

# Synergy of multiple partners, including freeloaders, increases host fitness in a multispecies mutualism

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**Understanding cooperation is a central challenge in biology, because natural selection should favor “free-loaders” that reap benefits without reciprocating. For interspecific cooperation (mutualism), most approaches to this paradox focus on costs and benefits of individual partners and the strategies mutualists use to associate with beneficial partners. However, natural selection acts on lifetime fitness, and most mutualists, particularly longer-lived species interacting with shorter-lived partners (e.g., corals and zooxanthellae, tropical trees and mycorrhizae) interact with multiple partner species throughout ontogeny. Determining how multiple partnerships might interactively affect lifetime fitness is a crucial unexplored link in understanding the evolution and maintenance of cooperation. The tropical tree *Acacia drepanolobium* associates with four symbiotic ant species whose short-term individual effects range from mutualistic to parasitic. Using a long-term dataset, we show that tree fitness is enhanced by partnering sequentially with sets of different ant symbionts over the ontogeny of a tree. These sets include a “sterilization parasite” that prevents reproduction and another that reduces tree survivorship. Trees associating with partner sets that include these “parasites” enhance lifetime fitness by trading off survivorship and fecundity at different life stages. Our results demonstrate the importance of evaluating mutualism within a community context and suggest that lifespan inequalities among mutualists may help cooperation persist in the face of exploitation.**

*Acacia drepanolobium* | cooperation | plant defense | life history theory | ant-plant

Cooperative partnerships between species (mutualisms) are among the most widespread (1) and economically important (2) species interactions. Equally widespread are species that exploit these partnerships: rhizobia that use plant sugars but fail to fix nitrogen (3), cleaner fish that consume tissue but ignore ectoparasites (4), and caterpillars eat the broods of their ant defenders (5). Because natural selection should favor such freeloaders if they can reap benefits without reciprocating, the persistence of mutualisms is a central puzzle in biology (6).

Most theoretical studies of mutualism evolution have focused on strategies for deterring or excluding exploiters while rewarding good partners (e.g., refs. 6–8). These approaches generally calculate the costs and benefits of interacting with a given partner species independent of an individual’s life stage and its interactions with other partner species. In nature, however, mutualists often occur within species-rich networks (9), and longer-lived species often interact with a variety of shorter-lived partners at different stages of their lives (10–12). However, we know little about how such successive interactions might cumulatively and nonadditively influence the lifetime fitness of long-lived mutualists (13, 14). Considering such ontogenetic variability may enhance our general understanding of how species interactions evolve (15) and, for mutualisms, how cooperation persists. Because so much of the world’s biodiversity (e.g., coral-reef and tropical-forest communities) and agricultural production (many

plants and their root symbionts) rests on mutualisms (16, 17), understanding the dynamics of these relationships is of practical significance as well.

Our study focuses on a long-lived (>100 y) obligate ant plant, *Acacia drepanolobium*, and four specialized ant symbionts. In most ant–plant mutualisms, multiple ant species compete for housing and/or food provided by host plants in exchange for protecting those plants from herbivores, pathogens, or encroaching vegetation (18). In *A. drepanolobium*, as in many other ant–plant systems, the quality of services provided by individual ant associates is variable: Some species appear to exploit plants by taking up residence while providing little or no protection (19–21), and others sterilize their hosts (22–25).

*Acacia drepanolobium* is widely distributed throughout East Africa. Plants provide housing (swollen-thorn domatia) and food (extrafloral nectar) for resident ants. At our site in central Kenya, ants compete in a dominance hierarchy (*Crematogaster sjostedti* > *Crematogaster mimosae* > *Crematogaster nigriceps* > *Tetraponera penzigi*) for exclusive occupancy of host trees (26). Tradeoffs among ant species in colonization and competitive ability help maintain coexistence in this guild (27) and produce a stereotypical succession of ant occupants as trees age (28). Transitions between ant species on individual host plants are frequent, occurring on 8–10% of trees per year (26). Each ant species differs in the short-term benefits it provides and costs it imposes upon its host (Table 1). Notably, *C. mimosae* and *C. nigriceps* aggressively defend host plants from herbivores, whereas *T. penzigi* and *C. sjostedti* are moderately and weakly aggressive toward herbivores, respectively (29). Finally, both *C. sjostedti* and *C. nigriceps* appear to be “parasites” within this mutualist network: *C. sjostedti* actively facilitates attack on host plants by cerambycid beetles and is associated with high host-plant mortality (20), whereas *C. nigriceps* sterilizes host plants while in residence by destroying floral meristems throughout the canopy (23).

To determine how successive interactions with multiple ant partners cumulatively determine lifetime plant fitness, we monitored annual survival, growth, reproduction, and ant occupancy of 1,750 *Acacia drepanolobium* (0.1–6.5 m in height) over 8 y. Using this long-term dataset, we constructed demographic models of *Acacia* growth, reproduction, and survival as functions of tree size, ant identity, and size-specific ant-transition probabilities. Specifically, we asked: (i) Does the inclusion of putative “free-loader” ant

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**Table 1. Variation among ant species in benefits provided to and costs imposed on *A. drepanolobium* host plants**

Ant species	Dominance rank*	Colonization rank <sup>†</sup>	Avg. no. trees per colony (± SEM)	Host plant defense <sup>‡</sup>	Percent shoots browsed <sup>§</sup>	Sterilization of host plant?	Extrafloral nectar use <sup>¶</sup>	Beetle damage**
Cs	1	††	22.0 (4.8)	Low 1.3 (0.3)	8.0 (1.1)	No	Low 0.1 (0.1)	6.6 (1.3)
Cm	2	3	4.4 (0.3)	High 17.6 (1.7)	3.3 (0.4)	No	High 2.0 (0.4)	1.4 (1.0)
Cn	3	2	2.5 (0.2)	High 15.0 (1.5)	2.5 (0.7)	Yes	High 3.8 (0.4)	0.44 (1.2)
Tp	4	1	1.3 (0.3)	Medium 5.4 (0.7)	3.8 (0.6)	No	None	4.5 (1.1)

Note that the most competitively dominant ant species appears to be a relatively ineffective host-tree defender. Cs, *C. sjostedti*; Cm, *C. mimosae*; Cn, *C. nigriceps*; Tp, *T. penzigi*.

