

CHAPTER SIXTEEN

The trophic structure of tropical ant–plant–herbivore interactions: community consequences and coevolutionary dynamics

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Introduction

The first part of this paper examines the consequences of an interlocking set of mutualisms, involving ants, plants, bacteria and phloem-feeding insects, for the structure and functioning of herbivore-based food webs in tropical communities. This part draws heavily from important recent work by Davidson and colleagues (Davidson 1997; Davidson *et al.* 2003) and extends their discussion of community-level implications of their findings. The second part explores how trophic interactions evolve when coevolution produces specialized symbiotic ant–plant mutualisms, and is based largely on our own work on interactions between ants and *Leonardoxa* myrmecophytes of African rainforests. The paper complements a recent general review of ant–plant protection mutualisms (Heil & McKey 2003).

16.1 Ant–plant–herbivore interactions and tropical food webs

How food webs function, and how trophic interactions shape communities, have long been central questions in ecology. Interactions between organisms at adjacent trophic levels – predators and prey, parasites and hosts – and competitive interactions among organisms at the same trophic level, all occupy major roles in theories to explain the great species richness and other traits of tropical-forest ecosystems (Wright 2002). Following the lead of classic studies like those of Hairston *et al.* (1960) and Paine (1966), investigations of how communities function have increasingly taken into account not only these direct interactions, but

also indirect interactions that extend across several trophic levels. Do natural enemies of herbivores have measurable impacts on fitness of individual plants, on relative abundance of plant species, on primary productivity or on plant species diversity? Conversely, does variation in productivity or other processes at the first trophic level, through its effects on herbivores, influence processes and patterns at higher trophic levels? The frequency of such 'trophic cascades' in different ecosystems (Halaj & Wise 2001; Schmitz *et al.* 2000; Shurin *et al.* 2002), and the respective roles of 'bottom-up' and 'top-down' forces in the web of indirect effects (Dyer & Letourneau 2003; Terborgh *et al.* 2003; van Bael *et al.* 2003), are questions widely debated today (Chapter 15, this volume).

Compared with investigations of competition and predation as structuring forces, studies that address the roles of mutualisms in shaping communities are underrepresented (Wimp & Whitham 2001). A host of mutualisms form an important part of the structural glue of tropical forests. Among these are transport mutualisms, which permit, for example, the persistence of outcrossing plants at very low densities (Janzen 1971) and the escape of animal-dispersed seeds from density-dependent mortality of seeds and seedlings (Wright 2002); nutrition mutualisms, which allow plants to assimilate minerals rapidly in leached tropical soils and can affect community composition in complex ways (Kiers *et al.* 2000); and protection mutualisms, in which plants attract natural enemies of herbivores and as a result suffer less damage. This last category is particularly underrepresented in community-level studies. Protection mutualisms can by their very nature have far-reaching effects in food webs, because they involve not only direct (and often indirect) trophic exchanges between the two mutualists, but also interactions with at least one additional trophic level. Furthermore, selection acts on the mutualists to increase the strength of these interactions. Protection mutualisms may thus be particularly likely to generate effects that cascade well beyond the two mutualistic partners.

Ants are among the principal predators of arthropods in tropical forests (Novotny *et al.* 1999; Floren *et al.* 2002), and protection and nutritional mutualisms between ants and other organisms are a large part of the reason why. Ants participate in three kinds of mutualisms that are of key importance in determining their impact on the structure of ecological communities. First, many plants provide ants with direct rewards – energy-rich extrafloral nectar or pearl bodies – that encourage the presence and activity of these predators on the plant. Ants thus attracted can increase plant fitness by reducing damage caused by herbivores and/or pathogens. Second, many ants are engaged in protection mutualisms with herbivores, principally phloem-feeding hemipterans (formerly known as 'Homoptera' (von Dohlen & Moran 1995)) such as aphids, membracids, scale insects and mealybugs. The carbohydrate-rich excretions of these 'trophobionts' provide ants with an energy-rich food source. Ants also protect other

myrmecophilous herbivores, most notably caterpillars of many lycaenid butterflies (Pierce *et al.* 2002). Relationships with lycaenids are important for some plants, but in terms of importance at the community level they are dwarfed by those with hemipterans. Associations between ants and their trophobionts can have widely varied effects on plants (Cushman & Addicott 1991; Chapter 17). In some cases, ant-tended trophobionts are probably the plant's principal herbivores and the effect on the plant is negative. In other cases, the protective benefits (e.g. against chewing insects) conferred by trophobiont-tending ants appear to outweigh the costs to the plant, resulting in a three-partner mutualism of ant, trophobiont and plant.

In all the above-mentioned kinds of mutualisms, the rewards produced for ants are carbohydrate-rich, with low contents of nitrogen and highly unbalanced amino acid compositions (Davidson & Patrell-Kim 1996). Profiting from these abundant but unbalanced food resources appears to require – or at least is greatly aided by – the involvement of ants in a third type of mutualism, with endosymbiotic microbes that help to repair such nutritional imbalances. Although little studied so far, ant-microbe mutualisms appear especially important for tropical arboreal ants, the ecological group of ants for which exudates derived directly or indirectly from plants are of greatest importance in the diet (Davidson *et al.* 2003). Ant-tended hemipterans are in turn dependent on their own microbial symbionts (Delabie 2001).

Thus ants, the most important predators of arthropods in tropical forest canopies, are largely sustained by an interlocking set of mutualisms. Without these mutualisms, food webs in tropical forest communities would probably be very different from those we know. Before developing this argument, we will briefly review what is known about the three types of mutualisms directly involving ants (see also Heil & McKey 2003).

Ant-plant protection mutualisms based on direct food rewards

Extrafloral nectary-bearing plants are diverse and abundant in many tropical ecosystems (Schupp & Feener 1991; Pemberton 1998; Rico-Gray *et al.* 1998), although their frequency varies substantially among biogeographical regions (Heil & McKey 2003), habitats (e.g. Cogni *et al.* 2003) and plant life forms (Bentley 1981; Blüthgen *et al.* 2000). A variety of functions have been proposed for extrafloral nectaries. These include nutritional benefits to plants that attract soil-nesting ants to their base, resulting in better soil quality (Wagner 1997), and the distraction of ants from visiting flowers (Wagner & Kay 2002) or tending hemipterans (Becerra & Venable 1989). However, the most frequently demonstrated benefit to plants is attraction of protective ants (recently reviewed by Heil & McKey (2003)). Herbivory induces increased rates of nectar production by existing nectaries (Heil *et al.* 2001) and can even increase the number of nectaries formed by the plant following damage (Mondor & Addicott 2003). Whereas most nectaries are

fairly conspicuous structures, some are quite cryptic, and current surveys may thus underestimate their frequency. Most tropical biologists would probably be surprised, for example, to know that a plant as abundant and familiar as cassava, *Manihot esculenta* Crantz (Euphorbiaceae), secretes nectar at the base of petioles of young leaves (Bakker & Klein 1992); externally evident nectar-secreting structures are absent. The frequency of another type of direct food reward, pearl bodies – lipid- or carbohydrate-rich glandular trichomes harvested by ants (Schupp & Feener 1991) – is probably even more seriously underestimated, because unlike most nectary-bearing plants, once these ant-attractant food bodies are harvested, no evidence of any secretory structure is left behind. Only Schupp and Feener (1991) appear to have adequately surveyed the frequency of glandular trichomes, by examining plants grown in a screened growing house. Even in this study, the proportion of species whose glandular trichomes actually function as food bodies was not determined.

