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Authors

Liu, Kunpeng
Mansor, Asyraf
Ruppert, Nadine
[et al.](#)

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SHORT COMMUNICATION



Rattan litter-collecting structures attract nest-building and defending ants

Kunpeng Liu, Asyraf Mansor , Nadine Ruppert , Chow Yang Lee, Nur Munira Azman , and Nik Fadzly 

School of Biological Sciences, Universiti Sains Malaysia, Minden, Malaysia

ABSTRACT

Rattan is an important climbing palm taxon in Malaysian tropical rain forests. Many rattan species have unique structures directly associated with certain ant species. In this study, four rattan species (*Daemonorops lewisiana*, *Calamus castaneus*, *Daemonorops geniculata* and *Korthalsia scortechinii*) were inspected and documented in a field survey concerning their relationships with several ant species. We noticed that two rattan species (*D. lewisiana* and *C. castaneus*) were more likely to be associated with ants compared to their neighbouring rattan (*Plectromia griffithii*). However, *D. lewisiana* and *C. castaneus* did not directly provide shelters for ant colonies, but possessed unique structures: upward-pointing spines and funnel-shaped leaves, which are equipped to collect more litter than *P. griffithii*. To test our litter collecting hypothesis, we measured the inclination of spines from the stem. Our results showed the presence of ant colonies in the litter-collecting rattans (*D. lewisiana* and *C. castaneus*), which was significantly higher compared to a non-litter-collecting rattan (*P. griffithii*). We propose a complex and novel type of adaptation (litter-collection and provision of nesting materials) for rattans, which promotes interactions between the rattan and ants through the arrangements of leaves, leaflets, and spines. In return, the rattan may benefit from ants' services, such as protection, nutrient enhancement, and pollination.

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Rattan; spine; leaf structure; leaf litter; ants

Introduction

Rattans are spiny palms belonging to the subfamily Calamoideae. About 600 species of rattans belonging to 13 genera are recorded worldwide.¹ Some rattans are climbers, which possess climbing structures, such as cirrus or a flagellum, but some are acaulescent or non-climbing species.² The flexible stems of certain rattan species are used by humans for matting, binding, and furniture production.³ In Peninsular Malaysia, rattans can be found from sea level to mountains over 1000-m high. They are an important component of the tropical primary rainforest and secondary forests but remain poorly understood.²

Ants are often regarded as the most successful eusocial animals. Their relationships with plants have long been established. These interactions include leaf-harvesting for fungal gardens;⁴ seed-harvesting and seed-dispersal;^{5,6} Plants bearing domatia for ant colonies are called myrmecophytes, benefiting from symbiont ants' protection against herbivores,⁷⁻¹¹ and protection from *Crematogaster*, which are the obligate ant partner of *Macaranga*, regulated by the food supply (food bodies) of their host plants.^{12,13} Several cases showed that ants can also serve as pollinators.¹⁴

Rattan-ant relationship across various species has been reported in the past.^{2,3,15-18} Sunderland¹⁷ reported on a variety of ant species colonizing various parts of several rattan species in Africa, with some ant species showing a specific preference towards certain rattan species, both in terms to their protective behavior and relationships with the resident scale insects. In the tropical rain forests of Southeast

Asia, *Korthalsia* is a common rattan genus associated with ants.^{2,15,18,19} Other rattan taxa with similar relationships include *Calamus* sp. and *Daemonorops* sp.²⁰

Dransfield² reported six rattan adaptations to cater for associated ant colonies. Ocreas (inflated extension of leaf sheath) are hollow chambers that form desirable shelters for ant colonies in some *Korthalsia* sp. and a few *Calamus* sp. *Calamus longipinna*'s sac-like ocreas are domatia for ant nesting.²¹ Another type of elongated ocreas (only known in *Korthalsia hispida*) provides tube-like chambers for ants to colonize.² Furthermore, ocreas are armed with spines which may provide protection for ant colonies. *Korthalsia furtadoana* has an obligate symbiont ant species, *Camponotus* sp.¹⁸ *K. furtadoana* enjoys healthier leaves if colonized by certain ant species.¹⁹ In addition to *Korthalsia*, *Daemonorops verticillaris*, has overlapping spine structures that provide cavities for ants. In return, the ants help the rattan absorb nutrients and water at higher efficiency.²² Simple adaptations involving leaflet or inflorescences as well as adaptation with leaf sheath auricles are known but rarely studied.²

