10 Integrating Ecological Complexity into Our Understanding of Ant-Plant Mutualism: Ant-Acacia Interactions in African Savannas

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Introduction

Ant-plant protection mutualisms, and mutualisms more broadly, are typically defined as "+ / +" interactions, indicating that species on each side of the interaction have a positive effect on the per capita growth rate of their partner. But that simple representation belies potentially great complexity: each "+" sign represents the net effects of the interaction's costs and benefits on the lifetime fitness of participants, and these costs and benefits may shift both spatially and temporally with environmental conditions, with variation in the guild of mutualist partners, and with variation in the community of interacting species outside of the mutualism. As these conditions change, so too may the strength of mutualism, with consequences that can strongly influence the communities in which these interactions are embedded. To understand mutualism, therefore, requires moving beyond traditional pairwise approaches (Stanton, 2003), and accounting for both the complexity inherent in mutualist networks and the ways in which the surrounding environment affects these interactions. Doing this accounting correctly is important: our entire understanding of mutualism, from the evolution of traits and behaviors to the stability of mutualism itself, is predicated on understanding how these interactions integrate to influence the lifetime fitness of the participants.

To illustrate the complexity of mutualism, and to provide examples of how this complexity may affect its ecological and evolutionary dynamics, in this chapter we review ant-acacia interactions within the savannas and bushlands of East Africa. In particular, we focus on research investigating the well-studied mutualism between *Acacia* (*Vachellia*) *drepanolobium*, a widespread and abundant myrmecophyte

(ant-plant), and its suite of symbiotic ant associates. Our approach highlights the "community ecology" of this ant-plant association, shedding light on the spatio-temporal variability of the ant-plant interaction, and examining both how the broader community and environment impacts the mutualism, and how the mutualism in turn affects the broader community. We focus on *A. drepanolobium* because it has been more intensively studied than other ant-plant associations in East Africa. There are many other extrafloral nectar-bearing species in the region, many of which are visited by suites of obligate or facultative ant associates, still awaiting research addressing the nature of these ant-plant interactions.

Natural History of the *Acacia drepanolobium* – Ant Symbiosis

Large areas of eastern and southern Africa are underlain with high-clay vertisols called "black cotton" soils. Over much of these, a wooded grassland community has developed dominated by a single tree species, *Acacia drepanolobium*. This tree is an ant acacia, providing food and housing to ant colonies, and receiving protection from herbivores from at least some of its ant associates (Madden and Young, 1992; Stanton and Palmer, 2011). The tree serves as an important source of forage for a variety of mammals, including giraffe, rhino, and other large browsing herbivores (Madden and Young, 1992; Martins, 2010).

In Laikipia and elsewhere (e.g., the Athi Plains in Kenya, many areas within the Great Rift Valley, and the Grumeti area of the Serengeti in Tanzania), *A. drepanolobium* is a foundation species (sensu Dayton, 1972), forming a virtual canopy mono-culture (>90 percent of the woody cover), and capable of achieving high densities (> 1500 stems (> 0.5 m tall)/ha, Young et al., 1998). The tree is defended by pairs of straight spines (modified stipules) at each branch node, which effectively reduce herbivory by large mammals, and whose length can be induced by large mammal herbivory. In addition, approximately one pair of spines in four is swollen at the base to produce a large (2–5 cm) hollow structure, which serve as domatia which several (but not all) symbiont ant species use for living space and to rear brood. In addition, the leaves of *A. drepanolobium* are characterized by extrafloral nectaries along the lower petiole, on which some (but not all) symbiotic ant species feed. This ant-plant symbiosis was first described in depth by Hocking (1970), and has since become an iconic example of the richness and complexities of mutualism (Young et al., 1997; Palmer et al., 2000; Martins, 2010).

Throughout its range, *A. drepanolobium* associates with a guild of ant species that vary strongly in their interactions with the host plant (Table 10.1). Here we discuss the four best-studied ant associates, and what is currently known about each unique association between these ant species and their host plant. The first three species, *Tetraponera penzigi*, *Crematogaster mimosae*, and *C. nigriceps*, are obligate associates of the host plant that appear to depend solely on the swollen spine domatia of the acacia for brood rearing. The fourth species, *C. sjostedti*, is a more generalized twig and cavity nester (a condition thought to be ancestral to residing within

Table 10.1 Ant Species Vary in Their Relationships with *Acacia drepanolobium*

ANT SPECIES	Dominance rank of mature colonies[1]	Avg # (± s.e.) trees per colony[2]	Dominance rank of queens[3]	Anti-herbivore defense[4]	Use of nectaries	Scale tending?	Domatia density[6]	Fruiting of host plants[7]
Crematogaster sjostedti	1	13.2 (2.4)	–	LOW	LOW	YES	MED	HIGH
C. mimosae	2	4.8 (1.1)	3	HIGH	HIGH	YES	MED	MED
C. nigriceps	3	2.8 (0.7)	2	HIGH	HIGH	NO	HIGH	–[8]
Tetraponera penzigi	4	1.2 (0.1)	1	MED	N/A[5]	NO	LOW	MED

[1] Dominance ranks taken from Palmer et al. (2000); [2] average colony size differs significantly among ant species; ANOVA, $F_{3,159} = 78.07$, $p < 0.0001$; [3] in contests among queens for establishment sites in swollen spine domatia (*Crematogaster sjostedti* colonies appear to spread primarily by fission, and independent foundress queens have not been observed), Stanton et al. (2002); [4] Palmer and Brody (2007); [5] *Tetraponera penzigi* destroys host tree leaf nectaries, Palmer et al. (2002); [6] for size-matched trees, see Palmer (2004); [7] from Brody et al. (2010); [8] *C. nigriceps*-occupied trees rarely flower because this ant species castrates host plants Stanton et al. (1999).

Note: The most competitively dominant ant species (*C. sjostedti*) appears to be a relatively ineffective host-tree defender.

specialized domatia, Davidson and McKey, 1993; Chomicki et al., 2015), and can be found in cavities within both live *A. drepanolobium* and dead snags, as well as hollows within the trunks of other woody plant species in these habitats.