\*Dominance ranks for interspecific competition among mature colonies for nest sites, taken from ref. 26.

<sup>†</sup>Colonization ability ranks taken from ref. 27.

<sup>‡</sup>Numerical data shown are mean number of workers recruiting in response to simulated disturbance (± SEM), from ref. 29.

<sup>§</sup>Percentage of total shoots (± SEM) with mammalian browsing damage from randomly selected size-matched trees [ANOVA ( $F_{3,92} = 10.6$ ;  $P < 0.0001$ )], from ref. 29.

<sup>¶</sup>Numerical data shown are mean number of workers tending nectaries (± SEM) for 50 scans of different host plants occupied by each species. Note that *T. penzigi* does not use extrafloral nectar, because this species destroys all host-plant nectaries.

\*\*Number of new cerambycid beetle scars (± SEM) accumulating on host plants over an 18-mo period, from ref. 20.

††*C. sjostedti* colonies do not appear to colonize new host plants via aerial dispersal.

species within the mutualist network weaken the lifetime benefits of ant association relative to what they would be if these ants were not present? (ii) Are the fitness benefits to the longer-lived mutualist (trees) of interacting with a particular short-lived partner (one ant species) independent of interactions with other short-lived partner species?

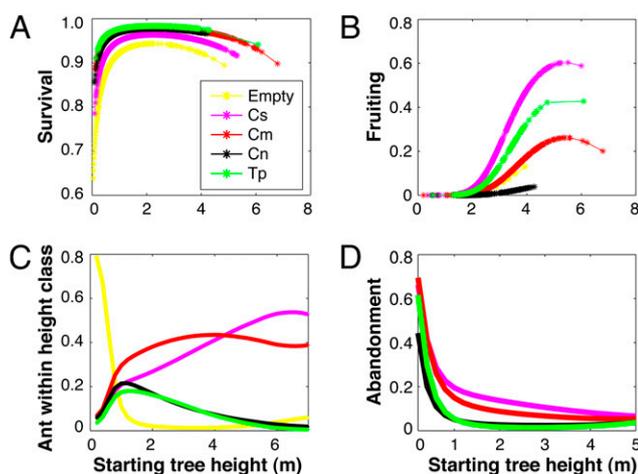
## Results and Discussion

**Contrasting Effects of Different Ant Partners on Survival and Reproduction of Trees.** Our demographic models revealed that none of the four symbiotic ant species is a “perfect” partner, with different species having contrasting effects on *Acacia* survival and reproduction throughout ontogeny (Fig. 1). We first considered each ant species independently, finding that occupancy by any ant species increased survival of acacias of all sizes relative to plants that lacked ants (Fig. 1A), and, with the exception of the sterilizing symbiont *C. nigriceps*, the same was true of fruiting (Fig. 1B). However, the ranking of ants’ effects on survival vs. reproduction

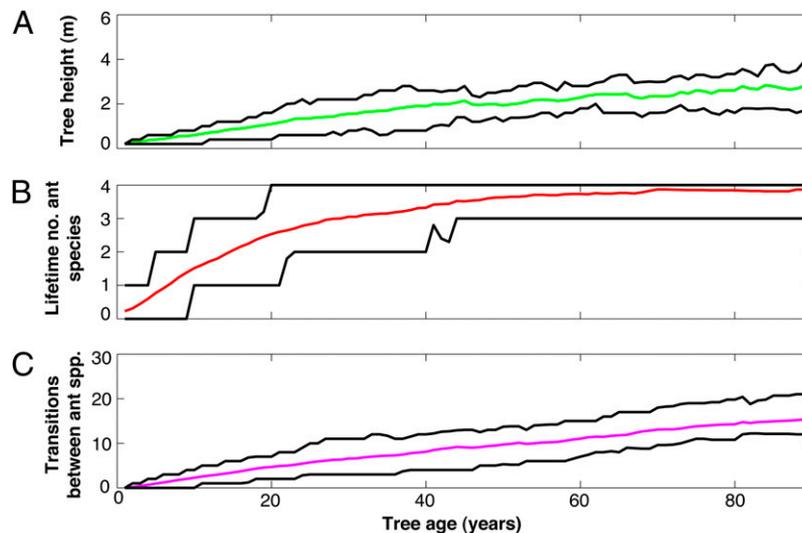
differed, with *T. penzigi* and *C. nigriceps* producing highest survival rates and *C. sjostedti* producing the greatest fruiting frequencies.

As mentioned above, individual host trees associate with multiple ant species and typically undergo many transitions between ant partners during ontogeny (Fig. 2). Importantly, the probabilities of specific ant transitions depended on both tree size and the identity of the current ant occupant. As trees grew, the most probable ant partner changed in a predictable, quasi-successional way, from strongly colonizing species with small colonies (*T. penzigi* and *C. nigriceps*) to competitively dominant species with larger colonies (*C. mimosae* and *C. sjostedti*) (Fig. 1C and Table 1) (see also refs. 26 and 28). Thus, by the time a tree reached an age of 54 y, it had a 90% chance of having partnered with three of the four ant species, and a >50% chance of having partnered with all four ant species (Fig. 2B). At that age, 90% of trees can expect to have had six or more transitions in ant occupancy (median, 10 transitions; Fig. 2C).

