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Coadaptation and coevolution of *Macaranga* trees and their symbiotic ants

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INTRODUCTION

Ants are everywhere on earth. When combined, all ants in the world weigh about as much as all humans (Hölldobler and Wilson, 1994). As they are the chief predator of insects, many plants and insect herbivores (e.g. aphids, scale insects and butterfly larvae) have struck hands with ants and get the ants protect them from enemies. In return, they give sugary secretions and/or domiciles to the ants. This mutualism between ants and other organisms has greatly contributed to the numerical dominance and diversity of ants (Tobin, 1994; Davidson, 1997) and their 'wards' (Pierce, 1987; Davidson and McKey, 1993). The intriguing aspect of such ant-ward mutualism is that the strength of the interactions varies widely from facultative and/or diffuse relationships to obligate and highly co-evolved associations.

The ant-plant defensive mutualism represents a prominent system for study of ecology and evolution of specificity in mutualism. Facultative mutualism between ants and EFN (extra floral nectar)-producing plants is common in temperate and tropical region worldwide (Schupp and Feener, 1991). In this system, EFN plants are usually exploited and defended by a wide range of local ant fauna, thus represent low specificity to ants. In contrast, the interaction between ants and myrmecophytes (plants that provide domiciles for the ants) is obligate, that is, neither of the party could live without the other, and the interaction is more specific. For example, Fonseca and Genade (1996) showed that, in Amazonian rainforest, every myrmecophyte-dwelling ant species was associated with as few as 1 to 4 myrmecophytic plant species, and that phylogenetically-related plant species were usually associated with a group of related ant species. These patterns of specific association have also been reported many times for a variety of myrmecophytic taxa (see review in Davidson and McKey, 1993). A part of causes for the specificity has been explained by preadaptation of ants and plants and/or competition among ant species. For example, plants with inhibitory hairs on stems are preadapted to be inhabited by timid small-bodied symbiotic ants which can walk through the hairs, while competitively dominant ants monopoly fast-growing pioneer myrmecophytes

which offer high rate of food production for ants (Davidson and McKey, 1993). On the other hand, evolutionary specialization also appears to shape the pattern of specificity in a number of ant-plant systems. In this congeneric ant species are often associated with different congeneric plant species (Chenuil and McKey, 1996; Ayala et al., 1996) although the adaptive significance and mechanism of maintenance in this fine-tuned specificity is to be determined.

Such high specificity in ant-myrmecophyte association stimulated a hypothesis of co-cladogenesis of ants and plants. But no evidence of cospeciation has been presented so far. Rather, recent works (Ward, 1991, 1999; Chenuil and McKey, 1996; Ayala et al., 1996) suggest that frequent host shifts and de novo colonization by ants to different plant taxa have determined the pattern of this association in the American and African tropics. In these regions, plant-ants are usually more habitat-specialized rather than host-specialized (e.g. Yu and Davidson, 1998). Recently, however, a rare case of cospeciation between ants and plants was documented in Southeast Asia (Itino et al., 2001b).

In this chapter, we review the current understanding of the species-specificity and coevolutionary history of *Crematogaster* ant-*Macaranga* plant association. For more detailed biological background, see Fiala et al. (1989, 1999), Itioka et al. (2000), Itino and Itioka (2001), Itino et al. (2001a, b) and Davies et al. (2001).

LIFE HISTORY

Macaranga is a genus of approximately 300 species distributed in the Paleotropics with its center of diversity in the Malesian region. In Borneo, they are a conspicuous component of the secondary forest and forest-gap flora (Davies et al., 1998). Twenty-six of the Southeast Asian *Macaranga* species house ants in their stems (myrmecophytes) and have a range of morphological specialization associated with this symbiosis (Fiala and Maschwitz, 1992a, b; Davies et al., 2001). These myrmecophytic *Macaranga* species are inhabited by several obligate ant species, mostly *Crematogaster* (subgenus *Decacrema*), which are highly species-specific to their host *Macaranga* species (Fiala et al., 1999; Itino et al., 2001b; Murase et al., 2002). In our main study site, a lowland mixed dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia, the investigated nine *Macaranga* species have close associations with four morphospecies of ants (Figure 1).