Within habitats, the abundance and diversity of ants at nectaries show marked variation among plant species (Hossaert-McKey *et al.* 2001) and across seasons (Rico-Gray *et al.* 1998). The importance of ants as protective agents is also likely to be highly variable among nectary-bearing plants. Ant protection appears to be a particularly important component of some plant strategies. An example is the mutualism between ants and the African wild yam *Dioscorea praehensilis* Benth. (Dioscoreaceae), in which ants provide protection during the most vulnerable stage of its unusual growth cycle (di Giusto *et al.* 2001). The plant is a perennial geophytic forest-canopy vine, which dies back to a large underground tuber at the beginning of the annual dry season. Near the end of the dry season, fuelled by tuber reserves, a single new stem repeats the climb from the ground to the forest canopy. Success depends on completing this trip as rapidly as possible, because only upon reaching the favourable light conditions of the canopy does the plant produce leaves that can restock tuber reserves and support flowering and fruiting. Rapid height growth is at such a premium that the stem does not branch until it reaches the canopy, a trip that requires at least two months. During this period, any herbivore attack of the plant's single apical meristem imposes a very great cost, because it can result in the loss of weeks of production by the entire aerial system, which lives only a single growing season. Cataphylls at the stem apex bear nectaries that attract ants to the meristem continually throughout this trip (di Giusto *et al.* 2001).

The *Dioscorea* example may be extreme (among opportunistic, non-symbiotic mutualisms) in the plant's likely dependence on ant protection. However, although the impact of ants attracted to extrafloral nectar (EFN) and other direct food rewards varies considerably, much work (most recently reviewed by Heil and McKey 2003) demonstrates that they often significantly reduce levels of attack by herbivores. Ants attracted to EFN and other direct rewards are important to the ecology of many tropical-forest plants.

Mutualisms between ants and hemipteran trophobionts

Community-level comparisons of herbivory have usually focused on chewing insects (e.g. Leigh & Windsor 1982; Coley & Barone 1996), the feeding activity of which is comparatively easy to quantify. Sucking insects have been neglected, although their community effects – thanks to widespread mutualism with ants – may dwarf those of chewing insects (Davidson *et al.* 2003). The biology of phloem-sucking hemipterans includes two key features that have led to the repeated evolution of protection mutualisms with ants (Delabie 2001). First, their food contains carbohydrates and water in excess. With little metabolic cost to themselves, they can excrete large amounts of an energy-rich liquid reward that is highly prized by ants. Second, their feeding behaviour ties them to a sedentary lifestyle. Their stylets are often deeply inserted into plant tissues, and reaching a suitable sap source takes minutes or hours. This makes active escape from predators difficult. Even if phloem-sucking insects could escape, the time lost afterwards in re-inserting the stylet would lower their foraging efficiency. Phloem-feeding hemipterans have thus evolved a wide range of anti-predator defences; mutualism with tending ants figures prominently among these.

Protected by ants from many predators and parasitoids, phloem-sucking insects often reach high densities. These densities should be vastly underestimated by canopy-fogging ‘knock-down’ experiments, because these insects die with their stylets inserted and are not ‘knocked down’. In the few studies based on direct observation in the canopy, numbers of ant-tended hemipterans rival those of ants themselves (Blüthgen *et al.* 2000; Dejean *et al.* 2000; Blüthgen & Fiedler 2002). In terms of biomass, they are thus likely to be the second most important insect group in the canopy, after ants.

For ants, association with phloem-sucking insects provides access to an abundant supply of energy-rich plant-derived resources, even on plants that do not produce direct rewards. Some hemipterans are facultatively associated with ants, whereas others are obligate myrmecophiles. Even in the latter case, associations are rarely specific, a given hemipteran often forming associations with several ant species, and vice versa (e.g. Blüthgen *et al.* 2000; Dejean *et al.* 2000). Different ant species also have different effects on the species richness, density and distribution of hemipterans (Itioka & Inoue 1999). Although plants vary in both their suitability as hosts for phloem-sucking insects (Gullan 1997; Blüthgen & Fiedler 2002) and the quality of the honeydew produced (Gullan 1997; Delabie 2001; Davidson *et al.* 2003), the host plant ranges of many hemipteran trophobionts are likewise often broad (Delabie 2001; Blüthgen & Fiedler 2002). Thus, association with hemipterans makes ants not only (quasi-)herbivores, but *generalist* herbivores. Dominant ant species can thus obtain energy-rich food from a large proportion of individual plants in the community, even in species-rich tropical forests. Furthermore, while some ant-tended hemipterans are largely restricted to young growth (Blüthgen & Fiedler 2002), many others (e.g. coccids

and stictococcids in African forests; D. McKey, personal observations) are capable of feeding on mature twigs. Thus, despite seasonal and other sources of variation, in tropical forest ecosystems honeydew is often much more continuously available in space and time than is extrafloral nectar, production of which is usually restricted to particular developmental stages of leaves and other organs and to particular times of day. The phenology of nectar production also varies among plant species.

Ants also harvest hemipteran trophobionts for protein (Carroll & Janzen 1973; Gullan 1997; Delabie 2001). Sap-sucking hemipterans present important contrasts with other potential sources of protein as regards their pattern of availability in space and time, as we have already seen in the case of energy. Most phytophagous insects in tropical ecosystems use ephemeral resources such as young leaves, flowers and developing fruits (Coley & Barone 1996). Their densities thus vary markedly in time, dependent on the phenology of their host plants. Sap-feeders may thus provide ants with a more regular and predictable supply of protein than they can gain from insects depending on other resources.

Little is known in quantitative terms about ant predation on their trophobionts (Davidson *et al.* 2003). In those systems that have been studied, the frequency of predation often appears to depend on the balance between availability to ants of carbohydrates and other resources (Gullan 1997; Delabie 2001). When food of ants is supplemented with more sugar, workers prey more frequently on the aphids they tend (Offenberg 2001). For this and other reasons, the mutualistic benefits to trophobionts are often dependent on their density (Morales 2000; Breton & Addicott 1992), which appears often to be regulated by ants (e.g. Larsen *et al.* 2001).

Do ant-hemipteran associations have positive or negative effects on plants? In most cases, the net effects of these associations on plants in tropical ecosystems are unknown (Chapter 17). Judging from temperate-zone examples (e.g. Karhu 1998; Karhu & Neuvonen 1998), these effects may be complex. In addition to the negative effects of loss of resources to sucking insects, there is also significant potential for the transmission of diseases by ant-tended hemipterans (Delabie 2001). However, little appears to be known about this aspect of the associations outside of agricultural environments. Positive effects include not only ant protection against other herbivores, mostly chewing insects, but also – in temperate-forest systems – improved physico-chemical properties of soil in ant nests (Wagner 1997), which are often located at the bases of trees harbouring large populations of hemipterans. Except for epiphytes (for which ant nests appear to be of widespread importance as substrates for establishment (Longino 1986)), the latter type of benefit is likely to be less important in tropical forests, where most ants that forage in tree crowns are also tree-nesting. If trophobionts are maintained at high densities and few chewing insects are present, or if ants do not effectively protect against those chewing insects that are present (Mackay

1991), the costs of ant-hemipteran associations will outweigh their benefits. On the other hand, if the protection ants provide against other insects is greater than the cost imposed by the hemipterans they maintain, then plants, ants and hemipterans are engaged in a three-partner mutualism. It is certain that ant-tended hemipterans play a currently underestimated role in tropical-forest ecosystems (Davidson *et al.* 2003). But whether, in each case, we have underestimated the cost of herbivory to plants or instead the investment of plants in protection mutualisms and indirect ('biotic') defence, remains to be established.