Our models assumed that ant occupants influence the demographic traits (e.g., growth, fruiting) of acacias rather than responding to preexisting differences in quality between trees. We used two approaches to validate this assumption. First, we experimentally switched the identities of ant occupants on host plants and then measured growth of these plants over 18 mo relative to control plants where resident-ant identity was not changed. This experiment demonstrated that different ant species exerted strong and contrasting effects on tree growth rate that were consistent with the correlations we observed between ant occupancy and plant growth in our 8-y demographic study (*SI Text* and Table S1). Second, we conducted three retrospective analyses of the 8-y demographic data. First, we added a variable (“tree growth over the previous annual transition”) to each of our 15 multinomial logistic models for ant-transition probabilities (Table S2) to see if past growth rates (an indicator of vigor) influenced ant transitions; in no case did this new variable improve model fit (*SI Text*). Second, we evaluated the causal direction of the strong correlation between *C. sjostedti* occupation and host-plant fruiting. Adding “fruiting (yes/no) in prior year” to our models for ant-transition probabilities did not increase their predictive power, nor did it improve the fit of a subset of models predicting only the takeover of large trees by *C. sjostedti* (*SI Text*). Finally, we used logistic regression to establish that occupation by *C. sjostedti* in prior years strongly predicted fruiting probability in future years (*SI Text*). Collectively, these results demonstrate that occupancy by different ant species strongly and differentially drives plant demographic traits, rather than vice versa (Table S2 and *Materials and Methods* for details).



**Fig. 1.** (A) Best-fit probabilities for survival of different-sized *Acacia* trees occupied by each of the four ant symbionts or unoccupied. (B) Best-fit fruiting probabilities for different-sized *Acacia* trees occupied by colonies of each of the four ant symbionts; (C) Best-fit probabilities of occupation by different ant species for different-sized *Acacia* trees. Cs = *C. sjostedti*, Cm = *C. mimosae*, Cn = *C. nigriceps*, Tp = *T. penzigi*. (D) Best-fit probabilities for abandonment of different-sized *Acacia* trees occupied by colonies of each of the four ant symbionts.



**Fig. 2.** Results from 10,000 stochastic simulations showing the 10th, 50th (median), and 90th percentiles for (A) height of surviving trees at different ages; (B) the total number of unique ant species (of four) ever occupying trees for surviving trees of different ages; and (C) the total number of transitions between different ant species on surviving trees at different ages. Results are shown up to 90 y, encompassing the usual range of ages for *A. drepanolobium*. A 1-y-old seedling has an average future life expectancy of 19 y and a 5% chance of reaching 40 y of age. A small but established plant (age 10 y) has a total life expectancy of 34 y and a 5% chance of reaching age 75 y.

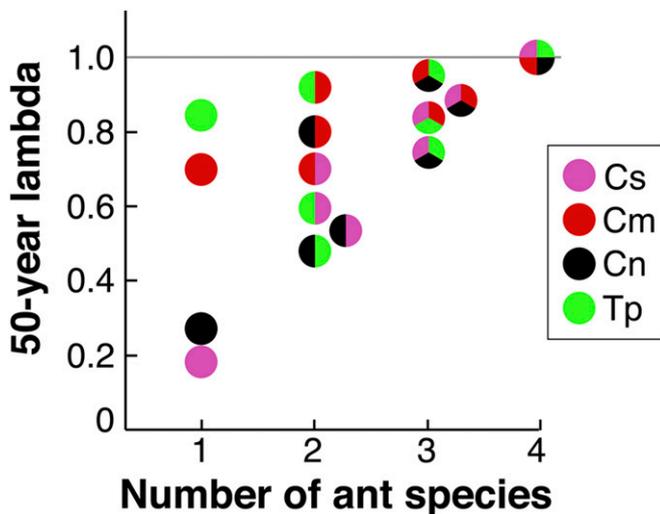
**Lifetime *Acacia* Fitness Benefits of Associating with Sets of All Four Ant Species (Including Putative Free-Loaders).** To determine how key components of *Acacia* fitness (survival and reproduction) were influenced by the contrasting effects of each ant species, we used our 8-y dataset to simulate *A. drepanolobium* demography in the presence of all four ant associates and then again with the simulated removal of one-or-more ant species. For these “reduced-community models,” the tree size- and ant-specific probabilities of transition to the ant species being removed were proportionally reallocated to the remaining possible occupancy states. In *SI Text* we discuss the realism of this assumption and explore alternative models that yielded similar results.

Our most surprising finding is that acacias sequentially associating with partner sets that included both the sterilizing *C. nigriciceps* and the poorly defending *C. sjostedti* had higher expected lifetime fitness than did acacias partnering with any single ant

species—even when that single species was *C. mimosae*, the one member of this guild that is both a very aggressive defender and a nonsterilizer. *Acacia* fitness was highest when trees partnered with all four ant species over their lifetimes and typically declined with the removal of one, two, or three ant species (Fig. 3). Our results show that the lifetime fitness of *A. drepanolobium* cannot be evaluated by summing the independent effects of associations with different ant partner species: Rather, fitness is a complex function of the duration, contrasting benefits and costs, and ontogenetic timing of a plant’s interactions with each partner ant species. Likewise, the net benefits to trees of interactions with a given ant species depend in part on the suite of other ant species with which the plant interacts (e.g., ref. 30).