These four ant species compete strongly both inter- and intra-specifically for *A. drepanolobium* trees; each tree hosts only a single ant species, and virtually all trees are occupied. Because of the high host plant densities in many areas, inter-specific and intraspecific conflicts among neighboring colonies for the possession of host plants are common, and the outcome of competition is determined largely by colony size (Palmer, 2004). There is a hierarchy in dominance of mature colonies of the four ant species (from low to high): *Tetraponera penzigi* < *C. nigriceps* < *C. mimosae* < *C. sjostedti*. This hierarchy is paralleled by a gradient in the mean average number of trees occupied by each ant species (and therefore colony size, Table 10.1). It also sets up a successional series, with the least dominant ant, *T. penzigi*, occupying the smallest trees on average, and *C. sjostedti* the tallest. In the sections that follow we discuss in turn each ant species, and its unique relationship with *A. drepanolobium*.

The Four Acacia Ant Species

Tetraponera penzigi, one of the most widespread associates of *A. drepanolobium* (Hocking, 1970), is a narrow-bodied, monogynous (one queen per colony) species with colonies that typically span only 1–2 canopies (Table 10.1). This species is a fungal farmer (Visiticao, 2011) which also gleans small food items (e.g., pollen, fungal spores) from surfaces of the host plant (Palmer, 2003). *Tetraponera penzigi* modifies host plants in two ways that decrease the frequency of takeovers by aggressive neighboring colonies. First, this narrow-bodied species maintains very small entry holes on swollen spine domatia, which are too small to permit passage of the larger-bodied *Crematogaster* species. Consequently, when taking over *T. penzigi*-occupied host plants, *Crematogaster* species must enlarge holes by chewing (Palmer et al., 2002). Second, *T. penzigi* workers chew and destroy virtually all leaf nectaries on their host trees. These "priority effects" increase the costs (hole enlargement) and decrease the benefits (nectary availability) of host plant takeover, reducing the probability of competitive displacement by aggressive *Crematogaster* neighbors (Palmer et al., 2002).

Crematogaster nigriceps is also a competitively subordinate, monogynous species, with colonies that typically span 2–3 host plants. This species also engages in behaviors that might be related to its position low in the dominance hierarchy, both forms of meristem pruning. First, they remove many (Stapley, 1998; Martins, 2013) or most (Stanton et al., 1999) of the axillary meristem at the nodes along the branches, leaving only those at swollen spines, and greatly reducing the number of leaves on each tree. The behavior also strongly reduces flower production, in some areas effectively sterilizing host trees (but see Martins, 2013; Tarnita et al., 2014). While the reasons for this sterilization behavior have not been identified experimentally,
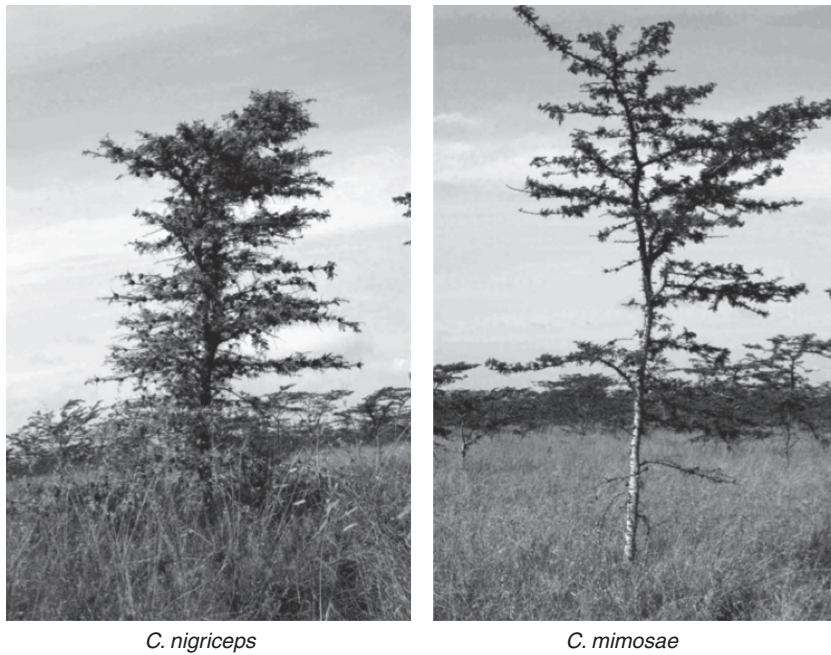
C. nigriceps   C. mimosae

Figure 10.1.   Contrasting effects of different resident ant species on *Acacia drepanolobium* architecture. *Crematogaster nigriceps* prunes host plant canopies, and their host trees (left panel) can be identified from a distance by their compact canopies, high level of branching, restricted lateral growth, and high densities of swollen spines. Contrastingly, host plants occupied by *C. mimosae* (right panel) have greater lateral growth, lower levels of branching, and lower swollen spine densities. Photo credit: Todd M. Palmer.

it may increase host plant allocation to domatia production to resident ants, as noted for other systems (Frederickson, 2009). Consistent with this hypothesis, *C. nigriceps*-occupied trees produce domatia in much greater abundance than trees occupied by the other three ant species (Figure 10.1). Second, *C. nigriceps* engages in selective pruning of apical meristems, reducing the lateral growth of their host trees, but largely in the direction of trees occupied by competitively dominant species, in particular *C. mimosae*, slowing or even preventing the physical contact between branches that serve as a corridor for ant takeovers (Stanton et al., 1999).