In this study, we approached the fundamental function of a rattan spine from a different perspective. We ask the question of whether the spines could function as a leaf litter collecting structure. We hypothesize that there will be ant colonies in litter-collecting rattans (*Daemonorops lewisiana* and *Calamus castaneus*) in comparison to non-litter collecting rattan (*Plectromia griffithii*). This study provides about a novel adaptation of certain rattan species which facilitates a relationship with ants, which has yet to be reported to date.

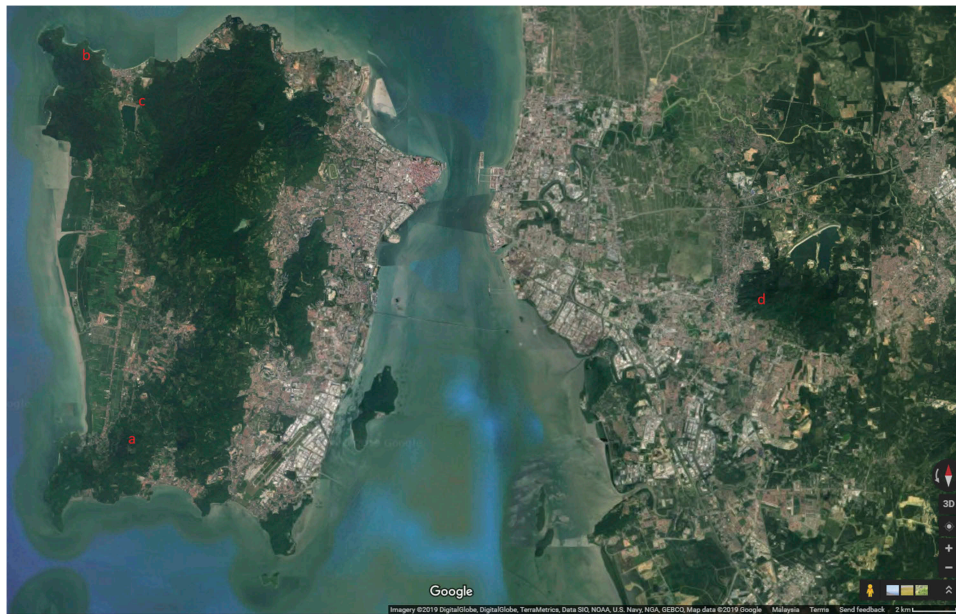


Figure 1. Study site locations at (a) Bukit Genting Hill, (b) Penang National Park, (c) Taman rimba, Teluk Bahang and (d) CheroK Tokun, Penang.

Materials and methods

Surveys on rattan–ant relationship were conducted in northern Peninsular Malaysia, Bukit Genting Hill (5°18'31.9"N, 100°13'14.0"E), Penang National Park (5°28'01.4"N, 100°11'56.0"E) and Taman Rimba, Teluk Bahang (5°26'52.51"N, 100°13'4.89"E) in Penang island, and in CheroK Tokun, Penang mainland (05°21'54.6"N, 100°28'58.7"E; **Figure 1**). Rattans were identified based on keys developed by Dransfield.² The associated ants were collected using forceps, kept in 70% ethanol, and transported to the laboratory for identification using keys developed by Hashimoto.²³

The three most abundant rattan species in Penang National Park and Taman Rimba, Teluk Bahang are *Plectomia griffithii*, *Daemonorops lewisiana* and *Calamus castaneus*. We recorded for each individual rattan clump (stem length > 50 cm) whether an ant colony was present, absent or abandoned. Any rattan with a sign of tunnels on the surface, but an absence of ants, was considered abandoned. Rattan seedlings (< 50 cm) were ignored as they were too small to collect leaf litter.

