

CHANGES IN ANT COMMUNITIES ACROSS A  
TROPICAL RAINFOREST LANDSCAPE WHICH  
INCLUDES OLD GROWTH AND TWICE-LOGGED  
AREAS IN SABAH, MALAYSIA

THOMAS E.M. BELL  
March 2015

A thesis submitted for the partial fulfilment of the requirements for the degree of Master of  
Research at Imperial College London

Formatted in the journal style of Ecological Entomology

Submitted for the MRes in Ecology, Evolution, and Conservation Biology

**Declaration**

The environmental data and ant specimens used for this study were collected by the Danum-Maliau Quantitative Inventory (DMQI) project, and sorted to family-level (Formicidae) by volunteers in the Soil Biodiversity Group, Life Sciences Department, Natural History Museum (London).

Identification to genus level was done by myself using the compound microscope. Photos for hard-to-identify individuals were taken using a compound light microscope, by myself with assistance from Elizabeth Psomas (Life Sciences Department, Imperial College London). A few images were sent to Tom Fayle (Forest Ecology and Conservation Group, Imperial College London) to confirm identifications.

I collated and somewhat processed the raw data on a Microsoft Excel spreadsheet. R code was written by myself, utilising the base R packages along with ggplot2 and betapart, which were downloaded through CRAN. Ordination was made using CANOCO 5.0, and was performed with the assistance of Paul Eggleton. Paul Eggleton was also helpful in suggesting tests to carry out in R, and reviewing some interpretations.

Thomas Bell, 26<sup>th</sup> March 2015.

Supervisor: Paul Eggleton (Natural History Museum)

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# CHANGES IN ANT COMMUNITIES ACROSS A TROPICAL RAINFOREST LANDSCAPE WHICH INCLUDES OLD GROWTH AND TWICE-LOGGED AREAS IN SABAH, MALAYSIA

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**THOMAS E.M. BELL**

*Department of Life Sciences, Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot, Berkshire, SL5 7PY, UK  
Email address: thomas.bell11@imperial.ac.uk*

26 March 2015

**Abstract**

1. The forests of Borneo, a global ant hotspot, are threatened by intensified logging and the conversion of forests into oil palm plantations. Previous logging has left a landscape including patches of old growth forest surrounded by twice-logged forests. The present study investigates the differences between leaf-litter ant communities in two old growth locations (Danum and Maliau) and one twice-logged location (SAFE).
2. Ants were collected from leaf-litter samples using Winkler bag extraction. Each ant was identified to genus level, and genera were classified into functional groups.
3. The three locations were found to have different genus compositions. Functional diversity between both old growth locations was very similar, but differed in the twice-logged location. These differences correlate strongly to location, but also to percentage of canopy cover.
4. All three locations are measurably different, highlighting the need to protect logged forests as well as old growth forests. SAFE is slightly more similar to Danum than Maliau, suggesting Danum as a preferable control for experiments in SAFE.

**Keywords:** Leaf-litter; community composition; ants; Formicidae; tropical forest; selective logging; land-use change; Sabah

## Introduction

Often overlooked, ants (Family: Formicidae) are key components of terrestrial ecosystems. Ant communities can constitute the largest biomass of any animal family in an ecosystem and carry out valuable roles in a range of ecosystem functions and services (Economo *et al.*, 2014). Ants are involved in various soil processes, pollination, and seed dispersal (Del Toro *et al.*, 2012). They act as ecosystem engineers (Bolton, 1994; Folgarait, 1998), creating their own microhabitats and redistributing nutrients (Del Toro *et al.*, 2012). Ant communities can be the largest consumer of rainforest vegetation (Wilson, 1987) and prey biomass, and thus primary production as a whole (Folgarait, 1998). They moderate pest populations and can control fungal outbreaks (Philpott & Armbrrecht, 2006). Ant communities exist in all rainforest strata, from the soil to the canopy (Brühl *et al.*, 1998), and are especially prominent in leaf-litter, where they can make up to 50% of leaf-litter macro-invertebrates (Brühl *et al.*, 2003). Understanding these communities is an essential part of understanding the ecosystems they are part of.

Ant species have huge diversity. Individual ants range from 1mm to 40mm, and colony sizes range from dozens to millions. Behaviour ranges from very docile to very aggressive, and dietary habits include carnivorous, herbivorous, and scavenging (Bolton, 1994). Despite this diversity, most ant species have only been studied taxonomically, leaving a great deal of ecological information undiscovered (Del Toro *et al.*, 2012). More than 12,500 species have been formally described, and perhaps that many again remain undescribed (Del Toro *et al.*, 2012). They are divided into 20 subfamilies, with this number likely to increase with further taxonomic analysis (Brady *et al.*, 2006). These 20 subfamilies comprise around 300 genera (Folgarait, 1998).

High species richness correlates with more extensive ecosystem functions (Gaston, 2000). Functional characteristics of ant communities strongly influence overall ecosystem properties, and species composition thus affects ecosystem functions (Hooper *et al.*, 2005). Ant communities have shown promise as environmental indicators and indicators for changes in biodiversity composition in other taxa (Majer *et al.*, 2007; Edwards *et al.* 2014), although there is disagreement on the matter (Lawton *et al.*, 1998).

Individual ant species can have strong effects on ant community composition (Del Toro *et al.*, 2012). The competitive exclusion and interference competition caused by an abundance increase of a dominant species can reduce overall ant richness (Andersen & Patel, 1994; Parr, 2008), and species have been found co-occur less than expected by chance (Sanders & Crutsinger, 2007). This can even reach the point where a change in community structure can

result in a decrease in species richness despite an overall increase in abundance (Folgarait, 1998). Similarly, in situations where a dominant species goes extinct, other species may flourish (Klimes *et al.*, 2011).

Ant communities are highly responsive to human impact, yet have strong resilience and can bounce back from temporary perturbations (Folgarait, 1998). Longer term changes, such as forest fragmentation or complete conversion of forest areas to agriculture, can lead to drastic declines in species richness (Brühl *et al.*, 2003; Philpott & Armbrrecht, 2006; Woodcock *et al.*, 2011). A small amount of disturbance, which opens up the forest, can actually increase species richness (Lawton *et al.*, 1998). Examples have also been seen where species composition and overall behaviour changes, yet overall species richness remains unaffected (Del Toro *et al.*, 2013).

The tropical forests of Sabah have some of the richest ant diversity in the world (Brühl *et al.*, 1998). This diversity is coming under threat. Only 8% of Sabah's original old growth forest is protected (Bryan *et al.*, 2013), and logging and other land-use conversion has in the past few decades intensified in unprotected areas (Brühl *et al.*, 2003). Of Sabah's forests in 1973, 40% was completely lost by 2010 (Gaveau *et al.*, 2014). Most of the remaining area, which is licenced for logging, has undergone a two-phases of selective logging. Under the existing logging regime, commercially valuable timber is selectively logged, and the forest is then left to regrow for 25 years before being logged again (Bryan *et al.*, 2013). 25 years is not a long time for forest regeneration, and even under that timeframe some areas have been logged prematurely (Reynolds *et al.*, 2011).

Selective logging not only damages commercially valuable tree species: around half of non-logged trees are also directly impacted by Sabah's logging activity (Bryan *et al.*, 2013). Over time the degradation of Sabah's forests have meant timber profits have fallen (Reynolds *et al.*, 2011). Recently there has been an expansion in oil palm (*Elaeis guineensis*) plantations throughout Malaysia. Such plantations are touted as tools of economic development (Basiron, 2007). One expansion of oil palm plantations is happening in a large area known as the Yayasan Sabah Forest Management Area, most of which is currently licenced for selective logging. The area also includes some virgin forests, including the protected Danum Valley Conservation Area and the protected Maliau Basin Conservation Area, as well as already existing oil palm plantations (Reynolds *et al.*, 2011). Further conversion of logged forest into oil palm plantation is ongoing in a location that is studied by the Stability of Altered Forest Ecosystems (SAFE) project (Ewers *et al.*, 2011).

The SAFE project's large-scale forest fragmentation experiment will increase understanding of the ecological impacts of such land-use changes. The presence of two old growth forest sites 100km apart (Danum and Maliau) presents an opportunity to assess natural variation. By examining this variation, and variation between these two old growth locations and the forests covered by the SAFE project, this study aims to gauge the variation in leaf-litter ant communities across the landscape covered by these sites, both old growth and twice-logged. This will be used to address the question of which old growth forest would be preferable as SAFE's old growth control. It is hypothesised that there will be variation between Danum and Maliau, but that they will be closer to each other than they are to SAFE. Leaf-litter ant communities will be quantified through examining genus richness, genus composition, functional composition, and overall abundance.

## Materials and Methods

This investigation sampled part of a larger collection curated as part of the Danum-Maliau Quantitative Inventory (DMQI), held by the Soil Biodiversity Group, Life Sciences Department, Natural History Museum (London).

