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Ant communities and their trophobionts shape the incidence of pests and diseases in Indonesia's coffee agroforestry system

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Abstract. *Muhammad FN, Rizali A, Rahardjo BT. 2024. Ant communities and their trophobionts shape the incidence of pests and diseases in Indonesia's coffee agroforestry system. Biodiversitas 25: 1127-1134.* Ants play various roles in a coffee agroecosystem, and their presence may impact biological control in coffee plantations. Despite the pantropical economic importance of coffee, most research is focused on the Americas. This study investigates how ant communities and their trophobionts shape the incidences of pests and diseases in the Indonesian shade coffee agroecosystem. Three 30 m x 30 m plots consisting of a total of 256 coffee plants were observed from January to March 2022. Ant communities and their trophobiont were observed using three methods: visual, tuna bait, and live bait. The ants found were classified into dominant and non-dominant based on their nesting behavior and dominance in the bait trap. Pest damage and disease intensity observation were also conducted three times. Generalized linear models were used to test the relationships between ant, hemipteran, coffee berry borer, twig borer damage and leaf rust disease intensity. Twenty-one species of ants were found, and five of them were categorized as dominant ants. Ants correlate coffee pest damage and disease intensity, their hemipteran trophobionts, or both. *Dolichoderus thoracicus* ant positively correlated with all trophobiont hemipteran and negatively correlated with twig borer damage. *Technomyrmex albipes* positively correlated with aphids but negatively with flatids. Meanwhile, *Tetraponera* sp.1 ant only positively correlated with flatids. In trophobiont hemipteran group, all except aphids positively correlated with coffee pests and disease. Scale insect *Coccus viridis* positively correlated with coffee leaf rust and twig borer infestation intensity, while flatid presence even positively correlated with all coffee plant pest and disease intensity. Indirectly, ants may reduce coffee pests and diseases through hemipteran suppression. The results suggest that the interaction of ants and their trophobiont hemipteran can act as a biological control agent for coffee pests and diseases.

Keywords: Biocontrol, coffee berry borer, complex interaction, leaf rust, twig borer

INTRODUCTION

The presence of ants has been known to have an impact on biological control that occurs in agroecosystems (Anjos et al. 2022). Ants can have a positive impact on plant cultivation in agroecosystems if they act as natural enemies or biological control agents. Plants and ants form a mutualistic symbiosis where ants will provide protection to plants from various herbivorous arthropods, while plants will provide shelter, food sources, and breeding grounds for ant colonies (Diamé et al. 2018). Due to the ability of ants to consume large numbers of pests, ants may replace insecticide treatment for controlling pests (Offenberg 2015). In addition, ants, with their hygienic behavior, are also known to suppress the spread of plant pathogens (Offenberg and Damgaard 2019). However, the beneficial role of ants is sometimes disturbed by the dominance of an ant species. In the ant community, the dominant species exhibits aggressive behavior and can monopolize a food source (Lessard et al. 2020). Non-dominant species can coexist with dominant species by foraging in different niches and at different times (van Oudenhove et al. 2018).

Besides being beneficial, the presence of an ant species can also be detrimental to plants. As a honeydew-tender, some species of ants may increase honeydew-producing pest abundance (Anjos et al. 2022). However, ants also choose which species can become trophobionts (Sanchez et al. 2020). In addition, several dominant ant species are also known to be vectors for the spread of pathogens, such as *Monomorium floricolae* whose presence increases *Phytophthora palmivora* incidence at cocoa plantations (Rizali et al. 2018). The danger from invasive ants is also important. The presence of invasive ants can damage ecosystems and displace local native species (Angulo et al. 2022).

One agroecosystem where the role of ants in biocontrol has been well-proven in coffee plantations. Shade-grown coffee is an important agricultural commodity for tropical nations harboring high biodiversity. Understanding how ants interact with the pest and pathogens of coffee is therefore important both economically and ecologically. Coffee is one of the important plantation commodities in Indonesia in addition to cocoa and oil palm. Coffee production in Indonesia reached 762,000 tons in 2020 (BPS 2021). With this, Indonesia has become the fourth-largest coffee exporter in the world (Statista 2022). However, coffee cultivation often faces problems from attacks by pests and diseases. Leaf rust (Talhinhas et al. 2017), twig borer (Túler et al. 2019), and coffee berry borer (CBB) (Johnson et al. 2020) are important pests and diseases of coffee plants in the world that can be found in Indonesia. CBB infestation can cause damage to up to 86.99% of coffee berries (Mubin et al. 2023). Meanwhile, coffee leaf rust can cause crop losses in the range of 10-70% (Jha et al. 2014).

