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Diversity and species composition of ants at coffee agroforestry systems in East Java, Indonesia: Effect of habitat condition and landscape composition

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Abstract. *Muhammad FN, Rizali A, Rahardjo BT. 2022. Diversity and species composition of ants at coffee agroforestry systems in East Java, Indonesia: Effect of habitat condition and landscape composition. Biodiversitas 23: 3318-3326.* Habitat condition and landscape composition are the main factors that shape biodiversity in agroecosystems. However, information on the effect of habitat conditions and landscape composition on biodiversity in agroforestry systems is lacking. Agroforestry systems possess habitats that are characterized by a high diversity of vegetation, that can support biodiversity both on the field or landscape scale. This research aimed to study the diversity and species composition of ants in coffee (*Coffea* spp.) agroforestry systems, and to investigate the effects of habitat conditions and landscape composition on ant communities. Field research was conducted in twelve coffee agroforestry systems in East Java, Indonesia. Ants were sampled with the fogging method for canopy ants and pitfall traps for ground-dwelling ants in 40 m x 30 m plots. In each location, habitat conditions aspects (such as cultural technique and tree age) were identified by interviews with farmers and vegetation observation. Meanwhile, landscape composition was characterized by ground checking and mapping the land-use type within a 500 m radius from plot centers. This research recorded 35 species and 4,622 individuals of ants from all coffee plantations. *Dolichoderus thoracicus* was the most dominant canopy ant, while *Pheidole* sp.2 was the most dominant ground-dwelling ant in all plantations. Based on the GLM analysis, different responses were found between canopy and ground-dwelling ants in relation to habitat conditions and landscape composition. Canopy and ground-dwelling ants were affected by habitat conditions (such as tree age and canopy cover). The species composition of ground-dwelling ants was also affected by habitat conditions. In conclusion, habitats in coffee plantations can affect ant communities with ground-dwelling ants being more sensitive than canopy ants. Meanwhile, landscape composition can affect the species richness of all ants and not affect each stratum (canopy and ground-dwelling ants).

Keywords: Abundance, ant, canopy, ground, similarity, species richness

INTRODUCTION

Habitat conditions and landscape composition are the main driving factors affecting biodiversity in agroecosystems. Habitat loss and fragmentation on the local and landscape levels have become threats to biodiversity (Horváth et al. 2019). Agriculture activity is the second general threat that can lead to biodiversity loss, after over-exploitation (Maxwell et al. 2016). Biodiversity loss can affect agricultural sustainability and environmental quality (Udawatta et al. 2019). The model system for studying the effect of agriculture on biodiversity is coffee production (Otero-Jiménez et al. 2018) and ants become the object to assess biodiversity (Silva et al. 2017). In South America, coffee plantations were proven to be the main reason for biodiversity loss across taxa, including ants (Philpott et al. 2008). However, the effect of habitats and landscapes of coffee plantations on ant taxa in Indonesia still lacks understanding.

Indonesia is one of the biggest coffee-producing countries in the world. In 2019, Indonesia produced approximately 741 tons of coffee beans with the domination of robusta (BPS 2020; Mutala'liah et al. 2017). However, coffee production in Indonesia also faces main pest problems such as the Coffee Berry Borer (CBB) *Hypothenemus hampei* Ferr (Coleoptera: Scolytidae) and coffee leaf rust disease caused by *Hemileia vastatrix* (Johnson et al. 2020; Ramírez-Camejo et al. 2021). Ants are one of the most important organisms in coffee plantations. Ants can deal with all main coffee pest problems (Perfecto and Vandermeer 2015). Vandermeer et al. (2010) explained that in South America, coffee plantations have autonomous pest control with *Azteca* ants as the key species. Other ant species that act as natural enemies of CBB in coffee plantations are *Dorymyrmex* sp., *Gnamptogenys sulcata* F. Smith, *Pheidole* spp., *Solenopsis* spp., *Tetramorium* sp., and *Oecophylla longinoda* Latreille (Philpott and Armbrecht 2006).

Ants are very sensitive to environmental change. Agriculture intensification, human disturbance, and land conversion are known to affect ant diversity (Solar et al. 2016; Rizali et al. 2020; Santos et al. 2021). Because of their sensitive and rapid responses, ants can become good indicators of change in the environment (Tiede et al. 2017). To maintain autonomous pest control by ants, the environment in coffee plantations must be suitable for ants. Optimal habitats in surrounding landscapes can also increase ant diversity and abundance (Vele et al. 2011). However, the effect of environments can vary for different species or types of ants such as canopy/arboreal and ground-dwelling ants. Canopy and ground ants have different species compositions (Antoniazzi et al. 2020). Different species compositions result in different responses of ant species/groups to environmental change (Andersen 2019) such as the isolation of agricultural land from its natural habitat (Rizali et al. 2021).