Two types of ant-association in *Macaranga* have been identified by Fiala and Maschwitz (1992b): myrmecophytes colonized by ants later in plant development (*M. hosei* in this chapter) and earlier-colonized myrmecophytes (the other eight *Macaranga* species in this chapter). The later-colonized *M. hosei* does not house ants until the sapling grows as high as 70 cm or so (Fiala et al., 1994; Itino and Itioka, 2001) because the food-body production starts only at this growth stage (Fiala and Maschwitz, 1992a). In earlier-colonized species, on the other hand, the food-body production starts earlier, and the seedling internodes swell and the pith degrades so that ant queens can colonize the seedlings of only 5-10 cm tall.

The nine *Macaranga* species are generally abundant in open habitat like forest gaps or riverbanks. Their habitat overlapped much, so that it was not uncommon to find more than five *Macaranga* species colonizing a single large forest gap, although there is subtle but detectable interspecific difference in microhabitat preference (Davies et al., 1998).

A queen ant colonizes a small *Macaranga* seedling and nests inside the swollen hollow stem. Nearly 100 % of 50-cm tall saplings of four 'earlier -colonized' *Macaranga* species are occupied by obligate ant colonies (Itino and Itioka, 2001). Workers actively patrol the leaves and protect the plants against herbivores and vines (Fiala et al., 1989; Itioka et al., 2000). They exclusively consume the food bodies secreted by the plants, the honeydew of small coccids (*Coccus* spp.) living inside the hollow stem, and the coccid themselves. The skewed age distribution of the coccids strongly suggests that the ants selectively eat younger coccid nymphs (T. Itioka, pers. obs.).

SPECIES-SPECIFICITY AND COADAPTATION

Historically the specificity of ants to *Macaranga* has been poorly understood and *Crematogaster borneensis* has been tentatively considered to be a highly variable ant inhabitant of *Macaranga* in peninsular Malaysia (Fiala and Maschwitz, 1990). Recently, however, Itino et al. (2001b) detected four morphological ant species in Lambir, Borneo (Figure 1) and Fiala et al. (1999) reported nine morphospecies in Southeast Asia. Moreover, both of the works demonstrated high degree of species-specificity in this symbiosis (Figure 1). Most of the symbiotic ants are members of subgenus *Decacrema* and most of the plants belong to section *Pachystemon*.

Because both ants and plants are not highly specialized to habitats (Davies et al., 1998) and several species usually coexist in the same forest gap, mechanisms maintaining the specificity appear not to include parallel specialization to habitat. Rather, coadaptation of ants and plants against enemies (herbivores and ant-predators) appears important. According to their enemies, seven *Macaranga* species are organized into three groups (Table 1, Itino and Itioka, 2001). The first group (two species) tends to suffer attacks by gall flies (Cecidomyiidae). The second group (four species) is often attacked by leaf eaters, and the third group (one species) by woodpeckers. The woodpeckers are not herbivores but ant-predators: they break the hollow stem and consume the ants inside. These three groups of *Macaranga* are inhabited by different ant species (Table 1, Itino et al., 2001b): the first group by *C. decamera*, the second group by *C. borneensis* or *C. sp. 4*, and the third group by *C. sp. 2*. This indicates that each ant species corresponds to different enemy fauna.

Interspecific variation in biotic and non-biotic (chemical/structural) defense of *Macaranga* are concerned with the enemy- and ant specificity (Table 1).

Interestingly, the degree of biotic and non-biotic defense varies inversely among

Figure 1. Phylogeny of symbiotic *Crematogaster* ants and phylogeny of the corresponding *Macaranga* hosts. For *C. borneensis* and *C. decamera*, principal host plants are indicated in the parentheses for each mtDNA lineage. Dashed lines indicate associations. The ant phylogeny is based on mtDNA sequences while the plant phylogeny is based on combined analyses of morphological characters and mtDNA sequences (Davies et al. 2001). Only nodes with >50 % bootstrapping support are presented as resolved. From Itino et al. (2001b).