Vandermeer et al. (2010) reported that ants can support or interfere with the cultivation of coffee plants. Ants can interact directly or indirectly with pests and diseases of coffee plants. In previous studies, key ant species from the genus *Azteca*, which are dominant in the South American region, can interfere with CBB colonization (Morris et al. 2015). In addition, *Plagiolepis* ants in Kenya can also be predators of black twig borer *X. compactus* (Egonyu et al. 2015). Philpott and Armbrecht (2006) also reported that several genera of ants, such as *Dorimyrmex*, *Pheidole*, *Gnamptogenys*, *Tetramorium*, and *Solenopsis*, can act as predators of coffee plant pests.

The purpose of this study is to find out how the ant community and its trophobionts shape incidences of pests and diseases in a tropical coffee agroforestry system. Research on the role of ants in the coffee agroecosystem has never been conducted in Indonesia. Nearly all publications about the role of ants as biocontrol of coffee pests and diseases came from the Neotropics and were very limited to the South American region, which is known as one of the largest coffee-producing regions in the world (Morris et al. 2018). Differences in entomofauna are the key differences between coffee plantations in Indonesia and South America. In previous studies, *Dolichoderus thoracicus* was the most dominant ant in coffee plantations, not *Azteca* (Muhammad et al. 2022). The results of this study can be used as recommendations for farmers in the practice of biological control of coffee pests and diseases.

MATERIALS AND METHODS

Study area

The research was conducted in three coffee plantations at UB Forest, Malang Regency, East Java, Indonesia (Figure 1). UB (Universitas Brawijaya) Forest is an educational forest managed by Universitas Brawijaya, covering an area of 554 hectares on the slopes of Mount Arjuno, East Java. The altitude of UB Forest ranges from 800 to 1600 meters above sea level. Land use in UB Forest was characterized as coffee agroforestry, pine forest, natural habitat, annual cropland, and settlement. Based on Karangploso Climate Station near the research location, the average temperature was 23.9°C and the average relative humidity was 77.5% (BPS Kabupaten Malang 2022).

Three 30 m x 30 m plots of arabica coffee (*Coffea arabica*) plants were selected for observation. There were different numbers of plants in each plot. In plot A, there were 84 plants. Plot B consisted of 82 plants. At the same time, plot C consisted of 90 plants. The plots were selected based on age similarity and habitat uniformity. The age range of observed coffee plants was 7-10 years. The canopy trees of all plots were only pines (*Pinus merkusii*). Low management intensity was applied throughout the plot. The distance between plants was 3 m x 3 m. Fertilizing and pruning were conducted only once a year.

