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Ant species on a facultative ant-plant (*Macaranga tanarius*) and their possible roles in herbivory protection

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ABSTRACT. Protective mutualism between ants and *Macaranga* genus plants ranges from obligate to facultative interactions. Unlike obligate ant-plant interactions, facultative mutualists like *Macaranga tanarius* lack specialized structures to house ant symbiont colonies but offer food rewards such as extrafloral nectary secretions and food bodies. These rewards attract opportunistic foraging ants that provide defense against insect herbivores. We hypothesized that the efficacy of this defense depended on the composition of the ant species. We assessed insect herbivory by recording leaf damage and monitored ant activity at different times of the day. We also conducted behavioral assays to test ants' response toward offered wax-moth larvae prey (representing lepidoptera larva that causes most leaf-loss damage of *M. tanarius*). Ant community composition did not differ between day and dusk, with almost half of the species (48.4%) active at both times. Saplings with foraging ants showed a trend of higher leaf loss (mean = 2.13%) than saplings without ants (mean = 1.32%), contrary to our expectations, although this difference was not statistically significant. This could be due to the short observation time in this study, as herbivore attacks on leaf loss may be accumulated over a longer period. Most ant visitors on *M. tanarius*, which relied on herbivory diets, ignored the prey items; only the yellow crazy ant *Anoplolepis gracillipes* consistently attacked offered prey. Future research should be carried out over a longer period, and the abundance of ant species patrolling *M. tanarius* should be recorded to understand the potential roles of ants on these plants.

Keywords	extrafloral nectary secretions, food bodies, wax-moth larvae, *Anoplolepis gracillipes*, behavioral assays
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INTRODUCTION

The genus *Macaranga* (Euphorbiaceae) is a group of trees widely distributed in the paleotropical regions between western Africa and the eastern Pacific Islands. These plants often take on the role of colonizers in disturbed and forest-edge habitats in the early to mid-stages of ecological succession (Whitmore 2008). Because of their fast growth rate compared to climax tree species such as dipterocarps, these colonizing plants can also make up the dominant tree species in disturbed habitats and secondary forests. *Macaranga* species growing in these habitats have been found to suffer from phytophagous insect herbivore attacks, such as Lepidoptera larvae, beetles in adult and larval stages, and grasshoppers (Fiala et al. 1989). Insect herbivory can account for up to 11% of annual leaf area loss in tropical forests (Coley & Kursor 1996) and has been recorded to be most severe in seedlings and immature plants (Itino & Itioka 2001), thus harming plant growth and reproductive success (Marquis 1984; Marquis & Braker 1994). Protective mutualism is a common strategy adopted by plants from the genus *Macaranga* in response to insect herbivory. In Southeast Asia, 26 species are known myrmecophytes (i.e. plants that live in an obligate association with a colony of ants), associated primarily with eight species of *Crematogaster* ants nesting in domatia (Feldhaar et al. 2016). The remaining ~200 *Macaranga* species are myrmecophiles (i.e. plants that lives in facultative association with ants), attracting ants by offering extrafloral nectary secretions and food bodies (Whitmore 2008).

Ant-associated *Macaranga* are generally well-defended against insect herbivores (Fiala et al. 1989, 1994) and elicit their ant-assisted defensive strategies through the production of food rewards in the form of small spherical food bodies that are rich in sugars, amino acids, lipids, phenols, and alkaloids (González-Teuber & Heil 2009) and extrafloral nectary secretions which are composed of sugars and amino acids. However, the precise nature of the plants' relationship with their ant partners differs depending on whether their interactions are myrmecophilous or myrmecophytic (Fiala et al. 1999).

In myrmecophilous interactions, foraging ants are attracted through the distribution of plant rewards across different plant parts such as nectar-secreting glands found on non-floral plant tissues (Souza et al. 2024). In myrmecophytic interactions, parts of the host plant are modified domatia that serve as nesting spaces for ant partners which are typically species specific. Myrmecophytic ants generally do not consider insect herbivores as a food source and respond by biting the insect into pieces or pulling it towards the edge of the leaf and dropping it from the tree (Shimizu-kaya et al. 2016).