**Dependence of Tree Fitness on the Timing and Duration of Association with Different Ant Partners.** Although the four ant species differ markedly in their defensive aggression (Table 1), the longer-term survival benefits to plants also depended on the timing and year-to-year consistency of occupation by each ant partner. In total absence of ants, host-plant survival was very low at all sizes (whether a small sapling or a larger abandoned plant) (Fig. 1A). Although *C. nigriciceps* sterilizes host plants and *T. penzigi* is only moderately aggressive, these species conferred high survival rates to host plants (Fig. 1A), in part because of their high year-to-year reliability. Both these rapidly colonizing species tend to occupy younger trees (Fig. 1C and Table 1), for which survival elasticities are highest (Fig. S1), and they rarely abandon their hosts (Fig. 1D), probably because their colonies are restricted to only one or a few host plants (Table 1). In contrast, small acacias with little nesting space are less desirable for the competitively dominant *C. sjostedti* and *C. mimosae* (31), both of which are highly polydomous, with single colonies typically occupying multiple host trees (Table 1). Although these two species will colonize and occupy smaller host plants, they more frequently abandon both small and large trees (Fig. 1D).

Although the poor survivorship of trees occupied by the poorly defending *C. sjostedti* is consistent with observations from prior studies (20), the relatively low lifetime fitness of host trees in simulated communities with only *C. mimosae* (the seemingly “best” mutualist) was unexpected. Although *C. mimosae* confers strong antiherbivore protection to its host trees, the resulting survival benefits are offset by this species’ propensity to abandon



**Fig. 3.** Long-term *Acacia* population growth rates ( $\lambda_{50}$ ) for simulated communities consisting of one, two, three, or four ant species. Species abbreviations are as in Fig. 1.

plants over longer time scales. These results emphasize that the fitness value of particular mutualists is conditioned by the temporal and/or spatial reliability of the services they confer, as noted for other mutualisms (32–36).

The effects of different ant species on lifetime *Acacia* reproductive output depended on the timing of their association with the plant. Predictably, reproductive elasticities were low for small plants and increased with plant height (Fig. S1). Although the sterilizing *C. nigriceps* has a direct negative impact on *Acacia* reproduction, it confers high survival and tends to occupy host plants early in their ontogeny, when reproduction is less important to fitness than survival. Thus, *C. nigriceps* exerted positive effects on overall *Acacia* fitness, provided that nonsterilizing ant species were available to colonize plants at later life stages (Fig. 3).

Conversely, an ant species that increases plant mortality may not necessarily diminish plant fitness if colonization occurs primarily during later life stages that have low survival elasticities. For example, although *C. sjostedti* negatively affects plant condition and survival (Table 1 and ref. 20), its presence was correlated with substantially increased reproduction (Figs. 1 and 4), possibly because of a tolerance response (37, 38) by plants to the high levels of herbivore and beetle damage associated with *C. sjostedti* occupation (e.g., ref. 39). (Because large trees occupied by *C. sjostedti* produced fewer, smaller swollen thorns and fewer active nectaries than similar-sized trees occupied by *C. mimosae*, *C. sjostedti* trees might have more energy available for reproduction.) We note that the reproductive benefits of *C. sjostedti* did not appear to hinge on the tempo of seedling recruitment into the host-tree population. Although most of our analyses assumed time-invariant recruitment probabilities, our results are robust even when we assumed episodic recruitment at intervals of 5, 10, or 20 y (*Materials and Methods*).

Surprisingly, the single ant species predicted to have the strongest positive effects on host fitness is *T. penzigi*, which is an only moderately effective defender. This effect resulted from the high year-to-year reliability of *T. penzigi* combined with moderately high fruiting success of larger trees occupied by this species. Mature trees occupied by *T. penzigi* may have more resources to allocate to fruiting because they do not produce nectar (40).

**Dependence of Ant Effects on a Host Plant's Association with Other Ant Species.** The dynamics of the ant–plant mutualism cannot be understood fully by comparing the costs and benefits of pairwise

associations between the different partners. Rather, it is necessary to consider the entire guild of ant symbionts and their cumulative net effects on lifetime host fitness. Although both the sterilizing *C. nigriceps* and the weakly defending *C. sjostedti* were predicted to have strong negative impacts on host-plant fitness in the absence of other ants, each generally increased lifetime plant reproductive output as a member of a mutualist set that included other ant species (Fig. 3). This increase occurred because long-lived host plants can accrue complementary benefits from the different ant partners at different stages of their ontogeny. The more rapidly colonizing *C. nigriceps* and *T. penzigi* conferred strong survivorship, especially to vulnerable, small host plants, because of their high interannual reliability, whereas acacias occupied by the late-successional *C. sjostedti* invested heavily in reproduction, offsetting the low survivorship associated with occupation by this nondefending ant partner (Fig. 4).