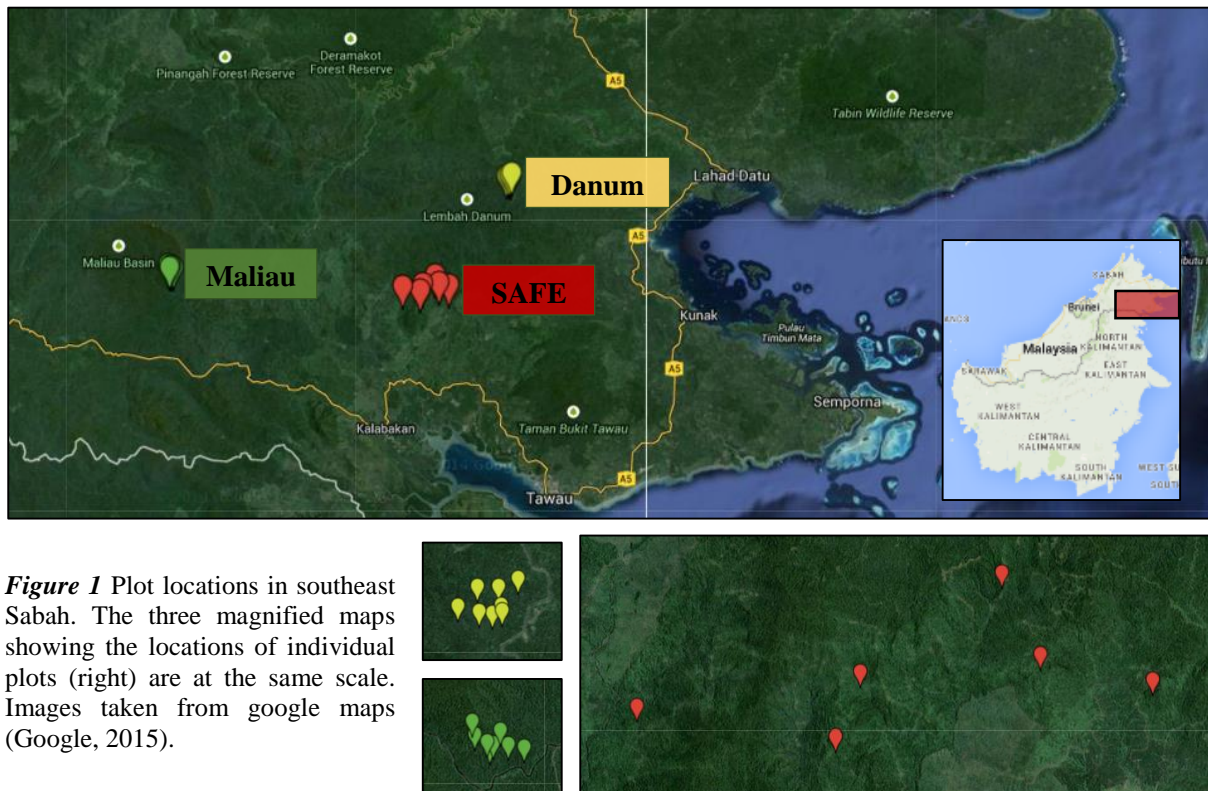
### *Study sites*

The DMQI collection was taken from three locations (Figure 1) in the southeast of the Malaysian state of Sabah. Sampling was conducted in September and October 2012. Two of the locations were old growth forest reserves: the Maliau Basin Conservation Area (4049'N, 116054'E) and the Danum Valley Conservation Area (4055'N, 117040'E). Eight plots were designated in each of these areas. The third location was an area of disturbed forest designated as a future oil plantation, which is the site of the Stability of Altered Forest Ecosystems (SAFE) project. Sampling here was from the standard six plots established by the SAFE project that have been disturbed to varying degrees by two rounds of selective logging (Ewers *et al.*, 2011).

### *Field sampling*

Among other sampling methods, a 100m transect was laid down in each plot, from which 1m<sup>2</sup> quadrats were designated every 7m. Leaf litter from each quadrat was collected into Winkler bag extractors, which were left to hang for 3 days, enough to collect an estimated 90% of ants

(Krell *et al.*, 2005). Soil temperature (sometimes referred to as temperature in this investigation) was recorded using a bi-metal thermometer. Soil moisture (sometimes referred to as temperature in this investigation) was measured using an SM200 probe and a HH2 meter, and was recorded as percentage of water-filled pore space (methodology employed in Carpenter *et al.*, 2012). Percentage of canopy cover (sometimes referred to as canopy cover in this investigation) was measured using a spherical densitometer, and latitude and longitude was taken from a GPS receiver.



**Figure 1** Plot locations in southeast Sabah. The three magnified maps showing the locations of individual plots (right) are at the same scale. Images taken from google maps (Google, 2015).

### Ant identification

This investigation uses leaf litter ant specimens from the Winkler bag samples, which were moved to the Natural History Museum and stored in 100% ethanol. Although analysis of specimens taken using a single sampling method has limitations in the quantification of ant biodiversity (Folgarait, 1998), Winkler bags for leaf-litter obtain the most ants per sample out of all standard ant capturing methods (Longino, Coddington & Colwell, 2002), even though they may miss the few ants longer than 15mm (Brühl *et al.*, 2003).

Ants were identified to genus using a Borneo ant-key (Fayle *et al.*, in prep. <http://www.tomfayle.com/Ant%20key.htm>) and through comparisons with the collections at the Natural History Museum. This was done using a compound microscope with a maximum magnification of 50x, supplemented with a compound light microscope equipped with an EOS



700D Canon camera for the few cases in which greater magnification was required. Only workers were counted, as they are responsible for ecosystem functions, as well as to reduce the probability of the inclusion of flying vagrants. Individuals were categorised to genus level. There is niche conservatism within genera (Andersen, 2000), so the genus level is useful for identifying functional roles. Genera were categorised according to divisions incorporating behaviour, dominance, feeding strategy, and temperature preferences set up by Andersen (2000) (Table 1). The few genera that contain species that fit into more than one category but were not included in the generalised myrmicinae category, were placed in just one. *Cerapachys* was classified as cryptic or specialist predator depending on subgenus; it is treated as cryptic here, cryptic being the functional group of the namesake subgenera *Cerapachys* *Cerapachys*. *Solenopsis* has one subgenera classified as cryptic, but the rest are tropical-climate specialists, and it is categorised as such here. Luke *et al.* (2014) classified some genera that were missing or vague in Andersen (2000) and was used to supplement Andersen (2000) for the following genera: *Nylanderia*, *Monomorium*, *Oechetullus*, *Paraparatrechina*, *Acropyga*, and *Anoplolepis*. *Pyramica* was classified as cryptic due to its close phylogenetic relationship and morphological resemblance to *Strumigenys*.

### *Statistical methods*

Statistical analyses were conducted using the R 3.1.2 statistics package (R Core Development Team, 2014) and CANOCO 5.01 (Petr Smilauer, 2014). Along with overall ant abundance, two simple measures of diversity were compared between locations using Kruskal-Wallis tests: genus richness, to see the range of ants supported, and Shannon index diversity using genera for species, as a quantifiable surrogate to represent changes in the tail and slope of genus rank-abundance curves. Kruskal-Wallis and pairwise Student's t-tests were used to test the combined signal of both old growth forests against the twice-logged SAFE plots. Generalised linear models were used to test abundance and both diversity measures for correlation to the environmental variables percentage of canopy cover, soil temperature, and soil moisture, using generalised linear models. An F-test was used to whether the variance in abundances differed between locations. Rank abundance was calculated using the BiodiversityR R package (Kindt & Coe, 2005).

A principal component analysis (PCA) and a redundancy analysis (RDA) were used to examine the correlative strength of the environmental variables with ant community composition, looking both at which genera are present and how many of each there are. The

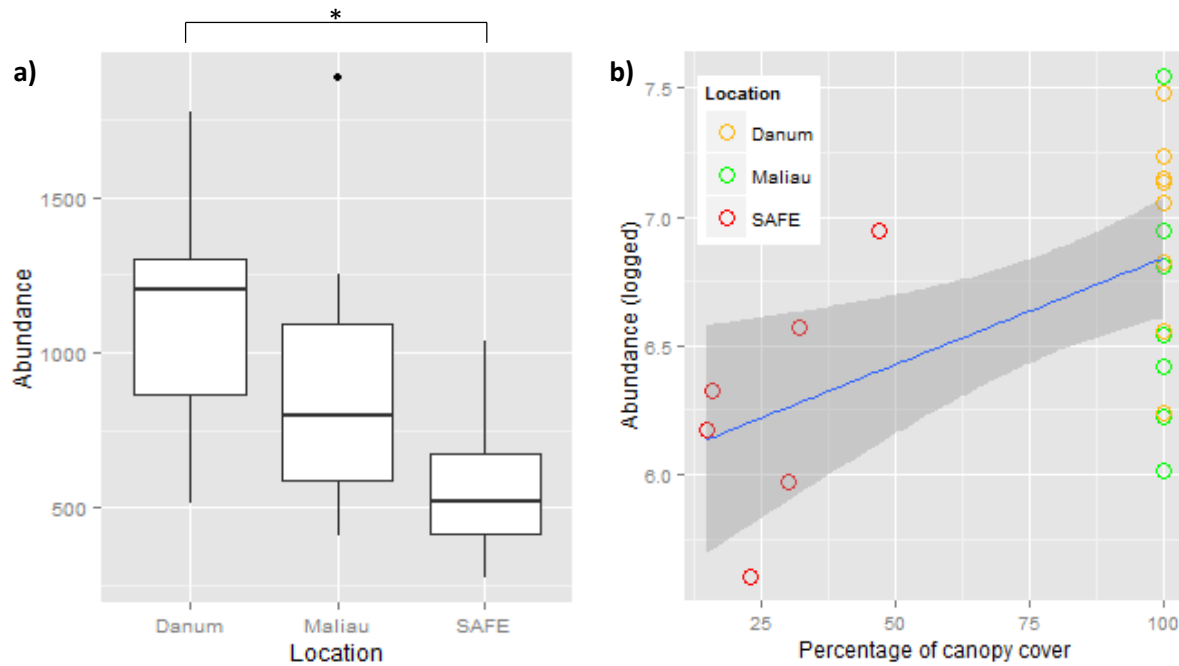
significance of each environmental variable's association with community structure was tested using Monte Carlo permutations with 499 randomisations. The RDA used forward selection to rank variables in by the closeness of their correlations, and selecting these with the highest marginal eigenvalues stepwise until the included variables covered enough variation that the missing variables were redundant. Beta diversity analysis between the three locations was examined using the Betapart R package (Baselga & Orme, 2012).