Nutritional mutualisms involving bacteria

The crucial role of endosymbiotic bacteria in the nutritional ecology of phloem-sucking hemipterans, including ant-tended trophobionts, is well-known (Delabie 2001). Much less known, but probably also crucial to the ecology of tropical herbivore food webs (Davidson *et al.* 2003), are nutritional mutualisms between bacteria and tree-dwelling ants. Several groups of tropical arboricolous ants harbour symbiotic bacteria. At least some species of *Camponotus*, a widespread genus well represented among tropical arboricolous ants, have intracellular bacterial endosymbionts (Schröder *et al.* 1996), although to our knowledge tropical tree-dwelling *Camponotus* have not been studied. Other genera harbour bacteria in the lumen of the gut, sometimes in specialized structures. These include *Cephalotes* (Jaffé *et al.* 2001), some *Tetraoponera* spp. (Billen & Buschinger 2000; van Borm *et al.* 2002), and *Cataulacus* (Caetano *et al.* 1994). All of these are groups that consume large quantities of nectar and honeydew, or whose diets also include unusual components such as epiphyllous non-vascular plants or wind-borne pollen and fungal spores. Both direct observations and isotopic data indicate that they have largely plant-derived diets, likely to be characterized by low protein content and unbalanced amino acid composition (Davidson *et al.* 2003). Although the functions of the bacterial symbionts in each case remain to be elucidated, patterns strongly suggest that they play roles in repairing these nutritional imbalances. For example, the localization of bacterial symbionts in *Tetraoponera*, near complexes of Malpighian tubules, suggests that they may function in internal nitrogen recycling (van Borm *et al.* 2002). Unravelling the functioning of ant-bacteria mutualisms is one of the key tasks facing ant ecologists in the next few years (Bourseaux-Eude & Gross 2000).

The trophic structure of opportunistic ant-plant interactions

Among this diversity of resources – direct (EFN and pearl bodies) and indirect (honeydew) energy-rich rewards, hemipteran trophobionts and other foliage-dwelling arthropods consumed as prey – what are the respective roles of each in ant diets? How important to tropical tree-dwelling ants are food sources that are not even indirectly derived from the plants they patrol, such as pollen, fungal spores and epiphylls? In short, what is the trophic structure of opportunistic

ant-plant interactions, and what are the implications of this structure for understanding community processes?

First, the relative importance of these different resources appears to vary among ant groups. Dolichoderines, for example, frequently tend large aggregations of trophobionts on plants, while also using extrafloral nectar (Davidson *et al.* 2003; Davidson *et al.* 2004). In contrast, most species of formicines are 'leaf foragers' that actively and solitarily scour vegetation for diverse resources. Although many formicines also tend trophobionts, and some are specialists in that activity, they appear to figure more prominently among consumers of EFN. Formicines also account for most of the observations indicating exploitation of unusual plant-derived resources such as pith and epiphylls (lichens and perhaps other groups). Pollen and perhaps fungal spores are suspected to be important in the nutritional ecology of many pseudomyrmecines and cephalotines (Baroni Urbani & Andrade 1997).

Plant-derived food sources supply most of the energy in the diets of all these ants. Studies of the natural abundance of stable isotopes indicate that tropical tree-dwelling ants also obtain a large part of their nitrogen from plant sources (Davidson *et al.* 2003), despite the low contents of nitrogen in most of the plant-derived foods. According to the hypothesis developed by Davidson (1997; Davidson *et al.* 2003), the dependence of tropical tree-dwelling ants on energy-rich, nitrogen-poor resources derived from plants is a key feature of their ecology, with enormous consequences for the communities in which they are key predators. Davidson's analysis (Davidson 1997; Davidson *et al.* 2003) of the consequences of the energy-rich, nitrogen-poor subsidy from plants in the ecology of tropical tree-dwelling ants is a *tour de force*, and constitutes one of the most thoroughly developed terrestrial examples of an emerging field, ecological stoichiometry (Elser *et al.* 2000), that has so far been nourished principally by examples from aquatic ecosystems (e.g. Gaedke *et al.* 2002). With abundant energy but limited by nitrogen, tropical tree-dwelling ants have evolved bacterial symbioses to compensate for nutritional imbalance; strategies of defence, physiology and morphology that spare nitrogen; and predation strategies that lavishly use plant-derived energy to gain animal protein (Davidson 1997). Experimental studies are beginning to supply evidence that honeydew- and nectar-feeding ants do in fact behave as if they were limited by nitrogen (Kay 2002).

Ant-plant interactions and the structure and functioning of tropical food webs

How have these interlocking mutualisms contributed to making ants such important predators in tropical forest canopies? Davidson (1997) has argued that the abundance of nectar, pearl bodies and hemipteran honeydew has allowed tropical tree-dwelling ants to evolve energetically costly prey-foraging strategies. Fuelled by plant-derived rewards and adapted to nitrogen-poor diets, ants can

reach higher densities, and maintain prey species at lower densities, than if they were solely dependent on animal prey. Plants should thereby benefit from decreased levels of herbivory. Davidson (1997) postulates in effect that top-down trophic cascades, from effects of ants on herbivores to the effects of herbivores on plants, are a dominant feature of the community ecology of tropical forests. (It should be noted that 'top-down' and 'bottom-up' effects are in this case thoroughly conflated, as the traits of predators are themselves dependent on the traits of plants.)

Such effects have been more or less well documented in the simplified interaction webs involving numerous myrmecophytes and their host-specific ants (Chapter 14) (e.g. Letourneau & Dyer 1998) and in several opportunistic interactions centred on EFN-bearing plants (reviewed by Heil & McKey (2003)). Do they occur at the community level? According to some current theory (Polis & Strong 1996), in highly diverse communities the effect of predators should have low penetration to lower trophic levels, because as predators reduce densities of some herbivores, other herbivores not affected by these predators take their place, so that the overall effect on plants is limited. However, there is evidence for top-down trophic cascades driven by other groups of predators in tropical forests (van Bael *et al.* 2003; Terborgh *et al.* 2003). Furthermore, as mentioned above, ants are both generalist predators and generalist herbivores; few herbivores might be unaffected by ants, and the penetration of their effects to lower trophic levels may thus remain high.

