with sandy versus clayey soils, we conducted ground surveys for the incidence of browse on clayey soils. Ground surveys revealed that elephants preferred to browse on nonmyrmecophytes (Tables S2 and S3), thereby reducing tree cover of subordinate (i.e., nonmyrmecophytic) woody plant species (multivariate analysis of variance [MANOVA] for megaherbivore effect on subordinate species: Wilks' $\lambda_{9,4}$ = 0.003, p < 0.0001; p < 0.01 for univariate F tests on five most abundant nonmyrmecophytes; Figure 3). Further, and consistent with analysis of remotely sensed data, ground surveys confirmed relatively low levels of browsing on *A. drepanolobium* by elephants (Tables S2 and S3) and nonsignificant impacts of elephants on tree cover of *A. drepanolobium* (p = 0.27; Figure 3). Other (nonelephant) browsers reduced cover of a single subordinate species (*Rhus natalensis*; Wilks' $\lambda_{9,4}$ = 0.05, p = 0.03; univariate F test for *R. natalensis*: p = 0.01).

To directly establish whether plant defense by *Acacia* ants influenced elephant browsing of host *A. drepanolobium* trees, we conducted a 12 month in situ ant removal experiment 2.5 km east of KLEE. We reduced ant abundances on host plants by removing approximately 100%, 60%, or 30% of existing colony members on individual trees, and then we assessed levels of elephant damage on these trees relative to unmanipulated plants after a 1 year period. The level of

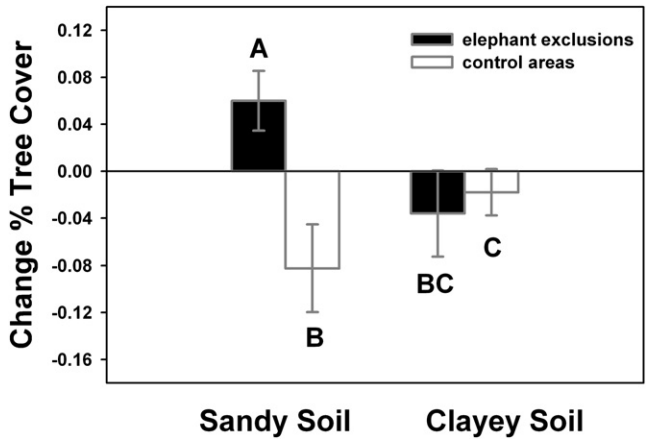


Figure 2. Landscape Change on Lewa Downs Conservancy and Mpala

Change in tree cover in elephant exclusions (black bars) and paired controls (white bars), 2003–2008. Virtually all trees on sandy soil are nonmyrmecophytes; ~95% of trees on clayey soil are the myrmecophyte *A. drepanolobium*. Means (±95% confidence intervals) from sandy soil represent averages across four exclusion plots and their paired controls from Lewa. Means from clayey soil represent averages across six exclusion plots and their paired controls at KLEE and two exclusion plots and their paired controls at Lewa. Letters associated with bars represent statistically significant differences between groups (p < 0.05).

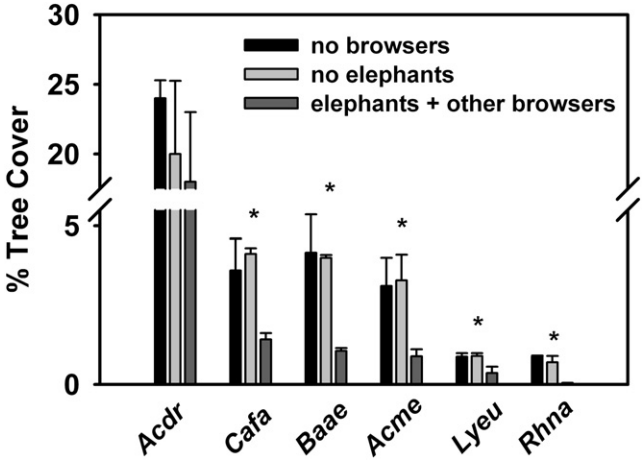


Figure 3. Differences in Tree Cover as a Function of Herbivore Treatment

Percent tree cover of the myrmecophyte *A. drepanolobium* (Acdr) and nonmyrmecophytes *Cadaba farinosa* (Cafa), *Balanites aegyptiaca* (Baae), *A. mellifera* (Acme), *Lycium europaeum* (Lyeu), and *Rhus natalensis* (Rhna) by herbivore treatment at KLEE in 2008. Black bars (±standard error of the mean) represent plots from which all browsers have been excluded, light gray bars represent plots from which only elephants have been excluded, and dark gray bars represent plots accessible to all browsers. *$p < 0.01$ is statistically significant between plots.

