

## A comparison of ground-dwelling and arboreal ant assemblages (Hymenoptera: Formicidae) in lowland forests of Cambodia

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**Abstract.** This paper presents the first comprehensive description of the ant fauna of Cambodia, most of which has not yet been extensively surveyed. The aim was to investigate ground-dwelling and arboreal ant fauna in three types of lowland forest in Cambodia and assess the bioindicator value of ant communities along forest disturbance gradient. The ground ant fauna was sampled by Winkler extraction, and the arboreal ant fauna by time unit sampling. A total of 101 ant species belonging to 40 genera in nine subfamilies was collected. Of these species, 41 were collected in the community forest (CF; habitat with high disturbance), 52 in regrowth forest (RF), and 61 in natural (undisturbed) forest (NF). Although the total species richness hence declined with the level of disturbance, it did not differ significantly among the three forest types. A comparison between ground and arboreal fauna showed an overlap of nine species (22%) in CF, 4 spp. (8%) in RF, and 7 spp. (11%) in NF. Non-metric multi dimensional scaling revealed that the ground ant fauna in CF greatly differed from the ground ant fauna in both RF and NF, which were rather similar in their species composition. Conversely, the arboreal ant fauna in the CF differed less from the arboreal ant fauna in RF and NF sites. However, there was much a higher occurrence of invasive ant species in CF than in the other forest types. The results suggest that higher level of disturbance due to logging and inundation common in community forests affects more the ground than arboreal ant fauna. The high number of ant species collected, well-defined vertical stratification of their communities, and the relatively high species turnover along the forest disturbance gradient confirm the importance of Cambodian lowland forests for biodiversity conservation programs and of the ants as usable indicator animal group of the disturbance.

**Key words.** conservation, disturbance, vertical stratification, time unit sampling, Winkler extraction, species composition

### INTRODUCTION

In terms of biomass and abundance, ants are well represented in all tropical rainforest strata (Hölldobler & Wilson, 1990; Dunn et al., 2009; Weiser et al., 2010; Jenkins et al., 2013). Inventories of lowland tropical rainforests in Sabah, Malaysian Borneo, have shown that ants account for more than 50% of all arthropod individuals at each site (Floren & Linsenmair, 1997). Similarly Tsukamoto & Sabang (2005) investigated the soil macro-fauna in a lowland primary forest of Sarawak, Malaysian Borneo, and found that 39% of all invertebrate individuals were ants.

Numerous studies on ant diversity have been conducted in tropical Asia (e.g., Ito et al. [2001] in Java, Indonesia; Yamane et al. [2002] in northern Vietnam; Eguchi & Yamane [2003] in northwestern Borneo; Malsch et al.

[2003] in Pasoh, Peninsular Malaysia; Eguchi et al. [2004] in northern Vietnam; Jaitrong & Nabhitabhata [2005] in Thailand; Gunawardene et al. [2008] in Sri Lanka; Pfeiffer et al. [2011] in Borneo; Zryannin [2011] in southern Vietnam). However, the ant diversity of Cambodia has not been comprehensively investigated. Guénard et al. (2012) also suggested that Cambodia is one of the least explored countries for myrmecofauna in the world. Unfortunately, biodiversity surveys in Cambodia were disrupted from the time of the world war, until the termination of the Cambodian civil war in 1992, and for a long time, security risks and a lack of infrastructure have prevented access to most of the forest areas in Cambodia.

In his biogeographical analysis, Zryannin (2011) demonstrated that the ant fauna of Nam Cat Tien in southern Vietnam formed a cluster with the Indo-Malayan ant fauna from Bogor (E. Java), Poring, and Tawau (N. Borneo). Interestingly a similar pattern has been reported in butterfly assemblages from the Cardamom Mountains (Monastyrskii et al., 2011). These authors state that the southern regions of the Indochinese Peninsula, including Cambodia, are biogeographically interesting, having a strong relationship with the Sunda region in their insect species composition rather than with northern parts of Indochina. However, despite this biogeographical interest, ant fauna of Cambodia region remains understudied.

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While the majority of the primary forests in tropical Asia have been converted to monoculture plantations (e.g., rubber and oil palm), the primary forests of Cambodia have remained relatively unexploited. Indeed, more than 60 % of the country is covered by forests (Save Cambodia's Wildlife, 2006). In recent years, however, these pristine forests have come under threat from human activities, such as logging and commercial harvesting and plantations. Also, an increase in tourist activity (e.g., casinos and hotels) in the highland areas of Phnom Bokor National Park in southwestern Cambodia is threatening the natural habitats of several endemic plants and animal species (Mey, 2009; Hosoiishi et al., 2012). Consequently, the number of studies focusing on the development of sustainable biodiversity conservation initiatives is increasing (Hosoiishi et al., 2013; Toyama et al., 2015). These studies are considered to be particularly important as information on the faunal assemblages in unexplored countries can serve as practical data sources for forest conservation (Robertson, 2002; Deblauwe & Dekoninck, 2007; LaPolla et al., 2007).

Disturbance is generally considered to adversely affect ant community structure and reduce diversity (Vasconcelos, 1999; Kone et al., 2014; Kwon et al., 2014). Deforestation results in trees becoming sparser, causing the microhabitats on the ground to become drier and canopy trees to be widely separate from one another. All this may have a negative effect on leaf litter-associated and canopy ants. Examining more than one stratum will provide a more comprehensive understanding of forest dynamics and how these affect the ant fauna supported by the forest. Previous studies have shown that low species richness and evenness are typical for ground-foraging ant communities in disturbed forests (Brühl et al., 2003; Bickel & Watanasit, 2005; Fayle et al., 2010; but see Wang & Foster, 2015). Moreover, arboreal ants are known to be in particular affected negatively by forest disturbance, as the forest structure in logged and secondary forests is simplified compared to natural forests and offer thus less nesting microhabitats in the canopies (e.g. Pfeiffer et al., 2008; Fayle et al., 2010; Klimes et al., 2012). Both strata are endangered then by spread of invasive ant species, once forest is disturbed (Klimes et al., 2015). By intercepting solar radiation, trees reduce the amount of light that reaches the ground layer (Belsky & Amundson, 1992), which means that in open canopy habitats, such as logged forests and plantations, soil temperatures and potential evapotranspiration tend to be markedly higher than in closed-canopy forests. These characteristics make open-canopy habitats more stressful also for ground-dwelling ants, leading to a decrease in species richness and changes in community structure (Turner & Foster, 2006).