Let us assume for the moment that tree-nesting ants do generate effects that cascade from herbivores to plants, and that such effects are community-wide. This leads to the question of just how far to other community components the impact of ants may extend. As dominant predators, do they structure other guilds of natural enemies of foliage-dwelling arthropods? Almost 30 years ago, Rathcke and Price (1976) noted that parasitoids in tropical ecosystems should experience high rates of indirect predation by ants that eat parasitized hosts, and postulated that this could explain the apparently anomalous latitudinal gradient in diversity of parasitoid hymenoptera (with a peak not in the tropics, but at mid latitudes, for groups such as Ichneumonidae (Janzen 1975)). It soon became clear that tropical diversity in many parasitoid groups, as in other insects, had been underestimated, and this hypothesis was put aside. It is now being re-examined in more precise incarnations. Does indirect predation by ants shape the structure of parasitoid guilds in tropical ecosystems? Ant predation on larval insects could lead to greater representation of life-history strategies featuring rapid development in very early host stages (e.g. egg parasitoids (Gaston *et al.* 1996; Kruger & McGavin 1998)), or favour traits that otherwise reduce the probability of indirect predation. Another idea to explain parasitoid diversity gradients, the 'nasty-host hypothesis' (Gauld *et al.* 1992), could also be seen in a new light. According to this hypothesis, tropical phytophagous insects have

fewer parasitoids than do temperate-zone insects because they are more often chemically defended. If ant predation is an important contributor to the selection pressure that has favoured the frequent evolution of toxicity in tropical phytophagous insects, this could be seen as another important community-level consequence of the mutualisms that sustain ants.

The impact of ants might extend even further. The steep decline of ant diversity and abundance with elevation on tropical mountains (Janzen 1973) could contribute to explaining why small mammals, which potentially compete with ants for food, increase in diversity with elevation in the tropics (Samson *et al.* 1997; Heaney 2001). Not surprisingly, some hemipteran groups rich in ant-tended species also show sharp diversity gradients with elevation (Olmstead & Wood 1990).

All these postulated effects of ants on the ecology of tropical forest communities rest, of course, on the hypothesis that tree-nesting ants, in partnership with plants and hemipteran trophobionts, collectively reduce the densities of other foliage-dwelling arthropods. To our knowledge, this hypothesis has not been tested at the community level. Doing this would require the collaboration of teams of myrmecologists and other entomologists. A large-scale manipulative study would be technically difficult, but if current hypotheses are on the right track, the results of such a study should be striking.

16.2 Evolution of trophic structure in symbiotic ant-plant mutualisms

In all tropical regions, opportunistic interactions between plants and plant-foraging ants have repeatedly given rise to tighter associations, in which ant colonies reside permanently in structures of plants. Hemipteran trophobionts are frequent third partners in such symbiotic associations. In symbiotic associations, each participant becomes a more predictable feature of the other participants' environment, creating greater opportunities for (co)evolutionary specialization (Davidson & McKey 1993).

As symbiotic ant-plant mutualisms coevolve, new selection pressures acting on resource flows can modify the trophic structure of interactions in several ways. These evolutionary changes can affect the overall rate of resource flow from plants to ants, as well as the kinds of rewards that are offered and the chemical composition of each. These two aspects, quantitative and qualitative changes, will be considered in turn.

Overall rate of resource supply

Resource flow from plant to ant should increase with coevolutionary specialization, because plants that maintain larger resident ant colonies are better protected (Rocha & Bergallo 1992), and ants that better protect the plant reap more benefits. The lineages that have been studied conform to this expectation, with specialized myrmecophytes supplying food resources to their resident ants

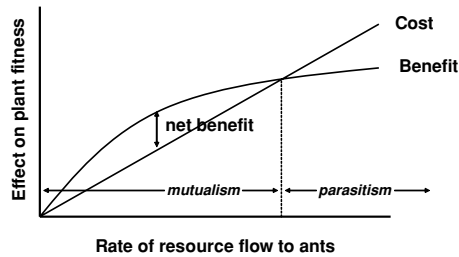


Figure 16.1 Graphical model illustrating the continuum between mutualism and parasitism in the effects of symbiotic ants on fitness of the host (adapted from Fonseca (1993)). Under certain circumstances, ants may have an interest in maintaining a rate of flow of plant resources to them that is greater than that optimal for the plant (where net benefits to the plant are maximized). See text for explanation.

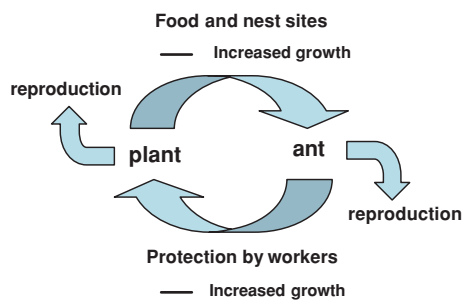


Figure 16.2 The potential for conflict between the two partners in horizontally transmitted symbiotic ant-plant mutualisms. The cycle of mutualistic benefits is provided by each partner's investment in the growth of the other. However, resources for reproduction are drawn from the same limited pool as growth, resulting in the potential for evolutionary conflicts between mutualists. Adapted from Gaume (1998).

at higher rates than do their less specialized congeners to opportunistic ants (reviewed by Heil & McKey 2003), and specialized plant-ants providing more effective protection than do opportunistic ants (Fiala *et al.* 1994; Nomura *et al.* 2000).

The cost to the plant of supporting its ants increases proportionally to investment: producing more resources entails greater costs. However, benefits to the plant plateau. At some point, supporting more ants confers little or no increased protection (Fonseca 1993). At very high rates of resource supply, costs may outweigh benefits (Fig. 16.1). Somewhere below this point, there is a rate of resource supply at which net benefit is maximized. If the interests of the plant and its ant colony were entirely congruent, this rate optimal for the plant would also be optimal for the ants. However, because ant-plant symbioses are horizontally transmitted (plant seeds and ant foundresses disperse independently), neither individual partner has an interest in the other's reproduction. Because resources allocated to growth (which increases mutualistic benefits) and reproduction of the tree or colony come from the same limited pool, this can lead to a conflict of evolutionary interests (Fig. 16.2). Selection on each partner should favour adaptations that increase its own benefits. These may come at the expense of partner reproduction. *Allomerus* plant-ants, for example, protect *Cordia nodosa* host-plants but castrate floral buds; resources thereby diverted from reproduction are channelled into increased growth, benefiting the ants (Yu & Pierce 1998). In turn, plants can modify the distribution of inflorescences (Raine *et al.*

2002), or of domatia (Izzo & Vasconcelos 2002), to limit contacts between ants and flowers and thereby presumably reduce such parasitism. The outcome of such battles for control over resource flow may be a coevolutionary tug-of-war with constantly shifting position. Alternatively, one of the partners may evolve an 'unbeatable strategy' that stabilizes the system – at least until it is beaten by the next surprising counter-adaptation.

Qualitative changes

As seen in a preceding section, food webs in opportunistic, non-symbiotic ant-plant interactions can be complex, with energy coming from nectar, honeydew and sometimes other plant-derived resources, and protein (and other nutrients) being supplied to some extent by these same resources, supplemented by bodies of hemipteran trophobionts and of insects captured on plants. Are food webs in specialized, symbiotic ant-plant mutualisms of comparable complexity?