Crematogaster mimosae* is often the most abundant ant species in the system, in some areas occupying ca. 50 percent of host trees (Hocking, 1970; Young et al., 1997; Palmer, 2004; Martins, 2010). Colonies of this species can be either monogynous (single-queen) or polygynous (multiple-queen) (Stanton et al., 2002, 2005), and typically occupy an average of 4–5 host plants. *Crematogaster mimosae* is among the most mutualistic of the four ant species, supporting high rates of plant growth and low host-plant mortality (Figure 10.2) (Palmer et al., 2008a). Nonetheless, in addition to harvesting nectar from the nectaries and foraging off-tree (as do all
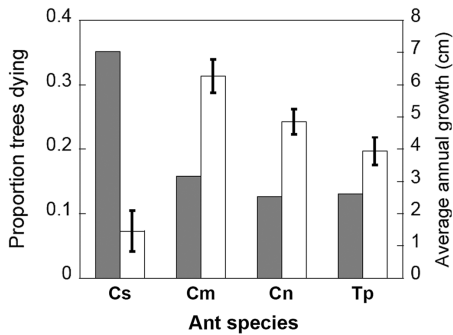
Figure 10.2.   Contrasting effects of different ant species on *Acacia drepanolobium* vital rates. Average annual growth rate (white bars ± SEM) and cumulative mortality (gray bars) for host trees occupied by the four acacia ant species over an eight-year observation period. Tp = *T. penzigi*, Cn = *C. nigriceps*, Cm = *C. mimosae*, and Cs = *C. sjostedti*. Host plants occupied by *C. sjostedti* suffer much higher mortality than those occupied by the other acacia ant species. *Crematogaster mimosae* promotes the highest rates of plant growth, followed by *C. nigriceps* and *T. penzigi* (adapted from Palmer et al., 2008a).

three *Crematogaster* species in this system) (Palmer, 2003, 2004), *C. mimosae* tends scale insects (Coccidae) on its host trees (*Hockiana insolitus* and *Ceroplastes* spp., Baker, 2015).

Crematogaster sjostedti is a non-obligate symbiont on *A. drepanolobium*, and can be found both on other acacia species (*A. seyal* var *fistula*, Young et al., 1997, and *A. zanzibarica*, Cochard and Edwards, 2011) as well as in hollow cavities within other woody plants and occasionally dead snags. This species occupies the greatest number of trees per (multi-queen) colony (Table 10.1), is competitively dominant, and is often found on the oldest and largest trees. Unlike the other three species, *C. sjostedti* does not live in swollen spine domatia, but instead occupies and raises brood in cavities in the stems of their host trees. (In some locations, *C. sjostedti* has been observed to construct and reside within papery nests on the outside of branches, Cochard and Edwards, 2011). Many of these cavities are excavated by the larvae of large cerambycid beetles, which *C. sjostedti* appears to facilitate (Palmer et al., 2008b), and which likely decrease the rates of plant growth and increase mortality (Figure 10.2). *Crematogaster sjostedti* is the least active against herbivores (Palmer et al., 2008b), and least mutualistic of the four ant species (Table 10.1) *Crematogaster sjostedti* also tends scale insects (*Ceroplastes* spp.), although at lower frequency than *C. mimosae*.

Species coexistence among the acacia ants – intense competition among colonies for host trees, coupled with a linear dominance hierarchy, motivates the question of how these four ant species coexist. Prior work has demonstrated that a number of mechanisms operate to support species coexistence in this guild, including competition-colonization tradeoffs, niche partitioning and priority effects (Stanton et al., 1999; Palmer, 2001; Palmer et al., 2002; Stanton et al., 2002; Palmer, 2003,

2004; Stanton et al., 2005). Tradeoffs in colonization versus competitive ability are particularly prominent in this system; *Tetraponera penzigi* and *C. nigriceps* are strong colonists, both investing reproductive effort heavily in the production of queens, while *C. mimosae* and *C. sjostedti* are dominant competitors, investing disproportionately in the production of workers (Stanton et al., 2002). Intriguingly, the dominance hierarchy in conflicts among queens for establishment sites (swollen spine domatia) is exactly the *opposite* of that for mature colonies (Table 10.1)! This ontogenetic reversal in competitive ability further reinforces the strong colonization and establishment success of *T. penzigi* and *C. nigriceps*. And for the dominant *C. mimosae* and *C. sjostedti*, rapid rates of colony growth are reinforced by these species' dominance in foraging for protein sources off of host plants (Palmer, 2004), and may be further supported by their tending of scale insects (K. M. Prior and T. M. Palmer, unpublished manuscript).

The four acacia ant species differ strongly, not only in their natural histories but also in the costs imposed and benefits provided to host plants. In the next section, we discuss this variation within the mutualism, and consider its ecological consequences.

Complexity within the *Acacia drepanolobium*-Ant Symbiosis: Variation in Benefits and Costs

The net benefits of mutualism are a balance between the goods or services obtained, and the costs that accrue in obtaining those benefits (Chapter 11). There may be several axes of benefit to plants in an ant-plant interaction, including protection from herbivory (Janzen, 1966), fertilization (Huxley, 1978; Sagers et al., 2000), and the pruning of neighboring plants (Janzen, 1969; Davidson et al., 1988; Fiala et al., 1989; Morawetz et al., 1992). So too can there be a variety of costs, including direct (e.g., metabolic) costs such as the production of extrafloral nectar, food bodies,and domatia, and other costs ("ecological costs," Frederickson et al., 2012) such as the collateral deterrence of beneficial insects such as pollinators (Ness, 2006), the tending by ants of scale insects or aphids (Styrsky and Eubanks, 2007, but see Pringle et al., 2011), and even sterilization by particular ant associates (Stanton et al., 1999; Yu et al., 2004). Predicting how the "balance of trade" in mutualism may shift across spatial or temporal environmental variation requires that we decompose mutualism into its constituent costs and benefits.

Variation in the Benefit of Defensive Symbiotic Ant Species

Acacia ants rapidly respond to host plant disturbances, emitting pungent alarm pheromones to which nestmates immediately respond and recruit (Wood and Chong, 1975). These workers swarm onto the muzzle of larger herbivores (or onto the bodies of invertebrate herbivores) and locate softer tissue (e.g., mucus membranes) and

bite down and/or sting. This defense can be quite formidable, as tens to hundreds of workers may swarm onto herbivores as they feed. The four acacia ant species vary strongly in their levels of aggressive response to disturbance (Table 10.1), as well as the extent of herbivore damage to their host plants. Following both real and simulated browsing, *C. mimosae* and *C. nigriceps* display the strongest recruitment of workers to the site of the disturbance, while *T. penzigi*'s response is relatively weak, and *C. sjostedti*'s response is almost non-existent (Palmer and Brody, 2007; Martins, 2010). Correspondingly, levels of both vertebrate and invertebrate herbivory tend to be higher on *T. penzigi*- and *C. sjostedti*-occupied trees, and lower on acacias occupied by *C. mimosae* and *C. nigriceps* (Palmer and Brody, 2007). These differences are clearly driven by differences in aggressive defense by symbiotic ants; in a five-year ant removal experiment, the overall levels of attack (by vertebrate browsers, cerambycid beetles, and stem- and leaf-galling insects) increased on ant-removal trees for *C. mimosae* and *C. nigriceps*, while attack rates on trees occupied by *C. sjostedti* and *T. penzigi* did not differ from their paired trees from which these species had been removed. Patterns of browsing by black are congruent with these findings. Martins (2010) found that rhinos fed on acacias occupied by the aggressively defensive *C. mimosae* and *C. nigriceps* significantly less often than expected based on their relative abundances, and fed more often than expected on acacias occupied by *T. penzigi*.