Several studies have shown that ant communities in coffee plantations are influenced by many factors. Habitat level, land management, shade cover, and vegetation diversity can affect the diversity, abundance, and composition of ant species in coffee plantations (Philpott et al. 2006; García-Cárdenas et al. 2018; Perfecto and Vandermeer 2020). Landscape composition can also affect ant communities in coffee plantations (Aristizábal and Metzger 2018). The studies that have been conducted, however, are all located in tropical coffee plantations in the Americas. There exist a small number of studies on ant communities in coffee plantations in Indonesia, such as for those in the provinces of West Java and Aceh (Susilawati and Indriati 2020; Jauharlina et al. 2021).

The objective of this research is to study the diversity and species composition of ants in coffee agroforestry systems in East Java, and to investigate the effects of habitat conditions and landscape composition on ant communities. The environment variables of in-site habitats that comprise tree age, variety, pesticide, fertilizer, canopy, vegetation, herbivore insect, and landscape composition were observed in all 12 coffee plantations. The hypothesis that is tested in this research is that landscape composition and habitat condition can affect the diversity and species composition of ants and there are different responses between canopy and ground ants.

MATERIALS AND METHODS

Study area and plot designation

Field research was conducted in twelve coffee plantations located in Malang Regency and Pasuruan Regency, East Java from December 2020 to February 2021 (Figure 1). These regions have a tropical wet climate with an average of air temperature is 24.3°C, relative humidity is 85.2%, and average monthly rainfall is 398.7 mm (BPS Kab. Malang 2022). Locations were selected based on the criteria of coffee plants in the productive stage, a minimum size of 1200 m^2 (Figure 2), and a distance of at least 1 km between locations with elevation ranges from 429 m asl to 1311 m asl. In the plantations, plots with a size of 40 m x 30 m were set up (Figure 2), consisting of two subplots with a 10 m x 10 m subplot for fogging method and a 25 m x 25 m subplot for pitfall traps and visual observation.

Sampling of ants

Sampling activity combined fogging, pitfall traps, and visual observation. The methods of fogging and visual observation were utilized to sample canopy ants, while pitfall traps were utilized to sample ground-dwelling ants. Fogging was conducted with usage of the DECIS 25EC insecticide and Krisbow Portable Insect Fogger 2L machine. Fogging was performed at 06:30 AM if in the early morning was not rain. In each study location, four trees were selected with a minimum distance of two trees between the sample trees. Before fogging was conducted, 2 x 2 m white sheets were placed under the selected trees. The selected trees were fogged for approximately a minute or until the whole canopy was fogged.