Functional group abundance differences between the three locations, and on a pairwise level between both old growth forests combined and SAFE, were examined using Kruskal-Wallis and pairwise Wilcoxon rank-sum tests. These tests were also used on pair-wise analyses between each pair of locations. Composition by functional group was analysed through a PCA and an RDA using the same methods used to analyse genus composition.

Satellite images were taken from Google Maps (Google Maps, 2015). Ordination images were made using CANOCO. Other graphs were made using R, using base R and the packages: BiodiversityR, betapart, and ggplot2 (Wickham, 2009).

**Table 1** The 70 genera found in this investigation broken down into the functional groups described in Andersen (2000). Those which could not be placed are grouped into Unknown.

Functional group	Genera included
Subordinate Camponotini (SC)	<i>Camponotus</i> , <i>Forelophilus</i> , <i>Polyrhachis</i>
Cold-climate specialists (CCS)	<i>Dolichoderus</i> , <i>Prenolepis</i>
Tropical-climate specialists (TCS)	<i>Acanthomyrmex</i> , <i>Acropyga</i> , <i>Aenictus</i> , <i>Anoplolepis</i> , <i>Cataulacus</i> , <i>Dilobocondyla</i> , <i>Euprenolepis</i> , <i>Gnamptogenys</i> , <i>Lophomyrmex</i> , <i>Lordomyrma</i> , <i>Myrmicaria</i> , <i>Oecophylla</i> , <i>Paratopula</i> , <i>Pristomyrmex</i> , <i>Proatta</i> , <i>Pseudolasius</i> , <i>Rotastruma</i> , <i>Solenopsis</i> , <i>Vollenhovia</i> , <i>Vombisidris</i>
Hot-climate specialists (HCS)	<i>Meranoplus</i>
Opportunists (O)	<i>Aphaenogaster</i> , <i>Cardiocondyla</i> , <i>Diacamma</i> , <i>Nylanderia</i> , <i>Odontomachus</i> , <i>Paraparatrechina</i> , <i>Paratrechina</i> , <i>Rhytidoponera</i> , <i>Tetramorium</i>
Generalised Myrmicinae (GM)	<i>Crematogaster</i> , <i>Monomorium</i> , <i>Pheidole</i> #
Specialist Predators (SP)	<i>Anochetus</i> , <i>Leptogenys</i> , <i>Myrmoteras</i> , <i>Pachycondyla</i> , <i>Platythyrea</i> , <i>Odontoponera</i>
Cryptic Species (C)	<i>Calyptomyrmex</i> , <i>Carebara</i> , <i>Cerapachys</i> , <i>Cryptopone</i> , <i>Dacatinops</i> , <i>Discothyrea</i> , <i>Emeryopone</i> , <i>Eurhopalothrix</i> , <i>Hypoponera</i> , <i>Leptanilla</i> , <i>Mayriella</i> , <i>Myopias</i> , <i>Myopopone</i> , <i>Mystrium</i> , <i>Pheidologeton</i> , <i>Plagiolepis</i> , <i>Ponera</i> , <i>Prionopelta</i> , <i>Probolomyrmex</i> , <i>Protanilla</i> , <i>Pyramica</i> , <i>Recurvidris</i> , <i>Strumigenys</i> #
Unknown (U)	<i>Lasiomyrma</i> , <i>Rhopalomastix</i> , <i>Secostruma</i>



**Figure 2** **a)** Ant abundance considered on the basis of location shows a significant difference between the plots of Danum and SAFE, but not between Maliau and either Danum or SAFE. **b)** Increasing ant abundance per plot correlates positively with increasing canopy cover. The grey shading represents the 95% confidence interval.

## Results

### *Trends in alpha diversity and abundance*

A total of 19,730 worker ants from 70 Genera were found across the 330 quadrats, with all but one quadrat containing ants. Genus richness was not significantly different across the three locations (Kruskal-Wallis,  $\chi^2 = 1.1776$ ,  $p = 0.555$ ) or between old growth forests and SAFE (Kruskal-Wallis,  $\chi^2 = 0.4478$ ,  $p = 0.5034$ ; Student's t-test,  $t = 0.6945$ ,  $p = 0.5063$ ), nor was it strongly correlated with percentage canopy cover (GLM, est = 0.01904,  $p = 0.405$ ), soil moisture (GLM, est = -0.01785,  $p = 0.875$ ), or soil temperature (GLM, est = 0.2843,  $p = 0.813$ ).

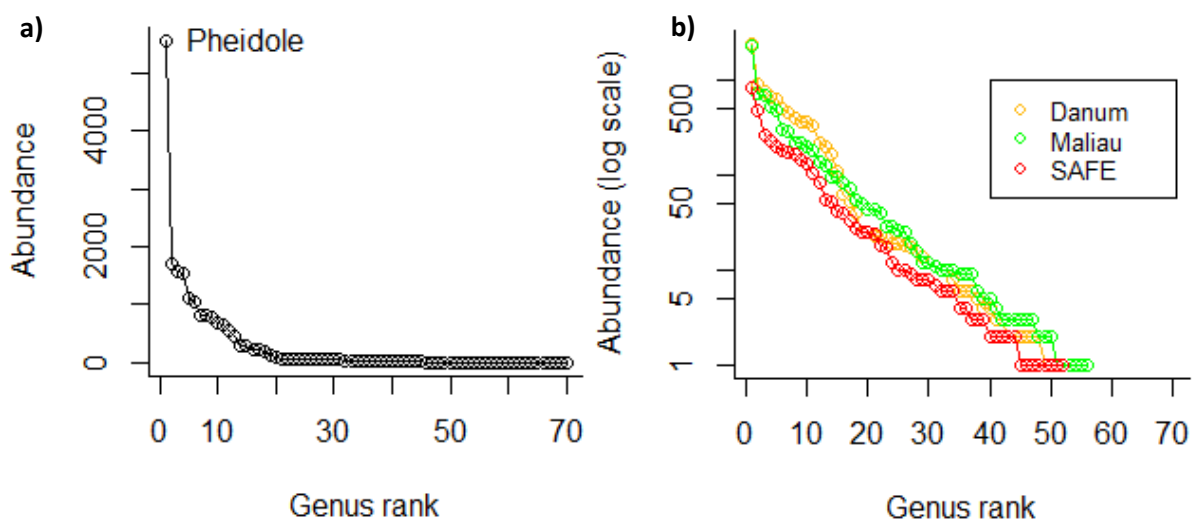
Community diversity, measured using the Shannon index, was undifferentiated across the three locations (Kruskal-Wallis,  $\chi^2 = 0.6709$ ,  $p = 0.715$ ) and between old growth and SAFE (Kruskal-Wallis,  $\chi^2 = 0.6576$ ,  $p = 0.4174$ ; Student's t-test,  $t = -0.8056$ ,  $p = 0.4308$ ), as well as being uncorrelated with canopy cover (GLM, est = -0.000838,  $p = 0.486$ ), moisture (GLM, est = 0.003660,  $p = 0.538$ ), or temperature (GLM, est = -0.06276,  $p = 0.3152$ ).

Total ant abundance was lower in SAFE than in the protected forests (Kruskal-Wallis  $\chi^2 = 4.7323$ ,  $p = 0.0296$ ; Student's t-test,  $t = 2.827$ ,  $p = 0.01272$ ), while not being significantly different between the two protected forests (Kruskal-Wallis  $\chi^2 = 1.5882$ ,  $p = 0.2076$ ; Student's t-test,  $t = 0.9441$ ,  $p = 0.3617$ ). However, Maliau by itself is not significantly different in

abundance from SAFE (Figure 2; Kruskal-Wallis  $\chi^2 = 2.209$ ,  $p = 0.1372$ ; Student's t-test,  $t = 1.6551$ ,  $p = 0.1254$ ), unlike Danum (Kruskal-Wallis  $\chi^2 = 5.4$ ,  $p = 0.02014$ ; Student's t-test,  $t = 3.0448$ ,  $p = 0.01025$ ). Total abundance also increases with canopy cover (Figure 2a; GLM,  $\text{est} = 0.4236$ ,  $p = 0.00887$ ). There is no difference in variance between abundances in the old growth forest plots and the SAFE plots (F-test,  $F = 0.9696$ ,  $p = 0.8692$ ). The very similar shapes of the rank-abundance curves of each location (Figure 3) imply the abundance changes are a net result of lower abundances in all genera, not a reduced number of genera.

### Comparison of genus composition

All three locations show very similar rank abundance curves (Figure 3), although each lacks some of the genera found in other plots. The eigenvalues for a PCA of genus composition and those of a constrained RDA (Figure 4) are not greatly different (Table 2), indicating no important environmental variables affecting genus composition differences have been missed. Monte Carlo tests (Table 2) indicate that canopy cover, moisture levels, location, latitude, and longitude all show a significant effect. However, an ordination using forward analysis leaves just canopy cover and location as significant, with the other explanatory variables being closely correlated with those two. The RDA shows clear cluster separation not only between the old growth forests and SAFE, but between both old growth forests. The Danum and Maliau plots are tightly clustered, the SAFE plots less so, with SAFE B even being slightly closer to the Danum sites than to the other SAFE plots.



**Figure 3** Rank abundance curves **a)** overall and **b)** per location. The four curves all follow very similar shapes, with the location abundances being represented on a log scale rather than an absolute scale. In each case *Pheidole* is by far the dominant genus. (For full details see the appendices.)