This study was undertaken to study for the first time the tropical forest ant communities of Cambodia along a forest disturbance gradient and assess their diversity and conservation value. We selected three forest types that have been subjected to varying levels of human disturbance, and sampled ants in both the ground and arboreal strata. In Cambodia, community forests (CF), regrowth forests (RF), and natural forests (NF) are all commonly found in the lowland of the country. The CF areas are most affected by

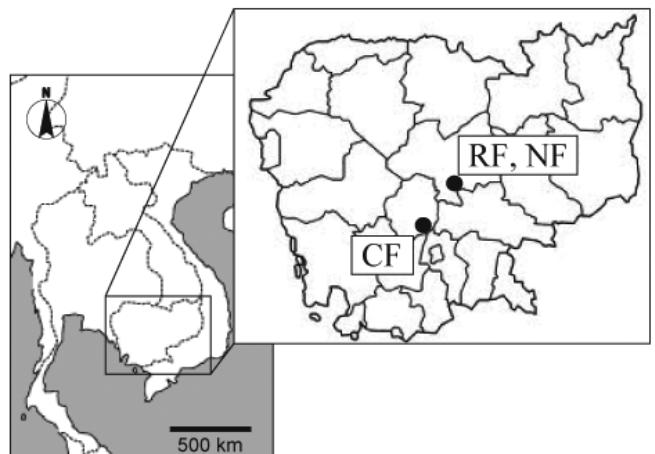


Fig. 1. Map of study sites in Kampong Chhnang and Kampong Thom Provinces, Cambodia. CF, community forest in Kampong Chhnang Province; RF, regrowth forest; NF, natural forest in Kampong Thom Province.

human disturbance, and RF areas are moderately disturbed. While the local people living in the vicinity of the CF areas use trees for fuel, they do not intensively use the RF areas for this purpose. The NF areas are not yet disturbed. The three forest types are dominated by evergreen tree species along with some deciduous trees such as *Dipterocarpus* spp. To better understand the characteristics of ground-dwelling and arboreal ants in Cambodia and their changes along the forest disturbance gradient, we compared ant species composition and dominant species among the three forest types. In addition, we present a preliminary survey of ant diversity and their species list in Cambodian forests in the hope that this information will facilitate future conservation initiatives that are undertaken in the country.

## MATERIAL AND METHODS

**Study sites.** The study was carried out in the three forest types in Cambodia: CF in Kampong Chhnang Province ( $11^{\circ}59'N$  and  $104^{\circ}44'E$ ), and RF ( $12^{\circ}38'N$  and  $105^{\circ}16'E$ ) and NF ( $12^{\circ}34'N$  and  $105^{\circ}23'E$ ) in Kampong Thom Province (Figs. 1, 2). The rainy season extends from May through October and the dry season from November through April, and the average annual precipitation and temperature are 1,700 mm and  $28^{\circ}C$ , respectively (Khun et al., 2008).

The three forest types are generally dominated by evergreen tree species, with deciduous trees such as *Dipterocarpus* spp. and *Shorea* spp. CF is most intensively affected by human disturbance as local people living in its neighbourhood use trees extensively for fuel, although they did not establish gardens there. RF consisted of forests that have regenerated after clearance for logging, shifting cultivation, or other activities, but did not contain yet high-canopy trees. NF consisted of undisturbed forests that are managed by the Cambodian Forestry Administration, supporting numerous large trees, including high-canopy trees. A total of 24 tree species have been recorded in the CF area, whereas 35 and 91 tree species occur in the RF and NF areas, respectively (Toyama et al., 2013). Generally, the forest floor of the CF

Table 1. Characteristics of community, regrowth and natural forests, showing their history of land use and vegetational characteristics at the time of the study. \*Data from Toyama et al (2013).

Study site	History of land use	Characteristics of the vegetation*	Tree species*
Community forest (CF)	Human exploitation	With a canopy height of 5.3–17.8 m	24 spp.
Regrowth forest (RF)	Abandoned after forest clearing	With a canopy height of 3.5–24.4 m	35 spp.
Natural forest (NF)	Natural	With a canopy height of 2.7–45.4 m	91 spp.



Fig. 2. Surveyed lowland forests of Cambodia. A, community forest in Kampong Chhnang Province; B, regrowth forest in Kampong Thom Province; C, natural forest in Kampong Thom Province.

area is covered with species of shrubs and weeds sparsely, which are abundant in RF and NF areas. The topography of the sampling sites in all the forest types is typically flat and the soil surface consists of sand and leaf litter. The CF area is normally flooded every year during the rainy season, but the RF and NF areas are not. Details of the study sites are given in Table 1.

**Ant sampling.** Ants were collected in the three forest types at the end of April and in mid-November of 2010. Three replicate sites were selected in each of the three forest types, with three transects (70 m × 10 m) established in each forest type to give a total of nine transects. Each transect had eight sampling points at 10 m intervals, and all transects were placed at a distance of at least 50 m from the forest edge to reduce edge effects.

This study focused on both ground-dwelling and arboreal ant communities and employed two kinds of sampling method. Ants on lower vegetation, hereafter called ‘arboreal ants’ for convenience’s sake, were hand-collected with forceps and an aspirator by time unit sampling method (modified from Ogata [2001]). This was performed for 15 min at a height of 0.5 to 2.0 m by searching for foraging ants on leaves and twigs, and repeated 8 times (once in each sampling point within transect, within 3 m around the point). The Winkler extraction method was used to collect ground-dwelling and cryptic ants. In each forest type eight samples of leaf litter (0.5 m × 0.5 m; top 3 cm soil layer) were collected at points at least 10 m apart from each other. The litter of each sample was sifted using a sieve with a mesh size of 6 × 6 mm and left for extraction in a mini Winkler apparatus for two days. A total of 72 time-unit samples from lower vegetation and 72 leaf litter samples were collected from the nine transects.

It should be noted that ‘arboreal ants’ term in this study is used for simplicity for all ants sampled by the time-unit method (on vegetation), although the samples sometimes also include ground-nesting species (e.g., *Camponotus rufoglaucus* and *Polyrhachis illaudata*) that are foraging on lower vegetation and vice-versa. Similarly, the ‘ground-dwelling ants’ category is solely used for ants collected by Winkler extractions. All of the specimens were keyed to genus (Bolton, 1994) and identified to species where possible using revisional papers (e.g., Bolton, 2000). Unidentified specimens (morphospecies) were given species codes (sp. 1, sp. 48 of SKY, etc.). Voucher specimens of all taxa are deposited at the Institute of Tropical Agriculture, Kyushu University, Japan.

