Sociobiology 66(4): 527-535 (December, 2019) DOI: 10.13102/sociobiology.v66i4.3743

Sociobiology
An international journal on social insects

RESEARCH ARTICLE - ANTS

Invasive Ants Affect Spatial Distribution Pattern and Diversity of Arboreal Ant Communities in Fruit Plantations, in Tarakan Island, Borneo

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Article History

Edited by
Gilberto M. M. Santos, UEFS, Brazil

Received	22 September 2018
Initial acceptance	11 November 2018
Final acceptance	10 November 2019
Publication date	30 December 2019

Keywords
Ants, plantation, invasive species, ant mosaic, species segregation

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Abstract

Human activities influence ant community structure. In tropical areas, the habitat characteristics of crop plantations frequently shape the structure of arboreal ant communities. The present study investigated the spatial distribution of arboreal ants dwelling in durian *Durio zibethinus* and citrus *Citrus amblycarpa* plantations in the Tarakan Island, North Kalimantan. Specifically, it was investigated whether ant communities are dominated by native or invasive species; and if ant arboreal mosaics occur. This study included two sites (A and C) comprising durian and citrus plantations and one site B with only citrus plantations. Ant workers dwelling on crop trees were collected by branch beating, and subsequently identified and counted. Across all sites, a total of 64,360 workers, from 22 ant species, were collected from 59 durian and 63 citrus trees. In site A, the invasive species *Tapinoma melanocephalum* and the native species *Oecophylla smaragdina* were numerically dominant. A null model analysis of species co-occurrence revealed that species segregation existed in this site. Conversely, in sites B and C the invasive species *T. melanocephalum* and *Technomyrmex albipes* were dominant, and native arboreal ants almost co-occurred with the two species. Moreover, the number of *T. melanocephalum* and *T. albipes* workers was negatively correlated with the species diversity index of arboreal ants. However, the number of *O. smaragdina* workers showed no significant correlation. The results suggest that the invasion and domination of non-native species dissasemble spatial structures and reduce the species diversity in arboreal ant communities. The community structures of arboreal ants in fruit plantations were varied, depending on the fruit species and the properties of dominant ants.

Introduction

Ants are an important ecological group both in natural and modified habitats (Hölldobler & Wilson, 1990; Lachet al., 2010). In tropical areas, their biomass and species diversity are much higher, leading to the formation of complexant community structures. Ant assemblages on forest canopies are suitable for exploring the factors influencing local community structures, species composition and richness, and spatial distribution (Yanoviak & Schnitzer, 2013). The canopies of individual trees are frequently isolated, functioning as a habitat island (Southwood & Kenedy, 1983; Harris, 1984; Adams et al., 2017). This is likely to limit the movement, resource use, and habitat preference of ant assemblages. Consequently, the habitat characteristics, tree species, tree size, and crown connectivity shape the structure of arboreal ant communities (Tschinkel & Hess, 1999; Ribas et al. 2003; Powell et al., 2011). Moreover, arboreal ants account for up to 90% of the arboreal insects' biomass, interacting with the other taxa and mediating a range of ecosystem processes (Davidson et al., 2003). Therefore, the community structures of arboreal ants strongly depend on the properties of the populations and communities of the taxa they interact with.

The community structure of arboreal ants is highly influenced by human activities (Morris, 2010). Simple forestry systems composed of a single or a few crop trees are

ISSN: 0361-6525

often invaded by non-native species, which tend to be more dominant than native species; this results in an increase in negative interactions (Sanders et al., 2003; Fayleet al., 2013). Additionally, in agricultural lands and disturbed secondary forests, the species composition and spatial distribution of arboreal ants frequently result in the formation of patterns that are referred to as ant mosaics. These are patchworks of territories dominated by different species that mutually exclude each other, and display nonrandom patterns of species co-occurrences (Majer et al., 1994; Jackson, 1984; Blüthgen & Stork, 2007; Rizali et al., 2008). The development of ant mosaic is catalyzed by two significant factors, namely interspecific competition, including resource use patterns, and dominant species territoriality (Room, 1975; Ribas & Schoereder, 2002). The existence of mosaic structures has been well-documented in plantations managed by farming activities, such as coffee, cacao, and cocoa farms, and palm oil plantations (Majer, 1976; 1992; Majeret al., 1994, Dejeanet al., 1997; Philpott, 2006; Fayle et al., 2013; Perfecto & Vandermeer, 2013). Pfeiffer et al. (2008) investigated palm oil plantations in the Borneo and Malay Peninsulas and found that ant mosaics were dominated by *Anoplolepis gracilipes*, *Technomyrmex albipes*, and *Oecophylla smaragdina*. In African cocoa plantations, *O. longinoda, Crematogaster* spp., and *Tetramorium maculeatum* are usually found and are usually found to be the most populous species among ant mosaics (Tadu et al., 2014).