The evolutionary conflicts developed above can shape not only the rate at which plants supply resources to ants, but also the kinds of resources offered. This is because some kinds of resources are more easily controlled by ants and others by the plant (Gaume *et al.* 1998; Itino *et al.* 2001). The clearest example is the contrast between rewards produced directly by the plant (EFN, pearl bodies) and those produced indirectly (hemipteran honeydew). Plants control their production of direct rewards, responding to variation in both resource availability (Linsenmair *et al.* 2001) and the likelihood of herbivore attack (Heil *et al.* 2001), and sometimes to the presence of the mutualist ant (Risch & Rickson 1981). Parasitic manipulation of plant production of direct rewards (Letourneau 1990) appears to be rare. In contrast, ants can more easily control rates at which plant resources are channelled to them in the form of honeydew (and hemipteran bodies), by regulating the number of trophobionts (among other mechanisms). While severe overexploitation of the plant by trophobiont-tending ants would lead to greatly reduced growth of the ant colony as well as of the plant (Fonseca 1993), traits leading to overexploitation that simply reduces plant reproduction would not be counter-selected. Also, because there is always a non-zero probability that the plant, or the ant colony, will die from causes independent of the efficacy of mutualistic exchange (e.g. physical disturbances), even exploitation levels that lead to modest reduction of host-plant growth could be favoured, if they increase the likelihood that the ants can reproduce before such an event occurs. If trophobiont-tending ants do exploit their hosts at levels greater than optimal for the latter, selection could favour plants that evolve mechanisms to reduce the rate of resource flow through trophobionts and increase the dependence of their symbiotic ants on direct rewards, whose production is more easily controlled by the plant.

Is there any evidence for such a scenario? Several observations suggest it. First, myrmecophyte symbioses often seem to originate from three-partner

ant–plant–hemipteran mutualisms. The high frequency of such tripartite systems in myrmecophytes is striking; systems including indirect rewards for ants are much more numerous than those in which only direct rewards are produced (Davidson & McKey 1993) (Chapter 17). One plausible interpretation of this finding is that ant association with trophobionts is often necessary, because the latter assure a regular and predictable, if not always rich, supply of protein that is usually not provided by direct rewards, at least those produced by unspecialized plants. This could have been a particularly crucial advantage at the outset of symbiosis, when predatory ants first became permanent residents of a single individual plant. Unable to buffer temporal variation in the abundance of phytophagous insects by hunting on many different plants, predators would have been dependent on hemipteran-supplied protein. Alternatively, these interactions may have been parasitic from the start, with ants tending hemipterans in stems while foraging little on plant surfaces. However, if this were the case, it would be difficult to understand why selection favoured the retention – and elaboration – of plant structures for housing ants.

Second, some of the most specialized myrmecophyte systems do not include trophobionts. In these, plants have often evolved direct rewards much richer in nitrogen than those produced by other myrmecophytes (e.g. Heil *et al.* 1998; Fischer *et al.* 2002). Did these symbioses originate via other pathways, not involving trophobionts, or have trophobionts been lost in these systems and replaced by direct food rewards? If the latter is the case, is there any evidence that evolution was driven by the conflicts described above?

The *Leonardoxa* case

Leonardoxa, a genus of small to medium-sized trees found in rain forests from northern Gabon to south-eastern Nigeria, offers an opportunity to examine these hypotheses, because very closely related taxa present dramatic contrasts in both myrmecophytic specialization and the structure of ant–plant–herbivore food webs. As currently circumscribed, the genus consists of a single polytypic species, *L. africana*, comprising of four vicariant taxa. These have been described as subspecies (McKey 2000), but they are clearly on different adaptive trajectories and are perhaps best considered as species *in statu nascendi*. One of these taxa, *L. a. gracilicaulis*, found in northern Gabon and southern Cameroon, is not a myrmecophyte. Like plants of many related genera, it has foliar nectaries that attract a diversity of opportunistic ants. Exclusion experiments show that the protective effect of these ants is at best weak (Gaume 1998). The three other taxa are all myrmecophytes bearing swollen twigs that function as ant domatia. Subspecies *rumpiensis* is an intriguing tree of submontane forests in the West Cameroon Dorsal. Thus far little studied, it is inhabited by a diversity of poorly known ant species. The two other taxa are lowland-forest myrmecophytes, each associated with a different, closely related formicine ant. Subspecies *letouzeyi* is found north

of the West Cameroonian Dorsal, in the Cross River area straddling Cameroon and extreme south-eastern Nigeria. It is associated with the ant *Aphomomyrmex afer*. Subspecies *africana* occurs south of the Dorsal, and is restricted to a narrow band of coastal forest southward to near the border between Cameroon and Equatorial Guinea. It is associated with the ant *Petalomyrmex phylax*. Both of these formicine genera are monotypic, and the two ants are sister species among extant taxa (Chenuil & McKey 1996). *Aphomomyrmex* shares numerous traits with related genera such as *Cladomyrma* and *Myrmelachista*, and is not host-specific, being known from at least one other host (*Vitex*, in the Lamiaceae (formerly placed in Verbenaceae)). In contrast, *Petalomyrmex* has evolved several morphological specializations, all of which appear to be adaptations to its sole host, *L. a. africana*, which is the most highly specialized myrmecophyte in the *L. africana* complex. The specializations of *Petalomyrmex* include most notably the strongly dorsiventrally flattened alates, matched to the slit-shaped prostoma (and *Petalomyrmex* entrance holes dug at the prostoma) of its host (Brouat *et al.* 2001).

Another difference between the two ants is that *Aphomomyrmex*, like most related genera, tends hemipteran trophobionts in the domatia of its hosts, whereas *Petalomyrmex*, alone among studied members of the tribe Myrmelachistini in this respect, never tends trophobionts. Mapping of characters on phylogenies of ants (Chenuil & McKey 1996) and plants (Brouat *et al.* 2004) indicates that as the system specialized, the lineage leading to *Petalomyrmex* lost an ancestral association with hemipteran trophobionts, while the host of this ant, *L. a. africana*, evolved larger and more numerous foliar nectaries and presumably higher rates of supply of direct rewards to its mutualist ant.

What selective pressures could have driven these evolutionary changes in the trophic structure of the symbiosis? Three arguments suggest that they resulted from evolutionary conflicts between mutualists and are due to adaptations of the plant, which has thereby gained a greater degree of control of resource flow. First, there is no clear reason why ants should cease to tend hemipteran trophobionts when plants increase the production of direct rewards, if by tending they can gain additional resources. (However, hemipteran-tending might be strongly counter-selected in resident ants if hemipteran-transmitted pathogens reduce the growth or survival probability of the ants' sole individual host.) Second, the absence of hemipterans in ant associations with *L. a. africana* appears to be due to a trait of the plant. The inner walls of the stem domatia of this plant are covered by a layer of sclerenchyma (Brouat 2000) that may constitute a physical barrier to phloem-sucking insects. Third, field studies of the tripartite mutualisms involving *L. a. letouzeyi*, *Aphomomyrmex*, and its hemipteran trophobionts provide circumstantial evidence of the kinds of conflicts between ants and plants that are postulated to have favoured plant adaptations permitting increased control.