**Data analysis.** Differences in species richness between the three forest types were compared by analysis of variance (ANOVA). Multivariate analyses were also conducted to detect differences of species composition in ant assemblages among the three forest types by non-metric multi-dimensional scaling (NMDS) performed using the PRIMER v6 (Clarke & Gorley, 2006). All NMDS ordinations were performed on a Jaccard index based on presence/absence data, which is employed widely in multivariate analysis of biological assemblage data. The NMDS algorithm attempts to place data points in a coordinate system in which the ranked distances are preserved. Since this method makes no assumptions and does not assume a linear relationship among variables, it is well suited for the analysis of non-normal data.

An analysis of similarity (ANOSIM) was then used to test whether the ant assemblage composition differed significantly among the three forest types. ANOSIM uses non-parametric permutation procedures applied to Jaccard similarity matrices based on rank similarities between samples. ANOSIM returns

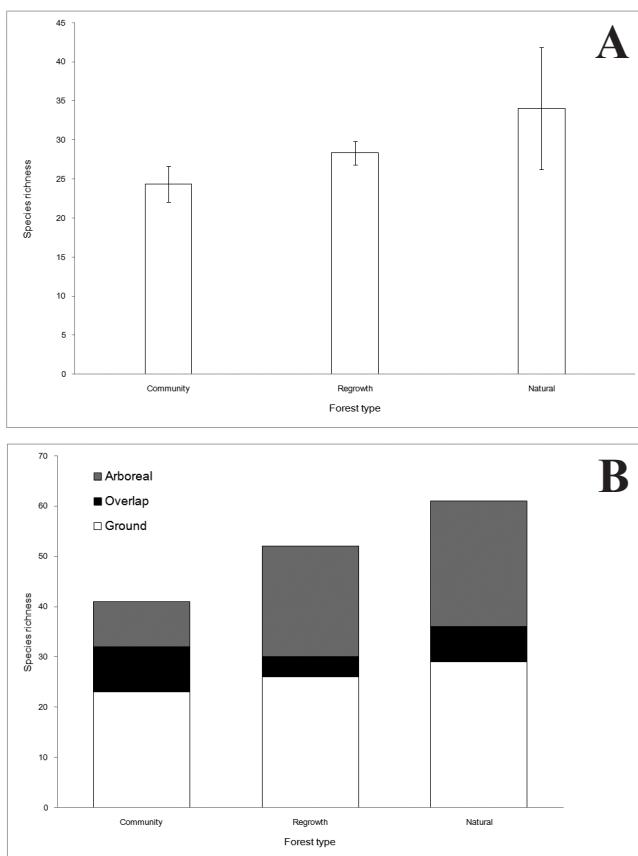


Fig. 3. A, Mean species richness (with S.D.) of ants per transect in community, regrowth and natural forests; B, Species richness in community, regrowth and natural forests of Cambodia. The dark band indicates the number of overlapping species between ground and arboreal samples.

a global R-static, which is an absolute distance measure among samples.

## RESULTS

A total of 101 ant species belonging to 40 genera in nine subfamilies was collected in the three forest types (Table 2). In terms of species number, the subfamily Myrmicinae was the best represented (45 spp. of 101 species), followed by the subfamilies Formicinae (27 spp.), Dolichoderinae (8 spp.), Ponerinae (7 spp.), and others (14 spp.). The most speciose genus was *Camponotus* with 11 species (11% of total), followed by *Carebara* with 8 spp. (8%), *Crematogaster* with 8 spp. (8%), *Tetramorium* with 8 spp. (8%), and *Pheidole* with 7 spp. (7%). Forty-one species were found in CF, 52 in RF, and 61 in NF, respectively. However, the total species richness per transect did not differ significantly among the three forest types (ANOVA, d.f.=2, 6;  $F=3.092$ ,  $P=0.119$ ) (Fig. 3A).

A comparison of the numbers of ground and arboreal species within different forest types showed that there was an overlap of 22% (9 spp.) in CF, 8% (4 spp.) in RF, and 11% (7 spp.) in NF (Fig. 3B).

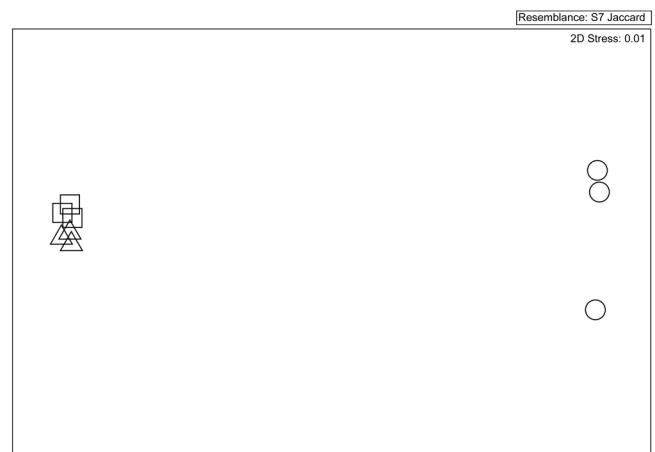


Fig. 4. Non-metric multidimensional scaling ordination for ground-dwelling ants in community forest (Kampong Chhnang), regrowth and natural forests (Kampong Thom). Circle: ground samples in community forest; triangle: ground samples in regrowth forest; square: ground samples in natural forest.

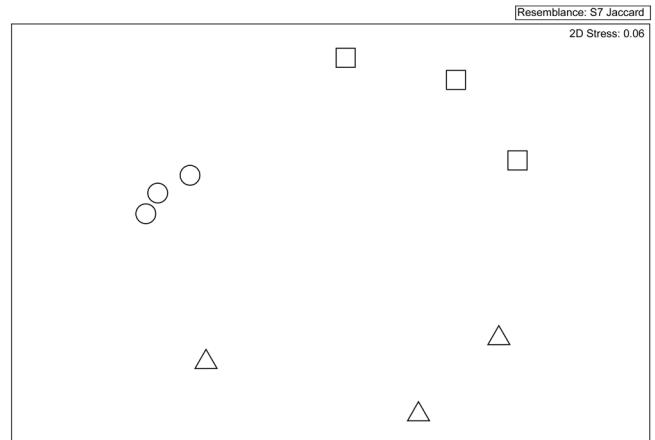


Fig. 5. Non-metric multidimensional scaling ordination for arboreal ants in community forest (Kampong Chhnang), regrowth and natural forests (Kampong Thom). Circle: arboreal samples in community forest; triangle: arboreal samples in regrowth forest; square: arboreal samples in natural forest.