The environmental condition in the plantations shape the peculiar structures of arboreal ant communities. However, the habitat characteristics of plantations differ among the planted crops, which differ in tree height, canopy area, crown connectivity, and other qualitative traits. Furthermore, the species composition of the herbivorous insects and arthropods using each crop as host plants is different. This leads to the difference in the ant communities interacting with them. The durian *Durio zibethinus* and citrus *Citrus amblycarpa* fruits are traditionally grown in the agroforestry systems of Indonesian Kalimantan (Siregar, 2006). To date, little is known about the communities of arboreal ants dwelling in the plantations of two these fruits. Moreover, in any fruit plantation in Kalimantan, it has been reported that ants monopolize the major part of the biomass in arboreal arthropods (Pfeiffer et al., 2008; Fayle et al., 2013; Diamé et al., 2017). However, Asfiya et al. (2015) suggested that intensive agroforestry practices promote the establishment of non-native ant species in the cocoa plantations of southeast Sulawesi. In the region of and Sulawesi and Indonesian Kalimantan, information on community structures of arboreal ants dwelling in plantations is currently lacking yet. The current study investigates the species composition and spatial distribution of arboreal ants in the plantations of durian and citrus fruits of the North Kalimantan area of Borneo. The following two topics were specifically investigated: (1) whether arboreal ant communities dwelling in the plantations of durian and citrus fruits are dominated by non-native species; and (2) whether ant mosaic structures occur in those communities. In addition, the effects of non-native species on the community structures were also investigated.

Materials and Methods

Study sites

Field research was conducted in the Tarakan Island of Borneo, Indonesia (Fig 1). Here, the monthly mean rainfall ranges from199 – 2008 mm^3. The mean annual temperature and humidity are 27.7 and 84%, respectively. Three plantation sites were selected (Fig 1): site A at Mamburungan (3°18’15’’N, 117°37’12’’E); site B at East Mamburungan (3°17’14’’N, 117°38’1’’E); and site C at Kampung Enam village (3°18’41’’N, 117°38’1’’E). The plantations at site A and C were established in open land where the densities of trees were relatively low. The plantation in site B was near to secondary forests. In the three plantations, we set up the study area (the area: 2.0 ha each) where many durian and citrus fruits were intensively planted. In site A and C, we selected 66 (durian: 44 and citrus: 22) and 30 (durian:15 and citrus: 15) trees as sampling trees, respectively (Table 1). Only 26 citrus trees were selected in site B. However, horticulture crops including included durians, citrus fruits, banana, mangoes, maize, cabbage, and other crops were planted and grown sporadically in all three sites. The horizontal positions of all selected trees were plotted on maps of each site by measuring the distribution within the study area. While the research was carried out farmers did not use the pesticide in the study area; however, weed killing and pest control were infrequently conducted with herbicides and insecticides.

Collection of arboreal ants on crop trees in studied sites

The collections of ants were conducted from March to September in 2016 and during March in 2017. On trees in the studied sites, 10 branches (length: 50-80 cm, diameter: 5-10 cm)