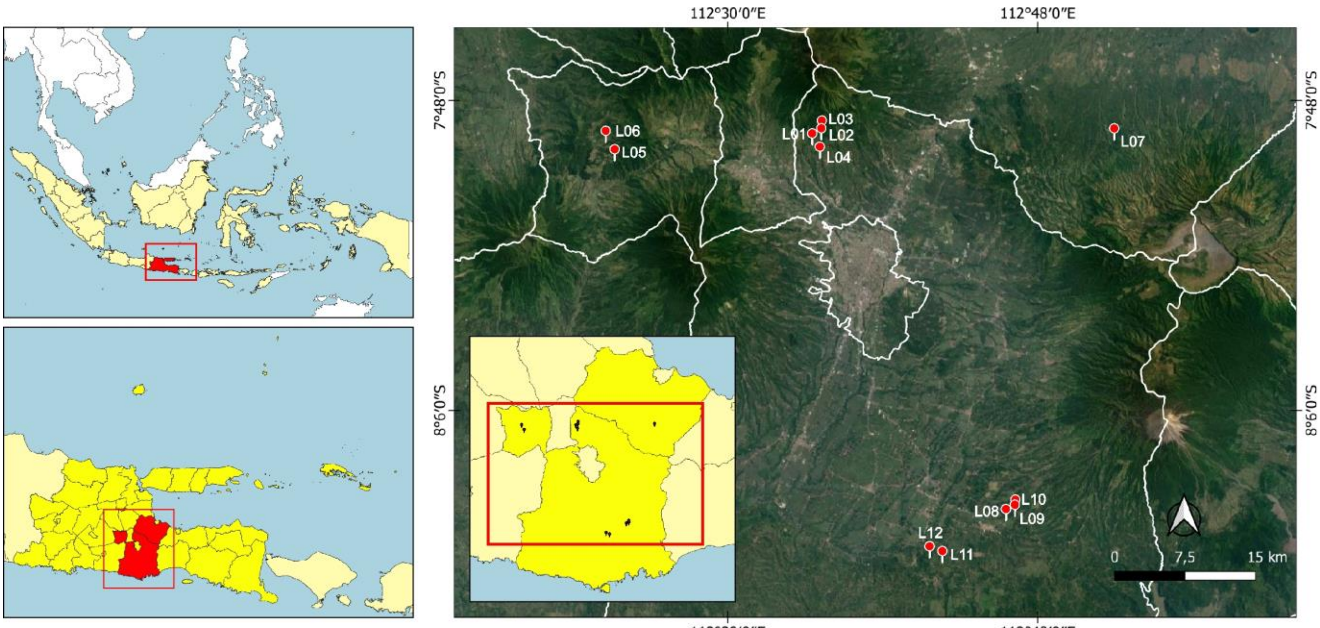


Figure 1. Research locations of twelve coffee plantations in East Java, Indonesia. Dots with letters indicate location codes. L01: UBF 1, L02: UBF 2, L03: UBF 3, L04: Bocek, L05: Ngantang 1, L06: Ngantang 2, L07: Puspo, L08: Dampit 1, L09: Dampit 2, L10: Dampit 3, L11: Sumawe 1, L12: Sumawe 2

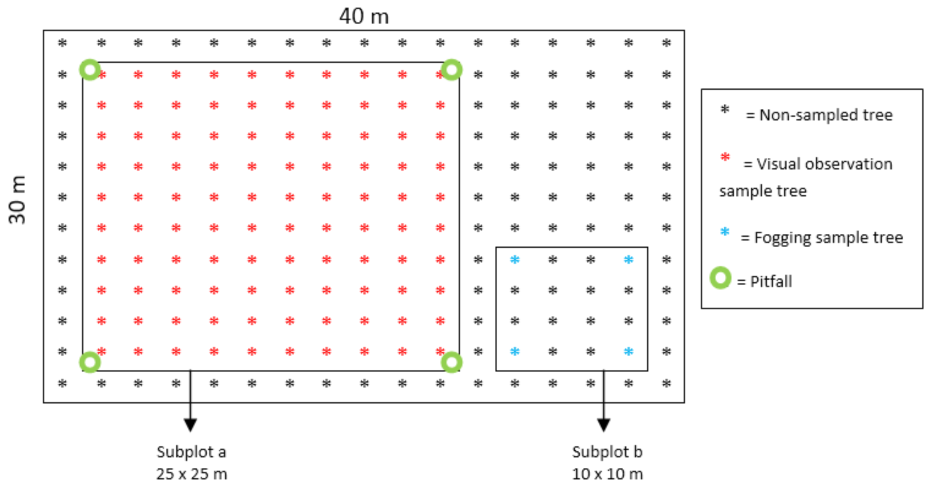


Figure 2. Design of the plot in each location. The plot consists of two subplots: (a) 25 m x 25 m for pitfall traps and visual observation and (b) 10 m x 10 m for fogging method. The two subplots were separated by a distance of one tree. Pitfalls were placed at every corner in subplot a. Meanwhile, the four fogging trees were located in each corner of subplot b

Approximately 30 minutes after fogging, the killed insects were then collected from the white sheet. The killed insects were stored in 15 ml plastic bottles containing 70% alcohol. For the pitfall trap method, four cups were placed in each corner of the plots. The cups were filled with detergent water to half-full. Specimens in the pitfall traps were collected after 24 hours and stored in 15 ml plastic bottles containing 70% alcohol. For visual observation, ants in 100 coffee trees in the 25 m x 25 m subplot were observed for five minutes per tree. The ants that were found were then taken with a brush and tweezers, and put in a microtube. In total, 1,200 trees were observed throughout the plantations. Visual observations were carried out to determine the percentage of occurrence of each ant species. Each method in this research was only carried out once per location.