Non-metric multi dimensional scaling showed that the ground-dwelling ant fauna differed among CF forest type and all other sites, while RF and NF aggregated together in the multivariate analysis (Fig. 4). By contrast, the arboreal ant fauna differed considerably between each forest type and also among sites within each forest type, with sites within both NF and RF more different from each other than those in CF (Fig. 5).

Overall, there was a significant difference in ant assemblage composition among the three forest types using ANOSIM (Global  $R=0.71$ ,  $P=0.001$ ), with the CF assemblage differing from RF and NF assemblages ( $R=0.815$ ,  $P=0.01$ ;  $R=0.981$ ,  $P=0.01$  for CF vs. RF, NF, respectively), and the RF assemblage differing slightly from NF ( $R=0.435$ ,  $P=0.06$ ). However, we could not find a significant difference when comparing ground or arboreal communities separately.

Table 2. Abundance (n=24) of ant species collected by Winkler extractions (ground-dwelling ants) and time unit sampling (arboreal ants). CFar: arboreal samples in community forest; CFgr: ground samples in community forest; RFar: arboreal samples in regrowth forest; RFgr: ground samples in regrowth forest; NFar: arboreal samples in natural forest; NFgr: ground samples in natural forest. \* indicates the invasive species.

Species	CFgr	CFar	RFgr	RFar	NFgr	NFar
AMBLYOPONINAE						
<i>Stigmatomma</i> sp. 1	1				1	
<i>Stigmatomma</i> sp. 2			1			
CERAPACHYINAE						
<i>Cerapachys</i> sp. 1					1	
<i>Cerapachys</i> sp. 2					2	
DOLICHODERINAE						
<i>Dolichoderus sulcaticaps</i> (sp. 9 of SKY)					4	
<i>Dolichoderus</i> sp.					1	
<i>Philidris</i> sp.			5	14	6	14
<i>Tapinoma melanocephalum</i> *	9	2				3
<i>Technomyrmex albipes</i> *						1
<i>Technomyrmex elatior</i>	5	3		2		
<i>Technomyrmex horni</i>	3		1		5	1
<i>Technomyrmex pratensis</i>			2			
ECTATOMMINAE						
<i>Gnamptogenys bicolor</i>					1	2
<i>Gnamptogenys binghamii</i>	1		1			
FORMICINAE						
<i>Acropyga butteli</i>	1		3			
<i>Anoplolepis gracilipes</i> *	1	5		2		2
<i>Camponotus rufoglaucus</i>		1		1		
<i>Camponotus</i> sp. 1		2				
<i>Camponotus</i> sp. 2				2		
<i>Camponotus</i> sp. 3				2		
<i>Camponotus</i> sp. 4				3		
<i>Camponotus</i> sp. 5						2
<i>Camponotus</i> sp. 6						1
<i>Camponotus</i> sp. 7						3
<i>Camponotus</i> sp. 8				1		
<i>Camponotus</i> sp. 9				1		
<i>Camponotus</i> sp. 48 of SKY	1				1	
<i>Lepisiota</i> sp. 1						2
<i>Lepisiota</i> sp. 2				3		
<i>Nylanderia</i> sp. 1	1	5			2	
<i>Nylanderia</i> sp. 2			4			
<i>Nylanderia</i> sp. 3			11		2	
<i>Oecophylla smaragdina</i>		19		4		1
<i>Paraparatrechina</i> sp.	2					
<i>Paratrechina longicornis</i> *					1	3
<i>Plagiolepis</i> sp. 1 of SKY	7					1
<i>Plagiolepis</i> sp.		4				
<i>Polyrhachis armata</i>				7		4
<i>Polyrhachis ilaudata</i>				6		7
<i>Polyrhachis laevissima</i>				2		
<i>Polyrhachis tibialis</i>						1
<i>Pseudolasius</i> sp.		2				

Species	CFgr	CFar	RFgr	RFar	NFgr	NFar
MYRMICINAE						
<i>Carebara</i> sp. 1	1		2		5	
<i>Carebara</i> sp. 3		3				
<i>Carebara</i> sp. 5			3		2	
<i>Carebara</i> sp. 6					1	
<i>Carebara</i> sp. 7					1	
<i>Carebara</i> sp. 8					1	
<i>Carebara</i> sp. 9			13		16	
<i>Carebara</i> sp. 10					3	
<i>Cataulacus granulatus</i>	1	8		2		3
<i>Crematogaster aurita</i>				2		
<i>Crematogaster biroi quadriruga</i>						1
<i>Crematogaster modiglianii</i>						16
<i>Crematogaster ferrarii</i>	3	19		11		1
<i>Crematogaster</i> sp. 1		10		8		1
<i>Crematogaster</i> sp. 2	1	13		2		5
<i>Crematogaster</i> sp. 3		5				1
<i>Crematogaster</i> sp. 4				3		
<i>Dilobocondyla</i> sp.				1		
<i>Lophomyrmex</i> sp.			2		11	5
<i>Monomorium</i> cf. <i>floricola</i> *		1				
<i>Monomorium pharaonis</i> *	6	1				
<i>Monomorium</i> sp.				1		
<i>Myrmecina</i> sp.						1
<i>Pheidole rabo</i>	1		1		5	
<i>Pheidole</i> sp. eg-94	4		1		8	1
<i>Pheidole</i> cf. sp. eg-111			1		3	
<i>Pheidole</i> sp. eg-141	2		1	1	3	4
<i>Pheidole</i> sp. 1					1	
<i>Pheidole</i> sp. 2					1	
<i>Pheidole</i> sp. 3			2	1		
<i>Proatta</i> sp.			3		1	
<i>Strumigenys feae</i> (sp. 44 of SKY)	7		7		11	
<i>Strumigenys</i> sp. 1			3			
<i>Strumigenys</i> sp. 2			2		1	
<i>Strumigenys</i> sp. 55 of SKY	1		1			
<i>Syllophopsis sechellensis</i>	12		3		3	
<i>Tetramorium aptum</i>	2					
<i>Tetramorium flavipes</i>	1					
<i>Tetramorium kraepelini</i>					1	
<i>Tetramorium scabro</i> group	2					
<i>Tetramorium</i> sp. 1	1					
<i>Tetramorium</i> sp. 2			4		11	
<i>Tetramorium</i> sp. 3			9		4	
<i>Tetramorium</i> sp. 63 of SKY	7					
<i>Trichomyrmex destructor</i> *	2					
PONERINAE						
<i>Anochetus graeffei</i> complex	4					
<i>Diacamma</i> sp.						3
<i>Ectomomyrmex</i> sp.			2		4	
<i>Euponera</i> sp.	1					
<i>Hypoponera</i> sp. 2 of SKY	7		7		11	
<i>Hypoponera</i> sp. 48 of SKY			5	1	5	
<i>Odontoponera denticulata</i>			2			1
PROCERATIINAE						
<i>Probolomyrmex vietii</i>	1					
<i>Probolomyrmex</i> sp.					1	