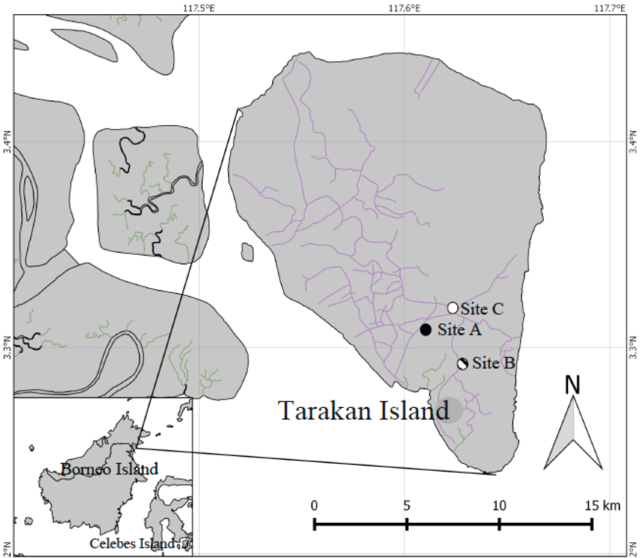

Fig 1. Location of the studied sites in the Tarakan Island of North Kalimantan.

Table 1. Collection data and characteristics of ant communities in three studied sites. As the index of diversity, the average pairwise niche overlap among species was shown.

Site	**A**	**B**	**C**
Area of studied site (ha)	2.0	2.0	2.0
Number of observed trees	66	26	30
Number of each crop species			
Durio zibethinus	44	0	15
Citrus amblycarpa	22	26	15
Collection data			
Species number of collected ants	22	21	15
Total number of collected ants	53461	7203	3696
Average of species number (/branch/tree)	11.3 ± 1.6	10.5 ± 2.1	3.9 ± 1.7
Range of species number	8-15	7-16	1-8
Average of collected number (/branch/tree)	810 ± 400.1	277 ± 89.2	123.2 ±83.8
Range of collected number	202-2202	120-561	14-309
Species diversity index			
Shannon-Wiener index (*H′*)	1.75	1.67	1.02
Overlap index			
Pianka index (*α*)	0.16	0.26	0.13
Czekanowski index	0.15	0.19	0.1

were selected and ants that were present on the branches were collected using the beating method. In addition, the number of ants walking on another 20 branches were also counted. The ant collection and counting were conducted 1-7 times in each site. All collected samples were stored in 99% ethanol and sorted in the laboratory. The species were identified using identification manuals and online resources i.e. Bolton (1997) and AntWeb.org (accessed on 2017). They were classified as belonging to one of the following three categories using information from databases: native species (N); invasive or tramp species (I); and unknown (U) (AntWeb, 2017; Pacific Invasive Ant Group, 2017; Antmaps, 2017).

Species collected in each site were classified as dominant species, if they met at least two the following criteria: (1) the collected number of workers was more than 5000 individuals in each site; (2) the frequency of collected workers was more than 25% of all collected workers in the site; and (3) there were polydomous nests in the sites (> 2 nests per tree were common finding). In site A, the territory ranges of colonies in dominant species were estimated by the observation of aggressiveness among workers. From each tree, 10 workers of each dominant species were collected. Workers from different trees were put into a transparent plastic container (the diameter: 40 mm, the depth: 25 mm) and the response among them was checked for 2-5 minutes. If they were mutually attacked by aggressive behavior, biting or pulling, they were regarded as members of different colonies. In one observation for a pair of trees, 10 replicates were conducted by using different 10 workers.

Statistical analyses

To analyze species composition and collection frequency in the sites, the average number of ant workers collected in one sample from one branch in each tree was calculated. The comparison of species diversity was evaluated using the Shannon-Wiener diversity index (*H′*) (Krebs, 1989). The degree of overlap among species in a tree was evaluated using the Pianka and Czekanowski niche overlap index (Pianka, 1973; Albrecht & Gotelli, 2001). Then, principal component analysis (PCA) was used to evaluate whether the ant communities were different among the sites or fruit trees. To confirm the existence of ant mosaics, we used C-scores as the metric to assess community-wide species co-occurrence (Gotelli, 2000; Pfeiffer et al., 2008; Fayle et al., 2013). In our study, C-score was the number of pairs of species and pairs of trees where each species occurs only once and two species occur at different trees. The higher the C-score, the greater the number of non-overlapping species distribution. Randomization of the original matrix was used to create the distribution of C-score expected under the null model which assumes random species co-occurrence. C-scores were simulated 1000 times randomly for the null model. Standardized effect sizes (SES) were calculated to evaluate the difference between the observed and expected C-scores. Positive and negative SES values indicate segregation between species and aggregation, respectively. The analyses were conducted using the Ecosim R function in the R package (Gotelli & Elison, 2013).

