MYRMECOPHAGY UNDERMINES ANT-PLANT MUTUALISMS: ANT-EATING *CALLOSCIURUS* SQUIRRELS (RODENTIA: SCIURIDAE) DAMAGE ANT-PLANTS IN SOUTHEAST ASIA

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Abstract. The hollow stems of many SE Asian ant-plants are frequently torn open by predators. These conspicuous injuries always occurred on previously ant-inhabited twigs. We discovered that they are caused by ant-eating *Callosciurus* squirrels. The major predator is probably the abundant Plantain Squirrel *Callosciurus notatus* Boddaert. We tested trapped squirrels in a large cage containing ant-inhabited and ant-free *Macaranga* treelets. *C. notatus* and *C. caniceps* tore open only the colonized twigs and left marks identical to those commonly observed in the field. In some areas, 100 % of all *Macaranga* ant-trees showed unmistakable traces of recent squirrel attacks. As a result, twigs often broke off and some young plants were even killed entirely. However, the frequency of stem damage caused by squirrels varied strongly with different localities. We present a tabular survey of known records of destructive myrmecophagy in ant-plants. The predators involved are birds, rodents and monkeys. These animals have good cognitive capacities and/or strong mouth-parts and thus appear to be well equipped to locate ant-plants and break open their hard domatium walls. None of them has been reported to be a specialist plant-ant predator and predatory behavior may often be learned. Damage caused by myrmecophagy occurs in many ant-plant systems and appears to represent an important cost of myrmecophytism. *Accepted 16 February 1999.*

Key words: Callosciurus notatus, Callosciurus caniceps, *Sciuridae*, *myrmecophagy*, *ant-plant*, *myrmecophytism*, *mutualism*.

INTRODUCTION

Tropical ant-trees ("myrmecophytes") are impressive examples of mutualistic relationships between animals and plants (for reviews see Buckley 1982, Davidson & McKey 1993, Jolivet 1996). The symbiotic ants nest in preformed cavities ("domatia") provided by these plants. In return, they primarily benefit their host plants by defending them against herbivores or by pruning neighboring vegetation. As a rule, strong herbivory or vine overgrowth in myrmecophytes only occurs when the protective ant guard is absent.

Lodging ants, however, can bring about an unexpected danger. In the course of our studies on *Macaranga* and other SE Asian ant-plant genera, we frequently observed conspicuous stem injuries, which occurred exclusively on previously ant-inhabited trees. We found out that they were not caused by herbivores, but by ant-eating rodents, which could be identified in the present study as *Callosciurus* squir-

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rels. Here we report this striking case of myrmecophagy and the destructive effect of *Callosciurus* squirrels on many ant-plants in SE Asia. We will compare our results with other known instances of destructive myrmecophagy in ant-plants.

MATERIAL AND METHODS

Field observations and experiments were conducted in the North Selangor Peat Swamp Forest on the west coast of Peninsular Malaysia (3°30'N, 101°10'E, 10 m a.s.l.) from April to July of 1995 and January to April of 1996. We trapped squirrels by using rat traps with banana baits fixed to trees at 1–2 m above the ground. Feces samples were collected from 40 freshly trapped *Callosciurus* squirrels and checked for ant remains.

Squirrels were put individually into a cage (2 x 2 x 2 m) in which we had inserted two small treelets or ramified branches of *Macaranga pruinosa* (each being of similar size and consisting of 5 twigs on average). An ant-free "tree" (without entrance holes) was simultaneously tested against another one inhabited

by specific partner ants of the *Crematogaster* (*Decacrema*) species group. Each individual squirrel was tested only once (n = 13 squirrels). Two of the tests were conducted with small trees of the syntopic congener *M. puncticulata*, which is associated with a larger *Camponotus* (*Colobopsis*) species (Federle *et al.* 1998a). The squirrels were kept in the cage for 24 h. In order to provide them with sufficient nourishment we supplied bananas and water. After 24 h we checked the *Macaranga* twigs for squirrel traces. For each 24 h experiment, two new experimental *Macaranga* "trees" were set up in the cage.