To examine the leaf-collecting structures, we measured the inclination of spines from the stem. Ten spines were randomly chosen from each species. We compared the spine angles among the three species. The paired leaflet angles were also measured in *D. lewisiana* and *C. castaneus*. Using a protractor, we measured the angles of the paired leaflet from five randomly selected leaves of *D. lewisiana* and *C. castaneus*. We compared the angles among different pairs of leaflets within the same leaf (the 1st, 10th and the last pair of leaflets from base to apex) to determine the changes in the angle from the first to the last pair of the leaflet.

Results

Rattan-ant associations

In total, four rattan species (*Daemonorops lewisiana*, *Calamus castaneus*, *Daemonorops geniculata* and *Korthalsia scortechinii*),

Table 1. Ant genera found on various rattan species.

Individual	Rattan species	Location	Ant species
Daemonorops			
1	<i>D. lewisiana</i>	PNP	<i>Philidris</i> sp.
2	<i>D. lewisiana</i>	PNP	<i>Dolichoderus thoracicus</i>
3	<i>D. lewisiana</i>	PNP	<i>Crematogaster</i> sp.1
4	<i>D. lewisiana</i>	PNP	<i>Dolichoderus thoracicus</i>
5	<i>D. lewisiana</i>	PNP	<i>Philidris</i> sp.
6	<i>D. lewisiana</i>	PNP	<i>Philidris</i> sp.
7	<i>D. lewisiana</i>	PNP	<i>Philidris</i> sp.
8	<i>D. lewisiana</i>	PNP	<i>Crematogaster</i> sp.2
9	<i>D. lewisiana</i>	PNP	<i>Philidris</i> sp.
10	<i>D. lewisiana</i>	PNP	<i>Philidris</i> sp.
11	<i>D. lewisiana</i>	PNP	<i>Tapinoma melanocephalum</i>
12	<i>D. lewisiana</i>	PNP	<i>Philidris</i> sp.
13	<i>D. lewisiana</i>	PNP	<i>Philidris</i> sp.
14	<i>D. lewisiana</i>	BGH	<i>Technomyrmex</i> sp.2
15	<i>D. lewisiana</i>	BGH	<i>Technomyrmex</i> sp.2
16	<i>D. geniculata</i>	BGH	<i>Camponotus</i> sp.
17	<i>D. geniculata</i>	CT	<i>Crematogaster</i> sp.5
18	<i>D. geniculata</i>	CT	<i>Crematogaster</i> sp.6
19	<i>D. geniculata</i>	CT	<i>Dolichoderus thoracicus</i>
Calamus			
20	<i>C. castaneus</i>	TRTB	<i>Crematogaster</i> sp.3
21	<i>C. castaneus</i>	TRTB	<i>Crematogaster</i> sp.3
22	<i>C. castaneus</i>	TRTB	<i>Crematogaster</i> sp.3
23	<i>C. castaneus</i>	CT	<i>Tapinoma melanocephalum</i>
24	<i>C. castaneus</i>	CT	<i>Dolichoderus thoracicus</i>
25	<i>C. castaneus</i>	CT	<i>Pheidole</i> sp.
26	<i>C. castaneus</i>	CT	<i>Technomyrmex</i> sp.1
27	<i>C. castaneus</i>	CT	<i>Crematogaster</i> sp.4
28	<i>C. castaneus</i>	CT	<i>Pheidole</i> sp.
Korthalsia			
29	<i>K. scortechinii</i>	CT	<i>Camponotus beccarii</i>
30	<i>K. scortechinii</i>	CT	<i>Technomyrmex</i> sp.3.
31	<i>K. scortechinii</i>	CT	<i>Dolichoderus thoracicus</i>

* PNP is Penang National Park. BGH is Bukit Genting Hill. CT is CheroK Tokun. TRTB is Taman Rimba, Teluk Bahang.

with 31 rattan individuals, showed signs of association with seven ant genera (*Philidris*, *Dolichoderus*, *Crematogaster*, *Tapinoma*, *Technomyrmex*, *Camponotus* and *Pheidole*) (**Table 1**).