Results

From 2016 to 2017, 64,360 workers were collected from 59 durian and 63 citrus trees in the three sites (Table 1). They comprised of 22 species from 16 genera and five subfamilies (Table 2). The species composition was significantly different between the three sites (χ^2=22413.2, P<0.01, G-test). The average number of workers and species (in a branch per tree) was significantly different between the sites (collected number: $F_{2,119}$=17.5, P<0.001; species number: $F_{2,119}$=183.2, P<0.001, One-way ANOVA) and they were larger in site A than at other two sites. The species diversity in site A was also higher (Table 1). Workers of *T. melanocephalum, O. smaragdina* and *T. albipes* were the majority, with more than 60% of all catches in each site (Table 2). They usually monopolized the trees by nesting in branches and trees and building weaver nests on tree, therefore they were regarded as dominant species. Five species, *T. melanocephalum, T. albipes, Anoplolepis gracilipes, Iridomyrmex anceps,* and *Trichomyrmex destructor* were identified as invasive (Table 2). It is noteworthy that the workers of non-native species were collected in all sampled trees in all sites. Furthermore, more than 60% of all workers collected in each site were occupied by those of non-native species (site A: 74.5%, site B: 80.7%, site C: 66.1%). In particular, *T. melanocephalum* workers occupied more than 50% of trees in site A and B.

The PCA of the data collected from the 122 trees identified two main groups of ant communities with one group in site A and B and another group in site C, though the groups were not separated on the basis of the type of fruit trees from which the ants were collected. The first and second principal component explained only 11.6% and 8.3% of the variance of the communities respectively (Fig 2). The ant communities in site A and B were comprised of *Tapinoma melanocephalum*, *Oecophylla smaragdina*, and other subdominant ants, whereas the community in site C primarily comprised *Technomyrmex albipes*. The pattern identified by the PCA suggest that the habitats of *T. melanocephalum* and *T. albipes* tended to be separated, although *O. smaragdina* were coexisting with them.

Table 2. Species composition of ants collected in three studied sites. By the information of life history, they were classified with three groups: native species (N), invasive or tramp species (I), and unknown (U).

Subfamily	Species	Group	Site A		Site B		Site C	
			N	(%)	N	(%)	N	(%)
Ponerinae	*Ponera* sp. 1	N	4	0.01	1	0.01	0	0
Dolichoderinae	*Dolichoderus* sp. 1	U	2	0.001	2	0.03	8	0.2
	Iridomyrmex anceps	I	3771	7.1	371	5.2	64	0.2
	Philidris sp. 1	N	786	1.5	71	1.0	1	0.03
	Tapinoma melanocephalum	I	26808	50.5	4020	55.8	45	1.2
	Tapinoma sp. 1	U	288	0.5	45	0.6	30	0.8
	Technomyrmex albipes	I	3945	7.4	383	5.3	2363	63.9
Formicinae	*Anoplolepis gracilipes*	I	2325	4.4	697	9.7	11	0.3
	Oecophyllas smaragdina	N	8131	14.6	294	4.1	1033	27.9
	Camponotus sp. 1	N	57	0.1	7	0.1	1	0.03
	Polyrhachis sp. 1	N	29	0.05	47	0.7	8	0.21
Pseudomyrmicinae	*Tetraponera* sp. 1	N	325	0.6	66	0.9	8	0.21
	Tetraponera sp. 2	N	49	0.1	1	0.01	0	0
Myrmiciane	*Crematogaster sewardi*	N	2121	4.0	592	8.2	18	0.5
	Crematogaster sp. 1	N	806	1.5	65	0.9	48	1.3
	Crematogaster sp. 2	N	145	0.3	14	0.2	0	0
	Trichomyrmex destructor	I	2712	5.1	341	4.7	20	0.5
	Monomorium sp. 1	U	402	0.8	0	0	0	0
	Monomorium sp. 2	U	140	0.3	37	0.5	0	0
	Tetramorium sp. 1	U	586	1.1	119	1.7	38	1.0
	Tetramorium sp. 2	U	32	0.1	26	0.4	0	0
	Pheidole sp. 1	U	16	0.03	4	0.06	0	0

