THE RAFFLES BULLETIN OF ZOOLOGY 2011 **59**(2): 181–194
Date of Publication: 31 Aug.2011

TAXONOMIC AND FUNCTIONAL DIVERSITY OF ANTS (HYMENOPTERA:FORMICIDAE) IN AN UPPER HILL DIPTEROCARP FOREST IN PENINSULAR MALAYSIA

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ABSTRACT. **–** Studies of ant diversity provide valuable insights into the health and functioning of forest ecosystems, but ants are surveyed infrequently in many tropical forest ecosystems. The majority of lowland forests in Peninsular Malaysia was cleared for land development in the 1970s and 1980s, leaving upper hill dipterocarp forests as almost all remaining contiguous, primary forests in Peninsular Malaysia. The ant communities of these forests have not previously been documented. Our extensive survey of a 200 ha upper hill dipterocarp forest site in Temengor Forest Reserve captured 10,307 individual ants, representing 211 species from 60 genera and nine subfamilies. Myrmicinae was the most common ant subfamily censused, with *Pheidole* recorded as the most speciose genera (40 species) followed by *Polyrhachis* (19 species) and *Camponotus* (13 species). Generalised Myrmicinae was the most diverse functional group, followed by Cryptic Species, Subordinate Camponotini and Tropical Climate Specialists. Seven undetermined specimens of possibly new species were recorded, suggesting that the upper hill dipterocarp forest of Temengor Forest Reserve is home to numerous ant species that have not been documented before. Our findings can be utilised to better understand the ant community composition and function of primary upper hill dipterocarp forests in Peninsular Malaysia as compared to other dipterocarp forests. Our results can also serve as a baseline to understand post-disturbance changes to ant community composition and functional diversity.

KEYWORDS. **–** Ants, Upper Hill Dipterocarp Forest, Peninsular Malaysia.

INTRODUCTION

Arthropods are often underappreciated, even though they provide irreplaceable ecosystem services that must be taken into account when studying the functions of both intact and disturbed ecosystems (Seastedt & Crossley, 1984). Ants are especially important ecosystem engineers that contribute to numerous crucial functions, including nutrient cycling, decomposition of organic matter, soil aeration, the suppression of soil-borne diseases and pests, and the direct and indirect alteration of soil properties (Folgarait, 1998).

Given the importance of ants as bioindicators of disturbance and environmental stress (e.g., Andersen, 1997; Hoffmann & Andersen, 2003), it is valuable to go beyond identifying ant specimens at a taxonomic level by also assigning them to functional groups. Although ants can be hard to identify due to their small size and their hyperdiversity (Longino et al., 2002), ant diversity and functional group surveys have been successfully employed by land managers to gain insight into the health and functioning of ecosystems (Andersen, 1997; Andersen et al., 2002; Andersen & Majer, 2004).

Andersen (2000) made a careful study of the global ecology of rainforest ants to understand how the structure and function of ant communities differ across biomes. He classified four primary stressors of ants (low temperature, microhabitat structure and resource capture, nest site availability and food supply), and then identified seven ant functional groups based on ants' response to competition, disturbance and stress (Appendix 1). Andersen utilised these functional group classifications to analyse the distribution of ant functional groups before and after disturbance in humid tropical forests. He found a significant increase in ants categorised as Dominant Dolichoderinae, and a substantial decrease in individuals categorised as tropical climate specialists, indicating that the disturbance had a clear effect on ecosystem function. The study of ants in relation to their functional groups directly improves our ability to understand how anthropogenic disturbance affects the ecosystem services ants provide (King et al., 1998).

Dipterocarp forests (dominated by trees in the family, Dipterocarpaceae) account for more than three-quarters of all Southeast Asian forests, representing substantial carbon sinks and biodiversity pools in the region (Manokaran, 1995). In Malaysia, dipterocarp forests account for about 85% of the country's forested areas (Kamaruzaman & Ahmad, 2003) and are commonly composed of species from the genera *Anisoptera, Dipterocarpus, Dryobalanops, Hopea, Shorea* and *Parashorea* (Thang, 1987).

While the floristic composition and the charismatic megafauna of Malaysian dipterocarp forests tend to be well studied in both Malaysian Borneo and in Peninsular Malaysia, the study of non-charismatic fauna lags significantly behind (Chey et al., 1997; Godfrey et al., 1999). Despite several extensive ant studies that have been carried out in Malaysian Borneo (Chung, 1995; Brühl et al., 1998; Hashimoto et al., 2001), very little is known about ant taxonomy or ecology in Peninsular Malaysia (Agosti et al., 1994). Only a few preliminary studies of ant diversity have ever been carried out in Peninsular Malaysia (e.g., Fiala et al., 1994; Liefke et al., 1998). The most comprehensive study of ant diversity in Peninsular Malaysia took place in the lowland dipterocarp forest of the Pasoh Forest Reserve (PFR) in Negeri Sembilan (Bolton, 1998; Moog et al., 2003). A total of 427 species from nine subfamilies have been documented at PFR (Malsch, 2000).

However, the surveys of ant diversity at low-elevation PFR are not likely representative of ant diversity in the rest of the peninsula. The majority of lowland forests in Peninsular Malaysia was cleared in the 1970s and 1980s for urban development and agriculture, particularly oil palm and rubber plantations (Liow et al., 2002; Abdullah & Nakagoshi, 2006). As a consequence, almost all contiguous, primary forests in Peninsular Malaysia are now the less-accessible, steep hill and upper hill dipterocarp forests found at higher elevations. We know little to nothing about the ant communities of these forests, although we would expect them to differ from the ant communities found in lowland forests (Sanders, 2002).

The objective of this study is to undertake what is, to our knowledge, the first survey of ant diversity and function in a pristine upper hill dipterocarp forest in Peninsular Malaysia. Our findings may be used for future comparisons of the ant communities of primary upper hill dipterocarp forests in Peninsular Malaysia with the ant communities in dipterocarp forests at other elevations and across various other environmental gradients. Additionally, since our study provides the only description of the ant community in an undisturbed upper hill dipterocarp forest in Peninsular Malaysia, our results can serve as a baseline to understand post-disturbance changes to ant community composition and functional diversity. Our study is especially valuable as timber harvesting and other anthropogenic land-use changes continue to occur in upper hill dipterocarp forests in Peninsular Malaysia.

MATERIAL AND METHODS

***Sampling location.* –** The study was conducted in Compartment 44, Block 5 of the 9765 ha Perak Integrated Timber Complex (PITC) (5° 24' N, 101° 33'E), a primary hill and upper hill dipterocarp forest concession within Temengor Forest Reserve (TFR) (Fig. 1). TFR was declared a Permanent Forest Reserve under Malaysia's National Forestry Act in 1984. It lies on the western portion of the Titiwangsa Main Range of Peninsular Malaysia in the northern state of Perak, near the border of Thailand. TFR is located at an altitude of 400–1000 m above sea level. Our sampling in PITC was carried out within an altitude range of 550–810 m in a forest dominated by *Shorea platyclados* (Sloot et Foxw), *Dipterocarpus costulatus* (Pierre), *Koompassia malaccensis* (Benth) and *Intsia palembanica* (Miq), which places our sampling location within an upper hill dipterocarp forest (Wyatt-Smith, 1963).