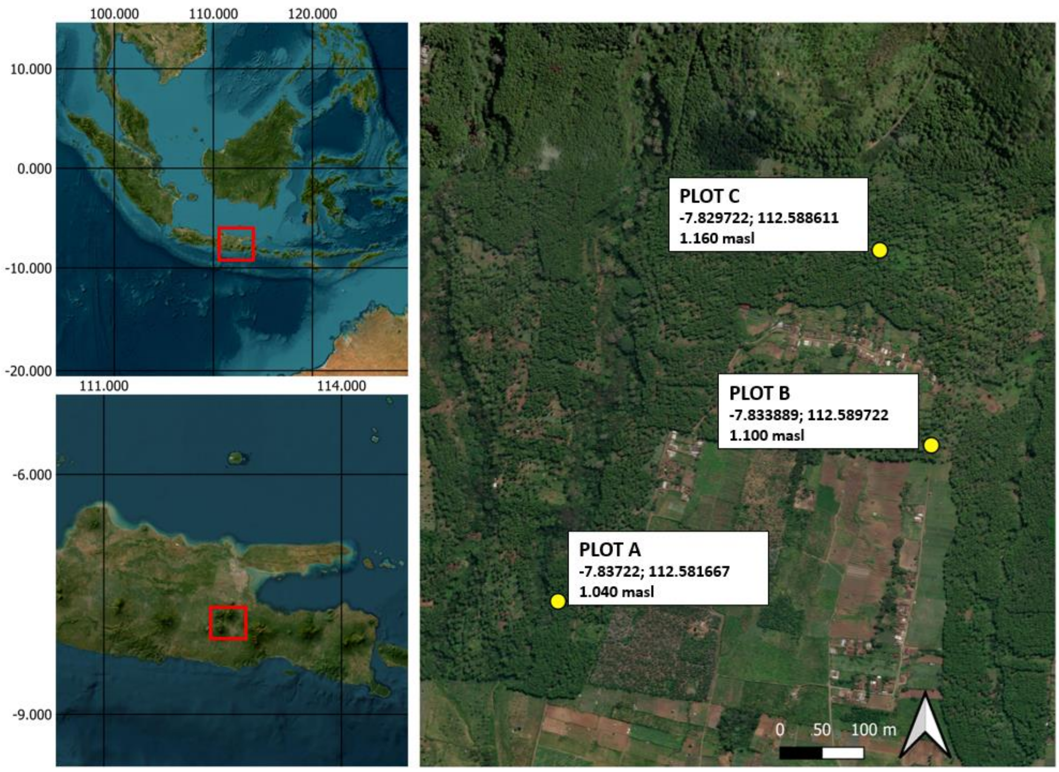

Figure 1. Map of three coffee plantation located in UB Forest area in East Java, Indonesia (QGIS.org 2022)

Ant and trophobiont hemipteran observation

Observation was conducted from January to March 2022. Ant community observation was conducted three times and once a month with three modified methods by Rizali et al. (2018): visual, tuna bait, and live bait. Each method was conducted on different days. Those methods were used to determine which species have dominant behavior by observing all 256 coffee plants from three plots. For observation with tuna bait, a 200 ml plastic cup was placed on a primary branch. A half tablespoon of tuna-based cat food was put and left for 2 hours. Then, the ants were observed to decide the dominant species. Meanwhile, the live bait was replicated in the day and at night on a one-day cycle. Two live larvae of *Tenebrio molitor* were put in a plastic cup for one hour. Ants were collected with a brush and were put into a 1.5 ml microtube. Ants were divided into dominant and non-dominant groups. Ants were considered dominant if they had the ability to build connected nests (polydomous nests) and/or were dominating bait traps that were characterized by a large number of individuals. Ants were identified at the genus level based on Nazarreta et al. (2021) and then separated into morphospecies based on external morphology. The purpose of this observation method is to prevent the dominant ant colony from being disturbed in future observations. Meanwhile, trophobiont hemipteran observation was conducted only visually. Visual observations of ant and trophobiont hemipteran were done by observing each plant sequentially within 5 minutes. Every trophobiont hemipteran that was associated with ants (trophobiosis) was directly recorded and photographed. The data obtained from this method was the presence/absence of ants and hemipteran trophobiont per plant.

Pest and disease observation

Pest and disease observation was conducted three times and once a month. The disease intensity of leaf rust (*Hemileia vastatrix*), and pest infestation intensity of twig borer (*Xylosandrus compactus*) and CBB (*Hypothenemus hampei*) were observed. A total of 256 samples of the same plants as ants and trophobionts were observed from three plots. Incidences of each pest and disease were counted based on the intensities at the tree level. The disease intensity of leaf rust was calculated using Merle et al. (2020) method with modification. The number of symptomatic leaves and the total number of leaves on the branch samples were counted. The intensity of twig borer infestation was calculated using Indriati et al. (2017) method with modification. A number of wilted and hollowed twigs, together with the total number of twigs in the sample branches, were counted. Meanwhile, the intensity of CBB infestation was calculated using Husni et al. (2019) method with modification. The number of hollowed berries, together with the total number of berries in the sample branches, was counted. The intensity value was obtained by dividing the number of symptomatic plant parts by the total plant parts and multiplying by 100. The modification made was to only observe the intensity of pests and diseases on four sample branches of each plant according to the method of Prastowo et al. (2019). Sample branches were selected based on compass points (North, East, South, West).