Philidris and *Crematogaster* were the most common ant genera found. All *Philidris* were found only on *D. lewisiana*, while *Crematogaster* were found on three rattan species

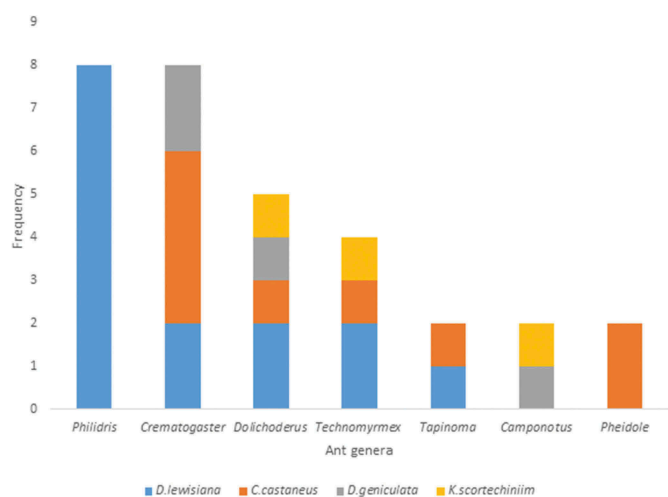


Figure 2. Ant genus associated with rattan species.

(Figure 2). Other ant taxa were found in relatively fewer numbers, with no clear patterns of their relationship to specific rattan species (Figure 2). However, the presence of those ant colonies on rattan plants was unlikely to be incidental, because of the high occurrence of ants on *D. lewisiana* and *C. castaneus*, but not on *P. griffithii*. We also found yellow crazy ants (*Anoplolepis gracilipes*) tending the aphid *Cerataphis orchidearum* on *D. lewisiana* (Figure 3a) and *Dolichoderus thoracicus* gathered at the surface of *Calamus diepenhorstii* (Figure 3b). However, because their nests could not be located on the rattan, we excluded both from our results.

Thirty individuals of *D. lewisiana* were found in Penang National Park, of which 13 were associated with at least one ant colony. Other four of these showed signs of abandonment by ants. *Calamus castaneus* were found in Taman Rimba, Teluk Bahang and Cherok Tokun. Of the 15 *C. castaneus* found, nine had at least one ant colony. *Plectomia griffithii* plants were found in all three study areas, but none had ant

colonies or signs of abandonment in the 19 individuals of *P. griffithii*. *D. lewisiana* is significantly associated with ants (57%) compare to *P. griffithii* ($\chi^2(df = 1, N = 50) = 13.44, p < .01$). There was also a significant difference between *C. castaneus* (60%) and *P. griffithii* (0%) ($\chi^2(df = 1, N = 34) = 12.58, p < .01$) in terms of their association with ants. Hence, it is significantly more likely to find an ant colony in leaf litter collecting rattans (*D. lewisiana*, *C. castaneus*) than non-litter collecting rattans (*P. griffithii*). In Bukit Genting Hill, we found that two *D. lewisiana* and one *D. geniculata* had ant colonies. In Cherok Tokun, Penang, ants were present on three *D. geniculata* and three *Korthalsia sortechinii*. One hemipteran aphid species, *Cerataphis orchidearum* was found on two individual of *D. lewisiana*. The ants were also tending the aphids (Figure 4).

Rattan adaptations

Although *P. griffithii*, *D. lewisiana* and *C. castaneus* had many spines on their leaf sheaths and stems, the patterns of spine arrangement differed. Spines of *P. griffithii* normally grew in clusters. Every cluster had three to ten spines. On the main stem, spine clusters may link together to form a row of spines. Most spines were pointing downwards (angles of spines ranging from 60° to 90°; Figure 5a). Only a small amount of leaf litter was trapped by those spines (Figure 6a). The arrangement of spines on *C. castaneus* was more irregular compared to *P. griffithii*. The inclination of spines was vertical to the stem or pointing slightly upwards (angles of spines ranging from 90° to 130°; Figure 5b). Spines were rarely pointing downwards, and a large amount of leaf litter was trapped by those spines (Figure 6b). The spines of *D. lewisiana* were shorter (< 4 cm) than those of *C. castaneus* (>6 cm), but they were also able to trap a substantial amount of leaf litter. Most spines had greater angles than *C. castaneus*, ranging from 120° to



Figure 3. (a) Yellow crazy ants (*Anoplolepis gracilipes*) were tending aphids (*Cerataphis* sp.) on rattan *D.lewisiana*; (b) *Dolichoderus thoracicus* gathered in the knee area of *Calamus diepenhorstii*.