***Sampling design.* –** Sampling occurred within a 200-ha area of PITC where 24 sampling plots were established (Fig. 1). Each sampling plot consisted of a 20 × 80 m rectangle that contained four square subplots (20 × 20 m) delineated within them. Each subplot was further divided into four 10 x 10 m quadrats. Each plot consisted of eight baits, eight ground pitfall traps, eight arboreal pitfall traps and four sets of leaf litter sifting.

***Sampling methods.* –** Four sampling methods were employed in order to thoroughly survey ant diversity, target ants present in different strata and capture ants with different functions. Sampling was conducted in Mar.2008 and repeated in Mar.2009. The sampling methods chosen were baiting (Keeler, 1980), ground pitfall traps (Fichter, 1941), arboreal pitfall traps (Samson et al., 1997) and leaf litter sifting (Olson, 1991). All methods were modified to suit the forest topography as detailed below.

Baiting – Baiting ants is commonly used to estimate the composition and richness of ground-foraging ant fauna (Greenslade, 1972). We placed a teaspoon of tuna and a cotton ball moistened with a 20% honey and 80% water solution on transparent plastic plates in quadrats 2 and 4 of each subplot, for a total of eight replicates in each plot. After 60 min, visual counts of all ants at the baits were completed and identifications were recorded to morpho-species. Opportunistic hand collections of ants using soft forceps were also carried out.

Ground pitfall traps – Ground pitfall traps are generally used to obtain an estimate of the abundance and species composition of ants active on the soil surface. Each ground pitfall trap was established in quadrats 1 and 3 in each subplot by embedding a hard plastic cup (5-cm diameter) in the soil until the mouth of the cup was even with the soil surface. 20 ml of water mixed with fragrance-free detergent was placed in the cup to serve as a killing agent. A coarse wire net was placed over the mouth of the cup to exclude larger organisms and to support a transparent plastic plate (15-cm diameter) approximately 2.5 cm above ground that shielded the trap from rainfall. All pitfall traps were left in the field for 48 hours before they were retrieved for species identification in the laboratory.

Arboreal pitfall traps – Extensive arboreal ant sampling can be carried out using fogging techniques that are expensive and require a substantial investment of time and effort by researchers (Delabie et al., 2000). A simpler and more cost-effective way to analyse ant composition at the arboreal level is to use arboreal pitfall traps. This sampling method is a modified form of the ground pitfall trapping method (Bestelmeyer et al., 2000). Arboreal pitfalls were constructed by twist-tying disposable plastic cups with snap-on lids onto

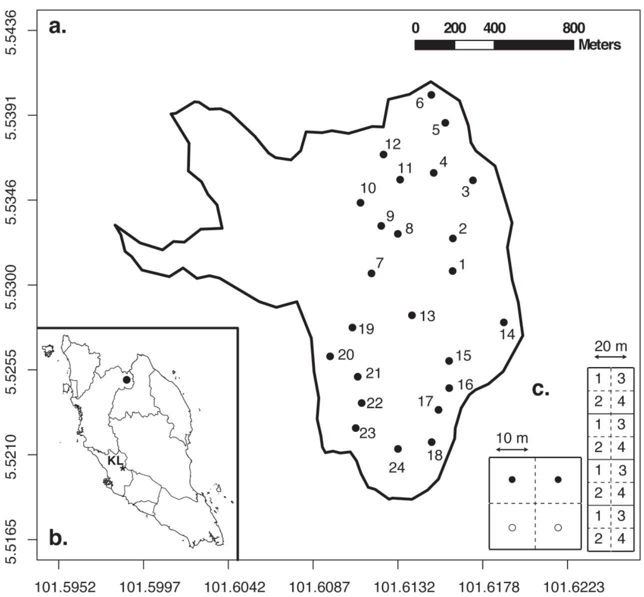

Fig. 1. a. Sampling occurred within a 200-ha area of the Perak Integrated Timber Complex (PITC) where 24 sampling plots were established. b. Filled circle shows the location of PITC in the Temengor Forest Reserve in northern Peninsular Malaysia. c. Each sampling plot consisted of a 20 × 80 m rectangle that contained four square subplots (20 × 20 m) delineated within them. Each subplot was further divided into four 10 × 10 m quadrats. Open circles indicate placement of arboreal pitfall and ground pitfall traps and filled circles indicate placement of baits and leaf litter sifting in each quadrat.

tree trunks (5–20 cm dbh) at a height of 1.3 m in quadrats 1 and 3 of each subplot. Arboreal pitfall traps were baited and filled with killing agent and left for 48 hours before they were collected.

Leaf litter sifting – Ants are most commonly found in the leaf litter layer on top of the soil surface. Therefore, leaf litter sifting is particularly well-suited for use in structurally complex habitats with abundant leaf litter, such as our upper hill dipterocarp forest study site (Bestelmeyer et al., 2000). We surveyed ant diversity within leaf litter in quadrat 3 of each subplot, for a total of four replicates in each plot. We sieved leaf-litter for 30 min in each quadrat by screening batches of the leaf litter over a 100 × 80 cm white sheet using a coarse (5 × 5 mm) rectangular (15 × 30 × 3 cm) wire sieve. All sieved ants were collected in vials.

Identification and analysis. – Collected specimens were brought to the laboratory where pinning and identification were conducted to the genus level according to Bolton (1994) and Hashimoto et al. (2001). When possible, specimens were identified to the species level; when this was not possible, identifications were left as morpho-species. Identifications to the species level were made by direct comparison of collected specimens to the collection at Kagoshima University (collector: Seiki Yamane).

A rarefied species accumulation curve of individuals was created for each sampling year to determine if species in the site were adequately sampled (Brühl et al., 1998). Species diversity estimations were calculated to determine the sampling efficiency. Ant genera were later assigned to functional groups following Andersen's (2000) classifications (Appendix 2), in order to characterise the ecosystem services provided by ants in TFR. All analyses were computed using the Vegan: Community Ecology Package (Oksanen et al., 2009) and Biodiversity R Package (Kindt & Coe, 2005) in R (R Development Core Team, 2009).

RESULTS

The four sampling methods (ground pitfall traps, arboreal pitfall traps, baiting and leaf litter sifting) that we employed to survey ant diversity in TFR led to the cumulative capture of 10,307 individuals, representing 211 species from 60 genera and nine subfamilies (see Appendix 2 for complete species list, abundances and functional classifications). The estimated total species richness ranged between 177.7 and 271.7, which yielded more than 70% sampling efficiency (Table 1). Sampling efficiency was calculated by dividing the number of actual species caught by the number of estimated species. A combined species accumulation curve representing the sampling completed in both years approached an asymptote after 40 plots were sampled (Fig. 2). Separate species accumulation curves for the sampling carried out in 2008 and 2009 both begin to approach asymptotes after approximately 20 plots were sampled.