Myrmecophytic *Macaranga* often have wax crystals covering the stem surface that facilitate the exclusion of non-partner ant species as only symbiotic ants with the 'right' claw tips can move without difficulty on the waxy stem surface (Brechka 2024). This is coupled with the structure of the host plant stipules, which are ecological isolation mechanisms that prevent access to the food bodies by non-symbiotic ants (Fiala & Maschwitz 1991; Federle et al. 1997; Linsenmair et al. 2001; Feldhaar & Fiala 2021). In myrmecophilous interactions, plants such as *Macaranga tanarius* have adopted a broader strategy by scattering the food rewards widely on the dorsal surfaces of their leaves, petioles, and stems that can be accessible by any foraging insects, including ants (Fiala & Maschwitz 1991; Heil et al. 2000).

Because of this broad strategy of disseminating food rewards, myrmecophilous *Macaranga* do not maintain interactions with specific ant partners. Instead, these plants maximize their defense against insect herbivores by enticing free-ranging, opportunistic ant species to forage on the plant surfaces. A wide variety of ant species are enticed to forage on myrmecophilous plants. Protection of the plant from insect herbivores can be inconsistent as not all attracted species of ants may provide the same level of defense against insect herbivores for myrmecophiles (Fiala & Maschwitz 1991).

In this study, we first surveyed the ant species that foraged on the myrmecophile *Macaranga tanarius* at a secondary forest site in Peninsular Malaysia. This was undertaken at two distinct time points to capture as many foraging ant species as possible. We expected little overlap between the active ant species in the daytime and dusk due to temporal partitioning (Houadria et al. 2015). We also hypothesized that host plants with ants present were better protected than host plants lacking ants. Hence, the former host plants would have a lower percentage of leaf surface area loss. Lastly, to assess the response of ant species to insect herbivores, we performed behavioral assays by offering foraging ants wax moth larvae and recorded the response toward the offered herbivore. We hypothesized that the efficacy of this defense strategy depended on the species composition of ants in the given environment where ants with a more aggressive nature (such as ants hunting for protein prey) offered better protection against insect herbivores than ants that relied mainly on a generalist omnivore and floral diet. We thus expected that most ant species would ignore the offered herbivore and only visited the plants for the consumption of food rewards, with the exception of ants with omnivorous or predatory diets. This would indicate that ant presence was a deterrent rather than an active contributor to anti-herbivory defenses in facultative ant-plants (Fiala et al. 1989, 1994; Linsenmair et al. 2001; Yek et al. 2023).