Data analysis

Ant and hemipteran observation resulted in data on occurrences. Meanwhile, the pest infestation and disease intensity were obtained in percentage form. Differences in attack intensities of each pest and disease of coffee plants on different plots were analyzed by Analysis of Variance (ANOVA). If significant differences were found, then Tukey's post-hoc test was conducted. The relationships between dominant ants and hemipteran presence were analyzed using a Generalized Linear Model (GLM) with binomial distribution. The GLM with quasipoisson distribution was also used to test the relationship between the presence and absence of dominant ants and hemipterans to coffee pests and disease attack intensities. The Pearson Product Moment Correlation Test was also conducted to analyze the interaction between pest and disease attack intensity. Before conducting ANOVA and correlation test, the data were tested for normality with the Shapiro-Wilk Test. If the attack intensity data did not have normal distribution, the data were then transformed using log(x). All analyses were conducted using R Statistics version 4.2.0 (R Core Team 2023).

RESULTS AND DISCUSSION

Ant and trophobiont hemipteran community

The ants found at the study site represented five subfamilies, 13 genera, and 21 morphospecies (Table 1). The most commonly found subfamily was Dolichoderinae (46.5% of the entire plant), followed by Formicinae (23.7%), Myrmicinae (17.6%), Pseudomyrmicinae (10.1%), and Ponerinae (1.8%). In comparing each plot, Dolichoderinae ants were also the most commonly found ants. At the species level, the black ant *D. thoracicus* and white-footed ant *Technomyrmex albipes* were the most commonly found. The ant species with the greatest occurrence in plots A and C was *D. thoracicus*. Meanwhile, in plot B, the species with the greatest occurrence was *T. albipes*. Eleven species were shared on all three plots.

Eight of 21 ants were categorized as dominant ants. All dominant ants can be found in all plots except *Crematogaster* sp.1. That species was absent in plot A. In plot A, as much as 91.6% (77 of 84) of plants were occupied by dominant ants. In plot B, 82% (68 of 82) of plants were inhabited by dominant ants. Meanwhile, in plot C, 96.6% (87 of 90) of plants were inhabited by dominant ants. Dominant ants can be found from one species to four species per plant (Figure 2). However, the occurrence of one dominant ant species on one plant was more common in plots B by 60% (41 plants) and C by 61.1% (55 plants). Whereas in plot A, less than half (49.3% or 38 of 68) of the plant population only has one dominant ant species. One plant could contain up to four dominant species. Twenty-four plants from all plots were only occupied by non-dominant species or were not occupied by ants. Each dominant species had different types of nests in the canopy.

Five species of trophobiont hemipterans were found during sampling (Table 2). The most frequently occurring hemipteran trophobiont was *Flatidae* sp.1, followed by the green scale *Coccus viridis*. *Flatidae* sp.1 was the most common in plot A, while *C. viridis* was the most common in plots B and C. *Coccus viridis* can be found on twigs, leaf stalks (petioles), and leaves. The flatids can be found on twigs and petioles, while aphids can be found only on lower leaf surfaces.

The presence of all trophobiont hemipterans was affected by dominant ants (Table 3). *C. viridis* positively correlated with *D. thoracicus* presence. Flatid presence positively correlated with *D. thoracicus* and *Tetraponera* sp.1 presence but negatively correlated with *T. albipes* presence. Meanwhile, aphids positively correlated with *D. thoracicus* and *T. albipes*. There was no correlation between trophobiont hemiptera.

Table 1. Ant species composition in three coffee plantation plots. Given are the names of the morphospecies and the number of morphospecies occurrences in the plots. Occurrence value based on the presence of ants at tree level

Morphospecies	Subfamily	Plot (Occurence)		
		A	B	C
Dolichoderus thoracicus	Dolichoderinae	48	13	77
Tapinoma sp.1	Dolichoderinae	2	0	6
Technomyrmex albipes	Dolichoderinae	9	59	13
Technomyrmex sp.2	Dolichoderinae	6	4	0
Technomyrmex sp.3	Dolichoderinae	12	2	2
Camponotus sp.1	Formicinae	7	1	5
Camponotus sp.2	Formicinae	5	4	5
***Camponotus* sp.3**	Formicinae	28	12	20
Polyrachis armata	Formicinae	23	5	5
Polyrachis sp.2	Formicinae	6	0	2
Polyrachis sp.3	Formicinae	0	1	0
Brachyponera sp.1	Myrmicinae	1	0	0
***Crematogaster* sp.1**	Myrmicinae	0	5	13
Crematogaster sp.2	Myrmicinae	0	3	1
Monomorium sp.1	Myrmicinae	7	1	6
Pheidole sp.1	Myrmicinae	5	5	4
Tetramorium sp.1	Myrmicinae	1	16	13
Tetramorium sp.2	Myrmicinae	0	10	5
Diacamma sp.1	Ponerinae	3	0	3
Odontoponera sp.1	Ponerinae	3	0	1
***Tetraponera* sp.1**	Pseudomyrmicinae	41	12	2

Notes: The morphospecies written in bold are the dominant species.