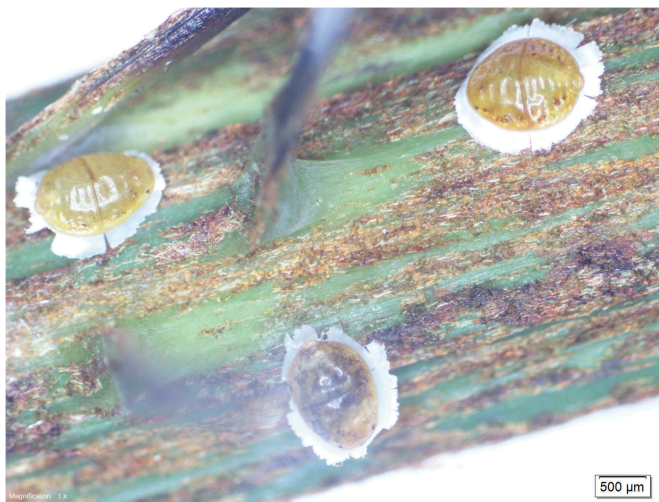


Figure 4. *Cerataphis orchidearum* was found attached to *Daemonorops lewisiana* in Penang National Park.

170° (Figure 5c). The spine angles of the three species were significantly different [F (2, 27) = 31.293, $P = .000$]. A Tukey post hoc test revealed that spine angles of *P. griffithii* ($65.5 \pm 21.4^\circ$) were significantly smaller than the spine angles of *C. castaneus* ($103.0 \pm 10.6^\circ$, $p = .001$) and *D. lewisiana* (138.0 ± 26.3). Spine angles of *C. castaneus* were also significantly smaller than those of *D. lewisiana*.

Leaf shape also facilitated litter accumulation in the two rattan species, *D. lewisiana* and *C. castaneus* have a similar leaf shape, with long and narrow leaflets asymmetrically arranged on both sides of the rachis. Every leaflet pair on both sides formed an angle, and the angles changed from wide to narrow from the upper to the lower part of the leaf. Leaflets on the upper parts had a wider angle (180°). On the bottom part of the leaf, the leaflets narrowed towards each other and the angle between the leaflets became smaller (ranging from 45° to 90°; Figure 7). For *D. lewisiana*, there were significant differences among leaflet angles of different positions [F (2, 12) = 122.757, $p = .000$]. Tukey post hoc test showed that the first pair of leaflets ($73.0 \pm 12.0^\circ$) was significantly smaller than the 10th pair of leaflets ($129.0 \pm 14.3^\circ$) and the last pair of leaflets ($180 \pm 0.0^\circ$). For *C. castaneus*, there was also a significant difference in leaflet angles of different positions [F (2, 12) = 161.110, $p = .000$]. Tukey post hoc test showed that the first pair of leaflets ($45 \pm 11.2^\circ$) was significantly smaller than the 10th pair of leaflets ($144 \pm 18.2^\circ$) and the last pair of leaflets ($180 \pm 0.0^\circ$). The leaflets at the bottom part formed an inverted funnel that trapped leaf litters (Figure 9a).

In *D. lewisiana*, some leaves showed one protruding leaflet growing around the middle part of the rachis (Figure 8a). This particular leaflet arrangement may be able to trap litter from falling to the ground. Due to this unique leaf shape of *D. lewisiana* and *C. castaneus*, leaf litter from the canopy was always trapped in the bottom part of the leaves (Figure 9a). Ant colonies may use the leaf litter to establish their nests (Figure 9b). The leaves of *P. griffithii* did not demonstrate any leaf-collecting capability and no leaf litter or ant colonies were found (Figure 8b).



Figure 5. Inclination of rattan spines: (a) *P. griffithii* (mean 65.5°); (b) *Calamus castaneus* (mean 103°); (c) *Daemonorops lewisiana* (mean 138°).

Discussion

In this study, ants were more likely to associate with litter-collecting rattans. However, there was no clear evidence of an obligate relationship between the rattan and ant species. It seems therefore to be a case of mutualism rather than symbiosis.