MATERIALS AND METHODS

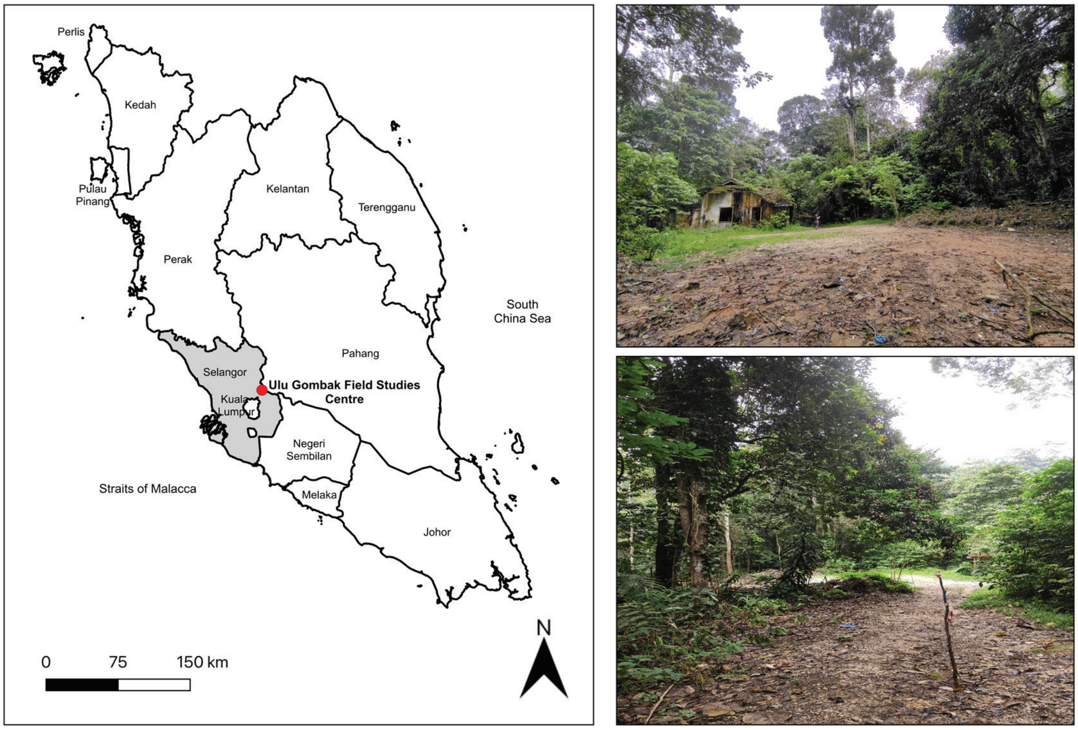
Study site and sampling criteria

We conducted our experiment and data sampling activities at the University of Malaya, Ulu Gombak Field Studies Centre (GB; 3°19'N, 101°45'E) between September and October 2022. The study site is a regenerated forest logged ~60 years ago before the area was designated as a forest reserve (Nor Hashim & Ramli 2013). The study area comprised of relatively open habitats exposed to sunlight with lush undergrowth (Ruziman et al. 2022). The forest stretch within the Field Studies Centre grounds is located along the edges of the forest reserve and the Karak Highway, one of the major roads leading to the eastern part of Peninsular Malaysia (Nor Hashim & Ramli 2013). It primarily comprises secondary-growth vegetation of pioneer tree species such as *Macaranga* spp., *Gigantochloa scortechinii*, and *Piper aduncum* (Ruziman et al. 2022) (Fig. 1). The two most abundant *Macaranga* at the study site were the obligate *Macaranga bancana* and the facultative *Macaranga tanarius* (Yek et al. 2023). The latter species being the subject of examination in this study.

Macaranga tanarius is a myrmecophile that elicits ant defense against insect herbivores through non-selective food rewards in the form of extrafloral nectary secretions and food bodies offered to attract a broad range of ant species that are found in the same habitat (Calixto et al. 2018). Because herbivory damage is most significant in seedlings and young plants (Itino & Itioka 2001), *M. tanarius* exhibits a growth-stage dependent trade-off in biotic ants-derived herbivory defense (Fiala et al. 1989; Heil et al. 2000). The plants' investment in food body production substantially declines once the trees have surpassed the height of 3 m and the plants have been shown to cease production of extrafloral nectary secretions once above 4 m in height (Fiala & Maschwitz 1991). As such, we enforced sampling criteria of only including plants equal to or less than 3 m in height in our survey.

Herbivory damage and ant species composition survey

Because herbivory damage tends to be focused on young leaves making up the crown of the plant (Folgarait & Davidson 1995), measurement of the herbivory damage incurred from external chewing insects (*e.g.,* lepidopteran larvae, beetles, and grasshoppers) in each plant was done by measuring the percentage of total leaf loss from the top three fully developed leaves of each surveyed tree. The top three fully developed leaves from plants exceeding the height of researcher's reach often grew along a downward slope, hence measurements were taken using a step ladder placed on sturdy ground, and with a vantage point from higher ground. Images of these top three leaves were captured using a mobile phone camera and processed using ImageJ software (Abràmoff et al. 2004) to quantify herbivory leaf damage. To quantify herbivory leaf damage, a horizontal photograph of the leaf was uploaded into the software, the percentage was calculated by comparing the total herbivory loss area (white) against the estimated total area of the reconstructed leaf (black) (Supplementary Figure) (Laflamme



Data source: GADM (2023).

Fig. 1. Map of Peninsular Malaysia where Ulu Gombak Field Studies Centre (red marker) is located northeast of Kuala Lumpur (left; version 4.1; GADM 2023). Photographs depicting the vegetation characteristics of the sampling site (photo credit: Zhi Hoong Wong; right top and bottom).

et al. 2016). Mechanical damage, defined in this study as leaf loss resulting from abiotic factors such as falling debris or human intervention was excluded from our calculations in the initial leaf-outline setting. The mean herbivory damage of the top three leaves was computed separately. The mean of the three herbivory percentages was then taken to be representative of the percentage of herbivory damage incurred in each *M. tanarius* sapling.