Yet even the most aggressive acacia ants do not appear to effectively deter all African browsers. For example, evidence for giraffe deterrence is equivocal. In one study conducted in the Kajiado district of Kenya, Martins (2010) found that Maasai giraffes (*Giraffa camelopardalis tippelskirchi*) fed on acacias occupied by *C. mimosae* and *C. nigriceps* significantly less often than expected by chance, while feeding on trees occupied by *T. penzigi* more frequently than expected. In the Athi Kapiti plains of Kenya, Madden and Young (1992) found that while *Crematogaster* ants shortened the duration of feeding bouts by giraffe calves, they did not reduce feeding bout durations for adult giraffes. In Laikipia, experimental density reductions of *C. mimosae* had no effect on giraffe damage to host plants over one year (Palmer and Brody, 2013), while in a 4.5-year ant removal experiment (Stanton and Palmer, 2011), damage consistent with giraffe feeding was significantly higher on paired ant-removal trees than ant-occupied trees for both *C. mimosae* and *C. nigriceps*.

Tolerance to herbivory appears to play a large role in *Acacia drepanolobium*'s defensive repertoire. In a longer-term ant removal experiment, acacias without resident ants grew faster and reproduced more than ant-occupied trees, despite much higher levels of herbivory on ant removal plants (Stanton and Palmer, 2011). These data suggest that acacia ants may impose large metabolic costs to host plants which may not be offset, at least over the shorter term, by protection from chronic but non-lethal herbivory. It is important to emphasize, however, that even this 4.5-year experiment is fairly short-term, relative to the long lifespan of this tree species (> 150 yrs). Over longer time scales, chronic herbivory, especially by the wood boring larvae of cerambycid beetles, is likely to have a large impact on plant growth and

Figure 10.3.   An African elephant (*Loxodonta africana*) sniffs an *Acacia drepanolobium*, assessing how well-defended the plant is by symbiotic ants. The four acacia ant species produce pungent and different volatile alarm pheromones (Wood et al., 2002) when they detect herbivores, which elephants may use as cues that indicate both the identity of the ant species in residence, as well as the density of the resident colony. Elephants tend to attack *Acacia drepanolobium* with very low densities of acacia ants, or those occupied by *Crematogaster sjostedti*, the least aggressive ant species. Photo: Kathleen Rudolph. (A black-and-white version of this figure will appear in some formats. For the color version, please refer to the plate section.)

survival (Palmer et al., 2008a). In general, tolerance of herbivory may have evolved in *A. drepanolobium* in part due to the variable nature of protection conferred by different ant species. Because ant species turn over frequently on host plants, tolerance of herbivory may enable plants occupied by poor defenders to continue to survive until they are replaced by more aggressive ant defenders. We discuss this possibility in greater detail later in this chapter.

Elephants: Key Drivers of the Acacia drepanolobium *-Ant Mutualism*

If ants impose such high metabolic costs to host plants, yet do not appear to provide sufficient benefits in the form of protection to offset these costs, then why associate with ants at all? The key to this puzzle, emerging from two decades of study of this mutualism, appears to be elephants (Figure 10.3). Elephants are a

distinctive herbivore in that they are capable of imposing catastrophic herbivory to trees, stripping branches, knocking down and destroying the main stem, and girdling trees by feeding on bark and phloem/cambium. Several studies have demonstrated that ants are highly effective defenders of host plants from catastrophic herbivory by elephants (Goheen and Palmer, 2010; Palmer and Brody, 2013). In the most comprehensive of these, Goheen and Palmer (2010) used a combination of experiments, feeding trials with captive elephants and remote sensing to show that acacia ants regulate woody plant cover in *A. drepanolobium* savannas by strongly deterring elephant herbivory. The efficacy of ant defense likely results from a combination of high ant densities on host plants (up to 90,000 workers on some trees, Hocking, 1970) and their tendency to attack areas of thin skin and mucous membranes by biting down and holding fast with their mandibles. Despite the massive size and eponymous thick skin of these pachyderms, the "Achilles heel" of these herbivores appears to be their trunks, whose inside surfaces are highly innervated to allow for fine motor coordination and sensitivity. While giraffes use their long, prehensile tongues to swipe away ants from their muzzles (Palmer and Goheen, unpublished data), elephants must use their trunks to feed, essentially inserting their "noses" directly into a canopy swarming with aggressive ants. Elephants also avoid attacks by bees (Vollrath and Douglas-Hamilton, 2002), further suggesting that swarming Hymenoptera may be a potent defense against these enormous and powerful herbivores.

Although catastrophic herbivory by elephants can occur, the annual risk to any individual plant is likely fairly low, owing to the relatively low abundance of elephants and high density of trees in many savanna and bushland systems. As a consequence, ant removal experiments over shorter time periods (relative to the long lifespan of the tree) may (Palmer and Brody, 2013) or may not (Stanton and Palmer, 2011) reveal these risks. Nonetheless, because intense herbivory by elephants can greatly reduce fitness, this rare form of herbivory likely generates potent selection on acacias for strong defense against these herbivores (Goheen and Palmer, 2010). Maintaining ant colonies, despite their high metabolic costs, appears to act as a critical "insurance policy" against rare but potentially lethal elephant herbivory. In this and other ant-plant systems (Pringle et al., 2013), rare events may be easily missed in short-term experiments, highlighting the need to conduct long-term studies of ant-plant associations, particularly when host plants are long-lived.