Table 2. Occurrence of trophobiont hemipteran at three coffee plantation plot in UB Forest. Occurrence value based on the presence of trophobiont hemipteran at tree level

Morphospecies	Plot (Occurence)		
	A	B	C
Aphididae sp.1	4	4	5
Aphididae sp.2	0	2	3
Coccus viridis	23	28	46
Flatidae sp.1	68	22	43
Flatidae sp.2	26	7	23
Total	121	63	120

DT	DT	DT	DT-C3	DT	DT	DT-C3	DT-T1	DT	DT
DT-T1-C3	DT-C3	DT-C3	DT	DT	DT	X	DT	DT.C3	DT.C3
0	DT-C3	0	DT	DT-T1	DT-C3	X	DT	T1-C3	DT-T1-C3
X	X	X	T1	X	T1	DT-T1	DT-T1	DT-T1-C3	DT-T1-C3
T1	T1	T1	TA.C3	0	0	DT-T1	DT-T1-C3	DT	DT
T1-C3	X	T1-C3	DT-T1-C3	T1	C3	DT	0	X	T1
DT-T1-C3	X	T1-C3	DT-C3	X	X	C3	0	T1	T1
T1	TA-T1	TA	X	DT-TA	DT-T1	TA-T1	DT-T1	T1	X
DT-T1	C3	C3	TA	TA-T1-C3	DT-TA	X	DT-T1	DT-T1-C3	T1
DT-T1	T1	DT-TA-C3	T1	T1	DT	X	X	0	DT-T1

A

TA	TA	TA	TA	TA	TA	TA-C3	TA-C3	TA	0
C1	X	TA	TA-T1-C3	TA	TA	TA-C3	C3	0	DT-TA-C3
TA-T1-C1	TA	TA	TA	TA-T1	DT-C3	TA	0	DT-TA-T1-C3	TA-C3
TA	TA-T1	DT-TA	DT-TA	0	TA	0	0	TA-C3-C1	T1
TA	DT-TA	TA	TA	DT-TA	X	X	X	X	TA
TA	0	TA	DT	X	TA	TA	X	X	T1-C1
TA	X	TA	DT-T1	TA	DT-TA	X	X	X	TA
TA-T1	TA	TA	DT-TA	TA	X	TA	X	DT-TA	DT-TA
0	TA	X	X	X	T1	TA-C3	TA	TA-C1	TA-C3
X	TA-T1	0	T1	0	TA	0	0	0	0

B

DT-C1	X	DT-C3	DT	DT-TA-C3-C1	DT	DT-TA-C3	DT-TA	DT	DT
C1	C1	DT	DT-C1	DT-TA	DT	DT	DT	DT	DT-TA
C3-C1	C1	C1	X	DT	DT-C3-C1	DT	DT	DT-C3	DT
DT	C1	X	DT-TA-C1	DT	DT	X	X	DT-TA	DT-TA
DT-C3	DT	TA-C3	DT-C3	DT-TA	DT-C1	DT-C3	DT-C3	DT	DT-TA
0	DT	DT	DT	T1-C3	TA-C3	DT-C3	DT	DT	DT
DT	DT	DT	DT-C3	DT	DT-C3	DT	DT	DT	DT
DT	DT	DT	DT-C3	DT	DT	DT	DT-T1	DT-C3	DT
DT	0	X	DT	DT	TA	DT	DT	X	X
DT	DT	DT	DT-C3	DT-C3	DT	0	DT	X	X

C

Figure 2. The dominant ant mosaic pattern in plots a, b, and c of coffee plantations in UB Forest. DT = *D. thoracicus*, TA = *T. albipes*, C1 = *Crematogaster* sp.1, C3 = *Camponotus* sp.3, T1 = *Tetraponera* sp.1, X = dead plant, and 0 = Only non-dominant ants or ants were absent