The insect specimens were initially sorted to the order level, with the ant group as additional identification. Ants were identified to the genus level with available references (Bolton 1994; Hashimoto 2003). When possible, they were identified to the species level with the antweb.org website (AntWeb 2021). The unidentified species were then separated to the morphospecies level based on external morphological differences (Lattke 2000). The abundance of herbivorous insects as potential prey and trophobiont of ants were also calculated.

Identification of habitat condition

Measurement of variables was conducted at the habitat level and landscape level. The habitat variables that were measured were canopy cover (%), number of vegetation species excluding coffee, coffee tree age, number of coffee varieties, pesticide application, and fertilizer type (Table 1). The canopy cover was measured with the photographic method. Four photos were taken four times in each location. The camera was placed 30 cm above the ground and photos of the canopy were taken. The resulting photographs were processed with ImageJ2 to measure the percentage of canopy closeness (Rueden et al. 2017). Vegetation species were counted in subplot a. Ten random places were selected for placement of the 1 x 1 m subplots. All species of understory plants and standing trees were counted from the subplots. Understory plants were identified according to Xu and Zhao (2017). Data on coffee tree age, number of coffee varieties, pesticide application, and fertilizer type were collected by interviewing the farmers. Based on the interview results, the age of the coffee trees was divided into three groups i.e. 5-8 year (young), 10-25 years (old), and 34-52 years (very old). Varieties of coffee were grouped into mono-variety and multi-variety. Pesticide variables were distinguished between with and without pesticides. While the fertilization variable was grouped into organic, inorganic, and mixed between organic and inorganic.

Characterization of landscape composition

At the landscape level, a ground check was initially carried out in a 500 m radius from the plot location, assisted by a printed map from Google Earth. The land use was recorded during the ground check. The results of the ground check were then digitized with QGIS (QGIS Development Team 2021). LecoS (landscape ecology statistics) plugins were utilized to calculate the class area (CA) and the number of patches (NumP) per class area in every location. Land use was classified into the seven categories of agroforestry, natural habitat, grassland, annual cropland, perennial cropland, open area, and settlement (Figure 3). Only the CA and NumP of the agroforestry and natural habitat categories were utilized in the analysis (Table 1).

Table 1. Habitat-landscape variable data in each coffee plantation. Location code refers to Figure 1

Location code	Vegetation diversity (species)	Age (year)	Pesticide	Fertilizer	Canopy cover (%)	No. of variety	Agroforestry class		Natural habitat	Herbivore insect	
							Class area (ha)	No. of patch		Species	Ind.
L01	11	7	Absent	Organic	64.29	1	23.72	1	Absent	7	12
L02	10	10	Absent	Inorganic	59.45	1	50.08	1	Absent	26	76
L03	10	7	Absent	Inorganic	78.83	1	70.22	2	Present	11	22
L04	12	52	Absent	Organic	65.69	1	4.49	3	Present	15	27
L05	9	8	Absent	Inorganic	79.33	1	51.62	1	Absent	9	17
L06	18	8	Present	Mix	58.06	3	40.60	3	Present	9	19
L07	7	35	Absent	Organic	80.72	4	56.84	1	Present	18	41
L08	6	21	Absent	Organic	76.80	3	61.79	3	Absent	27	193
L09	12	34	Absent	Mix	63.84	3	64.11	2	Absent	8	17
L10	6	25	Absent	Organic	72.88	2	53.92	2	Absent	5	12
L11	7	11	Present	Mix	39.33	1	53.80	1	Absent	28	94
L12	9	5	Present	Inorganic	65.01	1	31.48	5	Present	18	23

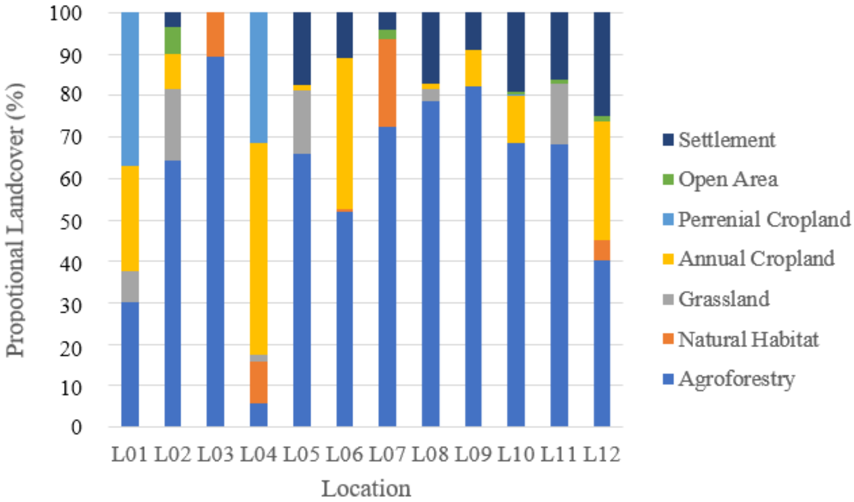


Figure 3. Landscape composition of the study areas. Location code refers to Figure 1