Table 1. Species estimation of ants trapped in 2008 and 2009 in Temengor Forest Reserve, Peninsular Malaysia. Numbers in parentheses indicate sampling efficiency*.

	Actual number of species	Chao estimates	First order Jackknife	Bootstrap
2008	152	219.6 ± 23.3 (69.2)	210.4 ±15.6 (72.2)	177.7 ± 7.7 (85.5)
2009	153	208.1 ± 19.1 (73.5)	207.7 ± 14.0 (73.7)	178.6 ± 7.3 (85.7)
All	211	264.4 ± 18.2 (79.8)	271.7 ± 13.2 (77.7)	238.4 ± 7.2 (88.5)

*Sampling efficiency was calculated by dividing the number of actual species caught by the number of estimated species (Brühl, 2001).

Table 2. Species richness and abundance trapped in 2008 and 2009 in Temengor Forest Reserve, Peninsular Malaysia, listed by subfamily.

Subfamily	2008		2009		Total	
	Species	Individuals	Species	Individuals	Species	Individuals
Amblyoponinae	–	–	1	1	1	1
Cerapachyinae	1	2	–	–	1	2
Dolichoderinae	5	97	6	264	7	361
Ectatomminae	2	62	3	54	4	116
Formicinae	42	593	36	780	50	1373
Myrmicinae	76	3936	0	3305	111	7300
Ponerinae	24	494	26	656	35	1150
Proceratiinae	1	1	–	–	1	1
Pseudomyrmicinae	1	2	1	1	1	3
Total	152	5187	153'	5061	211	10307

Overall, the subfamily Myrmicinae, yielded the highest number of species (111 species), followed by Formicinae (50 species), Ponerinae (35 species), Dolichoderinae (7 species) and Ectatomminae (4 species). Only one species from each of the four subfamilies Amblyoponinae, Cerapachyinae, Proceratiinae and Peudomyrmicinae was trapped (Table 2). The relative abundance of the nine subfamilies according to both total individuals and number of species did not differ between years, with Myrmicinae ranking highest, followed by Ponerinae, Formicinae, Dolichoderinae, Ectatomminae, Amblyoponinae, Cerapachyinae, Proceratiinae, and Pseudomyrmicinae (Table 2). The species richness of both Myrmicinae and Formicinae were higher in 2008 than in 2009, but the species richnesses of Ponerinae and Dolichoderinae were higher in 2009. The same species in Pseudomyrmicinae (*Tetraponera attenuate*) was found in both years. *Amblyopone reclinata* in the subfamily of Amblyoponinae was found only in 2009, while the subfamilies Cerapachyinae and Proceratiinae were found only in 2008. Of the total number of species trapped in both sampling years, 72.0% was captured in 2008 and 72.5% was captured in 2009. The dominant species composition was similar in the two sampling years. At the genus level, 63.3% of the 60 genera was trapped in both sampling years. The total species richness captured in the two sampling years was also very similar, with 152 species captured in 2008 and 153 species captured in 2009.

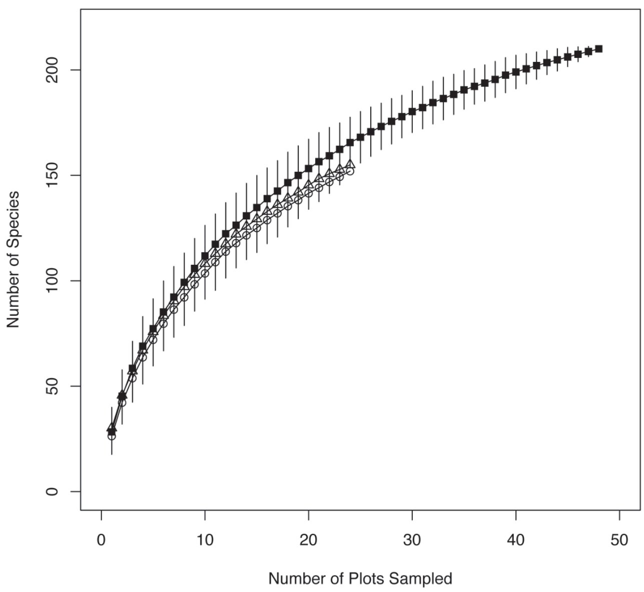

Fig. 2. Species accumulation curves with error bars for sampling in Temengor Forest Reserve, Peninsular Malaysia in 2008 [Δ], 2009 [o] and combined [■].

Pheidole was recorded as the most speciose genera (42 species, 19.9%; Table 3), followed by *Polyrhachis* (19 species; 9.0%) and *Camponotus* (13 species; 7.1%). The most abundant species was *Lophomyrmex bedoti* (Emery) with a total of 3265 individuals caught throughout the sampling period, followed by *Crematogaster* sp C with 683 individuals captured (Fig. 3). Both of these species belong to Myrmicinae. The third most abundant species was *Odontoponera transversa* (Smith) in the subfamily of Ponerinae with 330 individuals caught. *Euprenolepis procera* (Emery) was the most abundant ant in the Formicinae subfamily (187 individuals), while *Dolichoderus thoracicus* (Smith) was the most abundant Dolichoderinae (154 individuals). Of the 211 species trapped, 48.8% of species had a total number of captures of five or fewer individuals.

Table 3. Distribution of species by genus for ants sampled in Temengor Forest Reserve. Number of species is followed by percentage of total species in parentheses.

Genus	Total	Genus	Total	Genus	Total
Pheidole	42 (19.9)	*Platythyrea*	3 (1.4)	*Discothyrea*	1 (0.5)
Polyrhachis	19 (9.0)	*Echinopla*	2 (0.9)	*Emeryopone*	1 (0.5)
Camponotus	15 (7.1)	*Euprenolepis*	2 (0.9)	*Lepisiota*	1 (0.5)
Crematogaster	10 (4.7)	*Meranoplus*	2 (0.9)	*Lophomyrmex*	1 (0.5)
Hypoponera	10 (4.7)	*Myrmoteras*	2 (0.9)	*Lordomyrma*	1 (0.5)
Tetramorium	9 (4.3)	*Ponera*	2 (0.9)	*Mayriella*	1 (0.5)
Pachycondyla	8 (3.8)	*Recurvidris*	2 (0.9)	*Myopias*	1 (0.5)
Leptogenys	5 (2.4)	*Paraparatrechina*	1 (0.5)	*Odontomachus*	1 (0.5)
Myrmicaria	5 (2.4)	*Acanthomyrmex*	1 (0.5)	*Odontoponera*	1 (0.5)
Pheidologeton	5 (2.4)	*Acropyga*	1 (0.5)	*Oecophylla*	1 (0.5)
Strumigenys	5 (2.4)	*Amblyopone*	1 (0.5)	*Carebara*	1 (0.5)
Gnamptogenys	4 (1.9)	*Anochetus*	1 (0.5)	*Prenolepis*	1 (0.5)
Myrmecina	4 (1.9)	*Aphaenogaster*	1 (0.5)	*Proatta*	1 (0.5)
Paratopula	4 (1.9)	*Cataulacus*	1 (0.5)	*Pseudolasius*	1 (0.5)
Technomyrmex	4 (1.9)	*Cerapachys*	1 (0.5)	*Pyramica*	1 (0.5)
Monomorium	4 (1.9)	*Cladomyrma*	1 (0.5)	*Solenopsis*	1 (0.5)
Dolichoderus	3 (1.4)	*Cryptopone*	1 (0.5)	*Tetraponera*	1 (0.5)
Cardiocondyla	3 (1.4)	*Dacetinops*	1 (0.5)	*Vollenhovia*	1 (0.5)
Nylanderia	3 (1.4)	*Diacamma*	1 (0.5)		
Eurhopalothrix	3 (1.4)	*Dilobocondyla*	1 (0.5)		