*Analysis of beta diversity*

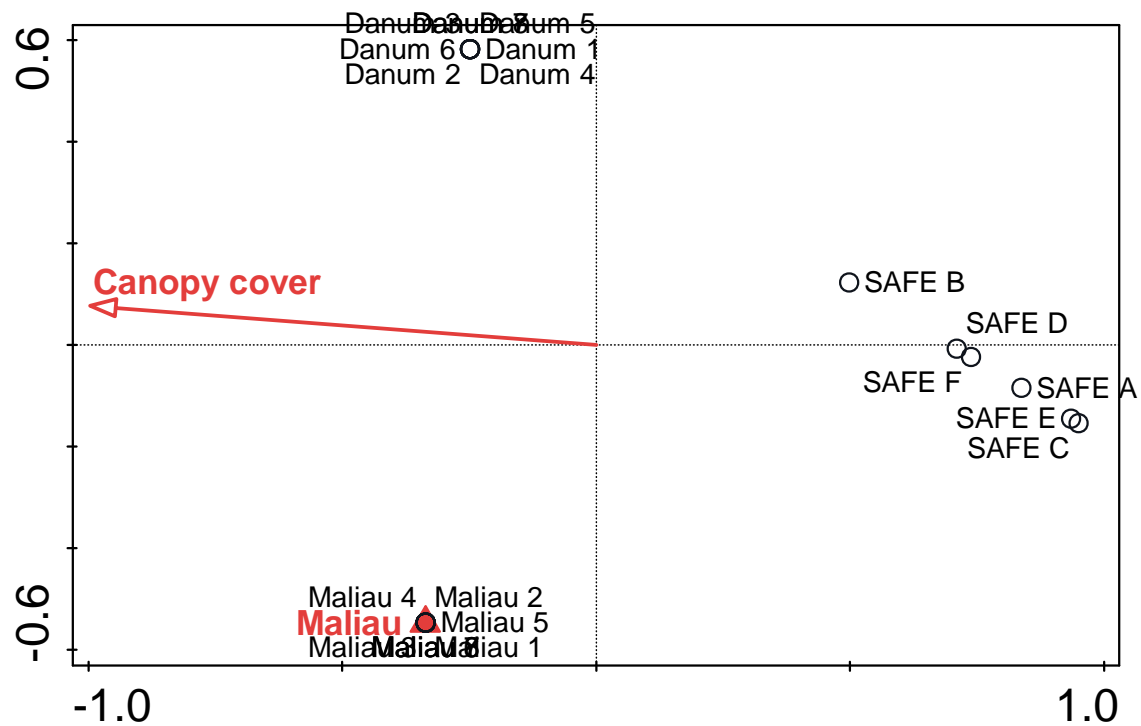
Beta diversity is mostly attributable to genus turnover (Figure 5), rather than a total gain or loss in genera. There is slightly less turnover between SAFE and Maliau than either has with Danum, although it is a very small amount compared to overall difference between all three. SAFE and Danum have slightly more similar composition than either has to Maliau, although the differences are not large. The rank-abundance curves for all three locations are very similar (Figure 3): all have fewer genera than the overall number, meaning some genera replaced others in the different locations, again highlighting the effect of turnover.

**Table 2** Eigenvalues for the PCA (unconstrained) and the RDA using the environmental variables (constrained) to examine genus composition, and the simple effects followed by the forward selection analysis for environmental variables in the RDA. Significant effects are in boldface.

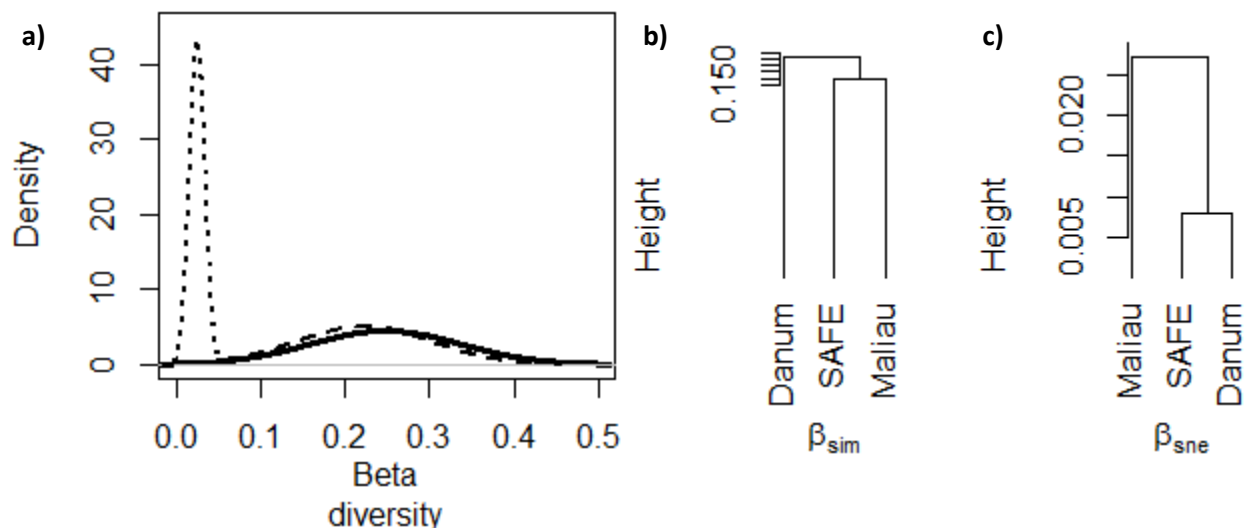
<i>Eigenvalues</i>		Axis 1	Axis 2	Axis 3	Axis 4
Unconstrained	Eigenvalues	0.1251	0.1023	0.0899	0.0727
	Explained variation (cumulative %)	12.51	22.74	31.73	39.00
Constrained	Eigenvalues	0.0750	0.0687	0.0378	0.1023
	Explained variation (cumulative %)	7.50	14.37	18.16	28.39

## Monte Carlo tests:

<i>Simple effects</i>	Explains %	Pseudo-F	<i>p</i> -value
<b>Canopy cover</b>	<b>7.4</b>	<b>1.6</b>	<b>0.006</b>
<b>Soil moisture</b>	<b>7.3</b>	<b>1.6</b>	<b>0.01</b>
<b>Location: SAFE</b>	<b>7.2</b>	<b>1.5</b>	<b>0.002</b>
<b>Location: Maliau</b>	<b>7.0</b>	<b>1.5</b>	<b>0.01</b>
<b>Longitude</b>	<b>6.8</b>	<b>1.5</b>	<b>0.006</b>
<b>Latitude</b>	<b>6.8</b>	<b>1.5</b>	<b>0.008</b>
<b>Location: Danum</b>	<b>6.7</b>	<b>1.4</b>	<b>0.014</b>
Soil temperature	5.6	1.2	0.168
<i>Conditional effects</i>	Explains %	Pseudo-F	<i>p</i> -value
<b>Canopy cover</b>	<b>7.4</b>	<b>1.6</b>	<b>0.006</b>
<b>Location: Maliau</b>	<b>6.8</b>	<b>1.5</b>	<b>0.002</b>



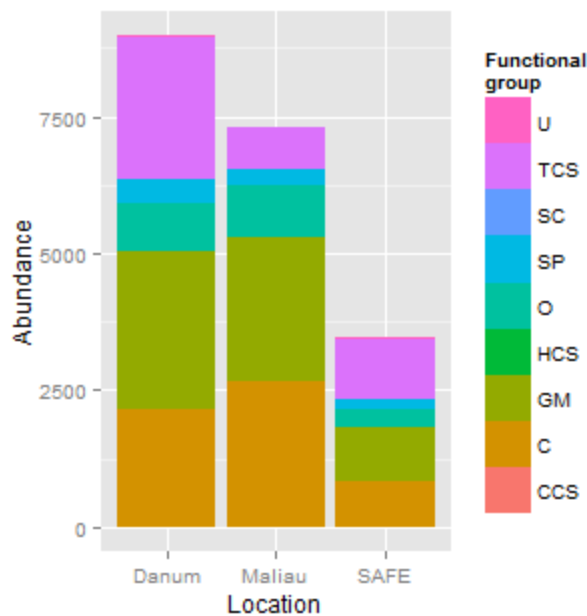
**Figure 4** An RDA run against canopy cover and the three locations show distinct clustering of plots around locations. SAFE is more spread out, with SAFE B being closer to Danum than SAFE. Although only one location is significant in the forward analysis and all three are included in the image, including each location on its own results in the same clustering effect.



**Figure 5 a)** Three different diversity measures are represented on this density plot. The overall Sørensen diversity (solid line) is a combination of Simpson's diversity (dashed line) and nested diversity (dotted line) (Baselga & Orme, 2012). The congruence of Sørensen diversity with Simpson's diversity indicates nested diversity plays a small role. **b)** There is slightly less Simpson's diversity difference between SAFE and Maliau than either to Danum. This is however by a very small amount compared to the long distance between all three. **c)** A pairwise analysis of nestedness places SAFE and Danum much closer to each other than either is to Maliau, although the overall effect is again small.

**Table 3** Different functional groups of ants (Table 1) showed different distribution patterns between the three sampled locations. The 3-location Kruskal is a Kruskal-Wallis test comparing all three locations. The other tests are pairwise Kruskal-Wallis and Wilcoxon tests. Old growth combines Danum and Maliau into one location for the purposes of that pairwise analysis. Significant results are in boldface.