To better understand the ant species that visited *M. tanarius*, we surveyed ant compositions found foraging on the plant. Because of the wide range of possible ant activity, we employed two spatial time point surveys – between 09:00 h to 12:00 h (Day) and 16:00 h to 19:00 h (Dusk) that accounted for variations in ant activity. Foraging ants could be found on the entire host plant; hence, the collection of ant samples included specimens collected from the entire plant. We collected a voucher for each ant species encountered on the leaves or stem of *M. tanarius* and only noted ant 'presence' and 'absence' for each species but not abundance data. Representative ant voucher specimens were brought back to the lab in ethanol for identification down to morphospecies level by the authors of this manuscript (HLT, ZHW, and SHY) using the identification guide of ant genera of Borneo (Hashimoto 2003). The morphospecies labeling of ants only applied to this study.

Ant behavioral assays

Leaves at the crown of the host plant are considered most susceptible to insect herbivore attacks (Folgarait & Davidson 1995). Hence, our bioassays focused only on the crown of the host plant. We tested the hypothesis that only predatory and highly aggressive ants attack insect herbivores by categorizing the ants into the following functional groups following Groc et al. (2014): ground omnivores (GO); arboreal omnivores (AO); ground-dwelling generalist predators (GGP); arboreal generalist (AG) and arboreal predators (AP). Morphospecies belonging to the same genus whose detailed dietary and nesting information are known were assigned the same functional group.

To assess the ants response when they encountered insect herbivores on host plants, we presented them with a live prey item and recorded their responses as described below. Our previous study at the same site found that most of the herbivory damage incurred by *M. tanarius* was from small phytophagous insects such as lepidopteran larvae (Yek et al. 2023). Therefore, we attempted to replicate this by using live waxworms (*Galleria mellonella*), in their third instar and weighing between 50-100 mg, as an approximation of lepidopteran larvae that local ant species might encounter while foraging on *M. tanarius*. A single live *G. mellonella* was placed on the center of the leaf when ants were observed foraging within the plant's top three to four leaves, composing the crown of each *M. tanarius* plant. To reach the crown of the *M. tanarius* plant, we chose trees at the downward slope and a step ladder placed on sturdy ground. Ant responses to the introduced prey item were recorded for 20 minutes (Fig. 2). This period was selected since it took time for foraging ants to recruit their nestmates if aggressive behaviors were displayed. Ant responses were recorded as binary traits: passive response (ants ignore introduced live prey) and active response (ants attacked introduced live prey directly, and/or recruited nestmates to move prey as a food item). We did not quantify the total time frame within which ants displayed passive or active responses. The behavioral assay experiments were also conducted at two time periods: between 09:00 h to 12:00 h (Day) and 16:00 h to 19:00 h (Dusk), mirroring the ant species composition survey we conducted. Repeated assays were conducted on some ant species, which were recorded on single trees during the observation period.