Twenty-five species were captured in an abundance of 100 or more individuals; 16 of these species belong to Myrmicinae, while five belong to Ponerinae, three to Formicinae and one to Dolichoderinae. Singletons of 38 different species were captured, representing five subfamilies: Amblyoponinae, Dolichoderinae, Formicinae, Myrmicinae and Ponerinae.

Generalised Myrmicinae was the most diverse functional group (54 species; 25.6%; Fig. 4), followed by Cryptic Species (38 species; 18%), Subordinate Camponotini (36 species; 17.1%), Tropical Climate Specialists (28 species; 13.3%), Opportunists (28 species; 13.3%), Specialist Predators (23 species; 10.9%), Dominant Dolichoderinae (three species; 1.4%) and Cold Climate Specialist (one species; 0.5%).When taking into account overall abundance, Tropical Climate Specialists were most abundant (3967 individuals), followed by Generalist Myrmicinae (2659

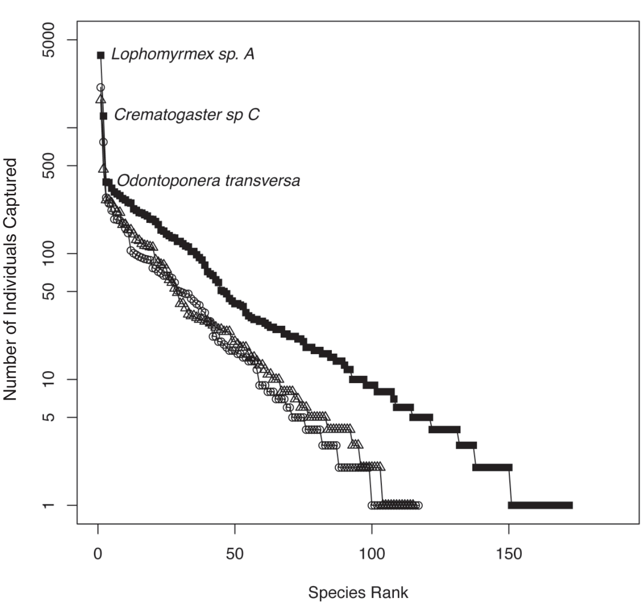

Fig. 3. Species rank abundance for number of ants caught during the sampling in Temengor Forest Reserve, Peninsular Malaysia in 2008 [Δ], 2009 [o] and combined [■].

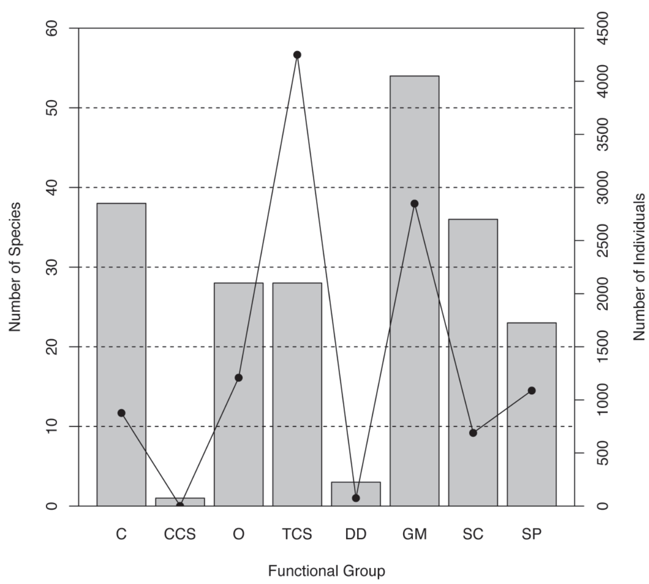

Fig. 4. Number of species (bars) and number of individual (lines) of ants from different functional groups. C: Cryptic species; DD: Dominant Dolichoderinae, GM: Generalised Myrmicinae; TCS: Tropical Climate Specialists; O: Opportunists; SC: Subordinate Componitini; SP: Specialist Predators.

individuals; Fig. 4). Cold Climate Specialists were the least abundant and diverse with only one species (*Prenolepis* sp two of NZA) and two individuals trapped.

DISCUSSION

Species accumulation curves calculated from sampling in 2008 and 2009 indicate that more sampling would need to be carried in order to adequately assess the entire ant community in TFR. However, when sampling from both years were combined, the species accumulation curve almost reached an asymptote, indicating that at least 40 plots are needed to adequately sample a 200-ha area of forest. The species estimation also indicates that the sampling efficiency falls above 70% throughout the study, which supports the efficiency of the trapping methods used (Table 1). Finally, the similarity of the separate species accumulation curves for 2008 and 2009 demonstrates the repeatability and reliability of our sampling methods.

Comparison to previous studies. – Taking into account the specimens trapped by all four sampling methods (ground pitfall traps, arboreal pitfall traps, baiting and leaf litter sifting) in both sampling years, ants from the following nine subfamilies were identified: Amblyoponinae, Cerapachyinae, Ectatomminae, Formicinae, Myrmicinae, Dolichoderinae, Ponerinae, Proceratiinae and Pseudomyrmicinae. Bolton et al. (2006) documented 21 subfamilies throughout the world, with twelve subfamilies occurring in the Indo-Australian region. A series of studies carried out in Malaysian Borneo, indicated the presence of all 12 Indo-Australian subfamilies of ants (Hashimoto et al., 2001). Similarly, a comprehensive study that sampled ants across multiple strata in Pasoh Forest Reserve (PFR), an unlogged lowland dipterocarp forest reserve in Peninsular Malaysia, also documented all 12 subfamilies (Malsch, 2000).

Our failure to document three of the 12 Indo-Australian subfamilies, Aenictinae, Dorylinae and Leptanillinae, which are composed of topsoil species, would likely have not occurred at TFR if more thorough topsoil sampling had been conducted (Bolton, 1994; Malsch, 2000). Aenictinae and Dorylinae are army ants, which are highly mobile and difficult to catch (Wilson, 1964), while Leptanillinae are subterranean species and very rarely recorded (Bolton, 1990). This calls attention to the importance of employing several trapping methods simultaneously when attempting to catalogue the ant diversity of an area. Our results also highlight the potential limitations of attempting a rapid ant diversity assessment in such a biologically diverse tropical forest.