Collateral Damage: Deterrence of Pollinators

Although the aggressive ant guards clearly benefit plants by attacking herbivores, these same ants could be a liability when it comes to beneficial visitors such as pollinators (Chapter 13). However, both *A. drepanolobium* and its closely related congener *A. zanzibarica* appear to have evolved mechanisms to deal with this conflict of interest. In a population of *A. zanzibarica* in Mkomazi, Tanzania, Willmer, and Stone (1997) demonstrated that resident ants are deterred from flowers during

the peak of pollen dehiscence, probably via a chemical in the pollen itself. In a later study that included both *A. drepanolobium* and *A. seyal* var. *fistula*, a related species with an ecotype that produces swollen spines, Willmer et al. (2009) similarly showed that floral volatiles produced by these species exerted a deterrent effect on ants, although the effects were weaker for these species than for *A. zanzibarica*.

Overall, the benefits provided by different acacia ants clearly vary substantially. But benefits are only one side of the "coinage" in the economy of mutualisms. In the next section, we turn our attention to the costs imposed by different ant species, again revealing strong variation and highlighting the strikingly high costs to host plants of maintaining ant associates.

Variation in Costs Imposed by Different Acacia Ant Species

Much of the research on ant-plant protective mutualisms has centered on identifying and quantifying the benefits of these interactions to participants, and in particular to host plants (reviewed in Heil and McKey, 2003). Interestingly, far less research has focused on the costs of mutualism to the participants, but research on the *Acacia drepanolobium* ant mutualism suggests that these direct costs can in some cases be quite high. For example, in a 4.5-yr study, removing the three *Crematogaster* species from host plants resulted in much higher rates of growth and higher rates of reproduction for host trees (Stanton and Palmer, 2011).

In contrast, host plants from which *Tetraponera penzigi* was removed did not grow or reproduce more than control trees where colonies were left in residence. *Tetraponera penzigi* destroys host plant nectaries and does not tend scale insects, suggesting that the high costs borne by trees occupied by the *Crematogaster* species largely result from photosynthate consumed by these three ant associates, both directly in the form of extrafloral nectar, and indirectly through honeydew exuded by scale insects, which are tended by both *C. mimosae* and *C. sjostedti*.

Extrafloral nectar and scale exudates are two very different pathways by which plant photosynthate is supplied to acacia ants. Rates of extrafloral nectar production appear to be under the plant's control, as EFNs are a plastic trait that responds to variation in herbivory, with trees producing fewer active nectaries when herbivores are experimentally excluded (Huntzinger et al., 2004; Palmer et al., 2008a). At the level of individual nectaries, it is not known how extrafloral nectar secretion is induced, but observations suggest it may be mediated by the acacia ants themselves. When resident colonies are experimentally removed from host plants, nectaries become inactive (Stanton and Palmer, 2011), and other non-acacia ant species (e.g., *Pheidole megacephala*) do not appear to be able to induce nectar production on these trees (Riginos et al., 2015).

When host plants change patterns of EFN production, shifts in host plant occupancy can occur, mediated through changes in the dynamics of competition between neighboring ant colonies. A reduction in active nectaries in response to an experimental reduction in herbivore pressure on host plants caused reductions in the size of *C. mimosae* colonies, making them vulnerable to takeover by neighboring

C. sjostedti colonies, which are less mutualistic (Palmer et al., 2008a). These results raise the intriguing possibility that *A. drepanolobium* may exert some control over the identity of its resident colonies through "partner screening" (Archetti et al., 2011), where the conditions established by the host plant select for the best adapted mutualist (Heil, 2013). When host plants are small (i.e., saplings) and have not yet emerged from the grass layer, competition or other forms of environmental stress constrain EFN production, which in turn favors the establishment and persistence of the moderately defensive and less metabolically demanding *T. penzigi* (Palmer, unpublished data). As acacias grow to larger sizes, nectar production may be less costly relative to the plant's overall carbon budget, allowing hosts to produce more nectar favoring the aggressive and metabolically demanding *C. mimosae* and *C. nigriceps* (Palmer et al., 2010).

As contrasted with EFN tending, colonies that tend scale insects have greater control of resource provisioning by their hosts. Tending scale insects may augment colony growth and activity level and buffer colonies from times when plants retrench their provisioning of extrafloral nectar (e.g., during drought or after exclusion of large herbivores, Palmer et al., 2008a). Recent experiments (K. M. Prior and T. M. Palmer, unpublished) point to the important role that scale insect associates play in the growth and energetics of *C. mimosae* colonies, an ecologically dominant species in many areas where *A. drepanolobium* occurs (Hocking, 1970; Young et al., 1997; Martins, 2010). Colonies whose scale insects were removed had lower activity levels and lower recruitment to simulated herbivory, and were more likely to be taken over by neighboring colonies than colonies whose scale insects were left intact. Scale-removal trees also produced more domatia (owing to increased branch growth) and more fruit, suggesting that scale tending by ants is costly to host plants. Yet despite these costs, the net effects of harboring scale insects may be positive for *A. drepanolobium*; acacias from which scale insects were removed were significantly more likely to be destroyed by elephants than trees where scale insects were present, suggesting that the increased colony activity and/or size driven by excess carbohydrates from scale insects feeds back to acacias through stronger ant defense.

The Costs of Ant Wars

Wars between neighboring colonies can have costly consequences for both ants and host plants. Following battles, one or both warring colonies are at increased risk for hostile takeovers from yet *other* neighboring colonies (Rudolph and McEntee, 2016; Ruiz-Guajardo et al., 2017), suggesting that these conflicts make colonies highly vulnerable to takeover by other neighbors. But *C. mimosae* may employ strategies to deal with those consequences, at least in intraspecific battles: in an elegant set of experiments, Rudolph and McIntee (2016) showed that for more than half of the intraspecific battles they experimentally induced, relatedness within the victorious colony declined, possibly as a result of the adoption of non-kin brood, or by queen-right fusion of the warring colonies. These results point to the primacy

of maintaining high worker densities within this intensely competitive community. Yet even with the possibility of colony fusion, post war colonies are typically at reduced densities, and as a result often suffer increased mammalian herbivory (Rudolph and McEntee, 2016), including catastrophic herbivory by elephants (Palmer and Brody, 2013).