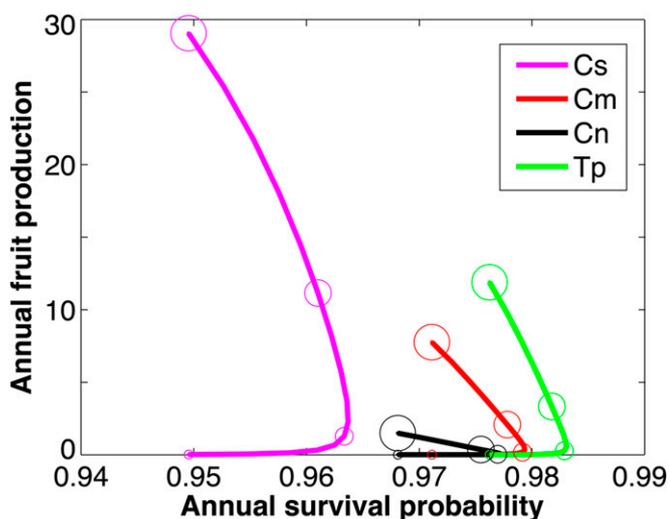
## Conclusions

**The Importance of Integrating Multiple Partner Effects.** Our data and analyses show that the effects of ant symbionts in an intensively studied ant–plant mutualism can be understood meaningfully only by considering the timing, duration, and sequence of a plant's lifetime interactions with the entire set of its associated ants. Multiple partnerships are a common feature of mutualism, and other studies describe ontogenetic succession of different partners (e.g., refs. 41–43). It has long been known that characterizing the net effects of interactions in multispecies communities entails understanding the direct and indirect effects of those species on one another (44, 45). However, natural selection acts on lifetime fitness, and the fitness of long-lived mutualists is determined by the temporally integrated effects of multiple partners. Thus, even knowing the net effects of the entire community of ants on *A. drepanolobium* over limited time scales is insufficient to describe this mutualism.

Likewise, the effects of individual ant species on plant fitness are conditioned by a plant's prior and future interactions with other ant species; two identical guilds of ant partners can have vastly different effects on plant fitness if they differ in the timing, sequence, or duration of their association with the plant. Integrating the effects of multiple partners is necessary to establish how natural selection shapes the life-history strategies of species embedded within mutualist networks.

**Sterilization "Parasites" as Mutualists.** Our work further demonstrates that some "parasites" are actually beneficial partners when considered within the broader context of the mutualist assemblage. In our system, as in others (22, 46), ant species identified as sterilizing "parasites" nonetheless can confer valuable protective benefits to host plants, often occupy host plants earlier in ontogeny, and are likely to be replaced by nonsterilizing ants as plants grow older. We show that when followed by nonsterilizing species later in ontogeny, these putative parasites can confer complementary benefits to plants. In other mutualisms, parasites have been shown to strengthen the relationship between mutualistic species (47, 48); in contrast, our results suggest that, in some cases, the persistent language of "mutualists" vs. "free-loaders" or "cheaters" may be misleading.

**Effects of Lifespan Inequalities Within Mutualisms.** Temporal mismatches in the lifespan of interacting mutualist partners may play a critical and currently unappreciated role in the maintenance of interspecific cooperation in nature, potentially increasing the persistence of mutualist networks where short-term partner quality is variable. Exploiters of mutualisms often display *r*-selected life-history strategies, such as strong early-colonization ability (49, 50). Where mutualists have a long lifespan relative to their partners, longevity itself may serve to hedge bets against a lifetime association with a weak partner.



**Fig. 4.** Predicted annual survivorship vs. fruit production for acacias occupied by each of the four ant species across different plant sizes. Increased bubble sizes around points on the line indicate increases in plant size in 1-m increments from 1 m (smallest bubbles) to 4 m (largest bubbles). Species abbreviations are as in Fig. 1.

More broadly, these results suggest that demographic methods and concepts can help establish the conditions under which long-lived mutualists tolerate or even benefit from apparently antagonistic partners and also explain how the existence of multiple partners might drive the evolution of life histories in mutualistic species. First, demographic models suggest that greater longevity generally should be favored by unpredictable environments (51, 52). For mutualists, variation in partner quality is effectively variation in the environment. Thus, interacting with multiple partners of varying quality might favor increased longevity in mutualist species. Second, demographic-sensitivity analyses can predict the relative importance of different demographic rates through ontogeny (53–55), providing a framework for understanding the age- or size-specific costs and benefits of different partners. Finally, stochastic demographic models show that negative correlations between different demographic performance measures through time can ameliorate the negative effects of environmental variability or even increase fitness (56), suggesting how sets of partners that generate such negative correlations in mutualists' vital rates might yield higher fitness than any single, seemingly optimal, partner. Such approaches and reasoning have been used recently to address the ontogeny of plant defense (15).

**Implications for Mutualism Stability.** Efforts to explain the apparent paradox of mutualism stability have described a range of strategies to enforce or incentivize good partner behavior, such as partner choice, host sanctions, and partner-fidelity feedback (57). Such stabilizing mechanisms are not necessary to explain the stability of this mutualism; instead, tradeoffs between survival and reproduction over the multidecadal lifespan of the longer-lived partner enable cooperation to persist when the short-term effects of ant partners range from cooperative to antagonistic.

## Materials and Methods

**Natural History of *Acacia drepanolobium* and Its Ant Mutualists.** This study was conducted at the Mpala Research Centre (0°20' N, 36°53' E) on the Laikipia Plateau, Kenya. Rainfall is variable, averaging 550 mm/y. Our study site is underlain by heavy clay vertisols dominated by *A. drepanolobium* (mature individuals 1.5–7 m tall, >95% of woody cover).

*Acacia drepanolobium*'s population size structure is L-shaped, implying healthy recruitment (28). A pair of straight, sharp spines is produced at each node. Approximately 5–10% of nodes house ants (in domatia  $\leq 5$  cm diameter), which feed partly from nectaries at the leaf bases (58). Virtually all trees >1 m tall have a single resident ant colony, although a single colony may occupy multiple trees (31). A wide range of herbivores feed on *A. drepanolobium*, including elephants, giraffes, and other large mammals, along with many species of insect (29).

**Long-Term Survey of *A. drepanolobium* and *Acacia*–Ant Dynamics.** In 1998 we established five permanently marked 200-m  $\times$  30-m belt transects. Along these transects we marked >1,750 *A. drepanolobium*, stratifying our sampling by host-plant size (five initial height classes: 0–0.50 m, 0.51–1.00 m, 1.01–1.5 m, 1.51–3.00 m, and >3.00 m) and ant occupant (five occupancy states: occupied by one of the four ant species or empty). Each tree was permanently tagged and scored for ant occupant and height (to the nearest 5 cm). We surveyed each tree annually from 1998 to 2007, recording vertical growth (to the nearest 1 cm), mortality, ant occupant, and number of fruits per tree.