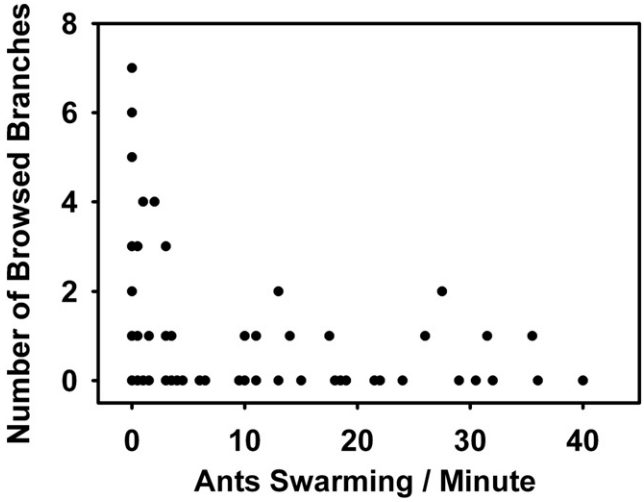


Figure 4. Responses of Elephant Browsing to In Situ Ant Removal from Trees

The number of *A. drepanolobium* branches browsed by elephants as a function of ant activity levels on trees from the ant-removal experiment ($\chi^2_1 = 28.41$, $p < 0.01$).

elephant browsing on host plants was significantly and negatively related to ant abundances on host plants (negative binomial regression: $\chi^2_1 = 28.41$, $p < 0.01$; Figure 4).

To further investigate whether protection by ant symbionts was the causal mechanism underlying observed patterns of landscape change, we conducted free-choice feeding trials on six 8-year-old elephants at the Sheldrick Wildlife Trust Reintegration Centre in Tsavo National Park, Kenya. We presented elephants with four groups comprised of ~20 1.5–2 m branches: (1) *Acacia drepanolobium* control, (2) *A. drepanolobium* ant removal, (3) *A. mellifera* control, and (4) *A. mellifera* ant addition. Browse surveys on sandy soils from Lewa demonstrated that elephants neither prefer nor avoid *A. mellifera* relative to other tree species on sandy soil (Table S4); thus, *A. mellifera* represents a typical nonmyrmecophyte from the perspective of an elephant. Groups of branches were spaced 10 m apart from each other, and their position in the elephant corral was determined randomly. Elephants were equally likely to feed on *A. drepanolobium* and *A. mellifera* in the absence of ants (Cox regression: $\beta = 0.33$, $p = 0.57$), indicating that, without its ants, *A. drepanolobium* is fundamentally palatable to elephants. Similarly, elephants avoided branches of both tree species if ants were present (Cox regression: $\beta = 3.61$, $p < 0.01$), demonstrating that symbiotic ants can deter elephant herbivory when alternative food plants are available (Figure 5).

Elephants are known to avoid swarming attack by other hymenopterans (bees [19]). The efficacy of ant defense may result from a combination of high densities of ants on host plants (up to 90,000 workers on some trees [20]), the species of ant occupant (*C. mimosae* and *C. nigriceps* swarm equally aggressively in response to disturbance [21] and occupy ~70% and 80% of trees at KLEE [22] and Lewa ["Lewa Browse Surveys" in Supplemental Experimental Procedures]), and the tendency of ants to attack areas of thin skin and mucous membranes by biting down and holding fast with their mandibles. Further, elephants are unique in that their nostrils are located away from their mouths at the apex of their feeding apparatus (trunk), rendering them vulnerable to swarming insects. In contrast, giraffes use their long, prehensile tongues to swipe away ants from their muzzles (unpublished data). Thus, despite their thick dermis, elephants are highly sensitive