There are few studies on rattan–ant relationship. Mattes et al.¹⁶ reported that two ant species of the genus *Camponotus* formed obligate association with the rattan *Korthalsia robusta* in Sabah, Malaysia. Edwards et al.¹⁸ stated that the only possible obligate



Figure 6. (a) Little amount of leaf litter trapped by *P.graffithii*. (b) Extensive amount of leaf litter collected and trapped by *C.castaneus*.



Figure 7. Leaflet angle of *Calamus castaneus* from the upper part to bottom part (from 3 to 1) is becoming smaller.



Figure 8. (a) A protruding leaflet growing on the middle of the rachis that may hinder leaf debris from falling. (b) The leaf of *Plectocomia griffithii* does not collect leaf debris or harbor ant colonies.



Figure 9. (a) Leaf litter trapped on the bottom part of *Daemonorops lewisiana* leaves. (b) Ant colony on the debris of leaves trapped by *Calamus castaneus*.

symbiont of *Korthalsia furtadoana* was two species of *Camponotus* in lowland dipterocarp forests of Borneo. Moog et al.²⁰ found that in Peninsular Malaysia four rattan species of the genus *Korthalsia*, one species of *Calamus* and four species of *Daemonorops* had a high occurrence of associations with *Camponotus* sp. Chan et al.¹⁵ reported that seven individual

clumps of *Korthalsia echinometra* were colonized by *Iridomyrmex* sp., and that four clumps of *Korthalsia rostrata* were colonized by *Dolichoderus* sp. and *Pholidris* sp. in Singapore. Sunderland¹⁷ surveyed rattans in Africa and found 11 rattan species associated with 12 ant species, but the evidence for a symbiotic relationship between rattan and ants was weak.

In this study, we propose a complex and novel type of rattan adaptation to promote ant association by leaf litter-collection and provisioning of nest materials through their arrangement of leaves, leaflets, and spines. According to Dransfield² there were six previously described adaptations of rattans that facilitate ant-rattan relationships: 1) casual adaptations (ants accidentally build nests in a rattan plant), and simple adaptations involving 2) leaflets; 3) inflorescences; 4) leaf sheath auricles; 5) ocreas; and 6) spine whorls. In relation to these, the ocrea in *Korthalsia* was the most studied adaptation.^{15,16,18,19,24} The ocrea in *Calamus* was also found to be colonized by ants.²¹ Rickson & Rickson²² reported spine whorls associated with *Camponotus*. Other adaptations were rarely studied and poorly understood.

Our results show that two rattan species (*C. castaneus* and *D. lewisiana*) have leaf arrangements that extend in every direction and expand horizontally in the shape of a vase or bowl and are thus able to collect leaf litter like in the well-known epiphytic fern *Platyserium*. At the bottom part of the rattan leaf, the angles of the leaflets become smaller and a funnel-like structure is formed at the end of every leaf. In addition, the gaps between two abreast leaflets are smaller than the litter falling from the canopy. Hence, leaves falling from the canopy are frequently trapped at the end of the rattan leaves.

Spines are normally considered to be a defensive weapon against herbivores, for instance from small climbing mammals such as squirrels that eat the apex of rattan stems.² Therefore, if spines are pointing down like in *P. griffithii*, this may potentially deter squirrels from climbing up. On the contrary, the spines on *D. lewisiana* and *C. castaneus* are always pointing upwards, and hence may be less effective to prevent small climbing mammals. We suggest that one of the main functions of spines on *D. lewisiana* and *C. castaneus* is to aid climbing and the leaf litter trapping may be incidental. Leaves falling from the canopy can easily be pierced by these spines and trapped along the rattan stems.

The leaf litter-collecting structure on an understory palm (*Asterogyne martiana*) was first described by Raich²⁵ in the rainforests of Costa Rica. It also has a funnel shape that collects nutrients in precipitation and organic debris. This leaf litter collecting structure also trapped a large amount of rainfall that is diverted down to the stem and is finally absorbed by the roots. The nutrient content from the stem flow was found to be much higher than nutrients from rainfall.²⁵ This nutrient-capturing hypothesis may also apply to rattan that has similar structures for collecting leaf litter.