**Modeling *Acacia drepanolobium* Demography.** Using height, survival, reproduction (2004–2007 only), and ant-occupancy data on 1,750 trees recorded annually for some or all years between 2000 and 2007, we fit a series of statistical models for mean tree growth, variance in tree growth, and fruit number if fruiting (general linear models); fruiting and survival probabilities (logistic regressions); and transitions in ant occupancy (ordinal logistic regressions). Five to 15 models were fit for each dependent variable (Table S2). Results of these analyses supported a set of predictive models for each *Acacia* demographic rate, with ant species having well-supported effects on all demographic rates (Fig. 1 and Fig. S2). Similarly, transition probabilities between ant species were influenced by both current ant occupant and tree height (Fig. S3).

We then used the best-supported model [determined using Akaike's information criterion (AIC)] for each demographic rate to construct a density-independent demographic model (first-order Markov chain) to describe *Acacia* growth, survival, reproduction, and ant-occupancy transitions as functions of tree size and ant occupancy state (Table S4). We used these regression models to estimate the demographic rates for trees in 35 height classes (0.2–7 m, in 0.2-m increments) times five ant states, for 175 combined categories. We created a final category for the seedlings, using data on trees <0.2 m from all years of our study to generate the initial frequencies of ant occupancy for the youngest and smallest size class (probabilities of 0.7637, 0.0673, 0.0810, 0.0563, and 0.0316, for empty, *T. penzigi*, *C. nigriceps*, *C. m.*, and *C. sjostedti* occupancy, respectively). The result was a deterministic demographic model for *A. drepanolobium* with 176 stage classes.

The one parameter in this model for which we have no field estimate is survival from seed to seedling establishment, which we set to 0.101 to yield replacement-level average tree fitness ( $\lambda = 1$ ) for the full ant community model. Thus, all our fitness measures (dominant eigenvalues for different demographic models) are relative to that of the current *Acacia* population, which we assume to be stable. We tested the sensitivity of our results to this assumption by using an alternative value for seed to seedling establishment derived from a separate 3-y empirical study (59) and found no change in the ranking of fitness for different ant communities.

We performed standard demographic analyses on our basic model, in which the ant community inhabiting and influencing trees includes all four species. To test the effects of different combinations of ant mutualists, we constructed modified reduced-community models with one or more of the four ants removed. Reduced-community models used all the estimated effects of the remaining ant species on *Acacia* performance (growth, reproduction, and survival) and on probabilities of transitioning from each ant species to all others. However, eliminating one or more ant species required us to modify the transitions between the remaining ant occupants to account for the missing probabilities of transitions to the now-missing ant species. To do so, we assumed that the probability of moving from any state (ant species  $\times$  height stage) to states involving excluded ants should be reassigned to the remaining, still-possible transitions (that is, involving ants in the hypothetical reduced community) in proportion to the originally estimated values for each transition probability. This assumption allows for the fact that many of the effects that result in ant abandonment of host (e.g., reduced host quality resulting from herbivore damage or overgrowth of saplings by grasses) are likely to occur in a density-independent manner, but alternative methods for modeling reduced communities produced qualitatively similar results (SI Text, "Analyses of Long-Term Transect Data"). Having created each modified matrix, we estimated  $\lambda$  and the frequency of ant states for the remaining stages. As is common practice (55), we interpret  $\lambda$  as a measure of lifetime fitness for acacias and focus on the effects of ant communities on this measure of plant performance.

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# Supporting Information

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## Key Assumptions and Tests of the Model

Our demographic modeling presented in the main text relies on several key assumptions, which we scrutinize here.

**Assumption 1: Our Basic Model for *Acacia* Demography and Ant Occupancy Accurately Reflects Patterns in Nature.** To test whether our basic model for *Acacia* demography and ant occupancy accurately reflects patterns in nature, we used the accepted approach of asking if the model predicts the stage distribution of the study population (1). We determined the observed distribution of *Acacia* heights and ant-occupancy rates across tree sizes at our study sites, using both the observed height and ant distributions from our long-term study and an independent survey of ca. 2,135 trees taken near our study sites. The stage distribution predicted by the model provided a good match to both observed distributions (Figs. S4 and S5). In both surveys, the predictions that *Tetraponera penzigi*, the fourth-ranked ant, would be most common on very small trees and that *Crematogaster sjostedti*, the first-ranked ant, would be most abundant on the largest trees were confirmed, and other patterns of size-dependent occupancy also matched the model predictions. Correlations between the frequencies of ant by 0.2-m height categories were 0.70 and 0.46 for the first and second data sets (Fig. S5). These correlations correspond favorably with the correlation in frequencies of the two data sets themselves (0.76). All three correlations are lowered by mismatches in abundance and ant-occupancy of the smallest trees. The smallest trees are those likely to be most dynamic over short spatial and temporal scales, for which we have the least data to fit ant frequencies, and which are least accurately sampled in the field. The correlations in frequencies were much higher ( $r = 0.94$  and  $0.85$ ) when the smallest size classes (trees  $\leq 1$  m tall) were excluded. These noncircular tests show that the *Acacia* demography and ant effects on which our results rest are reasonable.

**Assumption 2: The Demographic Traits That We Observe for Acacias Occupied by Different Ant Species Are the Result of the Ant Occupants Rather Than the Ants Responding to Quality Differences Between Trees.** Several independent lines of evidence indicate that causality is primarily in the direction of ant species differentially influencing tree performance, rather than vice versa. We detail these results here.