RESULTS AND DISCUSSION

Description of the stem damage. At our study site on the west coast of Peninsular Malaysia, we often observed conspicuous stem damage in the ant-plants *Macaranga pruinosa* and *M. puncticulata*. All these injuries looked similar (Fig. 1). On one side (mostly the upper side) the hollow twigs were torn open along a stretch of 5 to 30 cm, the myrmecodomatia being destroyed. The opening always began with a set of 2–3 characteristic double tooth marks. These marks never ran exactly in the direction of the twig, but at an angle of 40 ± 11° to it (average of 10 marks from different plants measured in top view). Each visible double tooth mark faced a small hole, which probably represents the impression mark of the opposite teeth. Similar small marks occurred regularly along the margins of the domatium openings, which suggests that the predator made further bites while stripping off the domatium wall. We found fresh domatium injuries (we considered twig openings with light, whitish wood and without plant callus to be "fresh") predominantly on young and slender twig sections that had thin and still poorly lignified domatium walls. In *M. puncticulata*, the maximum thickness of freshly damaged domatium walls was 3.5 mm (mean: 1.9 ± 0.6 mm; n = 125 fresh marks from 35 trees analyzed).

On most of the affected twig parts, abandoned ant entrance holes could still be seen. This indicated that these twigs had been previously occupied by ants. Moreover, all the damaged twigs were hollowed out. This finding is most significant in *M. pruinosa*, where the stems and twigs are filled with pith that has to be excavated by the colonizing *Crematogaster* (*Decacrema*) ants (Fiala & Maschwitz 1992). Even in larger trees (> 1.50 m) of this *Macaranga* species, only 50.5 % of the twigs are hollowed out (n = 5313 twigs

FIG. 1. Twig of *M. pruinosa* with traces of a recent colony foundation of *Crematogaster* (*Decacrema*) sp. (arrow), probably destroyed by a *Callosciurus* squirrel.

from 141 trees; see Table 1). However, in all of the *M. pruinosa* twigs damaged by the predator (n = 711 twigs from 77 trees), it was clearly visible that the pith had been excavated before. Interestingly, some damaged twig sections had obviously not been inhabited by large colonies, but had only contained claustrally founding queens. This could be easily recognized by the typical large entrance holes often sealed with pith (Fig. 1). Such traces provide evidence that the predator is capable of locating hollow "prey" twigs even when ants foraging on the twig exterior are absent. Ant entrance holes may therefore serve as an orientation cue.

The stem injuries were strikingly clustered on single trees or within groups of neighboring trees, whereas other trees were not affected at all (see Fig. 2). The distribution of damaged twigs among trees differed significantly from a random distribution (data from *M. pruinosa*; only trees with more than 20 hollowed-out twigs considered: n = 41 trees with a total of 1921 hollowed-out twigs of which n = 450

FIG. 2. *M. pruinosa* inhabited by *Crematogaster* (*Decacrema*) ants after predation by a *Callosciurus* squirrel. Damage shown by arrows.

were damaged; χ^2 = 460.8, df = 40, $P \ll 0.001$). As a rule, clustered injuries appeared to be of the same age, so that they may be caused by the visit of a single predator.

The shape of the twig marks suggested that the domatium predator could be an ant-eating rodent. We were able to confirm this assumption by direct observations and by cage experiments.

Identification of the predator (evidence for squirrels as predators). On two occasions, we observed a Plantain Squirrel (*Callosciurus notatus* Boddaert) from a distance, biting into twigs of large *Macaranga pruinosa* ant-trees. These bites were followed by some conspicuous head movements, in which the squirrel probably stripped off a domatium wall. After that the squirrel remained motionless for a short while, keeping its snout close to the twig. Both observed squirrels bit and tore open several twigs of the same tree; one of them was seen performing this behavior for more than 20 min. The bites of this squirrel caused a twig to break off the tree. In both of our observa-

tions, however, we were unable to see whether the affected twigs were inhabited by ants or not.