Data analysis

One-way ANOVA (Analysis of Variance) was used to analyze differences in species richness and abundance of ants toward different coffee tree age groups, the number of coffee varieties, presence of natural habitat, pesticide application, and fertilizer types. Prior to the analysis, the Shapiro-Wilk normality test was performed on each response variable. If the data were not normally distributed, data were transformed using log(x). Fisher's least significant difference test was then utilized if the ANOVA results were found significant differences.

The effects of all explanatory variables (i.e., canopy cover, number of vegetation species, prey abundance, as well as CA and NumP of agroforestry) on species richness and abundance of ants were analyzed by fitting a generalized linear model (GLM) and using a quasipoisson distribution to account overdispersion.

ANOSIM (Analysis of Similarity) was also carried out to determine the similarity of ant species compositions on different variables. Species composition was derived from a similarity matrix based on the Bray-Curtis index. All analyses were performed with R-statistic (R Core Team 2021) with an additional package of agricolae and vegan.

RESULTS AND DISCUSSION

Ant communities in coffee agroforestry systems in East Java

In total, 35 ant species and 4,622 individual ants were collected from all research locations (Table 2). The species belonged to 17 genera and 5 subfamilies. Different numbers of species were obtained from each method: 28 spp. with the fogging method, 17 spp. with the pitfall, and 30 spp. with the visual observation. *Dolichoderus thoracicus* F. Smith and *Anoplolepis gracilipes* Jerdon were the most abundant species (2,315 and 1,235 individuals, respectively Table 2). The most dominant species in the canopy was *D. thoracicus* (Figure 2a), while *Pheidole* sp.2 was on the ground (Figure 2b). Both of them were followed by *A. gracilipes* (Figure 2c). In visual observation, *Dolichoderus* was also the most dominant species (26.33%, Table 2). *D. thoracicus* was found in 26% of the total trees among all the plantations. This was the highest percentage of the occurrence. Susilawati and Indriati (2020) also found that *Dolichoderus* ants were the most abundant in coffee plantations in Indonesia. *Dolichoderus* ants were included in the dominant

Dolichoderinae ant functional group because of their dominant behavior (Santos et al. 2021). Meanwhile, *Pheidole* ants were the dominant ground ants in coffee plantations (Ennis and Philpott 2017). The *Pheidole* genera was the second-most abundant ants after the *Azteca* genera, as one of the dominant Dolichoderinae ants that are known to be coffee berry borer predators (Vandermeer et al. 2010). These patterns that occurred in South American coffee plantations were similar to the result.

The diversity of canopy and ground-dwelling ants in each location was different (Table 3). There is no difference in species richness between the canopy and ground ant ($F_{1.22}$ = 2.28, P = 0.145, Figure 3a). This is arguably due to the differences in preferences between canopy and ground ants in foraging for food and building nests (Floren et al. 2014). However, the abundance of canopy ants is higher than ground ants ($F_{1.22}$ = 22.9, P = <0.001, Figure 3b) which indicated the fogging method was more effective than pitfall (Leponce et al. 2021). There was difference in species compositions between fogging and pitfall captures (R ANOSIM = 0.637, P = 0.001, Figure 3c). This result was similar to Antoniazzi et al. (2020), who found that canopy and ground ants have different species compositions.

Effect of habitat condition and landscape composition on ant communities

Based on the analyses, habitat and landscape can affect the diversity and abundance of ants in coffee plantations. Canopy and ground ants showed different responses. Based on one-way ANOVA, coffee tree age affected the diversity of canopy ants (Table 4). In the GLM test, canopy cover had a negative relationship with the abundance of ground ants (Table 5). Meanwhile, in the similarity analysis, the composition of canopy ants in all variables showed similarity. However, for ground ants, there was dissimilarity in species composition between plantations with and without pesticide application (Table 6).