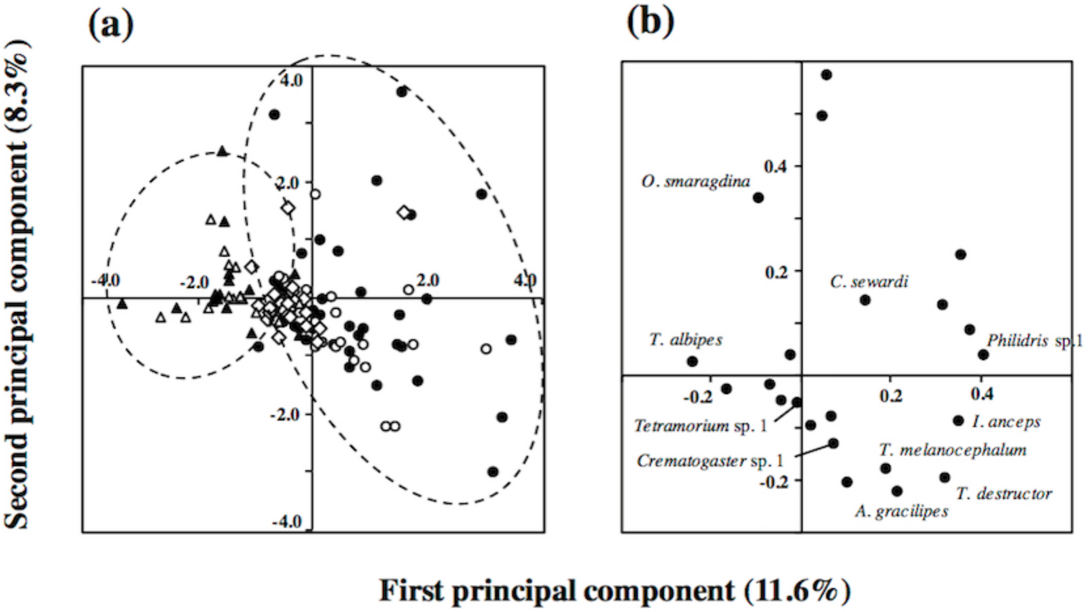

Fig 2. Biplot for the data of frequency and species composition of ants collected in 122 trees of three sites. (a) First and second principal components of ordinations of the trees. The circle, rhombus and triangle symbols represent site A, B, and C respectively. Black and white symbols mean durian and citrus trees. (b) The ordinations of the ant species. The names were shown in dominant and subdominant species of which the collection frequency was more than 1.0%.

Figure 3 shows the observed C-score index and frequency distribution of C-scores expected using null models in three studied sites. For site A, the observed C-score was significantly different from the mean value under null model (P<0.001, Table 3), i.e. species segregation was found in arboreal ant communities. In this site, two dominant species had multiple colonies (*T. melanocephalum*: six colonies, *O. smaragdina*: five colonies). Figure 4 shows the spatial distribution of territory ranges of the colonies. Within and among species, the distribution tended to be spatially segregated, though that certain large territories overlapped. Additionally, the average number (/branch/tree) of *T. melanocephalum* workers was negatively correlated with that of *O. smaragdina* workers (R^2=0.08, P<0.05). Probably, the two dominant species mutually avoid the overlap of territories. On the other hand, in site B and C, the observed C-scores were close to the mean values (Fig 3) and the differences were not significant (Table 3). Ant species in these two sites therefore co-occurred. Especially, the overlap index among species was highest in site B (Table 1).

Table 3. The observed C-scores(Obs.), mean metric values under null models (Mean null), standardized effect sizes (SES) and p-values (one-tailed t-test) for arboreal ant communities in three studied sites. Large C-score SES values indicate a greater degree of species segregation than would be expected at random.