In order to verify whether *Callosciurus notatus* is the predator responsible for the frequent stem damage, we trapped squirrels near the observation site. The trapped rodents were transferred individually to a cage (side length 2 m) containing one ant-inhabited and one ant-free experimental *Macaranga* tree and kept there for 24 h each.

In the cage experiments, 9 out of 13 Plantain Squirrels tested did open the *Macaranga* domatia. The marks they left on the twigs (n = 45) looked identical to those observed in the field. Moreover, *Callosciurus notatus* destroyed only the colonized plants (χ^2 = 9.0, df = 1; P = 2.7 x 10^{-3}). The ant-free plants, however, showed only a few tiny tooth marks on the stem surface, which we interpret as "testing" bites. Since the squirrels were very anxious when we approached the cage, we have not been able so far to see the twig-opening behavior from close up.

Our results indicate that *Callosciurus notatus* opens the domatia of *Macaranga* twigs in order to prey on ants and/or ant brood. This is in accordance with Lim (1965) as well as with Lim & Heyneman (1968), who also reported Plantain Squirrels to be myrmecophagous. However, *Callosciurus notatus* did not exclusively feed on ants. Like other squirrels, they also consumed fruits and seeds, so that ants represented only part of their diet. Feces samples of 40 *Callosciurus notatus* squirrels freshly trapped at our study site all contained plant fibers, seeds and fragments of insects, predominantly ants. In 2 of the 40 feces samples, we were able to identify workers of *Crematogaster* (*Decacrema*) spp. 1 and 2 (species numbers according to Fiala *et al.* 1999), which are associated with *Macaranga pruinosa*. As these ants never occur away from their host plant (which is *M. pruinosa* at our study site), the two squirrels had apparently visited a *M. pruinosa* tree and fed on its ants before they fell into the trap. In another 8 of the feces samples we also found fragments typical of *Crematogaster* (*Decacrema*) ants. However, these remains could not be determined unequivocally as they lacked the distinctive antennae necessary for reliable identification.

Apart from the abundant Plantain Squirrel, the syntopic congener *Callosciurus caniceps* also proved to be capable of tearing open the *Macaranga* domatia (1 out of only 3 trapped squirrels). None of the other small mammals tested inside the cage made any bites into the *Macaranga* plants offered: *Lariscus in-*

signis (Sciuridae, n = 1), *Sundamys muelleri* (Muridae, n = 3), and *Tupaia glis* (Tupaiidae, n = 5). However, our findings cannot rule out other animals also being responsible for the observed stem injuries.

Callosciurus notatus is very common in plantations and forests and widespread in SE Asia (Duckett 1982, Payne *et al.* 1985). It was the squirrel species we spotted most frequently at our study site and the most abundant animal among our trap captures (n = 46 in 485 trap-days). We directly observed *Callosciurus notatus* stripping bark off stems, which left traces commonly seen on many trees (including *M. pruinosa*). Moreover, we frequently saw Plantain Squirrels feeding on the fruits of female *Macaranga pruinosa* trees.

Occurrence of the damage. We observed the described damage in most of the myrmecophytic *Macaranga* species of West Malaysia, Borneo and Sumatra (Table 1). Besides *Macaranga* spp., a variety of other SE Asian ant-plants with hollow stem domatia often were found to be torn open in a similar manner. The affected plant species we observed are listed in Table 3. Many of them are hosts of *Cladomyrma* ants, e.g., *Neonauclea* spp. (Rubiaceae), *Saraca thaipingensis* (Caesalpiniaceae), *Drypetes longifolia* (Euphorbiaceae), *Spatholobus* cf. *bracteolatus* (Fabaceae), and *Crypteronia griffithii* (Crypteroniaceae); others are non-specific myrmecophytes (*Capparis buwaldae*, Capparaceae, *Myrmeconauclea strigosa*, Rubiaceae) inhabited by a variety of ants.