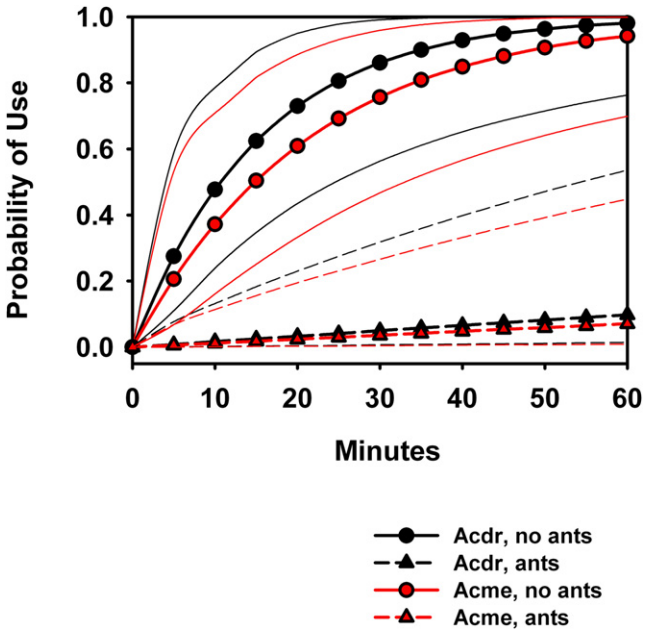


Figure 5. Free-Choice Feeding Trials with Elephants and *Acacia* spp.

Best-fitting Cox regression models as a function of food type: control *A. drepanolobium* (black triangles), ant-removal *A. drepanolobium* (black circles), control *A. mellifera* (red circles), ant-addition *A. mellifera* (red triangles). Solid and dashed thin lines represent 95% confidence intervals for probability of use of branches with and without ants, respectively. Elephants preferred branches without ants ($\beta = 3.61$, $p < 0.01$) but did not distinguish between tree species ($\beta = 0.33$, $p = 0.57$). The points in the graph are fitted from the model.

around their eyes and on the inner membranes of their trunks [23]; attack by scores of biting ants probably serves as a strong deterrent.

Classic experiments by Janzen [24] and subsequent studies by others [25–28] have elegantly demonstrated the capacity of symbiotic ants to prevent or greatly reduce herbivory and competition for light, thereby promoting the growth and survival of individual host plants. Ours is the first study to demonstrate that ant-plant symbioses can stabilize landscape structure at larger spatial scales by protecting adult trees from catastrophic herbivory. Because ants reduce palatability of their host trees, selective browsing on nonmyrmecophytes is at least partly responsible for creating the virtual monocultures of *A. drepanolobium* that typify black clayey soils in Laikipia [27, 29] and other regions of East Africa [10–13, 28]. A major challenge for the future is elucidating why *A. drepanolobium* is restricted to clayey vertisols, such that a diversity of nonmyrmecophytes thrives on other soil types. We hypothesize that characteristics of sandy soils (e.g., particle size, nutrient content, infiltration, etc.) favor nonmyrmecophytes and interact strongly with browsing to promote segregation of trees (*A. drepanolobium* and other myrmecophytes versus nonmyrmecophytes) across soil types (e.g., see [30]). In light of this, we expect that, on clayey soils, other determinants of savanna structure (i.e., rainfall and fire) or mortality factors affecting early life stages of trees (e.g., seeds, seedlings) will override browsing as drivers of tree populations, where plant defenses nullify elephants as important agents of mortality on adult trees [31].

Savannas typically are envisaged as unstable or disequilibrial systems in which climatic variability or disturbances generate the tree-grass mixtures that typify these ecosystems [1–3]. In Africa, browsing and killing of trees by elephants is often a critical force underlying the coexistence of trees and grasses [4–8]. Throughout much of their historic range, however, declines in elephant populations have triggered extensive increases in tree numbers, shifting open savannas to closed-canopy woodlands [8]. Elsewhere, and typically in response to confinement within protected areas, elephants have become "compressed," have overexploited trees, and have shifted savannas toward structurally simplified grasslands [8, 32]. Our study highlights the stabilizing effect that ant symbionts can confer on tree cover over expansive spatial scales. In sum, our experiments show that ant symbionts protect against catastrophic herbivory, effectively buffering a dominant tree against top-down control by megaherbivores. Because tree cover strongly regulates a host of ecosystem processes, including carbon storage, fire-return intervals, food web dynamics, nutrient cycling, and soil-water relations in our system [33, 34] and others [35, 36], these tiny bodyguards likely exert powerful indirect effects at very large spatial and temporal scales. As elephants and other large mammals in Africa exhibit chronic declines in some habitats and overabundance in others, identifying the ecological consequences of such landscape change remains an important challenge for wildlife managers in the future.