**An experimental test of the influence of *Acacia* ants on plant vigor.** To evaluate whether differences in host-plant demography are influenced by resident ant colonies, we compared the performance of acacias occupied by each of the three *Crematogaster* species with the performance of nearby trees on which each of these ant species was experimentally “switched” to another species. (Experimental switches were not practical for acacias occupied by *T. penzigi*; although this species is behaviorally the most subordinate, it strongly resists competitive displacement by other *Crematogaster* species.)

For each pairwise combination of *Crematogaster* species, we located 10 size-matched pairs of nearby trees and assigned five pairs to transitions from the more subordinate species to the more dominant species and five pairs to transitions in the opposite direction. For each pair, the tree occupied by the species to be displaced was termed the “target tree,” and the tree occupied by the displacing species was called the “invader tree.” We then located a size-matched “control” tree within 15 m of the target tree, occupied by the same species as the target tree (six combinations  $\times$  10 trees = 60 trees). On both control and target

trees, we tagged four arbitrarily chosen branches, one in each cardinal direction. We placed tags 20–30 cm from branch tips and recorded the exact distance from tag to tip.

We then determined colony size on both the target- and invader-tree (2). The colony of the dominant species (3) always was larger than the colony of the subordinate species. Because interspecific conflicts for the possession of host trees are won by attrition (2), staged conflicts in which the invader-tree species was dominant to the target-tree species were expected to proceed naturally toward the desired transition. By contrast, it was necessary to reduce colony size experimentally in conflicts in which the invader-tree species was subordinate to the target-tree species. For tree pairs assigned to transitions in which a more subordinate species would replace a dominant species on target trees, we reduced the size of the dominant colony in one of two ways, depending on the identity of the dominant species. In conflicts between *Crematogaster mimosae* and *Crematogaster nigriceps*, the dominant *C. mimosae* colonies were reduced in size by placing a Tanglefoot sticky barrier (Tanglefoot Company) at the base of nonfocal trees occupied by the same colony, preventing recruitment of workers from those trees to the focal tree. We reduced the size of the *C. mimosae* colonies until the total number of trees occupied by each colony was about half the size of the *C. nigriceps* colony.

Unlike the other two *Crematogaster* species in this system, *C. sjostedti* nests in hollowed-out cavities within the stem and branches of host trees and often creates entry holes to trees just above ground. As a consequence, it was difficult to create and maintain effective recruitment barriers on the numerous trees in their large colonies. Instead, for conflicts involving *C. sjostedti*'s replacement by a more subordinate species, we placed a Tanglefoot barrier at the base of each target tree, effectively restricting this species to a single-tree colony in each conflict. All sticky barriers were maintained carefully during the transition phase of the experiment (the 1-wk period during which conflicts played out).

After barriers to recruitment had been established, we pulled individual branches from the target and invader trees into contact and attached them with wire. We then allowed conflicts to proceed until the invader species had completely taken over the target tree. Complete takeovers, when only a single ant species could be found on branches and within swollen thorns on both trees, generally were achieved within 48 h of canopy contact. Control trees also were forced into conflict with a nearby tree of the appropriate invader-tree identity, but these conflicts were allowed to proceed for only 4 h before the trees were disconnected.

After 18 mo, we remeasured tagged branches to evaluate growth of target vs. control trees. We performed a  $2 \times 2$  factorial ANOVA on growth data, with “original ant species” and “subsequent ant species” as main effects. Both main effects and their interaction significantly influenced new growth on acacias (original ant species  $F_{2,2} = 26.98$ ,  $P < 0.0001$ ; subsequent ant species  $F_{2,2} = 5.47$ ,  $P < 0.01$ ; interaction term  $F_{4,4} = 2.68$ ,  $P < 0.05$ ). Planned contrasts revealed the effects of each ant species on branch growth after taking over target trees occupied by each of the other ant species, relative to the appropriate control trees (Table S1).

Past and present occupancy by different ant species had complex effects on branch growth rates. All three *Crematogaster* species influenced growth after taking over new trees (details are given in Table S1).

**Previously published results suggest that ants drive variation in plant vigor.** Recent studies of *Acacia drepanolobium* have shown negative correlations between average aggression of resident ant

species and herbivory on their host plants (4) and also have shown that saplings occupied by ants are browsed less than unoccupied saplings (5). Further, we previously have shown dramatic changes in rates of attack by wood-boring beetles (Cerambycidae) when ants are removed (6).

**Analyses of long-term transect data.** We performed four tests to determine whether competitively dominant ants choose better-performing trees, rather than our assumption that ant occupancy drives tree performance. First, we added a variable (“tree growth over the previous annual transition”) to each of our 15 multinomial logistic models for ant-transition probabilities (Table S2) to see if past growth rates (an indicator of vigor) influenced ant transitions. In no case did this new variable improve model fit; the minimum Akaike’s information criterion (AIC) of these models was 5.04 greater than the minimum AIC of the original models.

Our next three analyses were motivated by the puzzling result that *C. sjostedti* occupation was correlated with greater flowering probability and seed production within each tree-height class (Fig. 1 and Fig. S2). First, we asked whether the predictive power of our best model of ant succession, which already included current-ant and tree-size effects (Table S2), were improved by adding a tree’s reproductive status in the beginning year of each transition (flowering: yes/no). The model including reproduction had substantially lower predictive power ( $\Delta_{AIC} = 2.77$ ). We performed a similar analysis to determine whether past flowering influenced only the take-over of larger trees by *C. sjostedti*. Again, the addition of reproductive status lessened the model fit ( $\Delta_{AIC} = 2.00$ ). Finally, we used logistic regression to show that occupation by *C. sjostedti* in years  $t-1$  and  $t-2$  significantly increased fruiting probability, whereas occupation by *C. sjostedti* in the current and future year did not have consistent effects on current fruiting. These results collectively indicate that *C. sjostedti* increases fruiting rather than selectively invading high-reproduction trees.