The High Cost of Mutualism Constrains Host Plant Distribution

The high cost of hosting ant associates also appears to play a prominent role in restricting the distribution of *A. drepanolobium* to nutrient-rich black cotton soils. Many areas in which this tree species occurs are bordered by nutrient-poor sandy clay loam soils, which are dominated by less well-defended acacia species, support higher densities of herbivores, and from which *A. drepanolobium* is largely absent. This sharp disjunction appears to result from the interaction between herbivory and the costs of maintaining the defensive mutualism: in a set of transplant experiments, Pringle et al. (2016) demonstrated that resource addition and herbivore exclusion increased the performance of *A. drepanolobium* saplings transplanted to nutrient-poor red soils, while having no effect on *A. drepanolobium* establishment in nutrient-rich black cotton soils. Saplings exposed to herbivory on red soils had much lower survival than their black soil counterparts, and the overall higher level of herbivory on red soils constrained the number of domatia and EFNs produced by host plants. The authors concluded that resource limitation on nutrient-poor red soils constrains defensive investment for *A. drepanolobium*, increasing the vulnerability of this myrmecophyte to high levels of herbivory on red soils, and thereby restricting its distribution to more fertile black cotton soils. These results add to a growing body of literature demonstrating that mutualism can play important roles in constraining the realized niches of participant species (reviewed in Palmer et al., 2015).

With such variation in the costs and benefits of partnering with different ant species, it is perhaps unsurprising that each ant species differentially affects host plant vital rates. In the sections that follow, we review these differential impacts and how they integrate to affect the lifetime fitness of *A. drepanolobium*.

Ant Species Exert Strong and Differential Influences on Host Plant Vital Rates

Experiments and long-term observations have demonstrated that the four acacia ants exert very different impacts on host plant vital rates (Palmer et al., 2010); plants occupied by *C. mimosae*, *T. penzigi* and *C. nigriceps* have the highest growth and survival, while plants occupied by *C. sjostedti* have both the highest fruit production and the greatest mortality (Table 10.1, Figure 10.2). Intriguingly, the most "optimal" ant associate (from the host plant perspective) may change as trees progress through their ontogeny; at early ontogenetic stages, plants occupied by

T. penzigi and *C. nigriceps* have the highest survivorship, probably owing to the fact that these species seldom abandon small host plants. By contrast, *C. sjostedti* and *C. mimosae*, with colonies that often extend across > 5 host plant canopies, often abandon small "satellite" trees during periods of environmental stress (e.g., drought) – and abandoned trees have considerably lower survival rates than trees with any species of ant (Palmer et al.; 2010). As plants grow larger and gain more value to ant colonies, *C. mimosae* is less likely to abandon them, and plants occupied by this species have higher rates of growth and reproduction than those occupied by *T. penzigi* and *C. nigriceps*.

A Lifetime of Partnerships: Integrating Costs and Benefits to Host Plants across the Guild of Acacia Ants

With such strong variation in the costs and benefits of associating with different ant partners, including antagonists such as *Crematogaster sjostedti*, and sterilizing partners like *C. nigriceps*, it is reasonable to ask whether associating with these ants yield net benefits to host plants in the first place. Addressing this question requires evaluating the effects of partnering with different ant species on the lifetime fitness of host plants, a challenging task given the long (>150-year) lifespan of these trees. In a study that combined long-term (eight-year) monitoring of >1700 trees, demographic modeling and experiments, Palmer et al. (2010) showed that the fitness benefits to *Acacia drepanolobium* increased as trees interacted with more symbiotic ant species, including the sterilizing *C. nigriceps* and the antagonistic *C. sjostedti*. This seemingly paradoxical result emerged from the order in which different ant species typically occupy host plants (Figure 10.4). During early life stages, when survivorship is far more important than reproduction, *A. drepanolobium* is frequently occupied by *T. penzigi* and *C. nigriceps*, two species which promote high host plant survival due to their low rates of host plant abandonment. Later in life, *C. mimosae* becomes the most common occupant, and this species both protects host plants and is associated with moderate levels of reproduction. At very late life stages (Young et al., 1997), host plants become increasingly occupied by the less mutualistic *C. sjostedti*, investing less in ant rewards, and shunting resources toward reproduction (Table 10.1). Hence, host plants are able to trade-off survivorship and reproduction at different life stages, such that the full suite of ant occupants results in the highest rates of *A. drepanolobium* population growth (Palmer et al., 2010). Across a tree's lifetime, it is modeled to undergo many transitions in occupancy (> 15, Palmer et al., 2010) and to partner with each of the four acacia ant species.

Much about the dynamics of the *A. drepanolobium*-ant mutualism has been revealed from the study of host plants and ants, and it is found that no mutualism functions in isolation of the community that surrounds it. In the next section we turn our attention to the broader community in which this interaction occurs, examining both biotic and abiotic drivers that shape the dynamics of the mutualistic association.
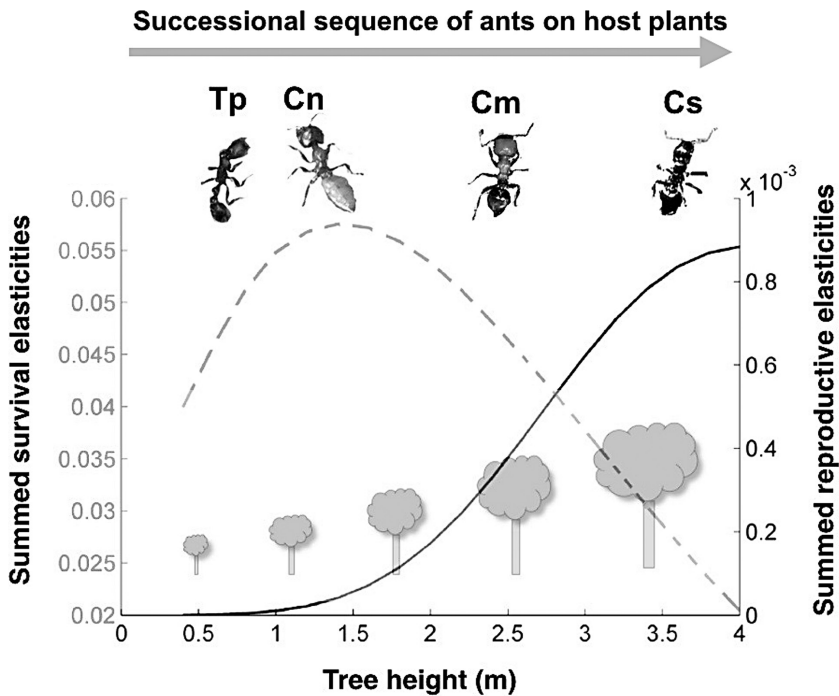
Figure 10.4. Sensitivity of *A. drepanolobium* population growth (🌳) to host plant survival (dashed line) and reproduction (solid line) across the ontogeny of the host plant. The successional sequence of acacia ants is shown at the top, Tp = *Tetraponera penzigi*, Cn = *Crematogaster nigriceps*, Cm = *C. mimosae* and Cs = *C. sjostedti*. Early in plant ontogeny, occupation by the strongly colonizing *T. penzigi* and *C. nigriceps* is most likely, and both species confer high survivorship benefits, while *C. nigriceps* temporarily sterilizes host plants while in residence. Later in life, occupation by *C. mimosae* becomes more likely; this species confers both strong survivorship and moderate reproduction. At late life stages, host plants are more likely to be colonized by the antagonistic *C. sjostedti* and invest heavily in reproduction while suffering higher rates of mortality. Host plants are able to trade off survival and reproduction at different life stages, maximizing fitness in the face of strong variation in the costs and benefits of associating with different symbiotic ant species (adapted from Palmer et al., 2010).