Experimental Procedures

Satellite Imagery and Aerial Photos

At Lewa, control plots paired with elephant exclosures were sampled from 200 m wide buffer strips around each exclosure, subject to the constraint that the buffer strip occurred entirely within Lewa boundaries. When an elephant exclosure abutted a neighboring property, we expanded the width of buffer strips to compensate for the area not sampled in that property. At KLEE, elephant exclosures consisted of the central hectare (ha) within each 4 ha fence.

KLEE Browse Surveys

From July 2007 to September 2007 at KLEE, we recorded canopy breadth, height, and diameter at breast height (DBH) on all individuals of the subordinate woody species (i.e., nonmyrmecophytes; n = 721). We paired each of the 721 individual trees with the nearest neighboring *A. drepanolobium*, subject to the constraint that the diameter of the *A. drepanolobium* was within 5 cm of the subordinate individual with which it was paired, and we recorded canopy breadth, height, DBH, and incidence of browsing. We used MANOVA to test for the effects of megaherbivores, wildlife, and cattle on percent tree cover of *A. drepanolobium* and the five most common, subordinate woody species: *A. mellifera*, *Balanites aegyptiaca*, *Cadaba farinosa*, *Lycium europaeum*, and *Rhus natalensis*. In addition, we included replicate as a fixed effect (random effects are extremely difficult to implement and interpret in MANOVA) in our analysis, because tree cover at KLEE increases from north to south. For each individual in the six plots accessible to megaherbivores (n = 332), we recorded the incidence of browsing by megaherbivores (elephant and giraffe). We ignored elephant browsing >1 year old, as evidenced by chalky, dull-colored wood. We used log-linear models to calculate odds ratios of browse by elephant and giraffe on each of the five most common nonmyrmecophytes (Table S3).

Ant-Removal Experiment

We removed ant colonies from host plants by inundating the host plant with smoke generated by burning dry grass in a bucket underneath the tree. *Crematogaster mimosae* displays an evacuation behavior when inundated by the smoke from burning grass, in which workers carry the majority of brood, eggs, pupae, winged reproductives, and queens from swollen thorn domatia into cracks in the soil at the base of the host plant over the course of 45–60 min. During smoke inundation, we made a rough approximation of the total number of workers on each tree. We then imposed treatments immediately following smoke inundation, either completely barring ants from recolonizing trees by applying a Tanglefoot sticky barrier at the base of the host plant (full ant removal) or allowing approximately 1/3, 2/3, or the entire colony to recolonize the host plant prior to applying a Tanglefoot barrier (for the 2/3 removal, 1/3 removal, and control treatments, respectively). On control trees, two small (6 cm) dead branches were wired to trees across the sticky barrier to allow ants to move freely across the sticky barrier.

Following the imposition of treatments, we then assayed trees for relative levels of ant defense at 6 and 12 months by disturbing a randomly chosen swollen thorn on each of two branches per tree (one in each of the north and south cardinal directions) and counting the number of workers swarming onto the tip of the uppermost spine of the disturbed swollen thorn over a 30 s period. Two researchers conducted these assays so that swollen thorns on two separate branches could be disturbed simultaneously. Overall levels of ant activity on trees were calculated as the average of these activity assays. Ant activity at 12 months was significantly correlated with ant activity at 6 months ($r = 0.64$, $p < 0.0001$), and our treatments were effective in generating a range of ant activities (Table S5). We then resurveyed each tree at the end of 12 months for browse damage inflicted by both elephants and nonelephant browsers.

Free-Choice Feeding Trials

We cut 1.5–2.0 m branches of *A. drepanolobium* and *A. mellifera* from trees at the periphery of Tsavo National Park near the town of Voi. At the time of collection, all *A. drepanolobium* in our feeding trials were inhabited by the ant *C. nigriceps*. We removed ants and swollen thorns from *A. drepanolobium* with wire cutters. Branches were transported to the holding corral and were presented to elephants within 2 hr of collection. Ants were added to *A. mellifera* by immersing branches for 5 min in a metal drum into which the ants and swollen thorns from the ant removal branches had been collected. A single observer, positioned ~20 m from groups of branches, recorded data on the number, type, and order of foods taken over a 1 hr period. Groups of branches were randomly placed 10 m apart within 10 m of the entrance of the holding corral.

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures, two figures, and five tables and can be found with this article online at doi:10.1016/j.cub.2010.08.015.

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