	3-location Kruskal	Old growth ~ SAFE		Danum ~ Maliau		Danum ~ SAFE		Maliau ~ SAFE	
		Kruskal	Wilcoxon	Kruskal	Wilcoxon	Kruskal	Wilcoxon	Kruskal	Wilcoxon
CCS	$\chi^2=2.0877$ $p=0.3521$	$\chi^2=0.0614$ $p=0.8043$	W=46 $p=0.8526$	$\chi^2=2.1429$ $p=0.1432$	W=24 $p=0.17$	$\chi^2=1.3333$ $p=0.2482$	W=20 $p=0.3123$	$\chi^2=0.1313$ $p=0.7171$	W=26 $p=0.7858$
C	$\chi^2=8.1383$ $p=0.01709$	$\chi^2=7.8478$ $p=0.005088$	W=86 $p=0.00351$	$\chi^2=5.404$ $p=0.4622$	W=25 $p=0.5054$	$\chi^2=6.0167$ $p=0.01417$	W=43 $p=0.01265$	$\chi^2=6.0167$ $p=0.01417$	W=43 $p=0.01265$
GM	$\chi^2=4.3903$ $p=0.1113$	$\chi^2=3.962$ $p=0.04654$	W=75 $p=0.04873$	$\chi^2=0.1765$ $p=0.6744$	W=36 $p=0.7209$	$\chi^2=5.4$ $p=0.02014$	W=42 $p=0.01998$	$\chi^2=1.35$ $p=0.2453$	W=33 $p=0.2824$
HCS	$\chi^2=9.3455$ $p=0.009346$	$\chi^2=9.0707$ $p=0.002597$	W=18 $p=0.003061$	$\chi^2=1$ $p=0.3173$	W=28 $p=0.3816$	$\chi^2=6.6943$ $p=0.009672$	W=8 $p=0.01219$	$\chi^2=4.4368$ $p=0.03517$	W=10 $p=0.04224$
O	$\chi^2=5.5481$ $p=0.06241$	$\chi^2=4.8941$ $p=0.02695$	W=78 $p=0.0296$	$\chi^2=1.2178$ $p=0.2698$	W=42.5 $p=0.2933$	$\chi^2=3.75$ $p=0.05281$	W=39 $p=0.05927$	$\chi^2=3.75$ $p=0.05281$	W=39 $p=0.05927$
SP	$\chi^2=1.8217$ $p=0.4022$	$\chi^2=0.6584$ $p=0.4171$	W=59 $p=0.4386$	$\chi^2=1.2196$ $p=0.2694$	W=42.5 $p=0.2929$	$\chi^2=1.35$ $p=0.2453$	W=33 $p=0.2824$	$\chi^2=0.0668$ $p=0.796$	W=26 $p=0.8463$
SC	$\chi^2=1.1089$ $p=0.5744$	$\chi^2=0.6781$ $p=0.4102$	W=38.5 $p=0.4353$	$\chi^2=0.4167$ $p=0.5186$	W=27 $p=0.5613$	$\chi^2=1.1433$ $p=0.2849$	W=17 $p=0.3208$	$\chi^2=0.1313$ $p=0.7171$	W=21.5 $p=0.7719$
TCS	$\chi^2=8.5563$ $p=0.01387$	$\chi^2=0.6576$ $p=0.4174$	W=37 $p=0.4494$	$\chi^2=7.4559$ $p=0.006323$	W=58 $p=0.004662$	$\chi^2=0.4167$ $p=0.5186$	W=29 $p=0.5728$	$\chi^2=4.2667$ $p=0.03887$	W=8 $p=0.04262$
U	$\chi^2=3.2365$ $p=0.1982$	$\chi^2=1.6459$ $p=0.1995$	W=65 $p=0.2131$	$\chi^2=1.953$ $p=0.1623$	W=45 $p=0.179$	$\chi^2=2.2793$ $p=0.1311$	W=35.5 $p=0.1487$	$\chi^2=0.5528$ $p=0.4572$	W=29.5 $p=0.4991$



**Figure 6** Total abundance broken into functional groups for the three locations. If all else was equal, the SAFE column would be  $\frac{3}{4}$  the height of the other two due to the different numbers of plots.

### Functional group composition

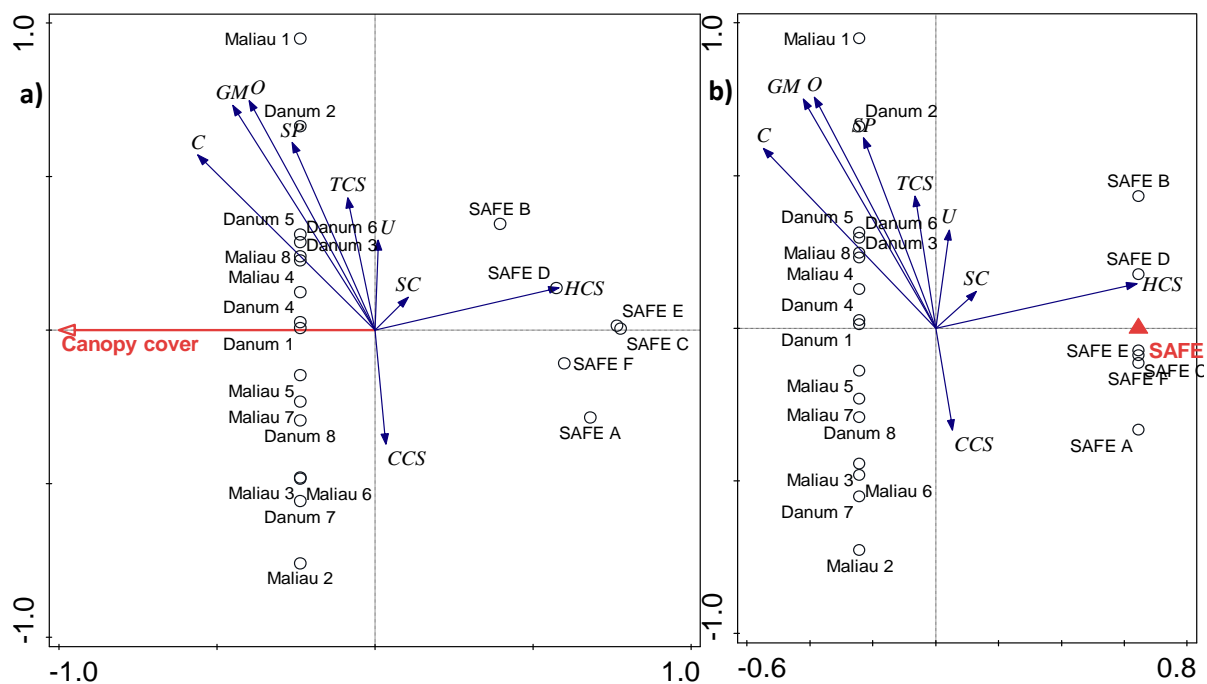
Cryptic species are significantly less abundant in SAFE than in either old-growth forests (Table 3). Opportunists showed a similar trend, although not as strongly, as although the old growth forest is significantly different to SAFE, the pairwise analyses of SAFE against the two old growth forests were not quite significant to the  $p < 0.05$  level, but were quite close ( $p < 0.10$ ).

Genera in the hot-climate specialist group showed the opposite effect, more common in SAFE than the old growth forests (Figure 6).

The abundance of the general myrmicinae functional group reflects that of the overall

functional group, with a difference between old growth and SAFE that is caused by Danum-SAFE differences, while Maliau is not significantly different from either. Tropical-climate specialists are relatively far fewer in Maliau than Danum and SAFE, while Danum and SAFE show no significant differences with each other.

There is a much larger difference in eigenvalues between the PCA and RDA when examining community composition based on functional groups (Table 4) than the one based on individual genera (Table 2). In the Monte-Carlo simple effects test, canopy cover was again significant, but in contrast to the effect when looking at all genera composition, only the SAFE location was significantly different, implying less distinction between Danum and Maliau. Furthermore, canopy cover and SAFE location both eliminate the other in forward analysis, implying a greater overlap in effect. Nonetheless, SAFE does cluster separately from Maliau and Danum, whose plots are this time undifferentiated, implying the difference in tropical-climate specialist abundance is outweighed by the similarities in the other functional groups.



**Figure 7** a) An RDA of canopy cover shows the SAFE sites separated from the main cluster, with a high level of hot-climate specialists. SAFE B is again closer to the old growth forests than the other sites, although there is no clear Maliau-Danum distinction. b) An RDA looking at the effect of just the SAFE location shows a similar pattern.



**Table 4** Eigenvalues for the PCA (unconstrained) and the RDA using the environmental variables (constrained) to examine functional group composition, and the simple effects followed by the forward selection analysis for environmental variables in the RDA. Significant effects are in boldface. The forward selection conditional effects are shown as two table because using either canopy cover or the SAFE location makes the other redundant, and so each is a separate analysis.

<i>Eigenvalues</i>		Axis 1	Axis 2	Axis 3	Axis 4
Unconstrained	Eigenvalues	0.3249	0.1724	0.1442	0.1328
	Explained variation (cumulative %)	32.49	49.72	64.14	77.42
Constrained	Eigenvalues	0.1405	0.1084	0.0549	0.0424
	Explained variation (cumulative %)	14.05	24.90	30.39	34.63

Monte Carlo tests:

<i>Simple effects</i>	Explains %	Pseudo-F	<i>p</i> -value
<b>Location: SAFE</b>	<b>12.4</b>	<b>2.8</b>	<b>0.016</b>
<b>Canopy cover</b>	<b>12.3</b>	<b>2.8</b>	<b>0.006</b>
Latitude	9.3	2.1	0.058
Soil moisture	8.9	1.9	0.076
Location: Danum	8.6	1.9	0.072
Location: Maliau	7.4	1.6	0.096
Longitude	6.8	1.5	0.192
Soil temperature	6.8	1.5	0.156

<i>Conditional effects 1</i>	Explains %	Pseudo-F	<i>p</i> -value
<b>Canopy cover</b>	<b>12.3</b>	<b>2.8</b>	<b>0.006</b>

<i>Conditional effects 2</i>	Explains %	Pseudo-F	<i>p</i> -value
<b>Location: SAFE</b>	<b>12.4</b>	<b>2.8</b>	<b>0.016</b>

## Discussion

The results illustrate significant differences between the ant communities in all three studied locations. These differences correlate with two main factors, the percentage of canopy cover, and the location itself. A reduction in canopy cover has important effects on a number of other factors, increasing the maximum air and soil temperatures, increasing the vapour pressure deficit, and lowering humidity (Hardwick *et al.*, 2015).