Squirrel predation is apparently not restricted to living plants. We observed fresh traces also on some dead and dry twigs, when these were inhabited by ants. Moreover, we rarely found twig marks in non-myrmecophytic members of *Macaranga* or other non-myrmecophytic genera (see Table 1). In these cases, the stems contained droppings typical of caterpillars, which indicated that the squirrels had not preyed on ants but on shoot-boring larvae.

Another type of domatium damage was found in *Macaranga*, but at much lower frequencies (*M. pruinosa*: only 4 out of 5313 twigs). The marks were round holes presumably made by woodpeckers or other birds feeding on ants or brood.

Influence on host plants and plant-ant colonies. The characteristic stem damage was very common in *Macaranga* (Table 1). Affected twigs often snapped down or broke off (49 out of 228 randomly selected, damaged *M. puncticulata* twigs; see also Fig. 2) and rarely

(2 observed cases in *M. puncticulata*), entire young plants were even killed. However, *Macaranga* trees showed considerable capacities of regeneration. We observed adult *M. puncticulata* plants surviving the complete destruction of all living shoots by forming new axillary sprouts. A one-year growth experiment with *M. pruinosa* even failed to demonstrate any negative effect of the predation. Out of 86 trees investigated (2.5–6.0 m in height), 23 were damaged (2–70 % of the twigs affected), and 63 were not. The growth rate of the damaged trees was 2.39 ± 0.85 m/year, whereas the undamaged plants averaged 2.19 ± 1.02 m/year.

The partner ant colonies were strongly affected by the squirrel predation. As a rule, queens of small colonies still inhabit young twigs with thin domatium walls, which are more easily torn open by squirrels (Fig.1). Since the *Macaranga* ant partners *Crematogaster* (*Decacrema*) spp. and *Camponotus* (*Colobopsis*) sp.1 are monogynous (Fiala & Maschwitz 1990, Federle *et al.* 1998b), entire colonies will die out when their queen has been killed. Colonies in heavily damaged *M. pruinosa* trees often contained many males and almost no brood, which indicates that their queen had been lost. In the one-year experiment with *M. pruinosa* (see above), the proportion of twigs colonized by *Crematogaster* (*Decacrema*) ants in the trees without damage increased by 15.1 %, but decreased by 5.8 % in the damaged group (U-test: P = 0.083 [n.s.], $n_{1 (damaged)}$ = 23; n_2 = 58; z = −1.78; only trees inhabited by *Crematogaster* (*Decacrema*) colonies considered).

M. puncticulata trees are less abundant in late successional forests. In one such stand, all of the 20 plants we investigated had damaged twigs. Although we observed many colony-founding *Camponotus* (*Colobopsis*) sp. 1 queens on these trees, larger colonies were absent. We assume that squirrel predation completely prevents the establishment of larger ant colonies at these sites.

Apart from its detrimental influence on the specific partner ants, the squirrels' predation led to a succession of secondary stem-nesting ant species. Out of 140 *M. pruinosa* twigs colonized by these ants (18 species of the genera *Tapinoma, Technomyrmex, Camponotus, Crematogaster, Pheidole, Tetramorium, Vombisidris,* and *Tetraponera*), 79 (= 56 %) were twigs with old marks (recognized by the presence of plant callus) of squirrel predation. Correlation between squirrel damage and the occurrence of secondary

TABLE 1. Frequency of twig damage apparently caused by squirrel predation in members of the genus *Macaranga* in SE Asia. All the investigated trees were > 1 m tall.

Macaranga species	Locality	n		damaged		%	
		twigs	trees	twigs	trees	twigs	trees
M. pruinosa (*)	West Malaysia: North Selangor Peat Swamp Forest	5313 [2532]	141 [108]	711	77	13.4 [28.1]	54.6 [71.3]
M. puncticulata	North Selangor Peat Swamp Forest	448	129	178	91	39.7	70.5
M. triloba	Ulu Gombak	271	120	24	21	8.9	17.5
M. hosei, M. hullettii, M. hypoleuca, M. motleyana ssp. *griffithiana*	(various localities in West Malaysia)	damage observed (no quantitative data available)					
M. aetheadenia, M. beccariana, M. caladiifolia, M. hosei, M. puncticulata, M. trachyphylla, M. triloba, M. winkleri	Borneo (various localities)	damage observed (no quantitative data available)					
M. pruinosa	Sumatra	damage observed (no quantitative data available)					
M. bicolor (**)	Palawan (Philippines)	damage observed (no quantitative data available)					