In a population of *L. a. letouzeyi* studied in Korup National Park, *Aphomomyrmex* was observed to tend two different hemipterans, with the coccid *Houardia abdita* being the sole or dominant trophobiont in about half the trees (= *Aphomomyrmex* colonies) studied and the pseudococcid *Paraputo anomala* the sole trophobiont in the other trees (Gaume *et al.* 1998). Among colonies overall, benefits to the tree of ant occupancy, as estimated by the amount of chewing-herbivore damage accumulated by leaves, increased with worker density in relation to number of leaves. However, comparing the two groups, this relationship was much stronger in trees whose ant colonies tended *Paraputo*. These results suggest that increasing the amount of resources supplied to ants resulted in increased protection, but that the strength of the relationship depended strongly on the identity of the third partner (Gaume *et al.* 1998). Not only did *Aphomomyrmex* confer greater benefits to the plant when it tended *Paraputo*, but the cost incurred by the plant may also be lower with this partner, if trophobiont biomass is correlated with the cost they impose. For comparable worker densities (number of workers in relation to domatia volume), dry biomass of associated trophobionts was between two and three times as great in trees whose colonies tended *Houardia* as in those with *Paraputo*. *Houardia* were dense and found in every domatium; *Paraputo* were sparse and mostly restricted to domatia in younger twigs.

Ant colonies tending *Houardia* thus appeared to impose greater costs and confer fewer benefits to their host plants than did those tending *Paraputo*. Their lower level of mutualism appears to pay off; for comparable colony size, production of alates was higher in colonies tending *Houardia* (Gaume & McKey 2001). Although the reasons for the differences in costs and benefits between colonies associated with different trophobionts must still be elucidated by experimental studies, observations suggest the following explanation (Gaume *et al.* 1998). Colonies tending *Houardia* depend on foliar nectaries for energy, exploiting the trophobiont for protein and using this abundant resource to increase the production of sexual brood. In contrast, colonies tending *Paraputo* exploit the honeydew they produce and are not dependent on foliar nectar. However, they apparently either do not consume *Paraputo* bodies or, if they do, gain insufficient protein from the low-density populations of this trophobiont. Limited by protein, they more actively patrol young leaves to hunt insect prey.

Plants that evolve adaptations favouring *Paraputo* over *Houardia* should have a selective advantage. Loss of nectaries would favour *Paraputo*, and this could explain why some individual *L. a. letouzeyi* lack foliar nectaries (McKey 2000). However, the plant has only limited control; *Houardia* remains in the system, and ant colonies that tend it require nectaries to reach the high density required for protective effect. Selection in opposing directions on nectary number could explain why this trait shows much greater among-individual variation in *L. a. letouzeyi* than in any of the other *Leonardoxa*, including the non-myrmecophyte *L. a. gracilicaulis* (McKey 2000).

Another possible plant response would be to evolve traits that exclude trophobionts altogether. By increasing the severity of nitrogen limitation, this could lead ants to intensify patrolling to capture insect prey, as we propose occurs when *Aphomomyrmex* tends *Paraputo*. However, temporal variation in herbivore abundance, coupled to the plant's phenology, may make complete dependence on such prey impossible for ants resident in a single host. Traits excluding trophobionts would thus usually be advantageous only if accompanied by the provision of direct rewards that satisfy all ant needs, including that for nitrogen. (This could be accomplished by an increase in the quality of direct rewards, by the reduction of ant requirements for nitrogen and other resources, or by some combination of the two.) Once direct rewards supply sufficient protein as well as energy, a situation results in which ants are likely to have more to gain by protecting the plant as a direct (and relatively constant and reliable) protein source than by using it to grow indirect protein sources (phytophagous insects), the abundance of which is highly variable in space and time. Control of resource flow by the plant thus has the effect of bringing the ants' interests closer to its own.

Another possible selective pressure favouring simplification of food webs in specialized ant-plant systems is the increased energetic efficiency that would result from elimination of a trophic level between plant and ant (Gaume *et al.* 1998; Itino *et al.* 2001). It is unclear how much the energetic efficiency of resource transfer to ants would be enhanced by eliminating hemipterans. This would depend in part on the extent of metabolic transformation of phloem sap before its excretion as honeydew.

Figure 16.3 summarizes our hypotheses about the evolution of trophic structure during specialization of ant-plant mutualism in *Leonardoxa*. Ants associated with the myrmecophilic *L. a. gracilicaulis* (Fig. 16.3a) eat foliar nectar, honeydew, hemipteran trophobionts and prey, in proportions that probably vary among species. *Aphomomyrmex*, symbiotic in *L. a. letouzeyi*, uses all of these resources, and probably epiphylls as well (D. McKey and L. Gaume, unpublished observations), like some other formicine ants (Davidson *et al.* 2003). When they tend *Houardia* (Fig. 16.3b), *Aphomomyrmex* obtain relatively more of their carbon from nectar and more of their protein from trophobionts; when they tend *Paraputo* (Fig. 16.3c), these ants obtain more carbon from honeydew and more nitrogen from chewing-insect prey. In both cases, ants use the plant to 'ranch' animal protein, either wild or domesticated. In contrast, our observations indicate that trophic structure in the highly specialized *L. a. africana* / *Petalomyrmex* symbiosis (Fig. 16.3d) is very simple, with ants obtaining both carbon and nitrogen mostly directly from the host. First, there is no indication that *Petalomyrmex* interacts in any way with epiphylls, which are much less commonly observed on *L. a. africana* than on *L. a. letouzeyi*. The latter grows in shadier, more humid forests; it also has tougher, perhaps longer-lived, leaves. Second, trophobionts are absent from