The eigenvalues for genus composition (Table 2) imply no important factors are missing, but location by itself is not ultimately very useful as a causative variable, and holds within it as yet unknown significant environmental factors. Given these are leaf-litter communities, strong effects are likely to come from factors affecting leaf litter, which future studies should measure. Variation in litter depth is known to influence ant assemblages (Zakaria, 2014). Vegetation structure and composition plays an important role in leaf litter decomposition (Vanconcelos & Laurance, 2005), heterogeneity (Barton *et al.*, 2010), and nutrient quantity (Sundarapandian & Swamy, 1999). Even the density of trees, something that would vary greatly in logged forests, affects leaf-litter structure (Donoso *et al.*, 2013).

Bornean rainforests are predominantly Dipterocarpaceae, but vegetation composition varies greatly on local scales (Slik *et al.*, 2003). In Danum Dipterocarpaceae shares its dominance with Euphorbiaceae (Newbery *et al.*, 1992). There seem to be few, if any, studies comparing vegetation structure in the Danum and Maliau areas specifically, but it is known Danum has more extensive ground cover while Maliau has taller trees (Benedick *et al.*, 2006).

### *Alpha diversity and abundance*

The effect of disturbance on alpha diversity is unclear. Most studies (Sakchoowon *et al.*, 2008; Woodcock *et al.*, 2011; Zakaria, 2014) see higher species diversity in old growth forests than logged forests, but this is not always the case. Bishop (2012) saw no change with disturbance. Luke *et al.* (2014) saw higher diversity in twice-logged forests. Lawton *et al.* (1998) found a parabolic relationship of species diversity with disturbance which rose from old growth forests and peaked in slightly disturbed forests, before decreasing. On the decreasing slope was mechanical disturbance of the sort that occurred in the twice-logged forests studied here. This study showed genus richness as unchanged between all studied locations.

Sakchoowon *et al.* (2008) found that although logged forests had lower abundance and species diversity, they had the same evenness as old growth forests. The lack of differentiation

in the Shannon index despite abundance changes and the similarity the location rank-abundance curves (Figure 3) indicate that evenness remained constant in this study as well.

Differences between all these studies may arise from a few reasons. This analysis, done at the genus level, will not pick up finer changes that many analyses, which work with species or morphospecies, pick up. Decrease will be obscured in genus-level studies as it is far more likely that a species will go extinct than every species in a genus. Similarly an increase will not be obscured if it is from an existing genus, which is especially plausible for a dominant genus such as *Pheidole*.

A second consideration to take into account is spatial scale. Woodcock *et al.* (2011) found that while there were species richness differences between old growth and logged forests at small spatial scales, such differences decreased as the areas being compared grew larger, meaning old growth forests had a higher density of species rather than more species overall. Different methodologies may thus produce different results, especially as the rate of change as the spatial scale increases may be different for different ant communities. This study took single long transects, and so would miss any smaller scale differences that methodology using independent quadrats would detect. Nonetheless, the lower abundance in SAFE suggests a density difference exists, as given there were on average fewer ants per quadrat, there are likely fewer genera per quadrat area as well, despite the overall equivalence of genus richness.

An important difference in methodology involves the strata examined. Each strata community has unique dynamics and responds to environmental change in different ways (Folgarait, 1998). 75% of ant species are found only in one strata (Brühl *et al.*, 1998), so although species richness between strata can sometimes correlate (Lawton *et al.*, 1998), there will be compositional differences. Canopy ants for example have been shown to be more abundant in secondary forests, yet are less resistant to perturbation (Klimes *et al.*, 2011). Luke *et al.* (2014) finding a higher abundance in logged forests and even oil palm plantations than in old growth forests is likely due to the strata examined: a lack of canopy cover will directly reduce the habitat available to leaf-litter dwellers, while ant species that nest in soil will still have sufficient nesting locations (Andersen, 2000).

Differing methodology also affects comparisons of abundance. As with genus richness, the methodology employed in this study took abundance at a plot level. A high level of variation is expected to be caused by this sampling, with the sampling method prone to anomalous high abundances if the single transect in each plot crosses areas of high abundance, such as nests and ant trails. Given this inherent variation, having a significant positive correlation between percentage canopy cover and abundance is a strong indication of

percentage canopy cover's importance. Luke *et al.* (2014) used an occurrence based method, summing up presence/absence across individual quadrats to get an overall plot value. This method eliminates extreme local variations that may be the product of ant nests and trails in exchange for gauging ubiquity across a plot. Their abundance results would thus differ from the ones in this study not only due to strata, but also due to being more varied on smaller scales.

### *Genus composition and structure*

Composition changes between old growth and logged forests have been seen in other studies (Sakchoowon *et al.*, 2008; Woodcock *et al.*, 2011). The genus composition differences found between Danum and Maliau here are not unique; Tawatao *et al.* (2014) also found species composition varied greatly between different old growth forest patches in Sabah. Brühl *et al.* (2003) found that common species were present across all forests, but fragmented forests lacked rare species, which is likely a linked effect to the spatial scale-richness interaction described above.

It is hard to determine what causes specific species assemblages (Gaston, 2000). Bishop (2012) suggests ant communities in old growth and highly disturbed habitats are both deterministically assembled, whereas those in areas of intermediate disturbance (such as selective logging) are stochastically assembled. Fayle, Turner & Foster (2013) describe how ant communities form mosaics in disturbed habitats, based on dominant species establishing territory, but that no defined mosaics are found in old growth forests.

Composition varied within SAFE far more than in Danum or Maliau. This may be due to the variance in percentage canopy cover, but may also be a spatial effect resulting from SAFE's plots being more spread out than Danum's or Maliau's (Figure 1). SAFE B is closer to Danum sites than the other SAFE plots, probably due to the effect of canopy cover (Figure 4), as SAFE B has the highest percentage canopy cover of all SAFE plots, at 50%.

As in this study, Luke (2010) noted high ant turnover between old growth and logged forests. Sharp (2014), in a study of beetle taxa from the same area, showed that beetle turnover was affected by both disturbance level and distance from the other plots. This study suggests a similar effect. That SAFE's plots, especially SAFE B, are slightly closer to Danum than Maliau (Figure 4) implies SAFE's genus composition is more similar to Danum's than Maliau's. The nestedness of Danum and SAFE (Figure 5) also supports this interpretation, although the effect is small and overshadowed by changes due to turnover.

*Functional identities*

Grouping the genera according to Andersen's (2000) functional groups clearly shows some functional groups dominating in abundance. General myrmicinae is the largest functional group, even though it only contains three genera: *Pheidole*, *Crematogaster*, and *Monomorium*. The general myrmicinae abundance trend reflecting the overall abundance trend is possibly a reflection on how dominant the three genera involved are in this environment. *Pheidole* by itself made up over a quarter of all ants found in this study (Appendix 1). Economo *et al.* (2014) notes *Pheidole* makes up 8% of all described ant species globally and is the dominant genus in tropical ecosystems, likely due to a propensity for adaptive radiation.

Cryptic species and opportunists appear to be disadvantaged by logging, reducing in relative abundance. Cryptic species are small and rely on leaf litter and dead wood to nest and forage in (Andersen, 2000), both of which are likely reduced in abundance in twice-logged forests with fewer trees. Opportunists are uncompetitive generalists (Andersen, 2000), and so it is hard to pinpoint why they are decreasing. They are potentially being pushed out of previously occupied niches by the small numbers of hot-climate specialists coming into SAFE.

The hot-climate specialist group, whose small abundance is nonetheless significantly higher in SAFE than elsewhere, consists only of the genus *Meranoplus*. Hot climate specialists are linked with higher temperatures (Andersen, 2000), and so may be responding to the increase maximum temperatures caused by logging. As they are absent from Danum and numbered only three in Maliau, they may be invading the area through the logged forests. Disturbance of an established species composition makes it easier for invaders to establish themselves (Hooper *et al.*, 2005). Other studies have found that the even more open oil palm plantations are open to invasives (Fayle, Turner & Foster, 2013; Konopik *et al.*, 2014). Luke *et al.* (2014) did not find hot-climate specialists, which may be an effect of examining different strata. They did however find dominant dolichoderinae only in the oil palms, a group not found in this study which is even more dependent on open space and high temperatures than hot-climate specialists (Andersen, 2000), and may represent a similar instance of invasion.

Other studies give clues as to what direct functional roles change. Gleave (2013) found invertebrates in logged forests play less of a role in seed dispersal than in unlogged forests; it may possibly be easier for vertebrates to access the seeds in a more open environment with less leaf litter. Senior *et al.* (2013) looking at the very open oil palm plantations found high abundances in many species from lower trophic levels that have very low abundances in forests. Bishop (2012) who looked at functional metrics rather than functional groups found 2 which

changed with habitat types. Interestingly one of the two metrics separated oil palm plantations from old growth and logged forests, while the other separated old growth from logged forests but separated neither from oil palm plantations, indicating that functional groups are not simply responding linearly to changes in canopy cover or other environmental variables.

Despite Danum and Maliau having very different genus compositions, they had very similar functional composition, implying any turnover was between species of the same functional group. Maliau's abundance difference with Danum is almost entirely due to a large drop in tropical-climate specialists (Figure 6). SAFE on the other hand shows no significant difference to Danum in relative tropical-climate specialist abundance. Tropical-climate specialist ants are often generalists except for their preference for humid areas (Andersen, 2000). Given the closer proximity of Danum and SAFE, there is possibly a humidity difference between those two areas and Maliau causing the abundance change. This may be because of their being closer to the coast than Maliau. Alternatively, the different vegetation structures discussed above may result in Maliau having microclimates unsuitable for tropical-climate species. Notably, as genus richness is undifferentiated, the tropical-climate specialist genera are still present in Maliau, but are unable to proliferate as they do in Danum and SAFE.