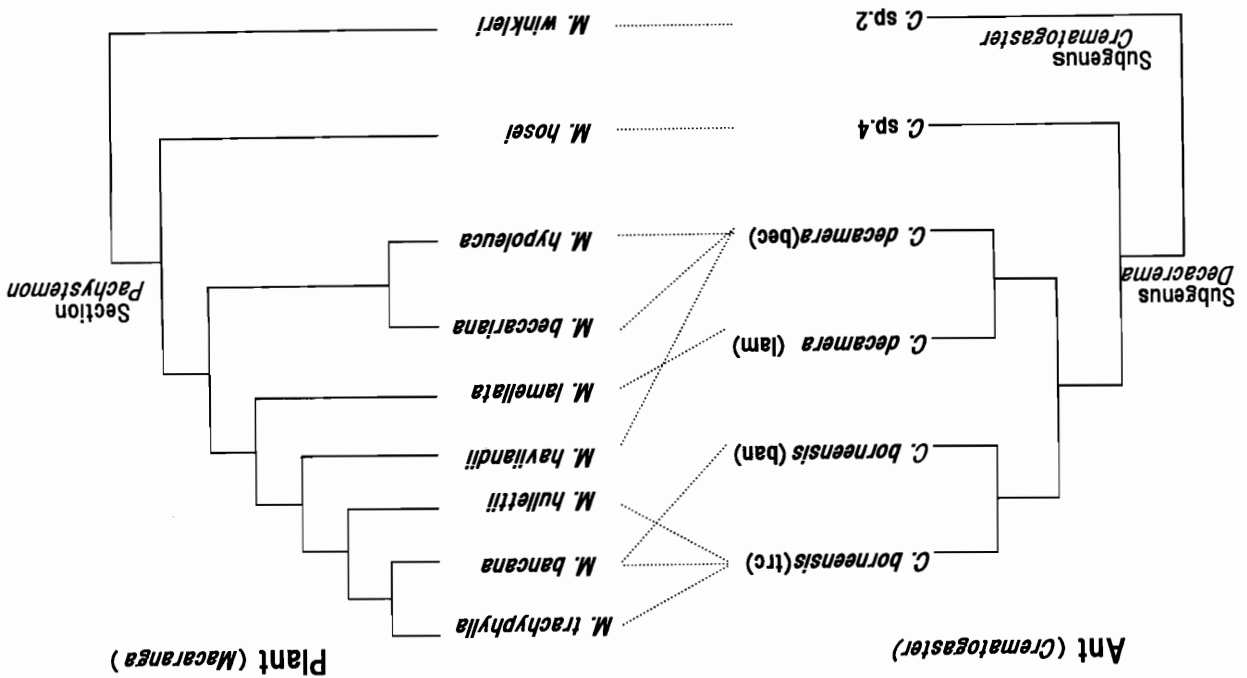


Table 1. Seven *Macaranga* species are organized into three groups based on their enemy fauna.

<i>Macaranga</i>	N	Percentage trees infested by ¹⁾				Principal enemies	Partner ants ²⁾	aggressiveness	density	quantity	main item	Chemical / structural defenses ⁵⁾
		gall makers	leaf eaters	wood eaters	wood peckers							
<i>M. deccariana</i>	81	24	17	5	8	gall makers <i>C. decamera</i> (bec)	+		+	scale insects	+++	
<i>M. lamellata</i>	9	31	5	31	8		<i>C. decamera</i> (lam)					
<i>M. bancana</i>	38	0	43	0	2	<i>C. borneensis</i> (ban)	++	++	++	scale insects	++	
<i>M. trachyphylla</i>	112	2	34	2	4		<i>C. borneensis</i> (trc)	++	++	++	food bodies	++
<i>M. hulleitii</i>	9	0	10	0	0	<i>C. borneensis</i> (trc)						
<i>M. hosei</i>	10	4	23	4	0		<i>C. sp. 4</i>					
<i>M. winkleri</i>	31	0	9	0	21	wood peckers <i>C. sp. 2</i>	+++	+++	+++	food bodies	+	

1) Itino and Itoka (2001)
 2) Itoka et al. (2000), Itino et al. (2001b)
 3) As *C. decamera* and *C. borneensis* are divided into different lineages in the molecular phylogeny, and each lineage corresponds to different specific host, principal host plants are indicated in the parentheses for each lineage (see Fig. 1)
 4) Itino et al. (2001a)
 5) Nomura et al. (2000)

Macaranga species, i.e. *Macaranga* species with weaker ant guards tend to have stronger non-biotic defense (Table 1, Itoika et al., 2000; Nomura et al., 2000).