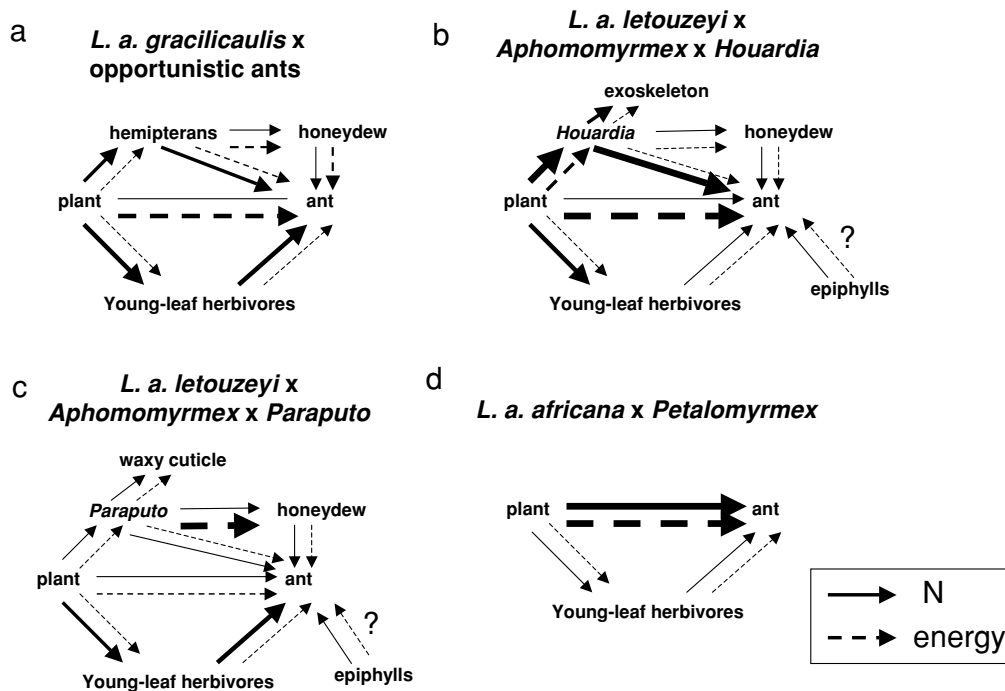


Figure 16.3 Summary of hypotheses about the evolution of trophic structure during the specialization of interactions between *Leonardoxa africana* and ant associates. a, The non-myrmecophytic, basal *L. a.* subsp. *gracilicaulis*, associated with a diversity of opportunistic ants. b, The ‘transitional’ myrmecophyte *L. a.* subsp. *letouzeyi*, associated with *Aphomomyrmex afer*, when colonies tend the coccid *Houardia abdita*. c, The same plant and ant combination, when colonies tend the pseudococcid *Paraputo anomala*. d, The highly specialized myrmecophyte *L. a.* subsp. *africana* associated with *Petalomyrmex phylax*, which does not tend trophobionts. Width of arrows indicates hypothesized relative magnitude of flows of nitrogen and energy in these systems.

the *L. a. africana* / *Petalomyrmex* system. Third, patrolling by *Petalomyrmex* workers is sufficiently intense that their main protective effect is probably to deter visits (and oviposition) by adult insects and to remove eggs and small immature stages. While *Petalomyrmex* workers do eat small caterpillars experimentally placed on the plant and dismember larger insects, transporting the pieces into domatia (L. Gaume, G. Debout and D. McKey, unpublished observations), the amount of protein they gain from herbivores they find under natural circumstances is probably limited.

According to these hypotheses, the adaptive function of patrolling young leaves has changed during evolutionary specialization of the system (Fig. 16.4). Opportunistic ants on *L. a. gracilicaulis* visit young leaves to hunt prey and to harvest foliar nectar. While nectaries are active only on mature leaves of *L. a.*

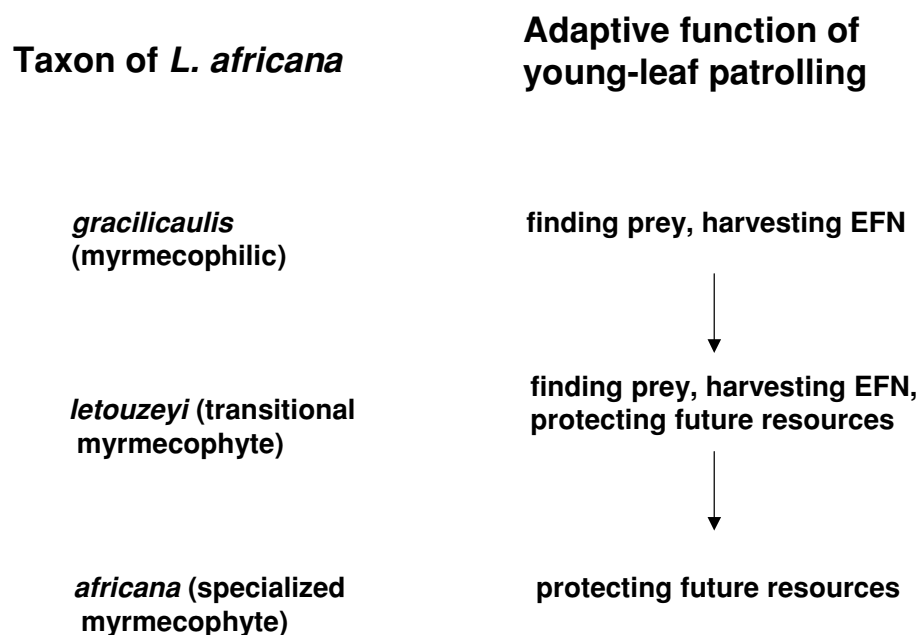


Figure 16.4 Summary of hypotheses about changes in the adaptive function of ant patrolling of young leaves during the evolutionary specialization of mutualism between *Leonardoxa* and its ant associates.

africana, young leaves also secrete nectar in *L. a. gracilicaulis* (Gaume 1998), as in most myrmecophilic plants. In the transitional myrmecophyte *L. a. letouzeyi*, *Aphomomyrmex* patrols young leaves to hunt prey (especially when associated with *Paraputo*, according to our hypotheses), but also to protect future resources and harvest nectar. In the highly specialized *L. a. africana*, *Petalomyrmex* appears to encounter little food on young leaves and patrols them to protect a future resource.

Preliminary data on natural abundance of nitrogen isotopes (A. Cason and D. McKey, unpublished) also indicate that *Petalomyrmex* obtains its nitrogen directly from plants. In general, the heavier isotope of nitrogen, ^{15}N , increases by 3–4‰ with each increasing trophic level (Scrimgeour *et al.* 1995). Values of ^{15}N for *Petalomyrmex* workers ranged from 1.2 to 5.6 ($n = 13$ colonies), values within the range of those obtained for ants that appear to derive most of their nitrogen from plant exudates (Davidson *et al.* 2003). Furthermore, ^{15}N values for *Petalomyrmex* colonies were correlated with those for their individual hosts and enriched on average by 2.9‰ relative to the plant (A. Cason and D. McKey, unpublished), indicating that plant and ant are separated by only a single trophic level (Scrimgeour *et al.* 1995). However, the degree of enrichment expected depends on a number of factors, including whether animals use plant amino acids or break down plant proteins (Davidson *et al.* 2003), and this is not known for

Petalomyrmex. The involvement of bacterial symbionts (abundant in hindguts of both *Aphomyrmex* and *Petalomyrmex*; C. Rouland, personal communication) might also affect enrichment (Davidson *et al.* 2003). Firm conclusions about the relative roles of plant- and insect-derived nitrogen in the diet of *Petalomyrmex* thus await further work.

Forest understorey as a habitat for plant-ants

In forest understorey, tree-dwelling ants are likely to be even more nitrogen-limited than those inhabiting other strata. Lower plant growth rates, well-defended long-lived leaves and other plant parts, and pulsed production of young leaves all contribute to variable and often low densities of phytophagous insects, probably including phloem-sucking insects. Tied to a single host in a prey-poor environment, understorey plant-ants may thus be particularly dependent on plant-derived protein and thus particularly adapted to a low and imbalanced nitrogen supply. Coevolution with an understorey ant-plant may thus have sharpened adaptations of ants such as *Petalomyrmex phylax* to scarcity of nitrogen. Nitrogen content (dry mass) of bodies of its workers is $10.8 \pm 0.5\%$ ($n = 13$ colonies; A. Cason and D. McKey, unpublished), within the range of mean values for other exudate-feeders and lower than values for legionary and other predatory ants (Davidson & Patrell-Kim 1996). If *Petalomyrmex* obtains most of its nitrogen directly from its host plant, as our observations suggest, it does indeed have a nitrogen-poor diet, for foliar nectar of *L. a. africana*, the only resource *Petalomyrmex* has been observed to harvest from its host, contains only $0.73 \pm 0.45\%$ nitrogen ($n = 4$ trees; A. Cason and D. McKey, unpublished). Using the standard conversion factor for 'crude protein', this represents about 4.6% dry mass protein. The abundant bacterial gut symbionts of *Petalomyrmex* (C. Rouland, personal communication), completely unstudied, seem likely to play significant roles in this ant's nutritional ecology, perhaps by synthesizing essential amino acids or recycling nitrogenous wastes, as suggested for symbioses between bacteria and other tropical tree-dwelling ants (van Borm *et al.* 2002; Davidson *et al.* 2003; Gil *et al.* 2003).