That species composition can change without affecting functional roles is supported by other studies from the same area. Luke (2010) found that ant and termite species assemblages change due to changes in the environment and the other's assemblage, but overall ant-termite interactions remain the same. Konopik *et al.* (2014) found that ant-predating frogs find similar prey in differently locations, again with different species. Fayle *et al.* (2015) found different assemblages of fern-associating ants carrying out the same roles in different locations.

### *Implications*

The redundancy seen between location and canopy cover in this study is a problem which could easily manifest in other studies, especially if there is only one control forest. Although a perfect control is impossible, problems such as this redundancy should be minimised as much as is possible. Despite the large differences between all three locations, this study does suggest that Danum's leaf-litter ant community is more similar to SAFE's than Maliau's is. In addition to being geographically closer, Danum and SAFE's more similar nested beta diversity indicates more shared genera, and their shared high abundance of tropical-climate specialists suggests the environments share similarities lacking in Maliau. Thus for SAFE, Danum seems to be a better old growth control site than Maliau. Although some studies have used Danum as their

chosen old growth site (eg. Fayle *et al.*, 2015), many others used Maliau (eg. Bishop, 2012; Luke *et al.*, 2014; Konopik *et al.*, 2014; Hardwick *et al.*, 2015).

This is not to say that Danum is closer to SAFE than it is to Maliau: both old growth areas share closer abundances in most functional groups. The twice-logged forest here clearly maintains a different ant community to that of the old growth forests. Happily, despite the overall degradation of Sabah's environment, protected areas are not just paper parks as the government enforces the protection afforded to them (Reynolds *et al.*, 2011). Additionally, the designation of two separate parks has resulted in a greater range of species being protected, as evidenced by their differences in genus composition in this study.

Less happily, as this study and many others mentioned above have indicated, these old growth forests do not protect all diversity. SAFE's different species composition means the existence of some protected pockets of forest is no reason to become complacent about species diversity and extinction risks. The spread of oil palm plantations may continue, especially if it becomes seen as an easy fix to a lack of commercial timber profit. These plantations not only directly destroy patches of forest, but break up the connections between the remaining areas. Ant species composition in continuous secondary Bornean forest has been found to be more similar to old growth reserves than fragmented patches of forest (Tawatao *et al.*, 2014). Selectively-logged forests can support up to 70% of their original species (Edwards *et al.*, 2014). If development of the areas must happen, it must aim to mitigate damage to these communities (Ewers *et al.*, 2011). For example, that long stretches of forest along riverbanks in oil palm plantations maintain much of the diversity of continuous logged forest elsewhere (Gray *et al.*, 2015) suggests that locating oil palm plantations in such a way that wildlife corridors are maintained, rather than the contiguous blocks that exist today, may be part of a solution.

Whatever the solution, many authors agree that twice-logged forests deserve as much protection as the current old growth forests have (eg. Luke, 2010; Gaveau *et al.*, 2014; Zakaria, 2014). Oil palm plantations maintain as few as 5% of original ant species (Woodcock *et al.*, 2011). The losses incurred in their development are not restricted to a loss in species diversity, but also a loss in the ecosystem functions and services they would otherwise provide. With palm plantations rapidly expanding over the already denuded forests of Malaysian Borneo (Bryan *et al.*, 2013), damaged forests remain preferable to anything that would replace them.

## Acknowledgements

Large thanks goes to Dr. Paul Eggleton, who supervised the project and provided guidance, as well as to the volunteers who sorted out the DMQI samples to family level. Thanks also to Elizabeth Psomas, who assisted with light microscopy and was a constant source of encouragement in the lab.

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**Appendices:** Ant genus abundances**Appendix 1** Overall

<b>Genus</b>	<b>Rank</b>	<b>Abundance</b>	<b>Proportion (%)</b>
<i>Pheidole</i>	1	5556	28.2
<i>Nylanderia</i>	2	1696	8.6
<i>Strumigenys</i>	3	1579	8.0
<i>Lophomyrmex</i>	4	1537	7.8
<i>Carebara</i>	5	1116	5.7
<i>Lordomyrma</i>	6	1055	5.3
<i>Hypoponera</i>	7	815	4.1
<i>Pheidologeton</i>	8	804	4.1
<i>Pseudolasius</i>	9	792	4.0
<i>Pachycondyla</i>	10	698	3.5
<i>Crematogaster</i>	11	652	3.3
<i>Ponera</i>	12	566	2.9
<i>Acropyga</i>	13	440	2.2
<i>Monomorium</i>	14	302	1.5
<i>Pyramica</i>	15	292	1.5
<i>Mayriella</i>	16	236	1.2
<i>Odontomachus</i>	17	210	1.1
<i>Solenopsis</i>	18	205	1.0
<i>Cardiocondyla</i>	19	118	0.6
<i>Myrmecaria</i>	20	82	0.4
<i>Acanthomyrmex</i>	21	73	0.4
<i>Odontoponera</i>	22	64	0.3
<i>Eurhopalothrix</i>	23	62	0.3
<i>Leptogenys</i>	24	58	0.3
<i>Vollenhovia</i>	25	54	0.3
<i>Proatta</i>	26	47	0.2
<i>Secostruma</i>	27	46	0.2
<i>Rotastruma</i>	28	46	0.2
<i>Cerapachys</i>	29	45	0.2
<i>Anochetus</i>	30	44	0.2
<i>Euprenolepis</i>	31	44	0.2
<i>Myrmoteras</i>	32	42	0.2
<i>Rhytidoponera</i>	33	33	0.2
<i>Cryptopone</i>	34	32	0.2
<i>Tetramorium</i>	35	29	0.1
<i>Meranoplus</i>	36	28	0.1
<i>Pristomyrmex</i>	37	22	0.1

Genus	Rank	Abundance	Proportion (%)
<i>Paratopula</i>	38	22	0.1
<i>Diacamma</i>	39	20	0.1
<i>Recurvidris</i>	40	19	0.1
<i>Prionopelta</i>	41	18	0.1
<i>Dacotinops</i>	42	14	0.1
<i>Aphaenogaster</i>	43	13	0.1
<i>Gnamptogenys</i>	44	12	0.1
<i>Platythyrea</i>	45	12	0.1
<i>Lasiomyrma</i>	46	8	0.0
<i>Polyrhachis</i>	47	7	0.0
<i>Myopopone</i>	48	6	0.0
<i>Oecophylla</i>	49	6	0.0
<i>Paraparatrechina</i>	50	6	0.0
<i>Protanilla</i>	51	6	0.0
<i>Myopias</i>	52	5	0.0
<i>Discothyrea</i>	53	5	0.0
<i>Mystrium</i>	54	4	0.0
<i>Rhopalomastix</i>	55	3	0.0
<i>Plagiolepis</i>	56	3	0.0
<i>Anoplolepis</i>	57	2	0.0
<i>Camponotus</i>	58	2	0.0
<i>Emeryopone</i>	59	2	0.0
<i>Aenictus</i>	60	2	0.0
<i>Dolichoderus</i>	61	2	0.0
<i>Forelophilus</i>	62	2	0.0
<i>Dilobocondyla</i>	63	2	0.0
<i>Calyptomyrmex</i>	64	1	0.0
<i>Vombisidris</i>	65	1	0.0
<i>Prenolepis</i>	66	1	0.0
<i>Paratrechina</i>	67	1	0.0
<i>Cataulacus</i>	68	1	0.0
<i>Leptanilla</i>	69	1	0.0
<i>Probolomyrmex</i>	70	1	0.0

**Appendix 2** Danum

<b>Genus</b>	<b>Rank</b>	<b>Abundance</b>	<b>Proportion (%)</b>
<i>Pheidole</i>	1	2404	26.8
<i>Lophomyrmex</i>	2	932	10.4
<i>Nylanderia</i>	3	759	8.5
<i>Strumigenys</i>	4	655	7.3
<i>Lordomyrma</i>	5	637	7.1
<i>Pseudolasius</i>	6	504	5.6
<i>Carebara</i>	7	465	5.2
<i>Acropyga</i>	8	389	4.3
<i>Pachycondyla</i>	9	367	4.1
<i>Hypoponera</i>	10	366	4.1
<i>Crematogaster</i>	11	327	3.6
<i>Ponera</i>	12	221	2.5
<i>Pyramica</i>	13	196	2.2
<i>Monomorium</i>	14	166	1.8
<i>Pheidologeton</i>	15	109	1.2
<i>Odontomachus</i>	16	64	0.7
<i>Mayriella</i>	17	52	0.6
<i>Myrmecaria</i>	18	40	0.4
<i>Odontoponera</i>	19	25	0.3
<i>Solenopsis</i>	20	25	0.3
<i>Cryptopone</i>	21	23	0.3
<i>Cerapachys</i>	22	23	0.3
<i>Anochetus</i>	23	22	0.2
<i>Secostruma</i>	24	19	0.2
<i>Proatta</i>	25	19	0.2
<i>Pristomyrmex</i>	26	18	0.2
<i>Vollenhovia</i>	27	17	0.2
<i>Rhytidoponera</i>	28	16	0.2
<i>Cardiocondyla</i>	29	14	0.2
<i>Prionopelta</i>	30	12	0.1
<i>Myrmoteras</i>	31	11	0.1
<i>Acanthomyrmex</i>	32	10	0.1
<i>Recurvidris</i>	33	10	0.1
<i>Lasiomyrma</i>	34	8	0.1
<i>Leptogenys</i>	35	6	0.1
<i>Eurhopalothrix</i>	36	6	0.1
<i>Oecophylla</i>	37	6	0.1
<i>Paratopula</i>	38	5	0.1