Interaction among ants, hemipterans, and coffee pests and diseases

The mean disease intensity of coffee leaf rust was 13.34%. Meanwhile, the mean of pest attack intensity by twig borer and CBB was 16.08% and 11.44%, respectively. When compared, there was no difference in the intensities of attacks by coffee leaf rust ($F_{2.253}$ = 0.033; P = 0.968) and twig borer ($F_{2.253}$ = 1.996; P = 0.138) among plots. Whereas for CBB, the attack intensity was different among plots ($F_{1.161}$ = 8.828; P < 0.001) and the highest intensity occurred in plot B. Coffee pest and disease attack intensities also correlated with each other. Based on correlation analysis results, positive correlations were found between leaf rust disease and twig borer (r = 0.311; P < 0.001), between leaf rust disease and CBB (r = 0.189; P = 0.015), and between twig borer and CBB (r = 0.302; P < 0.001). During observation, no *C. viridis* was infected by entomopathogenic fungi.

Coffee pest and disease incidences were affected by either ants or their trophobiont hemipterans (Table 4). Twig borer and CBB attacks were affected by both ants and hemipterans, while leaf rust disease attack was only affected by hemipterans. Leaf rust disease intensity was only positively affected by the presence of *C. viridis*. Twig borer attack was positively affected by all hemipteran presence but negatively affected by the presence of *D. thoracicus*. Meanwhile, CBB was positively affected by present flatids and aphids but negatively affected by the presence of the carpenter ant *Camponotus* sp.3. The connections among ants, hemipterans, and coffee pests and diseases represent a complex interaction (Figure 3).

Dolichoderus thoracicus presence positively correlated with all trophobiont hemipteran presence. *T. albipes* negatively correlated with flatids presence but positively correlated with aphids presence. While *Tetraponera* sp.1 only positively correlated with flatids presence. The presence of *C. viridis* had a positive relationship with both leaf rust disease and twig borer attack intensities. Flatid presence even had a positive correlation with all coffee pests and diseases. At the same time, aphids didn't correlate with all coffee pests and diseases. *Dolichoderus thoracicus* presence also negatively correlated twig borrer attack intensity. Due to the positive correlation between *D. thoracicus* and *Tetraponera* sp.1 with *C. viridis* and flatids, both ants may indirectly increase the intensity of attacks by coffee leaf rust, twig borers and CBB. On the other hand, the negative correlation that occurs between *T. albipes* and flatids means that *T. albipes* may indirectly reduce the intensity of pest and disease attacks on coffee plants.

Table 3. Generalized Linear Model of ant species and trophobiont hemipteran

	C. viridis		**Flatidae**		**Aphididae**	
	Estimate	**SE**	**Est**	**SE**	**Estimate**	**SE**
(Intercept)	-1.062**	0.334	0.020	0.295	-5.210***	0.970
Dolichoderus thoracicus - Present	0.710*	0.304	0.703*	0.304	1.848*	0.741
T. albipes - Present	0.454	0.317	-0.841**	0.311	1.392*	0.645
Tetraponera sp.1 - Present	-0.171	0.346	0.833*	0.371	0.799	0.672
Camponotus sp.3 - Present	0.173	0.309	0.471	0.337	-0.560	0.707
Crematogaster sp.1 - Present	0.699	0.508	0.133	0.529	1.183	0.879
C. viridis - Present	-	-	-0.010	0.285	-0.500	0.617
Flatidae - Present	-0.003	0.285	-	-	0.900	0.712
Aphididae - Present	-0.482	0.589	1.072	0.716	-	-

Notes: Estimate value followed by (*) indicate significant effect with significance level of 0.05. Estimate followed by (**) indicate significant with significance level of 0.01. Estimate followed by (***) indicate significant with significance level of 0.001

Table 4. Generalized Linear Model of ant species and trophobiont hemipteran against coffee plant pest and disease

	Leaf Rust Disease		**Twig Borrer**		**CBB**	
	Estimate	**SE**	**Estimate**	**SE**	**Estimate**	**SE**
(Intercept)	0.901***	0.028	0.786***	0.062	0.667***	0.087
Dolichoderus thoracicus - Present	0.009	0.025	-0.156**	0.056	-0.070	0.070
T. albipes - Present	-0.032	0.026	0.058	0.058	-0.079	0.071
Tetraponera sp.1 - Present	-0.022	0.028	0.004	0.062	0.018	0.073
Camponotus sp.3 - Present	-0.027	0.026	0.018	0.058	-0.120	0.073
Crematogaster sp.1 - Present	-0.025	0.044	-0.061	0.097	0.049	0.107
C. viridis - Present	0.055*	0.023	0.164**	0.050	0.042	0.064
Flatidae - Present	0.053*	0.024	0.183***	0.054	0.250***	0.071
Aphididae - Present	0.054	0.047	0.195	0.099	0.256	0.133