Species	CFgr	CFar	RFgr	RFar	NFgr	NFar
PSEUDOMYRMECINAE						
<i>Tetraponera allaborans</i>	1	6				
<i>Tetraponera extenuata</i>						1
<i>Tetraponera near attenuata</i>						1
<i>Tetraponera nitida</i>		8				
<i>Tetraponera</i> sp. 1				1		
Total number of species richness	33	18	30	26	36	32
Totals of ground plus arboreal ants		41		52		61

## DISCUSSION

This is the most comprehensive study of the ant fauna conducted up today in the lowland forests of Cambodia to our best knowledge. Although species richness did not differ significantly among the three forest types in our study, the composition varied greatly, especially between CF and undisturbed forests (RF, NF) for ground ants, and within RF and NF for arboreal ants. The region has a highly diverse ant fauna, and the undisturbed forests have greater ant diversity than disturbed forest, with the greater diversity being greatly attributable to many uncommon species.

**Ground-dwelling versus arboreal ant communities.** The NMDS ordination (Fig. 4) showed that the ground-dwelling ant communities in the RF and NF sites were more similar to each other than to the communities in the CF sites. The RF and NF communities showed less spatial variation and were closer than the communities in CF. There may be the higher difference in ground ant fauna at CF sites, may be due to the incidence of logging and inundation in this forest type, which are both higher than at the other two forest types. Also it may be due to higher proportion of invasive ant species in CF sites (54% of all 48 samples) (4% in RF; 21% in NF) (Table 2). In the CF forest sites, rainfall washes away the soil in the rainy season, causing severe damage to the nesting sites of ants. Conversely, the abundant leaf litter in RF and NF would have an effect of reducing soil erosion. Previous studies have shown that inundation affects ground ant fauna more strongly than arboreal ant fauna (Deblauwe & Dekoninck, 2007). For example, Wilson (1987) found a considerable reduction in ant species richness in an inundated area in Peru. Majer & Delabie (1994) also showed that soil-, litter- and shrub-associated species in the Brazilian Amazon were most strongly affected by inundation, whereas tree-foraging ants were not affected. The slightly higher difference then between CF forest sites appears to be influenced by the rare species. In contrast, the ground-dwelling ant fauna at both RF and NF sites had a similar species composition and high degree of species overlap. It may not be only due to the site proximity, and may be because the lower incidence of disturbance in those forest types allows for such a strikingly similar ground-dwelling species composition.

Some leaf litter-associated genera, e.g., *Carebara* and *Strumigenys*, were found in our samples. The RF and NF sites generally showed higher numbers of these species

than the CF sites, suggesting that the RF and NF sites have abundant leaf litter, fertile soil and stable conditions to host these small-body-sized and typically leaf-litter nesting taxa.

Unlike the ground fauna, arboreal ant fauna exhibited different composition patterns (Fig. 5). For example, the arboreal ant communities in CF sites have a higher similarity in species composition among the three sites sampled than found in the RF and NF communities, which were more scattered in the NMDS ordination. The higher variance among transects observed in RF and NF arboreal ant fauna may have been due to less frequent logging and higher number of tree species, which may permit establishment of certain rare arboreal ants at each site. Logging reduces the number of large trees and increases the abundance of shrubs, which generally have the effect of reducing the number of ant species, changing species composition (Widodo et al., 2004), and affecting the trophic structure (Woodcock et al., 2013). The lack of large trees and suitable arboreal nest sites can have especially negative effect on arboreal ants (Fayle et al., 2010; Klimes et al., 2012). Compared to contiguous forests, isolated trees are characterised by the absence of specialised arboreal species (Gove et al., 2009). Ant species diversity is typically much higher in primary forests than it is in secondary forests or highly disturbed forests and plantations (Vasconcelos, 1999; Hashimoto & Maryati, 2011; Klimes et al., 2012). Although the reason for the relatively higher species diversity in primary forests has been attributed in most of the studies simply to a high correlation of ant species richness with tree species richness (e.g. Ribas et al., 2003; Gunawardene et al., 2012), recently more careful studies suggested that rather structural diversity of suitable nest sites or other factors as seasonal and decomposition processes are main drivers of ant diversity in tropical forests (Donoso et al., 2010; Klimes et al., 2012; Sakchoowong et al., 2015).

**Vertical stratification of ants.** Although this study did not aim to show general pattern of vertical stratification, as we did not sample tree canopies and/or ant nests specifically, relatively high differences were still observed in the vertical distributions of ant assemblages in the three forest types among the forest floor and understorey sampling (Fig. 3A). A high percentage of species (92% in RF and 89% in NF), was restricted only to one of the two strata in RF and NF forests; however, this percentage was relatively lower (78%) in CF. Although we did not have sufficient data to explain this disparity, the forest structure (tree height, nest sites,

tree species) is considered to be an important factor and this may correspond to smaller canopies and less diverse plant communities in community forests in our study (Table 1).

Similar findings of high stratification of ants have been reported in primary rainforests of the tropics (Longino & Nadkarni, 1990; Itino & Yamane, 1995; Brühl et al., 1998; Yanoviak & Kaspari, 2000; Hashimoto et al., 2006; Vasconcelos & Vilhena, 2006). Brühl et al. (1998) collected ants from three strata in Bornean forests, i.e., leaf litter, lower vegetation, and canopy. Their results showed that the majority of species (ca. 75%) were restricted to each stratum. Longino & Nadkarni (1990) compared the ant fauna of leaf litter on the forest floor and in the epiphyte mats in the canopy of Costa Rican forests. They found that 33 species (62%) were restricted to one stratum out of a total of 53 species examined. Our results from the three forest types appeared to corroborate the findings of these previous studies. Although our study sites and sampling strata differed from theirs, the findings of the present study suggest that the well-preserved forests are characterised by well-defined stratification of ants.