Genus	Rank	Abundance	Proportion (%)
<i>Myopopone</i>	39	4	0.0
<i>Diacamma</i>	40	4	0.0
<i>Gnamptogenys</i>	41	3	0.0
<i>Parapatrechina</i>	42	3	0.0
<i>Myopias</i>	43	2	0.0
<i>Polyrhachis</i>	44	2	0.0
<i>Anoplolepis</i>	45	2	0.0
<i>Emeryopone</i>	46	2	0.0
<i>Dacotinops</i>	47	2	0.0
<i>Rotastruma</i>	48	2	0.0
<i>Aenictus</i>	49	1	0.0
<i>Paratrechina</i>	50	1	0.0
<i>Discothyrea</i>	51	1	0.0
<i>Probolomyrmex</i>	52	1	0.0
<i>Aphaenogaster</i>	53	1	0.0
<i>Calyptomyrmex</i>	54	0	0.0
<i>Vombisidris</i>	55	0	0.0
<i>Camponotus</i>	56	0	0.0
<i>Prenolepis</i>	57	0	0.0
<i>Meranoplus</i>	58	0	0.0
<i>Tetramorium</i>	59	0	0.0
<i>Mystrum</i>	60	0	0.0
<i>Rhopalomastix</i>	61	0	0.0
<i>Plagiolepis</i>	62	0	0.0
<i>Dolichoderus</i>	63	0	0.0
<i>Forelophilus</i>	64	0	0.0
<i>Cataulacus</i>	65	0	0.0
<i>Dilobocondyla</i>	66	0	0.0
<i>Leptanilla</i>	67	0	0.0
<i>Euprenolepis</i>	68	0	0.0
<i>Platythyrea</i>	69	0	0.0
<i>Protanilla</i>	70	0	0.0

**Appendix 3** Maliau

<b>Genus</b>	<b>Rank</b>	<b>Abundance</b>	<b>Proportion (%)</b>
<i>Pheidole</i>	1	2335	32.0
<i>Strumigenys</i>	2	740	10.1
<i>Nylanderia</i>	3	679	9.3
<i>Pheidologeton</i>	4	518	7.1
<i>Carebara</i>	5	482	6.6
<i>Hypoponera</i>	6	308	4.2
<i>Ponera</i>	7	290	4.0
<i>Lordomyrma</i>	8	222	3.0
<i>Crematogaster</i>	9	219	3.0
<i>Pachycondyla</i>	10	198	2.7
<i>Mayriella</i>	11	183	2.5
<i>Lophomyrmex</i>	12	137	1.9
<i>Odontomachus</i>	13	128	1.8
<i>Solenopsis</i>	14	96	1.3
<i>Cardiocondyla</i>	15	96	1.3
<i>Monomorium</i>	16	83	1.1
<i>Pyramica</i>	17	71	1.0
<i>Pseudolasius</i>	18	54	0.7
<i>Acropyga</i>	19	49	0.7
<i>Rotastruma</i>	20	44	0.6
<i>Euprenolepis</i>	21	43	0.6
<i>Acanthomyrmex</i>	22	39	0.5
<i>Odontoponera</i>	23	29	0.4
<i>Tetramorium</i>	24	29	0.4
<i>Proatta</i>	25	26	0.4
<i>Myrmoteras</i>	26	25	0.3
<i>Leptogenys</i>	27	19	0.3
<i>Eurhopalothrix</i>	28	16	0.2
<i>Diacamma</i>	29	12	0.2
<i>Anochetus</i>	30	12	0.2
<i>Paratopula</i>	31	11	0.2
<i>Secostruma</i>	32	10	0.1
<i>Cerapachys</i>	33	10	0.1
<i>Platythyrea</i>	34	10	0.1
<i>Vollenhovia</i>	35	9	0.1
<i>Recurvidris</i>	36	9	0.1
<i>Rhytidoponera</i>	37	9	0.1
<i>Gnamptogenys</i>	38	6	0.1



Genus	Rank	Abundance	Proportion (%)
<i>Prionopelta</i>	39	5	0.1
<i>Dacatinops</i>	40	5	0.1
<i>Aphaenogaster</i>	41	4	0.1
<i>Myopias</i>	42	3	0.0
<i>Polyrhachis</i>	43	3	0.0
<i>Meranoplus</i>	44	3	0.0
<i>Mystrium</i>	45	3	0.0
<i>Rhopalomastix</i>	46	3	0.0
<i>Discothyrea</i>	47	3	0.0
<i>Camponotus</i>	48	2	0.0
<i>Dolichoderus</i>	49	2	0.0
<i>Dilobocondyla</i>	50	2	0.0
<i>Calyptomyrmex</i>	51	1	0.0
<i>Vombisidris</i>	52	1	0.0
<i>Myopopone</i>	53	1	0.0
<i>Myrmicaria</i>	54	1	0.0
<i>Aenictus</i>	55	1	0.0
<i>Cataulacus</i>	56	1	0.0
<i>Anoplolepis</i>	57	0	0.0
<i>Emeryopone</i>	58	0	0.0
<i>Pristomyrmex</i>	59	0	0.0
<i>Prenolepis</i>	60	0	0.0
<i>Plagiolepis</i>	61	0	0.0
<i>Cryptopone</i>	62	0	0.0
<i>Oecophylla</i>	63	0	0.0
<i>Paratrechina</i>	64	0	0.0
<i>Forelophilus</i>	65	0	0.0
<i>Leptanilla</i>	66	0	0.0
<i>Lasiomyrma</i>	67	0	0.0
<i>Paraparatrechina</i>	68	0	0.0
<i>Protanilla</i>	69	0	0.0
<i>Probolomyrmex</i>	70	0	0.0

**Appendix 4** SAFE

<b>Genus</b>	<b>Rank</b>	<b>Abundance</b>	<b>Proportion (%)</b>
<i>Pheidole</i>	1	817	23.7
<i>Lophomyrmex</i>	2	468	13.6
<i>Nylanderia</i>	3	258	7.5
<i>Pseudolasius</i>	4	234	6.8
<i>Lordomyrma</i>	5	196	5.7
<i>Strumigenys</i>	6	184	5.3
<i>Pheidologeton</i>	7	177	5.1
<i>Carebara</i>	8	169	4.9
<i>Hypoponera</i>	9	141	4.1
<i>Pachycondyla</i>	10	133	3.9
<i>Crematogaster</i>	11	106	3.1
<i>Solenopsis</i>	12	84	2.4
<i>Ponera</i>	13	55	1.6
<i>Monomorium</i>	14	53	1.5
<i>Myrmicaria</i>	15	41	1.2
<i>Eurhopalothrix</i>	16	40	1.2
<i>Leptogenys</i>	17	33	1.0
<i>Vollenhovia</i>	18	28	0.8
<i>Meranoplus</i>	19	25	0.7
<i>Pyramica</i>	20	25	0.7
<i>Acanthomyrmex</i>	21	24	0.7
<i>Odontomachus</i>	22	18	0.5
<i>Secostruma</i>	23	17	0.5
<i>Cerapachys</i>	24	12	0.3
<i>Odontoponera</i>	25	10	0.3
<i>Anochetus</i>	26	10	0.3
<i>Cryptopone</i>	27	9	0.3
<i>Rhytidoponera</i>	28	8	0.2
<i>Aphaenogaster</i>	29	8	0.2
<i>Cardiocondyla</i>	30	8	0.2
<i>Dacatinops</i>	31	7	0.2
<i>Myrmoteras</i>	32	6	0.2
<i>Paratopula</i>	33	6	0.2
<i>Protanilla</i>	34	6	0.2
<i>Pristomyrmex</i>	35	4	0.1
<i>Diacamma</i>	36	4	0.1
<i>Plagiolepis</i>	37	3	0.1
<i>Gnamptogenys</i>	38	3	0.1

Genus	Rank	Abundance	Proportion (%)
<i>Paraparatrechina</i>	39	3	0.1
<i>Polyrhachis</i>	40	2	0.1
<i>Proatta</i>	41	2	0.1
<i>Acropyga</i>	42	2	0.1
<i>Forelophilus</i>	43	2	0.1
<i>Platythyrea</i>	44	2	0.1
<i>Prionopelta</i>	45	1	0.0
<i>Myopopone</i>	46	1	0.0
<i>Prenolepis</i>	47	1	0.0
<i>Mystrium</i>	48	1	0.0
<i>Mayriella</i>	49	1	0.0
<i>Leptanilla</i>	50	1	0.0
<i>Euprenolepis</i>	51	1	0.0
<i>Discothyrea</i>	52	1	0.0
<i>Myopias</i>	53	0	0.0
<i>Calyptomymex</i>	54	0	0.0
<i>Anoplolepis</i>	55	0	0.0
<i>Vombisidris</i>	56	0	0.0
<i>Camponotus</i>	57	0	0.0
<i>Emeryopone</i>	58	0	0.0
<i>Aenictus</i>	59	0	0.0
<i>Tetramorium</i>	60	0	0.0
<i>Recurvidris</i>	61	0	0.0
<i>Rhopalomastix</i>	62	0	0.0
<i>Dolichoderus</i>	63	0	0.0
<i>Oecophylla</i>	64	0	0.0
<i>Paratrechina</i>	65	0	0.0
<i>Rotastruma</i>	66	0	0.0
<i>Cataulacus</i>	67	0	0.0
<i>Dilobocondyla</i>	68	0	0.0
<i>Lasiomyrma</i>	69	0	0.0
<i>Probolomyrmex</i>	70	0	0.0