Increased coffee tree age can increase the species richness of canopy ants, but it has a limit. Coffee tree age was classified into three groups: young, old, and very old. The diversity of canopy ants was higher in coffee trees in the old group compared to the young and very old groups, based on Fisher's least significant difference test. Ant diversity increased as coffee tree age increased, but decreased when the coffee tree age was too old. This result is similar to the study by Conceição et al. (2019) in which it was found that older trees have higher numbers of canopy ants than younger trees. Increased coffee tree age can increase the aspects of the coffee tree, such as height and stem diameter (Rizali et al. 2013). Coffee trees that are taller and possess larger diameters provide more suitable habitat for canopy ants.

Plant variety did not affect the diversity or abundance of ants. Plant variety can affect ants through the presence of trophobionts or special chemicals from plants (Singh et al. 2021). However, in this research different varieties of coffee did not affect the composition of trophobionts and other herbivores. This is similar to the research by Offenberg et al. (2019) on ants and aphids in apple trees, where differences in apple varieties had no effect on ants or aphids.

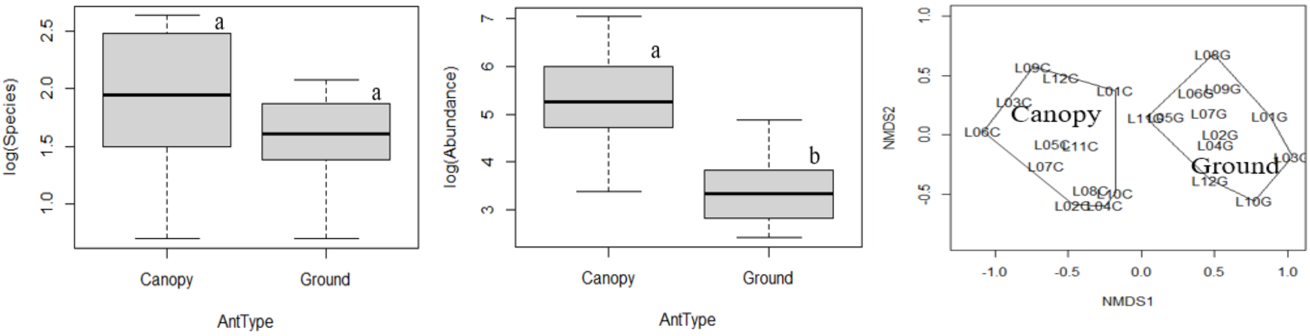
Table 2. List of ant species recorded from all studied plots in coffee plantations in East Java. Occurrence data are presented as the percentage of the total trees (n = 1200). Fogging and pitfall data are presented as the number of individuals

Morphospecies	Occurrence (%)	Fogging (ind.)	Pitfall (ind.)
Anoplolepis gracilipes	13.58	1152	83
Aphaenogaster sp.1	0.25	0	6
Camponotus sp.1	0.50	1	0
Camponotus sp.2	0	0	2
Crematogaster sp.1	8.33	181	2
Crematogaster sp.2	0.92	21	24
Diacamma sp.1	0	1	54
Dolichoderus thoracicus	26.33	2293	22
Dolichoderus sp.2	1.17	45	0
Dolichoderus sp.3	0.08	181	0
Dolichoderus sp.4	0.08	6	0
Hypoponera sp.1	0.17	1	4
Leptogenys sp.1	0.17	2	4
Leptogenys sp.2	0.17	1	3
Odontomachus sp.1	0	0	2
Odontoponera sp.1	0.33	0	79
Oecophylla smaragdina	4.00	0	0
Monomorium sp.1	0.75	52	0
Pheidole sp.1	0.08	31	39
Pheidole sp.2	0.58	2	113
Pheidole sp.3	0	0	14
Pheidole sp.4	0	0	2
Polyrhachis sp.1	4.50	9	0
Polyrhachis sp.2	0.08	2	0
Polyrhachis sp.3	0.08	3	0
Polyrhachis sp.4	0	3	0
Polyrhachis sp.5	0.08	1	0
Polyrhachis sp.6	0.08	1	0
Polyrhachis sp.7	1.17	4	0
Technomyrmex sp.1	2.75	6	0
Technomyrmex sp.2	0.58	49	0
Technomyrmex sp.3	1.25	44	0
Technomyrmex sp.4	3.00	26	0
Tetramorium sp.1	3.00	24	17
Tetraponera sp.1	8.58	10	0

Table 3. Species richness (S) and abundance (N) of the canopy and ground-dwelling ants in each location