Study site	C-score			
	Obs.	Mean null	SES	P
A	70.5	69.1	2.82	<0.001
B	10.4	10.2	1.23	0.11
C	15.8	15.7	0.24	0.37

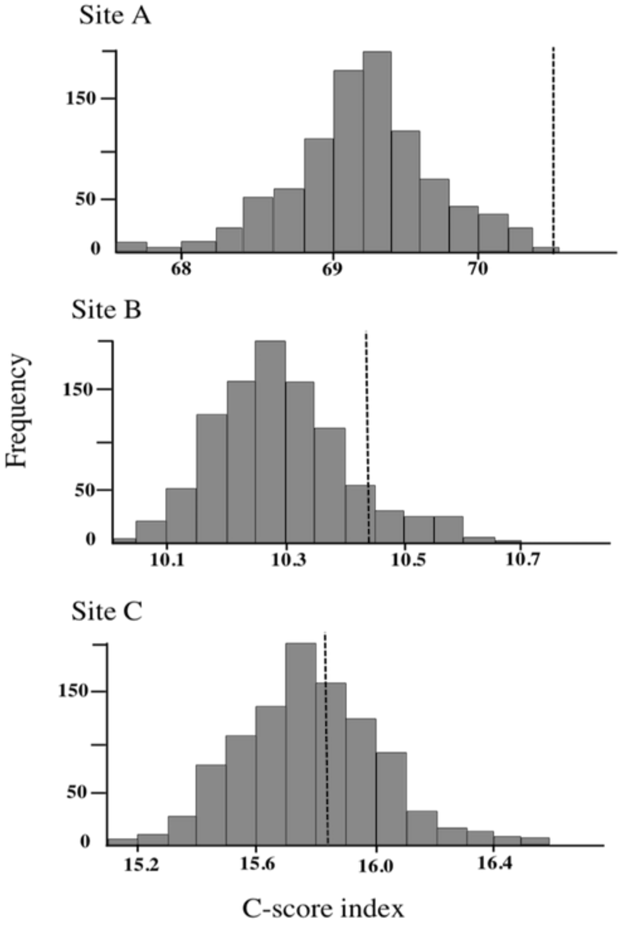

Fig 3. The observed C-score index (broken lines) and the frequency distributions of C-scores expected using null models in which there are no interactions between ant species for a tree in three studied sites. In site 1, the scores were significantly different (P<0.001, one-tailed t-test).

In the three sites, many trees were occupied by workers of a few dominant species. The average number (/branch/tree) of *T. melanocephalum* and *T. albipes* workers, both considered to be invasive and tramp species, was negatively correlated with the species diversity of arboreal ants at trees in all sites (Fig 5). However, the average number of *O. smaragdina* workers had no significant relationships, though it tends to be negatively correlated in site C. This suggests that the invasion and domination of non-native species reduces the number of ant species in trees and is associated with a reduction in species diversity of the arboreal ant community in fruit plantations.