Notes: Estimate value followed by (*) indicate significant effect with significance level of 0.05. Estimate followed by (**) indicate significant with significance level of 0.01. Estimate followed by (***) indicate significant with significance level of 0.001

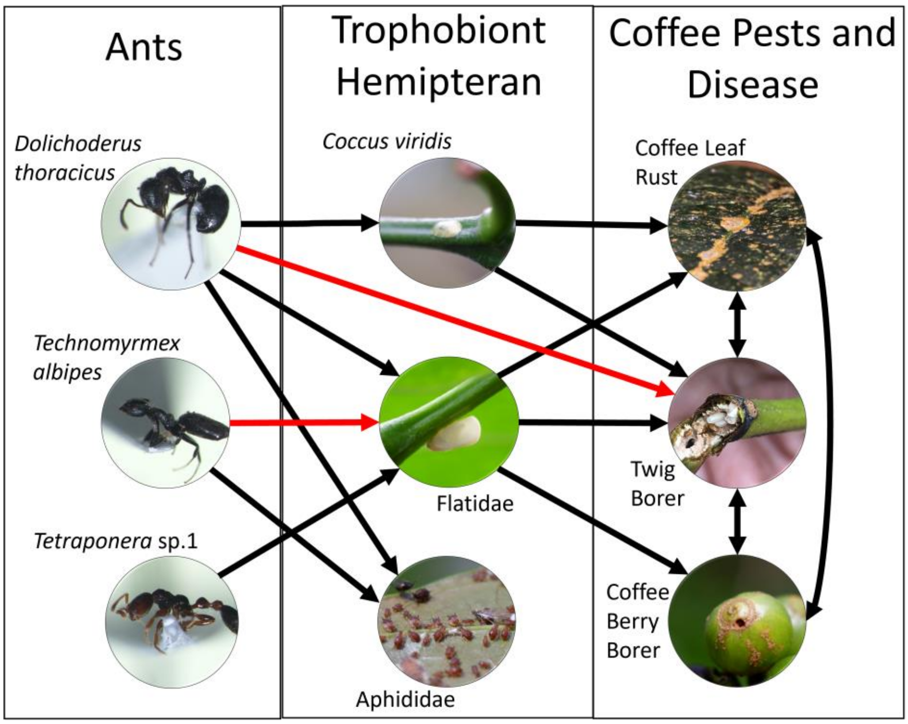

Figure 3. Complex interaction between ants, trophobiont hemipteran, and coffee pest and disease. Negative interaction are shown with red arrow line. Positive interaction are shown with black arrow line. Arrow lines are based on GLM on Table 3, Table 4 and correlation analysis. Photograph: Faiz Nashiruddin Muhammad, Ito Fernando, Yogo Setiawan

Discussion

Dominant species could share space with other dominant species. This is very important because, with minimal competition between dominant species, the biological control that occurs will not be disturbed. Each dominant species builds its nest in a different niche. *T. albipes* are known to nest on the ground or in the canopy (Sharaf et al. 2018). During the observation, *D. thoracicus* nests were found in the leaves that were attached to each other in the canopy. Meanwhile, *T. albipes* can be found behind the moss and lichen that grows on stems and twigs. Ants of the genus *Camponotus* and *Crematogaster* also have diverse nesting habits from ground to canopy (Fernandes et al. 2014; Ronque et al. 2018; Bujan and Yanoviak 2022). *Camponotus* sp.3 nests were found in the curling leaves, whereas several large *Crematogaster* sp.1 nests were found on the main stem of the coffee plant. Meanwhile, the nests of *Tetraponera* sp.1 were found in the cavities in the twigs that were formerly attacked by twig borers. Some species of *Tetraponera* can indeed build nests in the cavities of many plant stems (Ward 2022).