Location	Canopy ants		Ground ants		Total	
	S	N	S	N	S	N
L01	6	37	5	31	10	68
L02	11	29	5	52	15	81
L03	5	1147	3	15	8	1162
L04	14	140	8	40	19	180
L05	7	127	7	38	10	165
L06	4	493	5	76	8	569
L07	7	245	4	11	9	256
L08	13	148	4	25	16	173
L09	2	329	6	23	6	352
L10	14	286	2	11	15	297
L11	10	1073	6	130	13	1203
L12	3	98	8	18	9	116

Figure 2. The most common ant species: A. *Dolichoderus thoracicus*, B. *Pheidole* sp.2, C. *Anoplolepis gracilipes*



A B C

Figure 3. Differences of: A. Species richness, B. Abundance, and C. Species composition between canopy and ground-dwelling ants. Boxplots with different letters are significantly different at P < 0.05 according to Fisher's least significant difference test. Ant species compositions are shown with non-metric multidimensional scaling (NMDS) with a stress value = 0.199

Table 4. ANOVA results of the effect of habitat condition and landscape composition on species richness and abundance of the canopy and ground-dwelling ants

Variables	Canopy ants			ground ants		All ants	
	df	F-value	p-value	F-value	p-value	F-value	p-value
Species richness							
Natural habitat	1, 10	0.774	0.400	0.282	0.607	0.413	0.535
Variety	1, 10	0.003	0.958	3.281	0.100	0.246	0.631
Age group	2, 9	5.680	0.025	0.887	0.445	3.265	0.085
Pesticide	1, 10	1.085	0.322	1.399	0.264	0.542	0.478
Fertilizer	2, 9	2.017	0.189	0.472	0.638	1.760	0.226
Abundance							
Natural habitat	1, 10	0.828	0.384	0.487	0.501	0.560	0.471
Variety	1, 10	0.712	0.419	1.310	0.279	0.315	0.587
Age group	2, 9	0.018	0.983	0.380	0.694	0.008	0.992
Pesticide	1, 10	1.209	0.297	3.525	0.089	1.314	0.278
Fertilizer	2, 9	1.849	0.212	2.496	0.137	2.341	0.152

Note: p-value under 0.05 is significant

Table 5. Generalized linear model relating habitat variables and the species richness and abundance of canopy and ground-dwelling, ants

Variables	Species richness						Abundance					
	Canopy ants		Ground ants		All ants		Canopy ants		Ground ants		All ants	
	Estimate	P-value	Estimate	P-value	Estimate	P-value	Estimate	P-value	Estimate	P-value	Estimate	P-value
(Intercept)	3.493	0.024	2.427	0.047	3.382	0.002	1.715	0.152	5.794	0.001	6.076	0.024
Canopy	0.003	0.776	-0.007	0.502	0.000	0.935	-0.005	0.388	-0.043	0.004	-0.041	0.108
Vegetation	-0.081	0.238	0.000	0.986	-0.042	0.262	0.001	0.950	0.086	0.097	0.012	0.898
Prey	0.003	0.230	-0.000	0.953	0.003	0.111	-0.000	0.521	0.005	0.160	-0.004	0.596
CA.ag	-0.015	0.127	-0.008	0.264	-0.013	0.003	0.007	0.103	-0.004	0.570	0.047	0.081
NP.ag	0.113	0.403	0.052	0.598	-0.049	0.527	0.041	0.474	-0.166	0.268	0.095	0.759

Note: p-value under 0.05 is significant. Canopy: canopy cover, Vegetation: vegetation diversity, Prey: prey abundance) landscape (CA.ag: class area of agroforestry, NP.ag: number of patches of agroforestry)

Table 6. ANOSIM results of the effect of habitat condition and landscape composition on the species composition of the canopy and ground-dwelling ants

Variables	Canopy ants		Ground ants		All ants	
	R-ANOSIM	p-value	R-ANOSIM	p-value	R-ANOSIM	p-value
Natural habitat	0.109	0.188	-0.165	0.942	-0.032	0.586
Variety	-0.041	0.555	0.058	0.291	0.010	0.479
Age group	0.043	0.334	-0.112	0.793	0.068	0.290
Pesticide	-0.082	0.687	0.431	0.036	-0.008	0.503
Fertilizer	0.164	0.153	0.049	0.328	-0.021	0.545