The specialist herbivores for each *Macaranga* species appear to overcome the specific chemical and structural defense of *Macaranga* because ant-free plants were exclusively attacked by these specialist herbivores (Itino and Itoika, 2001). For example, *Macaranga* species susceptible to gall makers were not so susceptible to leaf eaters (Table 1), suggesting that they may differ in their allelochemical composition against herbivores. On the other hand, susceptibility to woodpeckers appears to be related to structural toughness of the stem: with weak stems, *M. winkleri* permits woodpeckers' easy access to symbiont ants, while *M. winkleri* is able to grow very fast (Davies et al., 1998) likely at a cost of the structural weakness.

On the other hand, food quantity offered by each *Macaranga* to the partner ants appears to be crucial for maintenance of ant specificity. The amount of food reward in *Macaranga* varies interspecifically (Itoika et al., 2000; Itino et al., 2001a; Hatada et al., 2002), and each amount appears suitable for each specific ant species. For example, a small-sized non-aggressive ant species (*C. decamera*) is associated with *Macaranga* species that provide few food rewards (Table 1, Itoika et al., 2000; Itino et al., 2001a). Even with limited rewards, *C. decamera* can effectively deter the main herbivore *Cecidomyiidae* (Itoika et al. 2000). On the other extreme, active and aggressive ant species (*C. sp. 2*) harbor the fast-growing and highly rewarding plant species (*M. winkleri*). Such aggressive behavior of the ants and plant's high rate of reward-offering are both indispensable to prohibit the vertebrates from destroying the plants and preying upon the ants.

Under these circumstances, the ant-plant specificity could be stably maintained. Suppose that the chemically and structurally defenseless *M. winkleri* were colonized by 'wrong' timid ant *C. decamera*, then it would suffer much damage by birds and generalist herbivores, and soon would wither to death. As such, the selection would favor the appropriate matching of ants and plants. Certainly, the fitness of particular associations were reported to vary in space and time in EFN plant-ant interactions (Schemske, 1983; Beattie, 1985) and in American myrmecophyte-ant mutualism (Davidson and McKey, 1993), which consequently inhibits the evolution of specificity. But fitness in *Macaranga*-ant mutualism seems highly stable spatially and seasonally: most of the ant-plant species-pairs coexist within a small spatial scale and they live in 'non-seasonal' forests without dry- or cool seasons (Davies et al., 1998).

HOW TO REAR ANTS: FOOD BODIES OR COCCIDS?

The primary food offered by plants to their partner ants differs among plant species: 1. homopterans only (homopterans themselves and their honeydew), 2. homopterans and specialized food bodies secreted by plants, or 3. food bodies only. American myrmecophyte *Tachigali* belongs to the first group (Fonseca, 1993) while most

myrmecophytic *Macaranga* belong to the second group. In the first group, the ants are able to take initiative in maximizing their fitness, because they can manipulate the homopteran population by eating or killing them to the level that is optimal for the ants but often not for the plants. However, such regulation of homopterans by ants may sometimes fail because the homopterans can potentially overcome regulation by the ants (e.g. by multiplying very fast or escaping spatially in the plant hollow stem) and increase to the ceiling level of carrying capacity. Fonseca (1993) reported that the homopteran population size in *Tachigali* was explained by plant leaf area and not by ant colony size, suggesting that the homopterans were free from ant regulation and reached the upper limit determined by food supply by the plants.