Within the nine subfamilies found at TFR, we captured 211 species, half of the number of species found in PFR where a comprehensive inventory of the lowland primary forest ant community was conducted (Malsch, 2000). It is important to note that the sampling effort employed in the study at PFR was much greater and involved the use of Winkler Extractors, the Berlese collection method, pitfall traps, baiting, the single rope technique and hand collection over a 10-month time period.

A comparison of our findings at TFR to the findings of Malsch (2000) at PFR shows that similar ant communities inhabit upper hill dipterocarp forests and lowland dipterocarp forests (Table 4). Only a higher percentage of Myrmicinae and Ponerinae were found at TFR as compared to PFR. The small differences in the taxonomic structure of PFR and TFR might be due to the fact that different methods were used in this study as compared to the study conducted in PFR. A second study conducted by Malsch (2000) that looked specifically at the diversity of ground foraging ants in PFR using a standard quadrat sampling yielded 120 species, in comparison to the 143 ground foraging ant species collected using ground pitfall trap, baiting and leaf litter sifting that were found in this study. Therefore, despite the rapid nature of our ant survey in TFR, we managed to capture about half of the overall ant species diversity of PFR and a greater number of grounds foraging ant species. This suggests that pristine upper hill dipterocarp forests in Peninsular Malaysia may be as diverse as lowland dipterocarp forests. However, in the future, a more intensive study should be carried out at TFR replicating the methods used by Malsch et al. (2000) in order to capture more of the rare upper hill forest specialist species.

Functional groups. – A large number of the species identified (55 species) are categorised as Generalised Myrmicinae (GM). GM ants occur abundantly and ubiquitously in primary forests throughout the tropics (Andersen, 2000). The most abundant species at our study site was *Lophomyrmex bedoti* (Emery) in the subfamily Myrmicinae. This generalist predator species is expected to be highly abundant in tropical forests and is commonly found on the forest floor where they forage (Rigato, 1994). Their heterogeneous diets enable them to survive in complex environments and dominate forest ant communities (Moffett, 1986).

The most diverse genus at TFR was *Pheidole* (42 species); these GM ants are also hyperdiverse and found to be abundant in most tropical forest sites worldwide (Wilson, 2003). This genus plays an important role in ecosystem functioning as it contains ant species that range from omnivores to scavengers to predators of other small insects. Eguchi (2001) reported that there are at least 52 species of *Pheidole* on Borneo. *Polyrhachis* was the second most diverse genus (19 species) at TFR. This genus is diverse and commonly abundant, but these Subordinate Camponotini (SC) ants are generally submissive to the Dominant Dolichoderinae (DD) and are ecologically segregated from them due to their large body sizes and nocturnal foraging (Andersen, 2000). DD diversity and abundance recorded in this study were low (three species; 1.4% of all individuals). DD prefer open and hot habitats, and in undistributed tropical rainforests, this habitat is found in forest gaps and in the canopy layer. Hence, it was caught less in the ground-level traps. More DD would likely have been collected, if the canopy had been fogged. The low abundance and richness of DD captured in TFR also imply that the forest's structure is relatively intact.

Tramp species of ants are closely associated with human activity and often nest in human structures (Schultz &

Table 4. Taxonomic structure of ants in Temengor Forest Reserve (this study) and Pasoh Forest Reserve (Malsch, 2000).

Subfamily	% Species TFR	% Species PFR	% Genera TFR	% Genera PFR
Myrmicinae	52.6	40.7	46.6	39.0
Formicinae	23.7	28.2	20.7	18.2
Ponerinae	16.6	14.9	20.7	19.5
Dolichoderinae	3.3	5.9	3.4	6.5
Ectatomminae	1.9	0.4	3.4	1.3
Cerapachyinae	0.5	2.9	1.7	1.3
Proceratiinae	0.5	1.4	1.7	3.9
Pseudomyrmicinae	0.5	1.4	1.7	1.3
Amblyoponinae	0.5	1.2	1.7	5.2
Aenictinae	0.0	2.5	0.0	1.3
Dorylinae	0.0	0.2	0.0	1.3
Leptanillinae	0.0	0.2	0.0	1.3

Andersen, 2000); only two tramp species were found in low abundances at TFR (*Technomyrmex albipes* (Forel) and *Tetramorium pacificum* (Mayr)). Even though these species are most likely native to Malaysia, their low abundance at the study site provides insight into TFR's overall health. These species are classified as Opportunists, meaning they pre-dominate sites when disturbance limits the productivity of other species (Andersen et al., 2000). Finally, no invasive species were trapped, providing further support for the classification of TFR as an undisturbed primary forest.

New species. – Seven undetermined specimens were discovered at TFR, which possibly correspond to new species. These seven undetermined specimens were only found in TFR, as compared to other undetermined species listed in Appendix 1, which were already present in the collection of Seiki Yamane at Kagoshima University. The finding of these species suggests that the upper hill dipterocarp forest of TFR harbors a high diversity of ant species that have not been thoroughly studied before. These specimens appear to be Cryptic Species, which are small and predominantly Myrmicinae and Ponerinae that nest and forage primarily in soil, litter and rotting logs. They are most diverse and abundant in forested habitats and are a major part of the leaf litter ant communities in tropical rainforests (Andersen, 2000). As Cryptic Species, they are able to avoid detection; their methods of crypsis include camouflage, nocturnal activity, subterranean lifestyles, transparency and mimicry (Zuanon & Sazima, 2006).

Conclusions. – Primary upper hill dipterocarp forests harbour diverse ant communities, and it is necessary to utilise a combination of sampling methods to ensure the accurate representation of an entire community. Our results can be used to compare the ant communities of primary upper hill dipterocarp forests in Peninsular Malaysia with dipterocarp forests in other floristic zones and at other elevations. Additionally, since our study provides the only description of the ant community in an undisturbed upper hill dipterocarp forest in Peninsular Malaysia, our findings can serve as a baseline to understand post-disturbance changes to ant species composition and functional diversity.

ACKNOWLEDGEMENTS

The Government of Malaysia, Forest Research Institute Malaysia (FRIM), and the Conservation of Biodiversity Project (CBioD) enabled us to conduct field sampling through co-funding by UNDP-GEF (MAL/04/G31) and ITTO [PD 165/02 Rev.3 (F)]. Our key partners in the CBioD Project, including the Perak Integrated Timber Complex, Perak State Development Corporation (SEDC), Forestry Department Peninsular Malaysia Headquarters and State Forestry Departments of Peninsular Malaysia granted us permission to conduct sampling in Peninsular Malaysia. This Project was conducted in collaboration with Duke University and was also supported by the National Science Foundation of the United States through a Graduate Research Fellowship to Hannah M. W. Salim. We would like to thank the Head of Entomology Branch at FRIM, Laurence G. Kirton, for his guidance and our field assistants, Noor Azmy Mohd Noor, Wan Shaina Mazuin, Mohd Shah Fadir Ishak and Nafaruding Che Nan for their hard work. We would also like to thank Prof. Seiki Yamane (Kagoshima University) and Dr. Bakhtiar Effendy Yahya (University Malaysia Sabah) for their supervision of species identification and involvement in improving this manuscript.