Note: p-value under 0.05 is significant

Pesticide application and fertilizer type also did not affect ant diversity and abundance. The farmers who applied insecticides only applied them four times a year to prevent CBB infestations on coffee fruits and to repel ants when harvesting. Gressel (2011) explained that low rates of pesticide application could accelerate mutations of subpopulations to pesticide resistance. Helps et al. (2017) also reported that there is still a high selection pressure even though the insecticide dosage was halved. The effect of pesticides differs depending on the ant species (Pereira et al. 2010). This causes differences in the compositions of ant species in coffee plantations where pesticides are applied and where they are not. The results of research by Widhiono et al. (2017) contrast with those of this research; in that research, inorganic fertilizers reduced ant diversity and abundance. This may happen because the farmers also apply inorganic fertilizers only twice a year. Less intensive application of pesticides and inorganic fertilizers can maintain ant diversity and abundance in coffee plantations.

Canopy cover negatively correlated with the abundance of ground ants. Increased canopy closeness can increase organic matter, such as leaf litter above the ground (Yuniasari et al. 2021). In addition to increasing leaf litter, a closed canopy can increase humidity and minimum solar radiation while decreasing temperature and wind effects (Kwon et al. 2014). However, the effects of canopy closeness are still unpredictable because of the different preferences of ant species on canopy closeness. According to Queiroz and Ribas (2016), specialist ants only prefer either a closed or an open canopy, while generalists can adapt to both closed and open canopies. Changes in canopy cover also have an impact on the shifting of ant functional groups from aggressive dolichoderinae to subdominant and opportunistic myrmicinae or specialist groups (Crist 2009). As such, in this research, the ground ants were specialists of an open canopy, while the canopy ants were generalists. Budiaman et al. (2021) also explained that clearcutting could change ant abundance, diversity, and even species composition.

Vegetation did not affect the diversity and abundance of ants. Dassou et al. (2017) explained that vegetation diversity couldn't modify ant nesting and foraging habits. With a foraging habit, vegetation only provides a part of their diets as omnivores. Most species of ants are polyphagous (Offenberg 2015). Meanwhile, with a nesting habit, ants usually nest where they start colonies (Dassou et al. 2017). Tree presence in all coffee plantations is the most important factor for ant nesting (Kuate et al. 2015).

Herbivore insects also did not affect ant diversity and abundance. We found 93 species and 553 individuals of herbivore insects from all locations. Orthoptera was the most abundant order, with 395 individuals. Herbivore insects can act as prey or trophobionts. Davidson et al. (2003) explained that ants could obtain nutrition from foraging or from their trophobionts. Every ant species has its own role in ecosystems such as predatory ants that usually interact with hemipteran trophobionts (Philpott and Armbrecht 2006). Due to predatory ants being grouped into specialist and generalist (Vieira and Hofer 1994; Hoenle et al. 2019), the diversity and abundance of ants, especially specialist predator, cannot be affected by the presence of herbivorous insects.

In this research, landscape composition had a relationship with the species richness and abundance of overall ants but had no effect on each stratum (canopy and ground-dwelling ants). The results are similar with the analysis by Marja et al. (2022) that landscape composition can enhance species richness and abundance of arthropods in agricultural landscapes, agroforestry was the most dominant class in almost all landscapes. Triyogo et al. (2020) showed that disturbed habitats (agroforestry) have greater ant diversity. Primary and secondary forests can hold high numbers of ant species (Solar et al. 2016) and increased forest area can increase ant diversity (Kuate et al. 2015). However, Philpott and Armbrecht (2006) explained that the agricultural intensification that occurred in coffee and cocoa plantations had a negative impact on the species richness of ants. Dauber et al. (2006) explained that sometimes more ant species are found in smaller areas than in larger areas. This proves that the increase in agroforestry areas can negatively impact ant diversity. In addition, natural habitats have no effect on ants in the coffee agroforestry system. The previous study also found the same pattern that area and patch number of agricultural lands are more affected by insect diversity than natural habitats (e.g., Ulina et al. 2019; Rizali et al. 2020).

In conclusion, this study has identified significant differences between a canopy and ground-dwelling ants. The abundance and species compositions of canopy and ground ants are different. Canopy ant diversity is only affected by tree age, while abundance is not affected by any variable. For ground-dwelling ants, abundance is only negatively affected by canopy cover. The species composition of ground-dwelling ants is also affected by pesticide application. Habitats in coffee plantations can affect ant communities, with ground-dwelling ants being more sensitive than canopy ants. Meanwhile, landscape composition can affect the species richness of all ants and not affect each stratum (canopy and ground-dwelling ants).

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