Effects of the Broader Community on the Acacia-Ant Mutualism: Biotic, Abiotic and Anthropogenic Effects

Termite Mounds Structure Competition and Patterns of Host Plant Occupancy among Acacia Ants

In some habitats where *Acacia drepanolobium* is found, strong spatial heterogeneity in soils is generated through the subterranean action of termites from the genus *Odontotermes*. Through their mound-building activities, these termites gener-ate "islands of fertility," with increased water infiltration (Arshad, 1981; Palmer,

2003; Fox-Dobbs et al., 2010), higher levels of organic carbon, nitrogen and phosphorus (Palmer, unpublished data), higher rates of *A. drepanolobium* growth and more abundant invertebrates, an important and N-rich prey source for the three *Crematogaster* species (Palmer, 2003; Fox-Dobbs et al., 2010; Pringle et al., 2010). This increase in the resource base favors more the more aggressively foraging *C. sjostedti* and *C. mimosae*, resulting in larger colonies of both of these species near mounds. The underlying heterogeneity in resources generated by the action of termites "cascades upward" to shape the spatial distribution of ants on host plants; in productive termite mound microhabitats, the competitively dominant *C. sjostedti* and *C. mimosae* are disproportionately successful in displacing the subordinate *C. nigriceps* and *T. penzigi* from large host plants, while these subordinate species are more successful in less productive inter-mound areas (Palmer, 2003).

Large Herbivores

Several lines of evidence suggest that large browsing herbivores – in particular elephants – strongly influence both the ecology and evolution of this ant-plant mutualism. In a long-term, large-scale exclosure experiment, we found that *A. drepanolobium* reduces its investment in both extrafloral nectar and domatia production in the absence of vertebrate herbivory. This reduction in investment in ant associates shifts the balance of competition from the nectar-dependent and strongly mutualistic *C. mimosae* in favor of the antagonistic *C. sjostedti*, which does not depend on host plant rewards (Palmer et al., 2008a). As a consequence, *C. sjostedti* becomes the most abundant ant occupant where herbivores have been eliminated, with negative consequences for host plants (Figure 10.1). Consequently, browsing by large mammals serves to reinforce the protective mutualism between acacias and *C. mimosae*, by inducing reward production that allows this strongly mutualistic species to retain its competitive edge. These are the very herbivores most threatened by human activities, including habitat conversion, competition with livestock and direct killing.

Fire

Africa has been called the fire continent, and much of this has been anthropogenic fire, which may date back to hundreds of thousands of years (Archibald et al., 2012; Archibald, 2016). Natural and anthropogenic fire are likely drivers of the evolution in *A. drepanolobium* of thick-bark (Midgley et al., 2016) and ready coppicing after the loss of aboveground biomass (Okello et al., 2001; Okello et al., 2008). However, perhaps even more striking evidence of fire as an evolutionary force in *A. drepanolobium* ecosystems is illustrated by the behavior of acacia ants. When both *C. mimosae* and *C. nigriceps* detect smoke, they quickly initiate an evacuation of host plants, rapidly moving brood and alates down the stem of the tree and into cracks within the heavy clay soil surrounding the tree's base (Palmer et al., 2008b). This evacuation behavior is highly effective;

survival rates after fires of colonies of *C. mimosae* and *C. nigriceps* are 85 percent and 70 percent, respectively (Sensenig et al. 2017). In contrast, fewer than 10 percent of the colonies of *T. penzigi* survived controlled burns. It appears that the behavior of *C. sjostedti* of living in stem cavities makes them less vulnerable to fires than living in swollen spines; approximately 50 percent of their colonies survive fires. Re-colonization of trees after fire occurs by two mechanisms. First, colonies that successfully evacuate domatia to safe havens belowground may simply emerge after the fire and return to their host tree. Second, trees that have lost their colonies can be recolonized by ants from nearby trees with surviving colonies. As a consequence, burned areas have disproportionately more *C. nigriceps* colonies and disproportionately fewer *T. penzigi* colonies than unburned areas (Sensenig et al. 2017).

Fuelwood Collection

Acacia drepanolobium is widely collected for fuelwood and charcoal production (Okello and Young, 2000). Because *A. drepanolobium* readily coppices after the loss of aboveground tissue, this harvesting usually does not kill the trees. However, when harvesting intervals are short (as they often are in fuel-limited environments), these coppicing trees are kept in small-statured populations (authors' personal observation, and Andrews and Bamford, 2008). We have visited two sites in different parts of Kenya (Athi Plains and Naivasha) characterized by intense repeat harvesting of *A. drepanolobium*. At both sites, the ant community was essentially limited to the early successional ant species *T. penzigi* and *C. nigriceps* (T. M. Palmer and T. P. Young, personal observation)

How Does the Ant-Plant Mutualism Affect the Broader Community?