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Appendix 1. The seven functional groups of ants, their abbreviations and their descriptions (adapted from Andersen, 2000).

Functional Group	Abbreviation	Description
Dominant Dolichoderinae	DD	Abundant and highly aggressive species that exert a strong competitive influence on other ants; favour hot and open habitats.
Subordinate Camponotini	SC	Behaviourally submissive to DD; ecologically segregated from DD because of large size and nocturnal foraging
Tropical-, Hot- & Cold-Climate Specialists	TCS, HCS, CCS	Found in arid zones (HCS), humid tropics (TCS) or cool-temperate zones (CCS); CCS and TCS are unspecialised, exist where DD are rare; HCS coexist with DD
Cryptic Species	C	Small species; found in soil, litter, rotting logs; most diverse/abundant in forests
Opportunists	O	Unspecialised, poorly competitive; predominate where stress or disturbance limit other ants
Generalised Myrmicinae	GM	Ubiquitous in warmer regions; compete with DD
Specialist Predators	SP	Medium to large size; only interact with other ants through direct predation because of special diets and small populations

Appendix 2. Complete species list, abundances and functional groups of all ants trapped in 2008 and 2009 in Temengor Forest Reserve, Peninsular Malaysia.

Subfamily	Species†	2008	2009	Total	Functional Group*
Amblyoponinae	*Amblyopone reclinata* (Mayr)		1	1	C
Cerapachyinae	*Cerapachys* sp 27 of SKY	2		2	C
Dolichoderinae	*Dolichoderus affinis* (Emery)	2	1	3	DD
Dolichoderinae	*Dolichoderus* sp 1 of NZA**		1	1	DD
Dolichoderinae	*Dolichoderus thoracicus* (Smith)	10	57	67	DD
Dolichoderinae	*Technomyrmex albipes* (Forel)	22	132	154	O
Dolichoderinae	*Technomyrmex horni* (Forel)	29	52	81	O
Dolichoderinae	*Technomyrmex kraepelini* (Forel)		21	21	O
Dolichoderinae	*Technomyrmex* sp 1 of NZA	34		34	O
Ectatomminae	*Gnamptogenys costata* (Emery)	59	39	98	TCS
Ectatomminae	*Gnamptogenys cribrata* (Emery)		7	7	TCS
Ectatomminae	*Gnamptogenys menadensis* (Mayr)		8	8	TCS
Ectatomminae	*Gnamptogenys* sp 1 of NZA**	3		3	TCS
Formicinae	*Acropyga nipponensis* (Terayama)	1		1	C
Formicinae	*Camponotus (Colobopsis) leonardi* (Emery)		1	1	SC
Formicinae	*Camponotus (Colobopsis) saunders* (Emery)	2	76	78	SC
Formicinae	*Camponotus (Colobopsis)* sp 62 of SKY	3		3	SC
Formicinae	*Camponotus (Colobopsis)* sp 98 of SKY	1		1	SC
Formicinae	*Camponotus (Myrmamblys)* sp 149 of SKY	21	19	40	SC
Formicinae	*Camponotus* (*Myrmotarsus*) *irritabilis* (Smith)		22	22	SC
Formicinae	*Camponotus* (*Myrmotarsus*) *rupifemur* (Emery)	58	14	72	SC
Formicinae	*Camponotus* (*Tanaemyrmex*) *festinus* (Smith)	3	5	8	SC
Formicinae	*Camponotus* (*Tanaemyrmex*) sp 1 of NZA	13	15	28	SC
Formicinae	*Camponotus* (*Tanaemyrmex*) sp 13 of SKY	7	6	13	SC
Formicinae	*Camponotus* (*Tanaemyrmex*) sp 15 of SKY	11	112	123	SC
Formicinae	*Camponotus* (*Tanaemyrmex*) sp 3 of NZA**	1		1	SC
Formicinae	*Camponotus* (*Tanaemyrmex*) sp 72 of SKY	35	9	44	SC
Formicinae	*Camponotus gigas* (Latreille)	14	5	19	SC
Formicinae	*Camponotus* sp 4 of NZA**	2	1	3	SC
Formicinae	*Cladomyrma petalae* (Agosti)		1	1	TCS
Formicinae	*Echinopla melanarctus* (Smith)	1		1	SC
Formicinae	*Echinopla tritshleri* (Forel)	4	9	13	SC
Formicinae	*Euprenolepis procera* (Emery)	44	143	187	TCS
Formicinae	*Euprenolepis varigata* (LaPolla)	28	26	54	TCS
Formicinae	*Lepisiota* sp 1 of SKY	1	1	2	O
Formicinae	*Myrmoteras barbouri* (Creighton)	4	5	9	SP
Formicinae	*Myrmoteras diastematum* (Moffett)	1	1	2	SP
Formicinae	*Oecophylla smaragdina* (Fabricius)	2		2	TCS
Formicinae	*Nylanderia* sp 1 of NZA**	6	20	26	O
Formicinae	*Nylanderia* sp 2 of SKY	180	22	202	O
Formicinae	*Nylanderia* sp 24 of SKY	27	1	28	O
Formicinae	*Paraparatrechina* sp 3 of NZA	5	172	177	O
Formicinae	*Polyrhachis* (*Campomyrma*) *equine* (Smith)	1		1	SC
Formicinae	*Polyrhachis* (*Myrma*) *carbonaria* (Smith)	1	1	2	SC
Formicinae	*Polyrhachis* (*Myrma*) *illaudata* (Walker)	1	10	11	SC
Formicinae	*Polyrhachis* (*Myrma*) *nigropilosa* (Mayr)	3	6	9	SC
Formicinae	*Polyrhachis* (*Myrma*) *obesior* (Viehmeyer)		5	5	SC
Formicinae	*Polyrhachis* (*Myrma*) *pubescens* (Mayr)		6	6	SC
Formicinae	*Polyrhachis* (*Myrmatophla*) sp 2 of NZA		7	7	SC
Formicinae	*Polyrhachis* (*Myrmhopla*) *abdominalis* (Smith)	1	21	22	SC
Formicinae	*Polyrhachis* (*Myrmhopla*) *arachne* (Emery)	17	4	21	SC
Formicinae	*Polyrhachis* (*Myrmhopla*) *armata* (Le Guillou)	42	3	45	SC
Formicinae	*Polyrhachis* (*Myrmhopla*) *furcata* (Smith)	19		19	SC
Formicinae	*Polyrhachis* (*Myrmhopla*) *maryatiae* (Kohout)		1	1	SC
Formicinae	*Polyrhachis* (*Myrmhopla*) *rufipes* (Smith)	1		1	SC
Formicinae	*Polyrhachis* (*Polyrhachis*) *bellicose* (Smith)	4		4	SC
Formicinae	*Polyrhachis* (*Polyrhachis*) *bihamata* (Drury)	5		5	SC
Formicinae	*Polyrhachis* (*Polyrhachis*) *orybria* (Forel)'	3	3	6	SC
Formicinae	*Polyrhachis proxima* (Roger)	3		3	SC
Formicinae	*Polyrhachis* sp 1 of NZA	3		3	SC
Formicinae	*Polyrhachis* sp 2 of NZA		3	3	SC
Formicinae	*Prenolepis* sp 2 of NZA	2		2	CCS

Appendix 2. Cont'd.