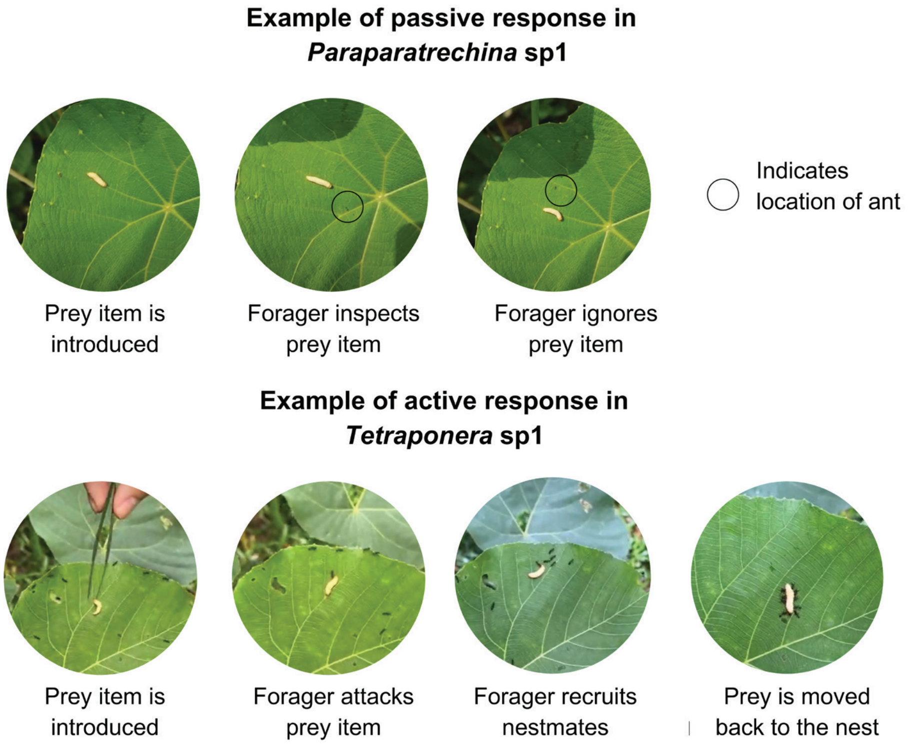


Fig. 2. Examples of the passive response of foraging ants to an introduced prey item (*Paraparatrechina sp1*) and the active response of foraging ants to an introduced prey item (*Tetraponera sp1*).

Statistical analyses

We carried out statistical analysis in JASP (Version 0.16.4; JASP Team 2024) and used the mean of the herbivory leaf loss for each tree as data points. For temporal ant species activity patterns, we visualized the distribution and overlap of ant species using a Venn diagram (Venny version 2.1; Oliveros 2007). To test whether the presence of ants affects the herbivory damage recorded on *M. tanarius* saplings, we used the Mann-Whitney U test and compared the herbivory damage between saplings with no ants detected (N = 33) and ants detected (N = 25). A chi-square test was performed to assess whether ant species differed in their responses to offered live prey, with the number of bioassays as replicates.

RESULTS

Herbivory damage and ant species composition survey

We sampled 58 saplings of the facultative ant-plant *M. tanarius* at GB and found that they had a mean surface area of total leaf loss of 1.62%, with two saplings (3.4%) not having any herbivory leaf damage. The leaf loss of all sampled plants ranged from no herbivory damage (0%) to 8.65%. A total of 33 saplings were found to have no foraging ants during the sampling period (Table S1). Of the remaining 25 saplings surveyed, 13 saplings were found to have foraging ants exclusively from 09:00 h to 12:00 h (Day) while four saplings had foraging ants exclusively from 16:00 h to 19:00 h (Dusk). The remaining eight saplings had foraging ants at both sampling times (Table S1). There was no difference in herbivory damage between ant-present and ant-absent plants (Fig. 3; Mann-Whitney U Test: z = 380.5, p-value = 0.62).

We recorded 31 ant species in our species composition survey spanning six subfamilies (Formicinae, Myrmicinae, Dolichoderinae, Ectatomminae, Ponerinae, and Pseudomyrmecinae) from17 genera (Table S2). The most common ant foragers detected on *M. tanarius* were *Paraparatrechina* sp1, *Anoplolepis gracilipes*, and *Tapinoma* sp1 (Table S2). Both *Paraparatrechina* sp1 and *A. gracilipes* (subfamily: Formicinae) are categorized as ground omnivores (GO) (Lynch et al. 1980; Groc et al. 2014) (Table S2).

Of the 31 recorded species, eight species (25.8%) were found to forage exclusively between 09:00 h to 12:00 h (Day), while eight species (25.8%) were found to forage exclusively between 16:00 h to 19:00 h (Dusk). Exclusive (Day) foragers included common ant species from genera *Crematogaster*, *Dolichoderus*, *Polyrhachis*, *Tapinoma*, *Tetramorium*, and *Tetraponera*. In contrast, the exclusive (Dusk) foragers consisted of ant species from *Camponotus*, *Paratrechina*, *Myrmicaria*, *Nylanderia,* and *Colobopsis*. The remaining 15 recorded ant species (48.4%) were found foraging on *M. tanarius* saplings during both 09:00 h to 12:00 h (Day) and 16:00 h to 19:00 h (Dusk) periods (Fig. 4). Of all the ant species recorded in our survey, only one – *Tetraponera* sp1 (subfamily: Pseudomyrmecinae) was categorized as an arboreal predator (AP) (Groc et al. 2014) (Table S2).