**Ant fauna in this study compared to neighbouring areas.** Several of the myrmecological studies conducted in other regions of the Indochinese Peninsula have produced lists of observed species. Faunal surveys of ants in neighbouring regions have reported a total of 272 species (68 genera) from Nam Cat Tien in southern Vietnam in March–June 2007 and January–November 2008 (Zryanin, 2011). In northern Vietnam, Yamane et al. (2002) collected 160 species (50 genera) from Cuc Phuong National Park in August 1998 and November 2001; Eguchi et al. (2004) collected 218 species (56 genera) from Ba Vi and Tam Dao during the years 1998–2002. The differences in the number species between this study and previous ones can be attributed to differences in the survey intensity and sampling methods. Our results were based on collection efforts spanning two weeks by one or two investigators. All of our samples were collected using standardised protocols for time unit sampling and Winkler extractions from quadrates of the same size. However, relatively small number of samples and transects we explored may contribute, why we did not find significant difference in community composition among forest types once the two strata were analysed separately (Figs. 4, 5).

In the three aforementioned studies, *Polyrhachis*, *Camponotus* and *Pheidole* were the most species-rich genera in Nam Cat Tien (Zryanin, 2011); *Leptogenys*, *Pheidole*, and *Camponotus* in Cuc Phuong (Yamane et al., 2002); and *Pheidole*, *Camponotus*, and *Leptogenys* in Ba Vi and Tam Dao (Eguchi et al., 2004). Our results also showed that *Camponotus* and *Pheidole* were the dominant genera and the absence of *Leptogenys* in our collections is likely due to our sampling methods. While Winkler extractions are often effective for collecting small cryptic species in leaf litter and soil, the method can be less effective for collecting large and active ant species such as *Leptogenys*. Similarly, our hand-collecting from vegetation might subsample e.g., small-bodied and cryptically-nesting species in twigs and

those restricted to the high canopy (e.g., Widodo et al. 2004; Klimes et al. 2015). The results presented here were thus partly affected by the limited methods used to collect ants. Further studies using additional collection methods, e.g., underground bait trapping, soil sifting, bait traps, and pitfall trapping, are considered necessary in order to obtain a more complete picture of the ant fauna in Cambodian lowland forests.

**Conservation implications.** The plant and animal biodiversity studies that have been conducted in recent years in Cambodia have been refined over time (Daltry & Momberg, 2000; Grismer et al., 2010; Toyama et al., 2013; Naiki et al., 2015), and many of these studies have provided useful checklists of species and descriptions of new species. However, of the Cambodian fauna studied to date, with the exception of several early taxonomic studies and isolated species descriptions (e.g. Fromantin & Soulié, 1961), the ants of Cambodia have received a little attention. Indeed, according to Guénard et al. (2012), Cambodia is one of the most unexplored countries in terms of its ant fauna. This study is the first necessary step toward providing a foundation for categorising the ant fauna of Cambodia at the genus level.

Faunal lists of ants do not only indicate the species names and the number of species, but they can also be used to infer the characteristics of the fauna. Several of the species collected in this study are also known in the neighbouring regions, e.g., *Hypoponera* sp. 2 of SKY is widely known from northern Vietnam (Yamane et al., 2002) and Borneo (Eguchi & Yamane, 2003). The collation of such data over the long term and the future work on taxonomy of those species which we were able to assign in this stage only to morphospecies names, will contribute to improvements in both taxonomic and biodiversity assessments of the fauna in these areas. It is possible that Cambodia is an integral part of the “Green Corridor” connecting the tropical rain forests in Southeast Asia with temperate deciduous forests in East Asia. Evidence for this connection may become more apparent as more unique taxa are discovered in the region. For example, several interesting *Crematogaster* species have been collected and new ant species from Cambodia, including new ant species described by Hosoihi & Ogata (2014), as well as lizards (Grismer et al., 2010), pitcher plants (Mey, 2009), and vascular plants (Naiki et al., 2015; Tagane et al., 2015). Much of the extensive area of Cambodia has yet to be surveyed for ants and other organisms. It is hoped that the information presented here will provide the foundation for a useful data set for biodiversity conservation planning in Cambodia.

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## LITERATURE CITED

Belsky AJ & Amundson RG (1992) Effects of trees on understory vegetation and soils at forest-savanna boundaries in East Africa. In: Furley PA, Proctor J & Ratter JA (eds.) *Nature and Dynamics of Forest-Savanna Boundaries*. Chapman and Hall, London. Pp. 353–365.

Bickel TO & Watanasit S (2005) Diversity of leaf litter ant communities in Ton Nga Chang Wildlife Sanctuary and nearby rubber plantation, Songkhla, Southern Thailand. *Songklanakarin Journal of Science & Technology*, 27: 943–955.

Bolton B (1994) *Identification Guide to the Ant Genera of the World*. Harvard University Press, Cambridge, USA, 232 pp.

Bolton B (2000) The ant tribe Dacetini. *Memoirs of the American Entomological Institute*, 65: 1–1028.

Brühl CA, Gunsalam G & Linsenmair KE (1998) Stratification of ants (Hymenoptera, Formicidae) in a primary rain forest in Sabah, Borneo. *Journal of Tropical Ecology*, 14: 285–297.

Brühl CA, Eltz T & Linsenmair KE (2003) Size does matter—effects of tropical rainforest fragmentation on the leaf litter ant community in Sabah, Malaysia. *Biodiversity and Conservation*, 12: 1371–1389.

Clarke KR & Gorley RN (2006) PRIMER V6: User Manual/Tutorial. PRIMER-E, Plymouth Marine Laboratory, Plymouth, 190 pp.

Daltry JC & Momberg F (eds.) (2000) *Cardamom Mountains Biodiversity Survey 2000*. Fauna and Flora International, Cambridge, UK, 252 pp.

Deblauwe I & Dekoninck W (2007) Diversity and distribution of ground-dwelling ants in a lowland rainforest in southeast Cameroon. *Insectes Sociaux*, 54: 334–342.

Donoso DA, Johnston MK & Kaspari M (2010) Trees as templates for tropical litter arthropod diversity. *Oecologia*, 164: 201–211.

Dunn RR, Agosti D, Andersen AN, Arnan X, Brühl CA, Cerdá X, Ellison AM, Fisher BL, Fitzpatrick MC, Gibb H, Gotelli NJ, Gove AD, Guénard B, Janda M, Kaspari M, Laurent EJ, Lessard JP, Longino JT, Majer JD, Menke SB, McGlynn TP, Parr CL, Philpott SM, Pfeiffer M, Retana J, Suarez AV, Vaconcelos HL, Weiser MD & Sanders NJ (2009) Climatic drivers of hemispheric asymmetry in global patterns of ant species richness. *Ecology Letters*, 12: 324–333.