In *Macaranga*, the primary food offered by the plants to the ants was different among four *Macaranga* species (Table 1, Itino et al., 2001a). Ants in *M. beccariana* and *M. bancana* relied on homopterans rather than food bodies. In contrast, ants in *M. trachyphylla* and *M. winkleri* relied primarily on food bodies rather than homopterans. In relation with this, the plant investment made in ants (ant dry weight / plant dry weight) was different among the four *Macaranga* species. The Homoptera-dependent *M. beccariana* harbored lower biomass of ants than the food-body dependent *M. winkleri*, suggesting that energy loss is involved in the Homoptera-interposing system, which has one additional trophic level (Itino et al., 2001a). Without homopterans, the energy and nutritional flow from plants to ants is more direct, thereby more resources should be available for the ants per unit plant biomass. Interestingly, the Homoptera-dependent *M. beccariana* is more chemically, rather than biotically, defended in comparison with the foodbody-dependent *M. trachyphylla* and *M. winkleri* (Table 1, Itoika et al., 2000; Nomura et al., 2000), possibly due to the higher cost for the plants in maintaining the ant colony.

These interspecific differences in food-offering system in *Macaranga* species provide us with a good opportunity to consider the evolution of reward-offering systems in ant-plant symbioses. In earlier stages of the coevolution, homopterans are thought to be the primary diet for the ants (Benson, 1985; Ward, 1991). At this stage, plants probably regulated ant populations via the size of domatia space, as was demonstrated in *Tachigali* (Fonseca, 1993), while the homopteran population was probably not well regulated by the ants. In the next stage, food bodies began to play a more important role in the evolution of the mutualism since FBs were a more stable, efficient and adjustable diet for the plants and ants.

Given these scenarios, why does Homoptera-dependent *M. beccariana* not produce more food bodies and abandon the less efficient and less adjustable homopterans? Similarly, why have many ant-plants in general not been free of homopterans, as ant plant *Acacia* has done (Janzen, 1966)? If the homopterans are just extra costs to and ultimately useless in the plant-ant symbioses, then selection would favor their abortion from the system. In fact, one species *Macaranga puncticulata* and its partner ants appears to have aborted the homopteran symbionts at some point in their evolutionary history and have never accepted them again (Federle et al., 1998a, 1998b). One explanation for the above question is that many ant-plant systems are still in the early stages of their evolutionary trajectories and so

have yet to become independent of Homoptera.

INTIMATE COEVOLUTION

Our survey has confirmed specificity between nine species of *Macaranga* and four morphological species of *Crematogaster* (Figure 1). Yet, the specificity looks one-sided: every *Macaranga* species is principally associated with a single ant morphospecies, whereas two of the four *Crematogaster* morphospecies had several plant associates. We hypothesized that such ant morphospecies might be a mixture of morphologically similar but reproductively isolated cryptic species or races that correspond to particular *Macaranga* species.

To test the hypothesis, we examined the mtDNA sequence variation of *Crematogaster* ants living in the nine *Macaranga* species (Itino et al., 2001b). The ant samples were collected from seven localities in Bornean and Peninsular Malaysia. A 496-base-pair part of the COI gene of mitochondrial DNA was sequenced for ants from 47 different plants. The ant phylogeny revealed six primary mtDNA lineages, suggesting that the previously detected four morphological species are in fact divided into six or more genetically differentiated lineages with different mtDNA types. Four of the six ant lineages have basically one specific partner plant species while the other two ant lineages have three associates each (Figure 1). Despite the insufficiency of free-living *Crematogaster* species sampled, the ant phylogeny suggests that *Macaranga*-associated *Crematogaster* have arisen at least twice, namely in subgenera *Decacrema* and *Crematogaster*. Based on the assumption that the mean rate of divergence in mtDNA sequences is 2.3 % per million years in arthropods (Brower, 1994), the age of diversification in plant-ant subgenus *Decacrema* can be estimated less than seven million years (Itino et al., 2001b).