Ants behavioral assay

A total of 48 behavioral assays were conducted at the study site (Table 1). Thirty of these were done on ant species that foraged on the plants between 09:00 h to 12:00 h (Day), while the remaining 18 were conducted on ant species that foraged between 16:00 h to 19:00 h (Dusk). There was a significant relationship between the ant species and their responses to offered live prey (Chi-Square test; $X^2_{(11, N=48)} = 39.36$, $p < 0.001$) indicating that ant species likely differed in their value as mutualist defenders. Only two ant species: *Tetraponera* sp1 (arboreal predator AP) and *Anoplolepis gracilipes* (ground omnivores GO) exhibited an active response to offered live prey. *Tetraponera* sp1 was aggressive in three out of five trials, whereas *A. gracilipes* was always aggressive when encountering offered prey (n = 5 trials; Table 1). There was one occasion when *Crematogaster* sp (ground omnivores GO) displayed an active response to the introduced waxworm initially but did not recruit nestmates and subsequently abandoned the live prey item after failing to immobilize it within the 20-minute observation.

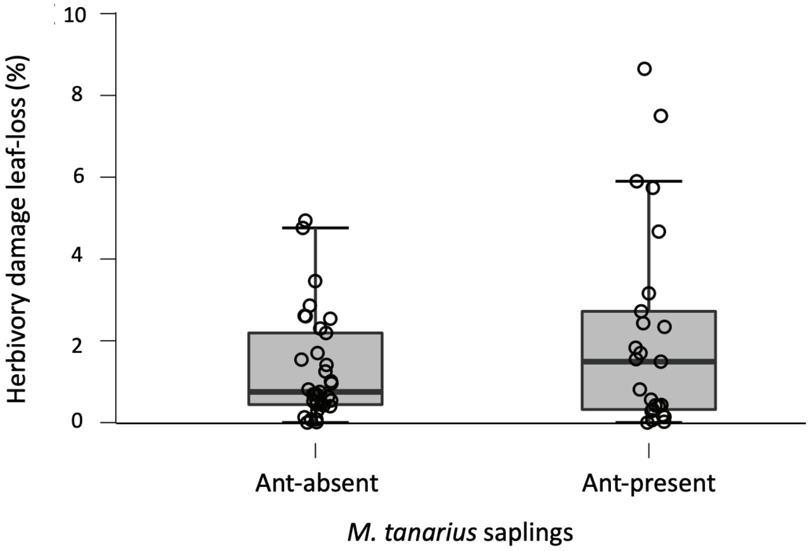


Fig. 3. The distribution of herbivory damage for *Macaranga tanarius* saplings with ant-present and ant-absent. Y-axis denotes the percentage of herbivory damage to leaf loss. Each data point corresponds to mean herbivory leaf-loss of a *M. tanarius* sapling. The midline in the boxplots showed the median leaf loss for ant-present and ant-absent saplings. In this study, ant -present saplings have herbivory damage of 2.13% and ant-absent saplings have herbivory damage of 1.32%.