Subfamily	Species†	2008	2009	Total	Functional Group*
Formicinae	*Pseudolasius* sp 3 of NZA	12	24	36	TCS
Myrmicinae	*Acanthomyrmex ferox* (Emery)	3	31	34	TCS
Myrmicinae	*Aphaenogaster (Deromyrma)* sp 1 *of NZA*	2		2	O
Myrmicinae	*Cardiocondyla* sp 1 of NZA		2	2	O
Myrmicinae	*Cardiocondyla* sp 2 of NZA	3	13	16	O
Myrmicinae	*Cardiocondyla* sp 3 of NZA	8	19	O	
Myrmicinae	*Cataulacus* sp 1 of NZA**	1		1	TCS
Myrmicinae	*Crematogaster longipilosa* (Forel)	19		19	GM
Myrmicinae	*Crematogaster modiglianii* (Emery)	4		4	GM
Myrmicinae	*Crematogaster* sp 1 of NZA	12	7	19	GM
Myrmicinae	*Crematogaster* sp 2 of NZA	94	66	160	GM
Myrmicinae	*Crematogaster* sp 3 of NZA	386	297	683	GM
Myrmicinae	*Crematogaster* sp 4 of NZA	40	68	108	GM
Myrmicinae	*Crematogaster* sp 5 of NZA		2	2	GM
Myrmicinae	*Crematogaster* sp 6 of NZA		4	4	GM
Myrmicinae	*Crematogaster* sp 7of NZA	1	12	13	GM
Myrmicinae	*Crematogaster* sp 8 of NZA	1		1	GM
Myrmicinae	*Dacetinops cirrosus* (Taylor)		2	2	TCS
Myrmicinae	*Dilobocondyla* sp 1 of NZA	1		1	TCS
Myrmicinae	*Eurhopalothrix omnivaga* (Taylor)		6	6	C
Myrmicinae	*Eurhopalothrix seguensis* (Taylor)		3	3	C
Myrmicinae	*Eurhopalothrix* sp 1 of NZA	2		2	C
Myrmicinae	*Lophomyrmex bedoti* (Emery)	1843	1422	3265	TCS
Myrmicinae	*Lordomyrma* sp 3 of SKY	1	3	4	TCS
Myrmicinae	*Mayriella* sp 1 of NZA		5	5	TCS
Myrmicinae	*Meranoplus malaysianus* (Schoedl)	2	1	3	TCS
Myrmicinae	*Meranoplus mucronatus* (Smith)	53	114	167	TCS
Myrmicinae	*Monomorium nr hiten* (Terayama)		4	4	GM
Myrmicinae	*Monomorium* sp 3 of SKY		3	3	GM
Myrmicinae	*Monomorium talpa* (Emery)		1	1	C
Myrmicinae	*Monomorium brocha* (Bolton)	7	3	10	C
Myrmicinae	*Myrmecina* sp 1 of SKY	1		1	TCS
Myrmicinae	*Myrmecina* sp 14 of SKY	1		1	TCS
Myrmicinae	*Myrmecina* sp 2 of NZA	1	1	2	TCS
Myrmicinae	*Myrmecina* sp 20 of SKY		5	5	TCS
Myrmicinae	*Myrmicaria* sp 1 of NZA	1		1	O
Myrmicinae	*Myrmicaria* sp 2 of NZA	1		1	O
Myrmicinae	*Myrmicaria* sp 3 of NZA	3		3	O
Myrmicinae	*Myrmicaria* sp 4 of NZA		135	135	O
Myrmicinae	*Myrmicaria subcarinata* (Smith)	14	4	18	O
Myrmicinae	*Carebara* sp 1 of NZA		1	1	C
Myrmicinae	*Paratopula* sp 1 of NZA	11	4	15	TCS
Myrmicinae	*Paratopula* sp 2 of NZA	35		35	TCS
Myrmicinae	*Paratopula* sp 3 of NZA	1		1	TCS
Myrmicinae	*Paratopula* sp 4 of NZA		25	25	TCS
Myrmicinae	*Pheidole* sp 1 of NZA	54	58	112	GM
Myrmicinae	*Pheidole algae* (Forel)	3	1	4	GM
Myrmicinae	*Pheidole annexus* (Eguchi)		2	2	GM
Myrmicinae	*Pheidole aristotelis* (Forel)	49	52	101	GM
Myrmicinae	*Pheidole bluntschlii* (Forel)		10	10	GM
Myrmicinae	*Pheidole cariniceps* (Eguchi)	6	5	11	GM
Myrmicinae	*Pheidole elisae/sauberi*		22	22	GM
Myrmicinae	*Pheidole longipes* complex (Latreille)	14		14	GM
Myrmicinae	*Pheidole lucioccipitalis* (Eguchi)	10	1	11	GM
Myrmicinae	*Pheidole plagiaria* (Smith)	1	1	2	GM
Myrmicinae	*Pheidole plinii* (Forel)	8	6	14	GM
Myrmicinae	*Pheidole quadricuspis* (Emery)	3	5	8	GM
Myrmicinae	*Pheidole quinata* (Eguchi)		14	14	GM
Myrmicinae	*Pheidole rabo* (Forel)	11		11	GM
Myrmicinae	*Pheidole retivertex* (Eguchi)		5	5	GM
Myrmicinae	*Pheidole rugifera* (Eguchi)	2	3	5	GM
Myrmicinae	*Pheidole* sp 10 of NZA	143	141	284	GM
Myrmicinae	*Pheidole* sp 11 of NZA		1	1	GM

Appendix 2. Cont'd.