Eguchi K, Bui TV, Yamane Sk, Okido H & Ogata K (2004) Ant faunas of Ba Vi and Tam Dao, North Vietnam (Insecta: Hymenoptera: Formicidae). *Bulletin of the Institute of Tropical Agriculture, Kyushu University*, 27: 77–98.

Eguchi K & Yamane S (2003) Species diversity of ants (Hymenoptera, Formicidae) in a lowland rainforest, Northwestern Borneo. *New Entomologist*, 52: 49–59.

Fayle TM, Turner EC, Snaddon JL, Chey VK, Chung AYC, Eggleton P & Foster WA (2010) Oil palm expansion into rain forest greatly reduces ant biodiversity in canopy, epiphytes and leaf-litter. *Basic Applied Ecology*, 11: 337–345.

Floren A & Linsenmair KE (1997) Diversity and recolonization dynamics of selected arthropod groups on different tree species in a lowland rainforest in Sabah, Malaysia with special reference to Formicidae. In: Stork NE, Adis J & Didham RK (eds.) *Canopy Arthropods*. Chapman and Hall, London. Pp. 344–381.

Fromantin J & Soulié J (1961) Notes systématiques sur le genre *Cremastogaster* avec description de trois espèces nouvelles du Cambodge (Hymenoptera Formicoidea). *Bulletin de la Société d'Histoire Naturelle de Toulouse*, 96: 87–112.

Gove AD, Majer JD & Rico-Gray V (2009) Ant assemblages in isolated trees are more sensitive to species loss and replacement than their woodland counterparts. *Basic and Applied Ecology*, 10: 187–195.

Grismer JL, Grismer LL & Chav T (2010) New species of *Cnemaspis* Strauch 1887 (Squamata: Gekkonidae) from southwestern Cambodia. *Journal of Herpetology*, 44: 28–36.

Guénard B, Weiser MD & Dunn RR (2012) Global models of ant diversity suggest regions where new discoveries are most likely are under disproportionate deforestation threat. *Proceedings of the National Academy of Sciences*, 109: 7368–7373.

Gunawardene NR, Majer JD & Edirisinghe JP (2008) Diversity and richness of ant species in a lowland wet forest reserve in Sri Lanka. *Asian Myrmecology*, 2: 71–83.

Gunawardene NR, Majer JD & Edirisinghe JP (2012) Correlates of ant (Hymenoptera: Formicidae) and tree species diversity in Sri Lanka. *Myrmecological News*, 17: 81–90.

Hashimoto Y & Maryati M (2011) Ground-dwelling ant diversity in Maliau Basin, Borneo: Evaluation of hand-sorting methods to estimate ant diversity. *Tropics*, 19: 85–92.

Hashimoto Y, Morimoto Y, Widodo ES & Maryati M (2006) Vertical distribution pattern of ants in a Bornean tropical rainforest (Hymenoptera: Formicidae). *Sociobiology*, 47: 697–710.

Hosoishi S, Le Ngoc A, Yamane SK, Ogata K (2013) Ant diversity in rubber plantations (*Hevea brasiliensis*) of Cambodia. *Asian Myrmecology*, 5: 69–77.

Hosoishi S & Ogata K (2014) Description and DNA barcoding of *Crematogaster fraxatrix* Forel, 1911 and two new closely related species from Cambodia and Indonesia (Hymenoptera: Formicidae). *ZooKeys*, 374: 57–68.

Hosoishi S, Park SH, Yamane Sk & Ogata K (2012) Species composition of ant prey of the pitcher plant *Nepenthes bokorensis* Mey (Nepenthaceae) in Phnom Bokor National Park, Cambodia. *Cambodian Journal of Natural History*, 2012: 3–7.

Hölldobler B & Wilson EO (1990) *The Ants*. Harvard University Press, Cambridge, Massachusetts, USA, 732 pp.

Itino T & Yamane SK (1995) The vertical distribution of ants on canopy trees in a Bornean lowland rain forest. *Tropics*, 4: 277–281.

Ito F, Yamane Sk, Eguchi K, Noerdjito WA, Kahono S, Tsuji K, Ohkawara K, Yamauchi K, Nishida T & Nakamura K (2001) Ant species diversity in the Bogor Botanic Garden, West Java, Indonesia, with descriptions of two new species of the genus *Leptanilla* (Hymenoptera, Formicidae). *Tropics*, 10: 379–404.

Jaitrong W & Nabhitabhata J (2005) A list of known ant species of Thailand (Formicidae: Hymenoptera). *The Thailand Natural History Museum Journal*, 1: 9–54.

Jenkins CN, Guénard B, Diamond SE, Weiser MD & Dunn RR (2013) Conservation implications of divergent global patterns of ant and vertebrate diversity. *Diversity and Distributions*, 19: 1084–1092.

Khun K, Mizoue N, Yoshida S & Murakami T (2008) Stem volume equation and tree growth for rubber trees in Cambodia. *Journal of Forest Planning*, 13: 335–341.

Klimes P, Idigil C, Rimandai M, Fayle TM, Janda M, Weiben GD & Novotny V (2012) Why are there more arboreal ant

species in primary than in secondary tropical forests? *Journal of Animal Ecology*, 81: 1103–1112.

Klimes P, Fibich P, Idigel C & Rimandai M (2015) Disentangling the diversity of arboreal ant communities in tropical forest trees. *PLoS ONE*, 10(2): e0117853. doi:10.1371/journal.pone.0117853.

Kone M, Konate S, Yeo K, Kouassi PK & Linsenmair KE (2014) Effects of management intensity on ant diversity in cocoa plantation (Oume, centra west Côte d'Ivoire). *Journal of Insect Conservation*, 18: 701–712.

Kwon TS, Lee CM & Sung JH (2014) Diversity decrease of ant (Formicidae, Hymenoptera) after a forest disturbance: Different responses among functional guilds. *Zoological Studies*, 53: 37.

LaPolla JS, Suman T, Sosa-Calvo J & Schultz TR (2007) Leaf litter ant diversity in Guyana. *Biodiversity and Conservation*, 16: 491–510.

Longino JT & Nadkarni NM (1990) A comparison of ground and canopy leaf litter ants (Hymenoptera: Formicidae) in a neotropical montane forest. *Psyche*, 97: 81–93.

Majer JD & Delabie JHC (1994) Comparison of the ant communities of annually inundated and terra firme forests at Trombetas in the Brazilian Amazon. *Insectes Sociaux*, 41: 343–359.