(*) 49.5 % of all investigated *M. pruinosa* twigs were not hollowed out and completely lacked squirrel damage (see text). Values in square brackets show data considering only the hollowed-out twigs. (Twigs of adult *M. triloba* and *M. puncticulata* are always hollow).

(**) *M. bicolor* is non-myrmecophytic, but its twigs are occasionally inhabited by shoot-boring caterpillars and secondary stem-nesting ants (see text).

colonizers was highly significant (Table 2). Queens of these ant species can only colonize twigs if the domatia are openly accessible. In the ant-plant *M. pruinosa*, secondary colonizers occurred much more frequently in adult trees (< 10 m: 1.3 % of 4425 twigs from 121 trees; > 10 m: 9.4 % of 888 twigs from 17 trees). This effect may in part be traced back to domatium-opening by squirrels.

Myrmecophagy in squirrels. In some areas of Malaysia, squirrel damage appeared to occur at lower frequencies than at our main study site. In the old secondary forests around Ulu Gombak, which are 100 km away from the North Selangor Peat Swamp Forest, twig marks on *M. triloba* trees were less common (difference from damage frequency (*M. puncticulata* + hollow twigs *M. pruinosa*): $\chi^2 = 54.1$; df = 1; $P \ll 0.001$;

Table 1). We cannot exclude the possibility that differences between host species lead to this effect (e.g., see the difference in damage frequency between the syntopic *M. pruinosa*$_{(hollow)}$ and *M. puncticulata*:

TABLE 2. Connection between squirrel damage and the occurrence of secondary stem-nesting ant species.

n (twigs)	domatia opened by squirrels	not affected by squirrels
with secondary stem-nesting ants	79	61
without	632	4541
$\chi^2 = 229.9$; df = 1; $P \ll 0.001$		

TABLE 3. Survey of recorded damage to ant-plants, caused by predators of ants and/or ant brood.
Evidence: T: traces found on plants, O: direct observation of predator.
Domatium: C: caulinar (hollow stems), L: leaf or stipule pouches, O: ochreae, P: hollow pitcher-bearing tendrils, T: stipular thorns.

Predator	Plant species	Ant species	Evidence	Domatium	Damage	Geographic region	Reference
woodpeckers: Dryocopus lineatus and probably other species	Cecropia spp., C. adenopus (= peltata)	Azteca spp., A. alfari, A. muelleri	O,T	C	stem domatia (young trunks and slender branches) pierced by woodpeckers (sometimes causing permanently deformed stems, which break off in windstorms)	Neotropics Northern Colombia, Central America	Fiebrig (1909); Abromeit (1911); Stitz (1913); Eidmann (1945); Skutch (1945); Janzen (1969); Janzen (1983); Carroll (1983)
woodpeckers	Macaranga spp.	Crematogaster spp., Campo-notus spp.	O,T	C	round holes in ant-inhabited twigs; observation of a woodpecker picking into twigs of M. hypoleuca in Borneo	SE Asia Borneo	Maschwitz et al. (1994); this study
birds: orioles (Icterus sp.) and woodpeckers (Centurus spp. ?)	Acacia spp., A. cornicera, A. collinsii, A. hindsii, A. melanoceras,	Pseudomymex spp., P. belti, P. ferruginea, P. nigrocincta, P. venefica	O,T	T	swollen thorns opened (by splitting, breaking, puncturing). Generally one out of 100-500 occupied swollen-thorn acacia at a given site (0.5-10 ha) showed predation by birds	Neotropics: Northern Colombia, Central America	Janzen (1966, 1969)
birds ?	Acacia spp.	?	?	T	"birds known as ant predators on the African Acacia trees"	Africa	Sjostedt (1908; ex Jolivet 1996)
birds ?	Humboldtia brunonis	several	T	C	domatia of many plants found damaged, apparently by a bird	India	D. McKey (pers. comm.)
birds ?	Dischidia rafflesiana	Iridomymex sp. [= Philidris]	T	L	"Round holes in the pitchers of D. rafflesiana are quite common, and I believe they are made by birds in search for ants' 'eggs'"	SE Asia Thailand	Kerr (1912)
woodpeckers ?	Humboldtia laurifolia	several	T	C	some plants with a considerable portion of internodes damaged; according to Escherich (1911), these wounds were "undoubtedly caused by woodpeckers"	Sri Lanka	Escherich (1911); Blatter (1928)
monkeys: Cebus capucinus	Acacia collinsii	Pseudomymex belti	O,T	T	thorns and branches ripped off; extensive destruction of some trees	Neotropics	Freese (1976)
monkeys: Cebus capucinus	Cordia alliodora	Azteca sp.?	O,T	C	swollen nodes bit open (unclear if ants were eaten)	Neotropics	Freese (1976)