Subfamily	Species†	2008	2009	Total	Functional Group*
Myrmicinae	*Pheidole* sp 12 of NZA	3		3	GM
Myrmicinae	*Pheidole* sp 13 of NZA		4	4	GM
Myrmicinae	*Pheidole* sp 14 of NZA		2	2	GM
Myrmicinae	*Pheidole* sp 15 of NZA	97	89	186	GM
Myrmicinae	*Pheidole* sp 17 of NZA	14		14	GM
Myrmicinae	*Pheidole* sp 18 of NZA	1		1	GM
Myrmicinae	*Pheidole* sp 19 of NZA		15	15	GM
Myrmicinae	*Pheidole* sp 2 of NZA	105	18	123	GM
Myrmicinae	*Pheidole* sp 21 of NZA	68	15	83	GM
Myrmicinae	*Pheidole* sp 23 of NZA	102		102	GM
Myrmicinae	*Pheidole* sp 28 of NZA		3	3	GM
Myrmicinae	*Pheidole* sp 29 of NZA	45		45	GM
Myrmicinae	*Pheidole* sp 3 of NZA	69	14	83	GM
Myrmicinae	*Pheidole* sp 36 of NZA	14		14	GM
Myrmicinae	*Pheidole* sp 37 of NZA		31	31	GM
Myrmicinae	*Pheidole* sp 4 of NZA	21	3	24	GM
Myrmicinae	*Pheidole* sp 44 of NZA	1	93	94	GM
Myrmicinae	*Pheidole* sp 5 of NZA	2	2	4	GM
Myrmicinae	*Pheidole* sp 6 of NZA	2	13	15	GM
Myrmicinae	*Pheidole* sp 7 of NZA	36	85	121	GM
Myrmicinae	*Pheidole* sp 8 of NZA	37		37	GM
Myrmicinae	*Pheidole* sp 9 of NZA		1	1	GM
Myrmicinae	*Pheidole tawauensis* (Eguchi)	1		1	GM
Myrmicinae	*Pheidole tjibodana* (Forel)	2		2	GM
Myrmicinae	*Pheidologeton affinis* (Jerdon)	32	76	106	C
Myrmicinae	*Pheidologeton pygmaeus* (Emery)	18	5	23	C
Myrmicinae	*Pheidologeton silenus* (Smith)	174	61	235	C
Myrmicinae	*Pheidologeton* sp 5 of SKY	17	83	100	C
Myrmicinae	*Proatta butelli* (Forel)		1	1	TCS
Myrmicinae	*Pyramica jacobsoni* (Menozzi)		1	1	C
Myrmicinae	*Recurvidris browni* (Bolton)	137	70	207	C
Myrmicinae	*Recurvidris kemneri* (Wheeler&Wheeler)		4	4	C
Myrmicinae	*Solenopsis* sp 1 of SKY	2		2	C
Myrmicinae	*Strumigenys bryanti* (Wheeler)		4	4	C
Myrmicinae	*Strumigenys koningsbergeri* (Forel)		1	1	C
Myrmicinae	*Strumigenys labidogenys* (Roger)	1		1	C
Myrmicinae	*Strumigenys rotogenys* (Bolton)		2	2	C
Myrmicinae	*Strumigenys* sp 1 of NZA	3	19	22	C
Myrmicinae	*Tetramorium brevispinosus* (Stitz)		7	7	O
Myrmicinae	*Tetramorium insolens* (Smith)	3		3	O
Myrmicinae	*Tetramorium kheperra* (Bolton)		12	12	O
Myrmicinae	*Tetramorium kraepelini* (Forel)		6	6	O
Myrmicinae	*Tetramorium laparum* (Bolton)	1		1	O
Myrmicinae	*Tetramorium pacificum* (Mayr)	26	20	46	O
Myrmicinae	*Tetramorium* sp 2 of NZA	8	18	26	O
Myrmicinae	*Tetramorium* sp 23 of SKY	33	16	49	O
Myrmicinae	*Tetramorium* sp 3 of NZA	3		3	O
Myrmicinae	*Vollenhovia fridae* (Forel)	2		2	C
Ponerinae	*Anochetus* sp 1 of NZA	2	11	13	SP
Ponerinae	*Cryptopone* sp 1 of NZA		5	5	C
Ponerinae	*Diacamma nr intricatum* (Smith)	14	50	64	O
Ponerinae	*Emeryopone* sp A	1		1	SP
Ponerinae	*Hypoponera* sp 11 of NZA	2	5	7	C
Ponerinae	*Hypoponera* sp 12 of NZA	1	2	3	C
Ponerinae	*Hypoponera* sp 13 of NZA	1		1	C
Ponerinae	*Hypoponera* sp 3 of NZA		9	9	C
Ponerinae	*Hypoponera* sp 4 of NZA	4	8	12	C
Ponerinae	*Hypoponera* sp 5 of NZA		2	2	C
Ponerinae	*Hypoponera* sp 6 of NZA	1		1	C
Ponerinae	*Hypoponera* sp 7 of NZA	20	9	29	C
Ponerinae	*Hypoponera* sp 8 of NZA	1	3	4	C
Ponerinae	*Hypoponera* sp 9 of NZA		1	1	C
Ponerinae	*Leptogenys diminuta* (Smith)	1	1	2	SP

Appendix 2. Cont'd.

Subfamily	Species†	2008	2009	Total	Functional Group*
Ponerinae	*Leptogenys kraepalini* (Forel)	3	6	9	SP
Ponerinae	*Leptogenys mutabilis* (Smith)		5	5	SP
Ponerinae	*Leptogenys* sp 1 of NZA	2	1	3	SP
Ponerinae	*Leptogenys* sp 23 of SKY	3	2	5	SP
Ponerinae	*Myopias* sp 1 of NZA	3		3	SP
Ponerinae	*Odontomachus rixosus* (Smith)	46	62	108	SP
Ponerinae	*Odontoponera transversa* (Smith)	149	181	330	SP
Ponerinae	*Pachycondyla* (*Mesoponera*) close to sp 7 of SKY	2		2	SP
Ponerinae	*Pachycondyla aff. rubra* (Smith)	1		1	SP
Ponerinae	*Pachycondyla astuta* (Smith)		1	1	SP
Ponerinae	*Pachycondyla chinensis* (Emery)	5	13	18	SP
Ponerinae	*Pachycondyla* sp 15 of SKY	1		1	SP
Ponerinae	*Pachycondyla* sp 1 of NZA		256	256	SP
Ponerinae	*Pachycondyla* sp 2 of NZA		14	14	SP
Ponerinae	*Pachycondyla* sp 3 of NZA	207		207	SP
Ponerinae	*Platythyrea paralella* (Smith)		2	2	SP
Ponerinae	*Platythyrea* sp 9 of SKY		2	2	SP
Ponerinae	*Platythyrea* sp 1 of NZA	22		22	SP
Ponerinae	*Ponera* sp 2 of NZA		2	2	C
Ponerinae	*Ponera* sp 3 of NZA	2	3	5	C
Proceratiinae	*Discothyrea* sp 2 of NZA	1		1	C
Pseudomyrmicinae	*Tetraponera attenuata* (Smith)	2	1	3	TCS

*C: Cryptic species; DD: Dominant Dolichoderinae, GM: Generalised Myrmicinae; TCS: Tropical Climate Specialists; O: Opportunists; SC: Subordinate Componitini; SP: Specialist Predators.
**Suspected new species that have not been found elsewhere. Based on comparison with Seiki Yamane's collection (Kagoshima University).

†Abbreviations of NZA and SKY refer to morpho-species in collectors' collections. SKY= Seiki Yamane's collection (Kagoshima University), NZA = Nur-Zati's collection (FRIM).