Given evidence for the high specificity between ants and plants, it is possible to test for cospeciation. The cospeciation hypothesis predicts the topology of ant- and plant phylogenies to be congruent and the timing of divergence to be simultaneous. The branching structures of the ant- and plant phylogenies are in fact highly congruent (Figure 1). We rejected the hypothesis that the ant phylogeny is independent of the plant phylogeny (Page, 1993, $p < 0.0012$, computed using 10,000 random trees) despite one major disagreement: a member of the *Crematogaster decamera* group seems to have once colonized *M. havilandii*, which had presumably been associated with a member of the *Crematogaster borneensis* group. In addition to the congruence of the ant and plant phylogenies, Tertiary climatic patterns in Borneo and the restriction of myrmecophytic *Macaranga* to aseasonal forests suggests that this clade of *Macaranga* diversified in the late Tertiary (Morley, 1998), which corresponds to the diversification period of *Crematogaster* subgenus *Decacrema*. These results suggest that the *Macaranga-Crematogaster* mutualism has been rapidly cospeciating and codiversifying over the past 6-7 million years (Itino et al., 2001b).

MACARANGA AS A MODEL FOR COEVOLVING INTERACTIONS

The intimate coevolution of *Macaranga* and *Crematogaster* is unique and present a striking contrast to the American and African ant-plant associations which are less specific (Fonseca and Ganade, 1996) and show no evidence for cospeciation (Ward, 1991; Chenuil and McKey, 1996). *Macaranga* is also ecologically unique among myrmecophytes in forming diverse communities of up to eight locally sympatric species, with each species inhabiting a slightly different microsite than the other species (Davies et al., 1998). The species-specificity of the ant guards appears to promote the coexistence of multiple *Macaranga* species on a small spatial scale, because each ant species defeats a restricted group of herbivores (Itino and Itioka, 2001) and thereby creates a novel enemy-free space (Holt and Lawton, 1993) for its host *Macaranga* species.

Macaranga system is interesting not only because the plants have intimately coevolved with ants, but also because they appear to have coevolved with many other organisms, i.e. symbiont coccids, herbivores and ant-predators (Heckroth et al., 1998; Itino and Itioka, 2001). Further ecological and phylogenetic treatment of this complicated but finely-organized association may provide a typical picture of intimately coevolving community in long-stable Southeast Asian tropical forests.

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SUMMARY

Many tropical plants house ants and thereby gain protection from herbivores. Although these ant-plant symbioses have been regarded as classical cases of coevolved mutualism, no evidence of cospeciation has been documented. Recent works showed, however, that the Asian ant-plant association between *Crematogaster* ants and *Macaranga* plants is highly species-specific, and that the molecular phylogeny of the ants parallels the plant phylogeny reflecting a history of cospeciation.

Because multiple (5-8) *Macaranga* species occur on a small spatial scale in tropical forests, we hypothesize that the ant-plant specificity is maintained not through parallel habitat specialization of the both parties but through their

coadaptation against specific enemies (herbivores and ant-predators). We examined whether or not the coexisting *Macaranga* species have different defense strategies against enemies. Interspecific comparison of leaf damage and enemy fauna of nine *Macaranga* species supported that the plants differ in their types of non-biotic (chemical/structural) defense: without ant protection, *M. beccariana*, for example, was resistant to leaf eaters but susceptible to gall makers. *M. trachyphylla* was heavily infested by leaf eaters, and *M. winkleri* was readily exploited by birds. Despite these variations in chemical/structural defense, ant-colonized plants were generally well defended by ants against most kinds of enemies. This, together with the differences in defensive behavior of the ant species, suggests that the individual host-specific ant mutualists are well adapted to deter the specific enemies, which can potentially overcome the chemical/structural defense of the host plants.

In parallel with the adaptive radiation of symbiotic ants in defense, the food-offering system of four *Macaranga* species was different. *M. beccariana* and *M. bancana* provide the ants primarily with scale insects which feed on plant sap inside the hollow stem, while *M. winkleri* and *M. trachyphylla* with food bodies produced by the plants. Ant biomass per plant biomass was lower in the scale insect-dependent *Macaranga* species than food-body dependent ones, suggesting that energy loss is involved in the scale insect-interposing symbiotic system, which has one additional trophic level.

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