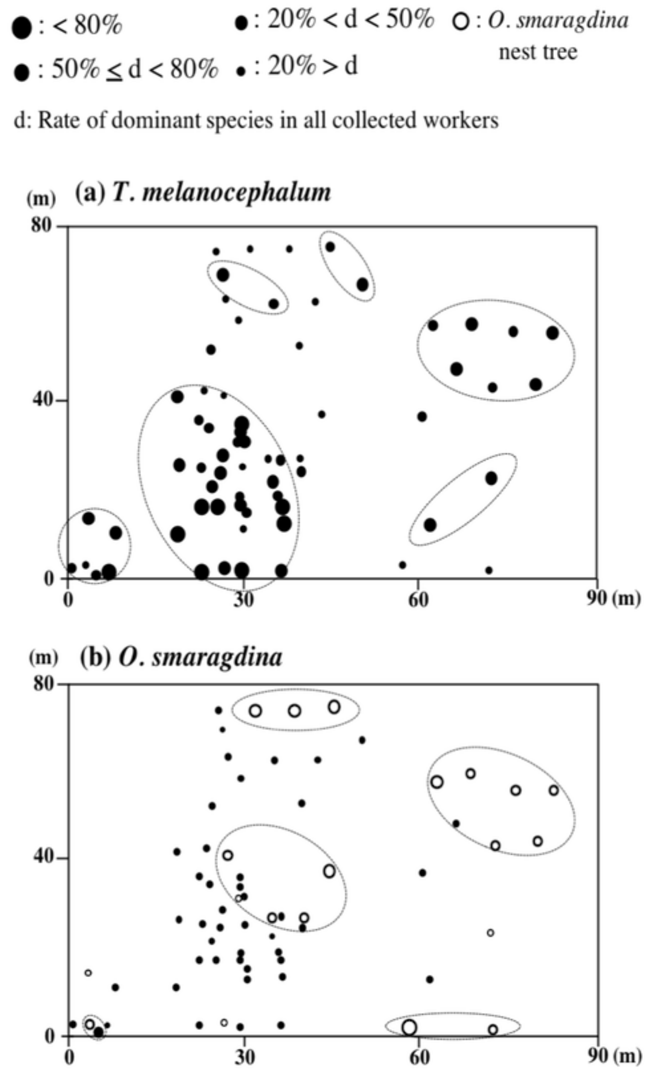

Fig 4. Spatial distribution of trees occupied by two dominant species, *T. melanocephalum* and *O. smaragdina* in site A. The symbol circle indicates fruit trees where ants were collected. Dotted line shows the territory ranges of colonies in each species.

Discussion

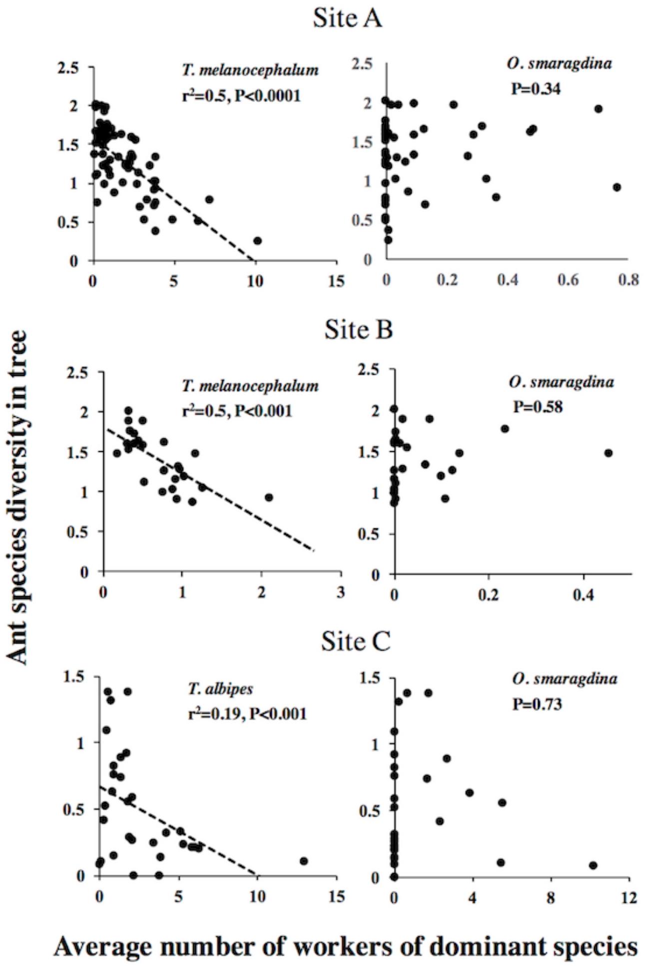

Fig 5. Relationships between average number of workers (/branch/tree) in dominant species and the species diversity of arboreal ants in tree. Species diversity is described as Shannon's diversity index.

The present study revealed the structure of arboreal ant communities in durian and citrus fruit plantations in Borneo. Ant communities were dominated three species, *T. melanocephalum, O. smaragdina* and *T. albipes,* which are also widespread in nearby natural forest and urban areas of Java, Celebes, and Kalimantan (Rizali et al., 2008; Rizali et al., 2011; Asfiya et al., 2015) as well as in other forests of southeast Asia (Pfeiffer et al., 2008; Elwood et al., 2016). The spatial distribution pattern of ants was different among three sites. The community structures of arboreal ants are varied, depending on the plantation conditions, micro environmenral factors, crop species and farming activities. Similar observations in other studies of plantations have also been made. Ribas and Schoereder (2002) tested whether 14 ant comunities in various crop plantations fit to the prediction of the ant mosaic model and showed the model to be valid in only about half of these cases.