The nutrient-capturing hypothesis can be further understood with the help of ant colonies. Beattie⁹ described a unique ant-plant relationship known as myrmecotrophy, in which the plants gain benefits from being “fed” by ants. Janzen²⁶ observed this phenomenon between several epiphytes and ant species in forests of Sarawak. Ants “fed” those epiphytes by placing the preyed insect in certain cavities of the plant. The plant wall of those cavities was able to absorb those prey bodies and their nutrients. Prey bodies were marked with radioactive elements, and these markers were found inside the plants, showing that nutrients from these insect bodies were absorbed by the plant tissues.²⁷ In

Thailand, the ants *Philidris*, *Crematogaster* and *Echinopla* collect organic debris to build nests inside the pitchers (modified leaves) of the epiphyte *Dischidia major*. Ants gained shelter, while their nest-building behavior benefited plants by providing them with extra nutrients.²⁸ Myrmecotrophy between rattans and ants was reported by Rickson and Rickson.²² *Daemonorops verticillaris* and *D. macrophylla* in Peninsular Malaysia have overlapping spines where ants build nests inside and they also collect falling litters at the top of the plant. Isotope tracers were used to demonstrate that water and nutrients from ant nests were absorbed into the plants and assisted in their growth.²²

Organic materials trapped by the plant may provide nesting materials and harborage for ants. And in return, the plant may receive more nutrients that are brought in by the ants. Overlapping leaf litter particles provides myriads of cavities for ants to build nests inside and debris or detritus from dead leaves can be used as building materials for ant colonies. For example, some *Crematogaster* species are arboreal foragers that collected decayed woods particles or rotting logs to build nests.²⁹ Rattan spines can provide structural support (frames) for their carton nests. Moreover, litter that traps rainfall²⁵ can provide a moist environment (water storage) for ant colonies. Water is crucial for colony formation in many ant species. For example, *Dolichoderus sulcaticeps* collects nesting materials from plant surfaces. Those materials can only be used for the construction of nests on the plant when soaked with water.³⁰

Ants provide both direct and indirect protection to their host plants.⁹ Direct interaction is established by plants that provide domatia (shelters), food bodies or extrafloral nectaries directly to attract ants. In return, the ants guard and protect their host plants against herbivores and seed predators. *Macaranga* provides shelter and food bodies for their symbiotic ants (*Crematogaster*) and ants significantly reduce herbivore damage.³¹

In our study, no rattan provided any food bodies or extrafloral nectaries to their ant residents. Although we observed that many ants (*Dolichoderus thoracicus*) gathered at the leaf sheath of the rattan *Calamus diepenhorstii* (Figure 9b), there could be extra attraction for certain ant species. However, we were unable to detect the reason for their accumulation. Previous studies showed that ants help to protect rattans together with their shelters which rattan provides. *Korthalsia furtadoana* experience less leaf damage when their ocreas were colonized by patrolling ants.¹⁹ Unlike rattan *Korthalsia* possessing ocreas that could serve as domatia for ant colonies, the rattans *D. lewisiana* and *C. castaneus* do not directly provide shelter for ants. However, the litter that they collect may also encourage ants to build nests and protect the plant.

In our study, most ants showed protective behaviors (swarming and biting) when we were collecting the rattan and ant specimens. Protective behavior was evident in *Philidris*, some *Crematogaster* species, *Tapinoma*, *Camponotus* and *Technomyrmex* ant species. Ant protection is crucial to a rattan’s development since ants may not only disturb some megaherbivores such as elephants, wild cattle, pigs and small herbivores like squirrels,² but also help

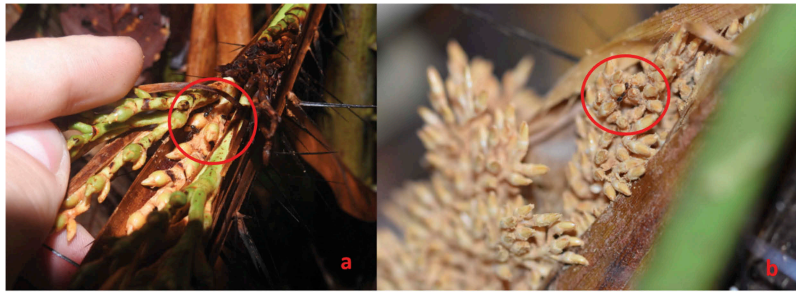


Figure 10. (a) Ants (*Dolichoderus*) inside a female flower of *Daemonorops lewisiana*. (b) Ants (*Philidris*) inside a male flower of *Daemonorops lewisiana*.