Because *Acacia drepanolobium* is a foundation species (sensu Dayton, 1972), the effects of acacia ants on plant vital rates have the potential to reverberate through the entire community. For example, Goheen and Palmer (2010) showed that by effectively protecting host plants from elephants, acacia ants play a central role in regulating woody plant cover in black cotton habitats. This is especially impressive when one considers that the average ant weighs about 5 mg, while a 5000-kg elephant (the size of a large male) is literally a billion times more massive! Because woody plant cover regulates a host of ecosystem properties in savannas, including carbon storage, fire-return intervals, predation-risk, food web dynamics, nutrient cycling and soil-water relations (Belsky et al., 1989; Pringle and Fox-Dobbs, 2008; Holdo et al., 2009; Riginos et al., 2009; Ford et al., 2014; Riginos, 2015), these minute yet pugnacious bodyguards can exert powerful indirect effects across entire landscapes.

The key role of the ant-acacia mutualism in shaping black cotton savannas is becoming increasingly evident with the advent of a recent invasion in some parts of
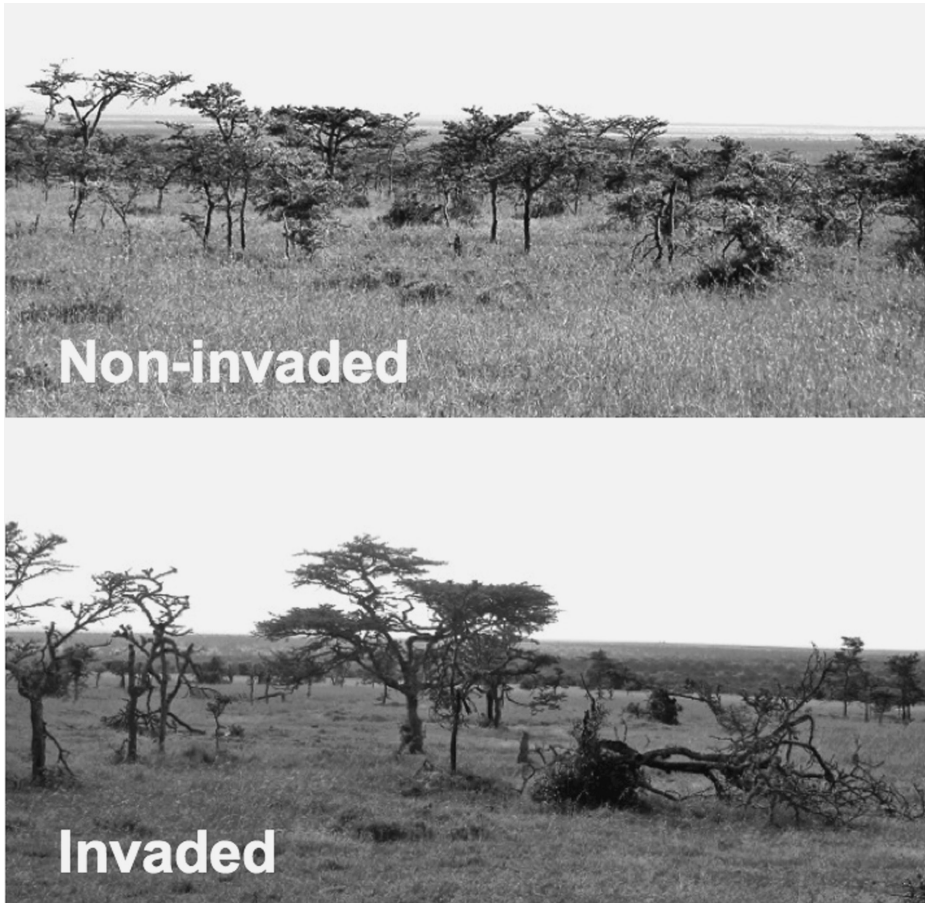
Figure 10.5. Elephant damage to *Acacia drepanolobium* increases strongly in areas where the native acacia-ant mutualism has been disrupted by invasion by *Pheidole megacephala*. The invasive ant displaces native acacia ants, but does not protect host trees from mammalian herbivores. Thus, invaded areas (bottom panel) have a much higher frequency of moderate to severe elephant damage to host plants, relative to non-invaded savannas (top panel). Photo credits: Todd M. Palmer.

East Africa by *Pheidole megacephala*, the "big-headed ant" (Chapter 15). *Pheidole megacephala* forms massive super-colonies and aggressively preys on arthropods while displaying little or no aggression toward larger animals. This species is a recent invader of the Laikipia region (ca. within the last decade), and in numerous areas is disrupting the *A. drepanolobium*-ant mutualism by nearly or completely exterminating native acacia ants on host plants. In contrast to native acacia ants, *P. megacephala* does not protect trees from vertebrate herbivores. As a result, in areas where it has invaded, browsing by elephants has increased substantially, resulting in higher levels of damage and mortality to host plants (Figure 10.5, Riginos et al., 2015). Over the longer-term, disruption of the ant-acacia mutualism by *P. megacephala*

may strongly alter the extent of woody plant cover in these savannas, with cascading consequences for the entire community.

Summary and Future Directions

More than two decades of research on *A. drepanolobium* and its ant associates has revealed much about the complex and variable nature of ant-plant symbiosis. The system has also served as a model for integrating the study of mutualism into a community context, revealing how both biotic and abiotic environmental variation can shape ant-plant interactions, and demonstrating how a foundational mutualism can structure its surrounding community at large spatial scales. Yet much remains to be learned about this widespread association: can host plants exert control over the identity of their ant occupants? What are the physiological mechanisms underlying host plant allocation to ant rewards versus other carbon demands? Does the multi-species nature of the ant-plant association buffer *A. drepanolobium* from environmental variation? What are the landscape-scale consequences of the mutualisms' disruption by *P. megacephala*? The list of questions is long, and research has only begun to scratch the surface of this intriguing study system.

Study of this symbiosis may also help to illuminate more general principles that underlie many of the worlds' mutualisms of conservation concern. Like corals and their dinoflagellate associates, and tropical trees and their pollinators or dispersers, *A. drepanolobium* is a long-lived species which interacts over its ontogeny with multiple shorter-lived partner species. A thorough understanding of the drivers of contingency in costs and benefits within mutualist networks may lead to a more predictive framework for understanding context-dependent outcomes in these widespread interactions. The broad distribution and highly tractable nature of the *A. drepanolobium*-ant interaction makes it an ideal candidate for these investigations.

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