	Barteria fistulosa	Tetraponera sp.			branches ripped open	Africa	Davidson & McKey
monkeys: Cercocebus albigena monkeys	Barteria fistulosa	Tetraponera sp.	O	C	branches ripped open	Africa	Davidson & McKey (1993); D. McKey (pers. comm.)
monkeys	Cecropia sp.	?	?	C		Neotropics	Terborgh (pers. comm. cit. in Davidson and McKey 1993)
rodents: Callosciurus notatus, C. caniceps	Macaranga spp. (see Table 1)	Crematogaster spp., Camponotus spp.	O,T	C	(see text)	SE Asia: Malay Pen., Borneo, Sumatra, Philippines	this study
rodents	Myrmeconauclea strigosa	several	T	C	swollen internodes rarely torn open	SE Asia: Borneo	J. Moog (own observ.)
rodents	Capparis buwaldae	several	T	C	hollow stems torn open. 6 out of 8 plants showed damaged stem parts	SE Asia: Borneo	Maschwitz et al. (1996)
rodents	Saraca thaipingensis	Cladomyrma petalae	T	C	previously inhabited internodes torn open, tooth marks	SE Asia: Malay Pen.	Maschwitz et al. (1996); J. Moog (own observ.)
rodents	Spatholobus bracteolatus	Cladomyrma petalae	T	C	internodes previously colonized by ant queens torn open	SE Asia: Malay Pen.	J. Moog (own observ.)
rodents	Drypetes longifolia	Cladomyrma petalae	T	C	twigs torn open along a stretch of 10–30 cm, tooth marks; sets of neighboring plants damaged	SE Asia: Malay Pen.	Maschwitz et al. (1996); J. Moog (own observ.)
rodents	Crypteronia griffithii	Cladomyrma crypteroniae	T	C	previously inhabited internodes torn open	SE Asia: Borneo	J. Moog (own observ.)
rodents	Neonauclea gigantea, N. paracyrtopoda N. sp. C.	Cladomyrma spp.	T	C	previously inhabited internodes torn open, tooth marks. At a study site in Sabah (Borneo), 50.4 % of n = 226 N. gigantea trees were damaged	SE Asia: Borneo	Maschwitz et al. (1996); J. Moog & T. Urschek (pers. comm.)
unknown	Nepenthes bicalcarata	Camponotus schmitzi	T	P	tendril domatia and pitcher parts damaged, tooth marks	SE Asia: Brunei	M. Merbach (pers. comm.)
unknown	Scaphopetalum thonneri	Technomyrmex kohli, T. laurenti	T	L	about 30 % of leaf pouches damaged [no details given in text]	Africa: Southern Cameroon	Dejean & Djieto-Lordon (1996)
unknown	Clerodendrum fistulosum	several	T	C	stem domatia of some plants torn open	SE Asia: Borneo	Maschwitz et al. (1994)
unknown	Korthalsia echinometra, K. scortechinii	Camponotus (Myrmoplatys) spp.	T	O	ochreae with slits or punctures probably pierced by birds	SE Asia: Malay Pen., Borneo	M. Werner & M. Lehmann (pers. comm.)