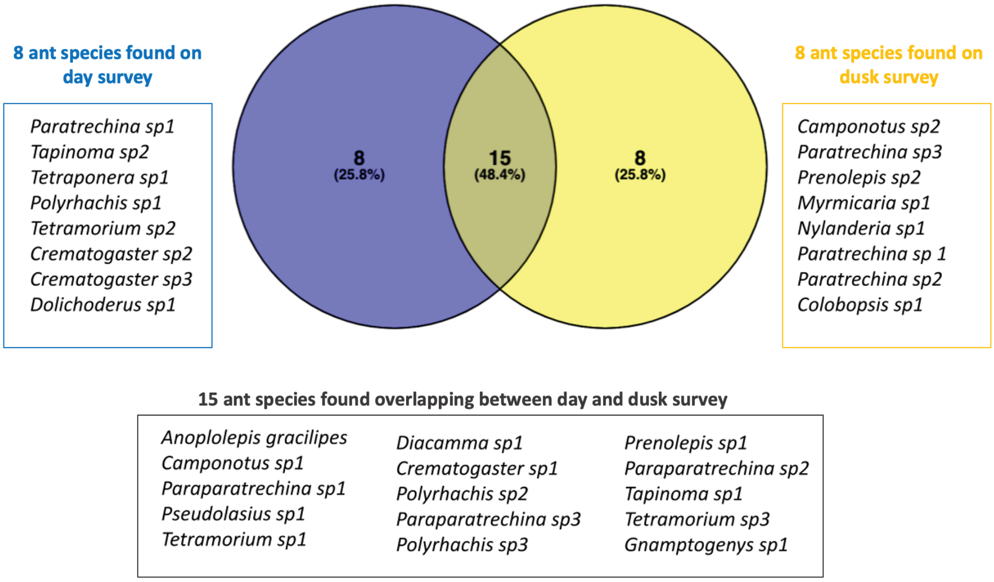


Fig. 4. Ant composition survey on *Macaranga tanarius* at day (09:00 h to 12:00 h), and dusk (16:00 h to 19:00 h). Half of the ant species (48.4%) can be found foraging on *M. tanarius* at both periods.

Table 1. Behavioral assays of ant species response to offered wax-moth larva. 0 indicates a passive response. 1 indicates active response, *i.e.*, attack, recruiting nestmates, and moving prey back to their nest.

Ant species		**Response**		**Total**
		0	1	
Anoplolepis gracilipes	Ground Omnivores	0	5	5
Camponotus sp1	Arboreal Omnivores	1	0	1
Colobopsis sp1	Arboreal Omnivores	1	0	1
Crematogaster sp1	Ground Omnivores	9	0	9
Gnamptogenys sp1	Arboreal Predators	1	0	1
Nylanderia sp1	Arboreal Omnivores	4	0	4
Paraparatrechina sp1	Ground Omnivores	5	0	5
Polyrhachis sp1	Arboreal/Ground Omnivores	5	0	5
Prenolepis sp1	Arboreal Omnivores	3	0	3
Pseudolasius sp1	Arboreal Omnivores	1	0	1
Tapinoma sp1	Arboreal Omnivores	8	0	8
Tetraponera sp1	Arboreal Predators	2	3	5
Total		**40**	**8**	**48**

DISCUSSION

The mean surface area of total leaf loss of 1.62% on ant-present and ant-absent *M. tanarius* was substantially lower than our previous studies looking at *M. tanarius* leaf surface area loss at the same site (mean = 5.76%; Yek et al. 2023). This was most likely due to the differences in precipitation levels and their relationship with the activity of herbivores. Using the same methods for assessing herbivory damage, Yek et al. (2023) measured leaf surface area loss between June and August, corresponding to the driest months with low precipitation levels. Lepidopteran larvae communities measured throughout the year was highest during these dry months (Itioka & Yamauti 2004). Consequently, our current study which measured leaf surface area loss between September and October corresponded to a period of elevated precipitation levels and decreased lepidopteran larvae communities detected on leaf surfaces (Itioka & Yamauti 2004).

Our study showed that ant presence does not influence the rate of herbivory. Although we observed a trend of higher leaf-loss area average for *M. tanarius* with ants, it was not statistically significant. This finding is contrasting with an earlier work by Fiala et al. (1994) where ants-excluded *M. tanarius* suffers significantly higher mean leaf damage than controls. We think this is due to the fact that our observation period was a snapshot of ants activity, whereas the herbivore attacks on leaf loss were accumulated over a longer period outside our survey window. A longer survey (at least five days) might reveal a different pattern, as Heil et al. (2000) found that artificial leaf-damage led to a significant induction of extrafloral nectary secretions production, and that the increased in extrafloral nectary secretions occurred gradually over the course of three days. Since ants forage on extrafloral nectary secretions on *M. tanarius*, we expect that a longer period would reveal a different pattern in ant activity. A different approach to assess whether ant presence influences the rate of herbivory is to simulate herbivory damage on *M. tanarius* young leaves and monitor the ant activity over the course of the next five days and measure the changed in rate loss due to herbivory damage.