eliminate invertebrate herbivores such as grasshoppers (*Chondracris rosea*, *Choroedocus capensis*, *Pachyacris vinosa*), moths (*Sesamia inferens*), butterflies (*Gangara thysis*) and more.³² Ants not only deter herbivores, but also help the plant to eliminate plant competitors. Ants constantly cut off foreign plant parts that encounter their host plants *Macaranga*.³³ The leaves of *K. furtadoana* were covered with fewer epiphylls when patrolling ants were present.¹⁹

Indirect interactions also existed among rattans, ants, and *Cerataphis* (Homoptera). *Cerataphis* is a rattan pest which sucks the sap from the rattan plant. However, they are constantly tended and guarded by ants since they excrete honeydew for ants.³⁴ In this complicated three-trophic system, even though plants are damaged by the homopteran pests, plants may still benefit from the ants, since ants will also protect the host plant from herbivores.^{9,10}

Protective effects may even emerge from the visual imitation of ants crawling on the rattan. Lev-Yadun and Inbar³⁵ suggested that black spots on the surface of stem and branches of *Xanthium trumarium* (Asteraceae) and other plant taxa look like ants swarming on the plants. Later, Lev-Yadun³⁶ showed that visual ant mimicry occurs in the flowers of many *Passiflora* species. This visual mimetic strategy may serve as a warning signal or as a masquerade to deter herbivores. Similar patterns of black spots were also found on *Amorphophallus bufo*, an understory plant in Malaysia forests which exhibits numerous black spots that may serve as a defensive strategy by mimicking ants.³⁷ Therefore, even if the ants on rattans did not show any protective behavior, having them constantly moving around the plant may indicate to herbivores that the plant is protected. Herbivores may avoid such a plant if they have previously experienced ant bites.

Ants may also serve as pollinators, although they are a much less common pollinator than bees and wasps, there are cases showed where certain ants are able to collect pollen grain from flowers and visit flowers systematically.^{9,10} Of the two ant-hosting rattan species discussed in this study, *C. castaneus* is mainly pollinated by stingless bees (*Trigona*) and paper wasps (Vespidae).³⁸ However, the pollinators of *D. lewisiana* are unknown. In our observations, the flowers of *D. lewisiana* were always enclosed by spiny bracts. Of all potential insect pollinators that visited the flowers, only ants could crawl inside their female flowers (Figure 10a) and male flowers (Figure 10b). This may suggest a role for ants in the pollination of *D. lewisiana*. More research is required to further substantiate this observation.

In conclusion, the leaf litter collection apparatus of certain rattan species may be a unique adaptation to attract symbiotic or mutualistic ant colonies as leaf litter is a nutrient trap that offers a suitable environment for nesting ants. For the rattan, its nutrient economy could be improved by ant colonies and ants could protect the rattan from herbivores or seed predators and even pollinate the rattan flowers. However, the relationship between these rattans and ants may not be obligate. Future studies should further evaluate and elucidate these complex associations.

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Author contribution

Kunpeng Liu, Asyraf Mansor, and Nik Fadzly conducted field experiments and identification. Chow Yang Lee helped with the ant's identification and ant nest analysis. Kunpeng Liu, Nadine Rupert, Nur Munira Azman, & Nik Fadzly wrote the manuscript, conducted the statistical analysis and proof editing the manuscript.

Conflict of interest

The authors declare that they have no conflict of interest.

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ORCID

Asyraf Mansor  <http://orcid.org/0000-0003-1255-7239>
 Nadine Rupert  <http://orcid.org/0000-0002-9760-0058>
 Nur Munira Azman  <http://orcid.org/0000-0001-5841-065X>
 Nik Fadzly  <http://orcid.org/0000-0002-6282-8423>

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