This research evidently showed that ants can act as biological controls for coffee pests. In this study, *D. thoracicus* was able to control CBB. Some ant species in the research by Philpott and Armbrecht (2006) had been known to act as biological controls in coffee plants. However, that study was only conducted in the African (Afrotropical) and American (Neotropical) regions. *Tetramorium* spp. and *Pheidole* spp. were included in the list as CBB predators by Philpott and Armbrecht (2006), but in this study, both genera were not behaviorally or numerically dominant because we only found a small number of workers foraging in the canopy or attending bait. For CBB attacks, these results suggest that the presence of ants may reduce CBB attacks due to indirect interaction through flatids suppression. This is in accordance with the study conducted by Gonthier et al. (2013), for which the results suggested that ants such as *Azteca*, *Pseudomyrmex*, *Tapinoma*, and *Wassmania* can prevent coffee pests from colonizing. In this study, the attack of *X. compactus* as a coffee twig borer was lower on plants with *D. thoracicus*. The research by Giannetti et al. (2022) also proved that female *X. compactus* avoids twigs containing foraging ants as hosts.

Regarding the relationship between ants and hemipterans, the ants may choose which hemipteran species would become their trophobionts (Nelson and Mooney 2022). The results of the study by Sanchez et al. (2020) showed that the dominant species *Lasius grandis* can reduce the population of psyllids *Cacopsylla* sp. in pear trees. On the other hand, ants can allow some species of hemipterans to become their trophobionts. The ants provide protection to the hemipterans; in return, the hemipterans provide honeydew to the ants (Anjos et al. 2022). When an artificial sugar solution has been provided in the field, ants can turn to prey on aphids (Pérez-Rodríguez et al. 2021). In coffee plants, *C. viridis* has been recorded as the trophobiont of many ant species (Philpott and Armbrecht 2006). In the Neotropics, *Azteca instabilis* interferes in the predation process of the coccinellid beetle *Azya orbigera* on *C. viridis* (Perfecto et al. 2014).

The positive correlations among leaf rust, twig borer, and CBB in this research suggested that pest and disease attacks can reduce plant resistance. Weak plant resistance causes plants to be easily attacked by pests and diseases. Júnior et al. (2015) also explained that *H. vastatrix* attacks can reduce the rate of photosynthesis of coffee plants. In addition, the twig-borer ambrosia beetle is also associated with several fungal species that can grow in boreholes (Giannetti et al. 2022). Several types of microbes known to be associated with ambrosia include *Aspergillus* spp., *Penicillium* spp., *Trichoderma* spp., *Fusarium* spp., *Acremonium* spp., and *Gliocladium* spp. (Tarno et al. 2016). *Fusarium* and *Aspergillus* were also known to be found in coffee fruits infected with CBB (Alves da Silva et al. 2020). Pest and disease attacks can reduce the supply of nutrients for plants, resulting in a decrease in the level of plant resistance (Huber et al. 2011). Another reason for the positive correlation between pests and diseases was suggested by de Bobadilla et al. (2022), who explained that a plant's resistance can be determined by sequential attacks from pests. Ants, which mostly have a positive correlation with hemipterans, also indirectly contribute to pest and disease attacks. Only *T. albipes* showed a negative correlation with one of the hemipteran trophobionts.

The positive association of *C. viridis* on coffee leaf rust contrasts with the results of previous studies (Jackson et al. 2012). The absence of the white halo fungus *Lecanicillium lecanii* associated with *C. viridis* leads to the absence of the role of *C. viridis* as an indirect biological control of coffee leaf rust. White halo fungus can act as an entomopathogen for scale insects and as an antagonist for coffee leaf rust (Jackson et al. 2016; Zewdie et al. 2021). The absence of white halo fungus may have resulted in a failure in the natural control of coffee leaf rust.

In conclusion, there are dominant and non-dominant species that shape the ant community. The presence of ants and their trophobionts affect the incidences of coffee pests and diseases. Each ant species has a different impact on pests and diseases of coffee plants, directly or indirectly. All the hemipteran trophobionts only have a negative impact on incidences of coffee pests and diseases. The absence of *C. viridis* infected with *L. lecanii* made its presence unable to control coffee leaf rust disease. Further research needs to be done to find out how the behavior and predation rate of ants to control coffee plant pests. This study also recommends ants as one of the ways to control pests and diseases in coffee commodities. Different regions in Indonesia have the potential for different entomofauna. Therefore, further exploration is needed to find out which ant species are beneficial for coffee cultivation.

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