The ecological diversity of ant-plant-herbivore interactions

This brief, partial discussion of the particular exigencies of forest-understorey environments opens the door to a vast and still poorly explored domain – the comparative biology of ant-plant mutualisms. The role of gradients of resource availability (e.g. between canopy and understorey, between pioneers and plants of mature forest) in structuring ant-plant interactions (Davidson *et al.* 1991; Davidson & McKey 1993) is but one theme. The diversity of nutritional ecologies encountered among tropical tree-dwelling ants is another important theme, in which broad-scale ecological and phylogenetic patterns are just now becoming clear (Davidson *et al.* 2003). A third central theme, so far based almost entirely on observations and correlations (Gaume *et al.* 1998; Davidson *et al.* 2003), is the

ecological diversity of the hemipteran trophobionts tended by ants. A fourth theme, barely addressed so far, is the ecological diversity of other phytophagous insects with which ants interact. Ecologically important traits of herbivores such as size, development time, phenology, and chemical composition should vary among host plants in predictable ways, affecting the traits required of effective ant mutualists (Meunier *et al.* 1999), but patterns in this diversity among ant-plant systems have scarcely been examined. The task is now to combine all these elements in highly integrative studies that consider each of these participants in multitrophic interactions as an actor that evolves, not simply a part of the environment of one or another focal partner. Ant-plant-herbivore interactions can then become an even richer set of biological models for testing questions of general importance in ecology and evolutionary biology (Heil & McKey 2003).

Perspectives

Finally, our reading suggests several more questions about the trophic structure of ant-plant-herbivore interactions that could be rewarding to explore.

- (1) How important are non-hemipteran insects as food sources for specialist plant-ants? Why do some specialist plant-ants simply discard insects found on the plant (e.g. Janzen 1966), whereas others consume them as prey? Do some specialist plant-ants use the host plant to 'ranch' these insects, just as they ranch phloem-sucking hemipterans? We have argued that herbivores other than hemipteran trophobionts would often be unreliable protein sources for host-restricted ants, owing to their intermittent and unpredictable availability, mirroring host-plant phenology. It is interesting that the case most suggestive of an important role of insects captured on the plant in the nutrition of the resident ant colony – *Azteca* plant-ants on *Cecropia* (Sagers *et al.* 2000) – involves a host plant with relatively continuous production of young leaves.
- (2) How important is resource flow from ant to plant? In an increasing number of 'protection mutualisms', ants appear also to confer nutritional benefits on plants (e.g. Sagers *et al.* 2000; Alvarez *et al.* 2001; Belin-Depoux & Bastien 2002), just as in many ant-epiphyte 'nutritional mutualisms'. Are adaptations to enhance such flows most widespread in forest-understorey ant-plants, as Janzen (1974) long ago suggested? Traits such as the canaliculate sclerenchyma lining the inner wall of domatia in *Leonardoxa a. africana* (Brouat 2000) suggest the possibility of exchange between the resident *Petalomyrmex* colony and its host, although what might be exchanged, and in which direction materials might flow, are completely unknown. Despite such suggestive observations, little is known, and plants bearing obvious structural adaptations to nutrient uptake from ant-occupied domatia (e.g. the structures from which *Maieta* plants absorb nutrients from debris in

leaf pouches (Belin-Depoux & Bastien 2002)) have not been studied experimentally. The only manipulative study of understory plants of which we are aware – of *Piper*, a plant that appears to lack such specialized absorptive structures – showed that ant-mediated nitrogen uptake by plants occurs but may not be quantitatively important (Fischer *et al.* 2003).

- (3) Although attention has focused on nitrogen/carbohydrate ratios, nitrogen is probably not the only nutrient in short supply in the unbalanced dietary regimes of tropical tree-dwelling ants (and of their hemipteran trophobionts). Stoichiometric analysis of ant-plant-herbivore systems should be extended to include other crucial elements. Given the status of phosphorus as a limiting nutrient for tropical-forest plants, especially on old, weathered soils (Vitousek & Farrington 1997) – and thus its likely scarcity in plant secretions – this element would appear to be a suitable candidate. Nitrogen/phosphorus ratios may affect growth rates of individuals, demography of populations, and thereby community processes (Elser *et al.* 2000). Do these ratios vary in the food of different groups of tropical tree-dwelling ants? In the round of studies that is sure to be stimulated by the work of Davidson *et al.* (2003), it would be interesting to include both elements right from the start.
- (4) With rising levels of atmospheric CO₂, will nitrogen be even more diluted in extrafloral nectar and honeydew? Will tropical tree-dwelling ants be subjected to even more severe nitrogen limitation?
- (5) The ability of introduced ants to form mutualisms with plants (Fleet & Young 2000) and with hemipterans – native or introduced (Helms & Vinson 2002) – makes ants often formidable biological invaders (Lach 2003; O'Dowd *et al.* 2003). By reducing the densities of both herbivores and of beneficial insects that visit nectaries, invasive ants may destroy many kinds of interactions.
- (6) The second part of this paper has focused on trophic rewards produced by plants for ants. How does the plant regulate the ratio of rate of supply of food resources with that of other resources, such as nesting space (Fonseca 1999)? If nesting space is more strongly limiting than food, ants might channel a greater proportion of plant-derived resources into reproduction (and dispersal) relative to colony growth. If food is more strongly limiting than nest space, this could favour parasitic manipulation of the rate at which the plant supplies food. Integrative studies must consider morphogenetic, physiological and evolutionary interactions between the two kinds of rewards.
- (7) Some ant-garden plants appear to constitute a partial exception to the statement that symbiotic ant-plant mutualisms are horizontally transmitted. *Anthorrhiza* myrmecophytes within the territory of a single *Dolichoderus* sp. colony are close relatives, owing to dispersal and planting of seeds by the

ants (Maeyama & Matsumoto 2000). In such systems, ants have an interest in the reproduction of their hosts. Does this have consequences for resource flows within these systems?

- (8) As for *Leonardoxa* and its ants, increasingly detailed phylogenetic information is accumulating for the species-rich ant-*Macaranga* associations (Davies *et al.* 2001; Blattner *et al.* 2001; Feldhaar *et al.* 2003; Vogel *et al.* 2003), and studies address a broad range of biological questions (e.g. Itioka *et al.* 2000; Nomura *et al.* 2000; Itino & Itioka 2001; and others reviewed by Heil and McKey (2003)). However, these radiations include only a fraction of the ecological diversity represented in ant-plant symbioses. Studies of ant and plant radiations that present ecological contrasts with these systems are now necessary to explore the diversity of trophic structures, and their evolution, in these complex biotic interactions.

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