**Assumption 3: Reduced-Community Models with Fewer than Four Ant Species Capture the Likely Dynamics of Those Communities.** When one or more ant species is removed from our models of tree demography, we assumed that all remaining transition probabilities (including abandonment and trees remaining unoccupied) would increase in proportion to their previous values (Materials and Methods, “Modeling *Acacia drepanolobium* Demography”). As detailed below, we consider this assumption to be the most realistic. However, we tested the effects of alternative assumptions by replicating our analysis with the assumption that the probability of a tree transitioning into an unoccupied state (being abandoned or staying empty) remained the same for all scenarios and that only the probability of transitions to remaining ant species would increase in reduced ant communities. This assumption produced results slightly different from our other models, with some reduced ant communities generating higher *Acacia* fitness than did a four-ant community (Table S3). However, our key results regarding relative effects of ants on host-plant fitness remain unchanged. Notably, the relatively high benefits of *T. penzigi* and *C. sjostedti* are even more pronounced, and *C. mimosae*, the presumed best mutualist based on short-term effects, is still not the best partner for lifetime tree fitness.

Although many of our results were robust, we consider this alternative assumption less realistic than that in our original models. Much colony abandonment of acacias appears to occur on host plants that have suffered either long-term (e.g., competition, senescence) or short-term (e.g., intense herbivory, trampling) reductions in vigor. Because all host plants are subject to these effects, we expect that the probability of a host plant transitioning to unoccupied status would remain proportional to other transition probabilities when one or more ant species is absent. Because the probability of host-plant abandonment by the high-fidelity ant associates *T. penzigi* and *C. nigriceps* is already low (Fig. 1), their proportional increases in abandonment in the

hypothetical reduced communities of our original models will be low also. Furthermore, the characteristic size-specificity of occupation by different ants suggests that in a reduced ant community some trees would be more likely to be abandoned or remain empty. Thus, not increasing the proportion of trees transitioning to unoccupied status when adjusting transition rates in hypothetical reduced communities is likely to misrepresent the dynamics of ants and tree abandonment and to produce artificially high  $\lambda$  values (e.g., the  $\lambda$  value for single-species communities of *T. penzigi* in Table S3).

### Test 1: Effects of Episodic Recruitment on Demographic Predictions.

Our main results are based on a deterministic model of *Acacia* demography. The most important potential effect of environmental stochasticity that could alter our results is highly episodic recruitment (i.e., years with strong recruitment of seeds separated by many years of low or zero recruitment). Our result that occupation by the antagonistic *C. sjostedti* can increase lifetime fitness of plants by increasing reproductive output implicitly assumes that trees with strongly pulsed annual reproduction over fewer years (followed by death) will have higher fitness than trees with higher survivorship that reproduce at lower levels for a longer period (a “trickle” strategy). If recruitment opportunities arise only during certain years (episodic recruitment), a trickle strategy might allow plants to hedge against environmental variability.

Strongly pulsed recruitment windows are not a likely scenario for *A. drepanolobium* in our study area. Prior study in this system shows that rainfall, rodents, seed production, and understory cover all independently influence recruitment in *A. drepanolobium* (7), with the result that recruitment occurs at low but relatively consistent levels from year to year. Nonetheless, to examine whether episodic recruitment would shift the relative fitness of acacias occupied by different ant sets, we modeled the lifetime fitness of acacias with different sets, assuming 1-, 5-, 10-, or 20-y recruitment windows. In the 20-y model, for example, recruitment probability is zero for 19 y and then high enough in the 20th year to maintain an average stochastic lambda of  $\sim 1$  for the full ant community. The results are qualitatively identical to those from our deterministic models of up to 10-y pulses (shown in Fig. 3). For 20-y windows, the addition of *C. sjostedti* to sets of other partner ant species that include *C. nigriceps* increases host fitness in two of three reduced communities. Where *C. sjostedti* reduced *Acacia* fitness, these effects generally were very small (Table S4). These results suggest that trees successfully trade off survivorship for strong reproduction in later life stages and that episodic recruitment is not likely to change our basic conclusions (Table S4).

### Test 2: Comparing Swollen Thorn and Nectary Production by Large Trees Occupied by *C. mimosae* Versus *C. sjostedti*.

To establish whether mature trees occupied by *C. sjostedti* invest fewer resources in ant partners than do trees occupied by *C. mimosae*, we surveyed the production of active nectaries and swollen-thorn domatia on mature trees occupied by both species. In August 2008, we randomly selected 14 pairs of size-matched *Acacia* trees (>4 m tall) occupied by each species. On each tree, we randomly selected four branches (3–4 m high) bearing new growth (one branch in each cardinal direction). On the distal 30 cm of each branch, we measured the number of growth nodes, number of swollen thorns, and diameter (at the widest point perpendicular to the branch axis) of each swollen thorn. We then surveyed the 10 most distal leaves on each branch for active nectaries.

Mature trees occupied by *C. mimosae* produced 36% more domatia and 50% larger domatia than those occupied by *C. sjostedti* (paired  $t$  tests, d.f. = 13; number of swollen thorns:  $t = 2.82$ ,  $P < 0.02$ ; average diameter of swollen thorns,  $t = 5.06$ ,  $P < 0.001$ ). Trees occupied by *C. mimosae* also produced 56% more active nectaries than trees occupied by *C. sjostedti* ( $t = 3.24$ ,  $P < 0.01$ ). The average number of growth nodes did not differ ( $P = 0.35$ ).