Malsch AKF, Rosciszewski K & Maschwitz U (2003) The ant species richness and diversity of a primary lowland rain forest, the Pasoh Forest Reserve, West-Malaysia. In: Okuda T, Manokaran N, Matsumoto Y, Niiyama K, Thomas SC & Ashton PS (eds.) *Pasoh: Ecology of a Lowland Rain Forest in Southeast Asia*. Springer-Verlag, Tokyo. Pp. 347–373.

Mey FS (2009) *Nepenthes bokorensis*, a new species of Nepenthaceae from Cambodia. *Carniflora Australis*, 7: 6–15.

Monastyrskii AL, Yago M & Odagiri K (2011) Butterfly assemblages (Lepidoptera, Papilionoidea) of the Cardamom Mountains, Southwest Cambodia. *Cambodian Journal of Natural History*, 2011: 122–130.

Naiki A, Tagane S, Chhang P, Toyama H, Hua Z, Dan SV & Yahara T (2015) Flora of Bokor National Park, Cambodia II: Four new species and nine new records of *Lasianthus* (Rubiaceae) from Cambodia. *Acta Phytotaxonomica et Geobotanica*, 66: 153–179.

Ogata K (2001) Time unit sampling: A protocol. *ANeT Newsletter*, 3: 18–19.

Pfeiffer M, Tuck HC, Lay TC (2008) Exploring arboreal ant community composition and co-occurrence patterns in plantations of oil palm *Elaeis guineensis* in Borneo and Peninsular Malaysia. *Ecography*, 31: 21–32.

Pfeiffer M, Mezger D, Hosoihi S, Yahya BE & Kohout RJ (2011) The Formicidae of Borneo (Insecta: Hymenoptera): A preliminary species list. *Asian Myrmecology*, 4: 9–58.

Ribas CR, Schoereder JH, Pic M & Soares SM (2003) Tree heterogeneity, resource availability, and larger scale processes regulating arboreal ant species richness. *Austral Ecology*, 28: 305–314.

Robertson HG (2002) Comparison of leaf litter ant communities in woodlands, lowland forests and montane forests of north-eastern Tanzania. *Biodiversity and Conservation*, 11: 1637–1652.

Sakchoowong W, Hasin S, Pachey N, Amornsak W, Bunyavejchewin S, Kongnoo P & Basset Y (2015) Influence of leaf litter composition on ant assemblages in a lowland tropical rainforest in Thailand. *Asian Myrmecology*, 7: 57–71.

Save Cambodia's Wildlife (2006) The Atlas of Cambodia: National Poverty and Environment Maps. Save Cambodia's Wildlife, Phnom Penh, Cambodia, 139 pp.

Tagane S, Toyama H, Chhang P, Nagamasu H & Yahara T (2015) Flora of Bokor National Park, Cambodia I: Thirteen new species and one change in status. *Acta Phytotaxonomica et Geobotanica*, 66: 95–135.

Toyama H, Tagane S, Chhang P, Kajisa T, Ichihashi R, Samreth V, Ma V, Sokh H, Katayama A, Itadani H, Tateishi M, Tachiki Y, Onoda Y, Mizoue N, Tachida H & Yahara T (2013) Inventory of woody flora in permanent plots of Kampong Thom and Kampong Chhang Provinces, Cambodia. *Acta Phytotaxonomica et Geobotanica*, 64: 45–105.

Toyama H, Kajisa T, Tagane S, Mase K, Chhang P, Samreth V, Ma V, Sokh H, Ichihashi R, Onoda Y, Mizoue N & Yahara T (2015) Effects of logging and recruitment on community phylogenetic structure in 32 permanent forest plots of Kampong Thom, Cambodia. *Philosophical Transactions of the Royal Society of London Series B*, 370: 20140008. doi: 10.1098/rstb.2014.0008.

Tsukamoto J & Sabang J (2005) Soil macro-fauna in an *Acacia mangium* plantation in comparison to that in a primary mixed dipterocarp forest in the lowlands of Sarawak, Malaysia. *Pedobiologia*, 49: 69–80.

Turner EC & Foster WA (2006) The impact of forest conversion to oil palm on arthropod abundance and biomass in Sabah, Malaysia. *Journal of Tropical Ecology*, 25: 23–30.

Vasconcelos HL (1999) Effects of forest disturbance on the structure of ground-foraging ant communities in central Amazonia. *Biodiversity and Conservation*, 8: 407–418.

Vasconcelos HL & Vilhena JMS (2006) Species turnover and vertical partitioning of ant assemblages in the Brazilian Amazon: A comparison of forests and savannas. *Biotropica*, 38: 100–106.

Wang WY & Foster WA (2015) The effects of forest conversion to oil palm on ground-foraging ant communities depend on beta diversity and sampling grain. *Ecology and Evolution*, 5: 3159–3170.

Weiser MD, Sanders NJ, Agosti D, Andersen AN, Ellison AM, Fisher BL, Gibb H, Gotelli NJ, Gove AD, Gross K, Guénard B, Janda M, Kaspari M, Lessard JP, Longino JT, Majer JD, Menke SB, McGlynn TP, Parr CL, Philpott SM, Retana J, Suarez AV, Vasconcelos HL, Yanoviak SP & Dunn RR (2010) Canopy and litter ant assemblages share similar climate-species density relationships. *Biology Letters*, 6 (6): 769–772.

Widodo ES, Naito T, Mohamed M & Hashimoto Y (2004) Effects of selective logging on the arboreal ants of a Bornean rainforest. *Entomological Science*, 7: 341–349.

Wilson EO (1987) The arboreal ant fauna of Peruvian Amazon forests: A first assessment. *Biotropica*, 19: 245–251.

Woodcock P, Edwards DP, Newton RJ, Khen CV, Bottrell SH & Hamer KC (2013) Impacts of intensive logging on the trophic organisation of ant communities in a biodiversity hotspot. *PLoS One*, 8: e60756.

Yamane SK, Bui TV, Ogata K, Okido H & Eguchi K (2002) Ant fauna of Cuc Phuong National Park, North Vietnam (Hymenoptera: Formicidae). *Bulletin of the Institute of Tropical Agriculture, Kyushu University*, 25: 51–62.

Yanoviak SP & Kaspari ME (2002) Community structure and the habitat template: Ant assemblages in the tropical canopy and litter. *Oikos*, 89: 259–266.

Zryannin VA (2011) Analysis of the local ant fauna (Hymenoptera, Formicidae) in Southern Vietnam. *Entomological Review*, 91: 198–211.