χ^2 = 24.7; df = 1; $P \ll 0.001$; Table 1). However, we have evidence that *Callosciurus notatus* squirrels trapped from plantations where *Macaranga* ant-plants were completely absent did not tear open hollow ant-plant twigs at all (unpubl. results). Therefore, we assume that preying on plant-ants is not innate, but rather acquired by learning.

Destructive myrmecophagy in ant-plants. For ant-predators capable of opening twigs, ant-plants probably represent an easily accessible and predictable source of protein food.

Table 3 gives a survey of all records known to us of destructive myrmecophagy in ant-plants. The list is certainly not exhaustive, since numerous ant-plant predators have not yet been identified. Moreover, many of the listed records are only based on the observation of twig marks. The predators recorded are birds (mostly woodpeckers), monkeys and rodents. These animals have in common that they are capable of breaking open hard domatium walls with their bills, incisors, or (the monkeys) with their skilful hands. None of the recorded predators is an obligate ant-predator and most of them are polyphagous. Moreover, the habit of preying on plant-ants in some species appears to be acquired by learning. This might be true for monkeys and for the *Callosciurus* squirrels investigated in the present study.

As discussed by Redford (1987), the extent to which ants are susceptible to predation varies with the type of colony defense. Heavily stinging species (e.g., members of the Ponerinae or Pseudomyrmecinae) may deter vertebrate ant-predators more strongly than workers of taxa without a functional sting. However, the data listed in Table 3 are still too meager to allow any interpretation concerning this issue. Similarly, host plants probably differ in their susceptibility to predation by having weaker or stronger domatium walls. The clearest evidence for this has been found in *Acacia*, where the small type-A thorns are more frequently split open by birds than the stronger type-B thorns. Moreover, type-B thorns predominantly occur on trees inhabited by monogynous *Pseudomyrmex* colonies, which suggests that the formation of stronger thorns is an adaptation to protect the colony queen against predation (Janzen 1969). In *Macaranga* and many other myrmecophytes, the queens of larger plant-ant colonies preferably stay in the trunks at the bottom of the trees, where they are well protected against predators and twig damage.

With regard to destructive ant-predators, colonization by partner ants seems to be unfavorable to host plants because stem injuries become more likely. However, many myrmecophytic associations have actually proved to be stable during long periods of evolution. If energy costs invested for the nutrition of ants plus the costs arising from ant-predator damage surpassed the benefits derived from the association with ants, we should expect a selection towards plant features rendering ant colonization more difficult (e.g., reduction of stem diameter, production of fleshy pith, loss of food offers, etc.). However, mass predation on ant-plants (as observed in this study) appears to be an evolutionarily young phenomenon for the following reasons.

Many of the ant-plants listed in Table 3 are typical pioneer trees and have become much more abundant in the course of recent logging activities by man. In SE Asia and the Neotropics at least, secondary forests are especially rich in ant-plants. At our study site, former forest clearings are now almost pure mass stands of *M. pruinosa*. Under these conditions, using plant-ants as a food resource may be much more profitable than in primary forests. Similarly, some predators abundantly occur in anthropogenic habitats (e.g., *Callosciurus notatus*, Duckett 1982), but appear to be less common in primary forests. Therefore, we conjecture that destructive ant-predators have not exerted a continuous selection pressure in the evolution of ant-plant mutualisms.

The destructive effect of myrmecophagy on ant-plants has been used as an argument against the "protectionist" ant-plant hypothesis (Fiebrig 1909, Escherich 1911). Few of the experimental studies that demonstrated a protective effect of plant-ants towards their host plants have taken into account the influence of ant-predators (e.g., Janzen 1966). Further work is needed to quantify the cost of myrmecophagy in relation to the benefits of myrmecophytism.

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