Half of the ant species (48.4%) were active at both 09:00 h to 12:00 h (Day) and 16:00 h to 19:00 h (Dusk) observation periods. This observation did not support the usual pattern found in tropical ant communities, whereby one fourth to one third of tropical ant species showed significant temporal distribution (Houadria et al.

2015). Heil et al. (2004) found no differences in overall ant activity on *Macaranga tanarius* during 24 hours of observations. However, Heil et al. (2004) did not identify the ants in their study. Temporal partitioning was perhaps not necessary for *M. tanarius* as most ants collected were ground or arboreal omnivores, and omnivorous ants exhibit plastic foraging times and adjust their foraging activity based on resource availability and hierarchical structure of the community (Traniello 1989).

Of the ant species tested, only *Anoplolepis gracillipes* and a *Tetraponera* sp1 attacked the offered prey. The highest active response interaction with live prey was from *Anoplolepis gracilipes*, commonly called the yellow-crazy ant, a widely distributed species considered invasive in many parts of the world, including Malaysia (Lee & Yang 2022). This is contrary to our expectation as we expected that only predatory species would attack the offered prey. However, our results were consistent with known *A. gracilipes* behavior as this species forms large colonies and often displays rapid nest expansion *via* the formation of supercolonies, displacing other ant species territories (Thomas et al. 2010; Hoffmann 2014; Gan et al. 2022) and diet niches (Lee & Yang 2022).

Although we expected *Tetraponera* species – an arboreal predator (AP) would attack offered prey all the time, *Tetraponera* sp1 only showed three active responses out of five trials. *Tetraponera* species are diurnal foragers that showed preference over carbohydrate and consistent proteinaceous foods (Norasmah et al. 2012). For *Tetraponera* sp.1 found in our study, the most reliable supply of carbohydrates was provided by the extrafloral nectary secretions of *M. tanarius* saplings, and the incidental presence of insect herbivores (i.e. offered live prey) provides an occasional but inconsistent protein source. We are unsure why sp1 displayed inconsistent response to the offered prey. The identification of the *Tetraponera* species, and the study of its dietary preference would help resolve this inconsistency in future study.

Two to four ant species were found foraging on the majority of *M. tanarius* saplings on-site at any given time (48 out of 58 surveyed plants; Table S1). This contrasts with myrmecophytic *Macaranga species*, which have only one symbiotic ant species patrolling the host plant (Fiala et al. 1999). In myrmecophilus *M. tanarius*, most ant species responded passively to introduced live prey, which supported our hypothesis that most ants visited myrmecophilous host plants for plant-based food rewards like extrafloral nectary secretions. In myrmecophytic *Macarang*a species, the symbiotic ant species showed strong aggressiveness and a mass recruiting system that significantly reduce herbivory leaf loss (Fiala et al. 1989). For myrmecophilous *Macaranga*, the ants presence predominantly likely functioned as a deterrent rather than an active defense strategy against insect herbivores (Koptur et al. 1998; Heil et al. 2004; Koptur 2005).

Current work did not account for ant abundance, which could affect the relationship between herbivory and ant presence. Ant abundance and species composition should be monitored in future studies during peak herbivore months between June to August (Itioka & Yamauti 2004). It would be interesting to investigate whether the increase in insect herbivores on host plants will directly affect the opportunistic ants foraging activity. The effectiveness of *A. gracilipes* in removing insect herbivores off *M. tanarius* leaf surface also begs further investigation. From the host plant perspective, these highly dominant ant species would be the best ant symbionts to attract. However, if *A. gracilipes* displayed characteristic invasive ant traits, their dominance would also decrease the diversity of ant communities in the surrounding area (Gerlach 2004; Abbott 2005), and hence the diversity of ant species foraging on host plants. Will this change in ant species composition affect the protective impact of ants on *M. tanarius*? Future research could be carried out at sites with similar ant communities, but have not seen a heavy influx of *A. gracilipes* in the respective ant communities. Another promising investigation angle is the generality and potential benefits of *A. gracilipes* in plant protections at disturbed habitats.

ESM

Electronic supplementary information for this article can be downloaded from the Asian Myrmecology website.

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DISCLOSURE STATEMENT

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