In site A plantation, where *T. melanocephalum* and *O. smaragdina* were dominant, non-random spatial segregation was clear, suggesting that an ant mosaic may be present. In this site, the distribution of territory ranges in *T. melanocephalum* and *O. smaragdina* colonies were unlikely spatially overlapping. Probably, the species segregation may be due to the distribution pattern. Spatial distribution of arboreal ant assemblages is affected by several factors, including interspecific interactions and territoriality of dominant species. In general, invasive species including *T. melanocephalum* heavily impacts their enviroments as competitors on other ants (Holway et al., 2002; Dejean et al., 2010; Falcão et al., 2017). Also, *O. smaragdina* is aggressive towards other ant species, defining its territory over multiple trees (Hölldobler & Wilson, 1990; Van Mele, 2008; Devarajan, 2016; Diamé et al., 2017). The interspecific interations with territoriality may be one of the factors giving rise to the species segregation. However, the effects on other ant taxa was different between the two species. The increase of *O. smaragdina* workers did not reduce the species diversity of ants on trees. As a reason, native ants that act as subdominant species could defend overlapping territories in the same way as dominant species (Leston, 1973). The species segregation among dominant species and the interactions of *O. smaragdina* with other ants appear to lead to high diversity of arboreal ants in site A. It indicates that native ants acting as dominant species facilitate arboreal ant communities with high species diversity.

In contrast, species aggregation was observed in site B and C where *T. melanocephalum* and *T. albipes* were generally and numerically dominant. The aggregation of species could be due to several factors. First, the subordinate ant community could have disassembled by *T. melanocephalum* and *T. albipes*. In many of the trees in these sites, >90% of ants collected were either *T. melanocephalum* or *T. albipes*. These two species are dominnant and frequently exclude other species, particularly in disturbed habitats (Holway et al., 2002; Pfeiffer et al., 2008; Klimes et al., 2011). Moreover, it has been suggested that the presence of dominant competitors increases the randomness of co-occurance in the subordinate ant communities (Gotelli & Arnett 2000; Sanders et al., 2003; 2007). Such behaviour leads to weaker separation of ant species. Second, severe disturbance to ant habitats increases the degree of species segregation (Floren et al., 2001; Souza da Conceição et al., 2015). Particularly, the plantation in site B was established near the secondary forests and trees other than durian and citrus were present within and around the plantation. Therefore, it is possible that the native ant communities move to the canopies of other native trees, resulting in the random distribution of native ants in durian and citrus fruit tress. To confirm this, the spatial distribution of ant species on the canopies of the native trees should be investigated in this site. Third, the number of observed trees in site B and C may be insufficient for robust statistical analyses. The number of observed tress in site A, where spatial segregation was clearly observed, was more than twice that in theses sites. Ant populations from additional trees in site B and C should be further evaluated to increase statistical robustness. However, since the increase of *T. melanocephalum* and *T. albipes* workers had negative effects on species diversity of arboreal ant communities, this suggests that the invasion and domination of non-native species can disassemble the spatial structures and reduce species diversity of arboreal ant communities in these fruit plantation.

The structures of arboreal ant communities are different among the fruit plantations. The invasion of non-native species appear to have any negetive effects on the structures. It is known that arboreal ants have an important role on predation of herbivorous insects and other arthropods in the plantations. For example, *O. smaragdina* is a predator that negatively impacts other insect groups, including polllinators, herbivores and parasites (Tsuji et al., 2004; Tanga et al., 2016; Appiah et al., 2014; Migani et al., 2017). It is also reported that a few species of the genus *Crematogaster* are predators of herbivorous insects in plantations (Tanaka et al., 2012; Castracani et al., 2017). Our results indicate the interactions of arboreal ants with other insects are also affected by the invasion of non-native ant species and the change of the community structures. Information about the factors affecting ant community structures will be useful for the efficient management of agroforestry system.

Acknowledgments

This study was founded by BPPLN-RISTEKDIKTI scholarship of Indonesian Ministry of Research, Technology, and Higher Education. We are grateful to Muttaqien, Wisnu Ageng, Philipus, and other staffs of the Agriculture Faculty in Borneo Tarakan University and laboratory of Ecology in Kanazawa University. Cordial thanks to the owners of the plantations as studied sites. We also thank to the editor and two referees for their reviews and comments on our manuscript.

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