Research Article

Selectively Logging Old Growth Rain Forest Twice Changes Canopy Ant Species Composition, While Conversion to Oil Palm Changes Composition and Reduces Species Richness and Diversity

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Abstract

Tropical forests around the world, and particularly in Southeast Asia, are being affected by anthropogenic habitat conversion and degradation. Ants, an ecologically important group in the rainforest canopy, have previously been demonstrated to be robust to a single round of selective logging, but are strongly affected by conversion to oil palm. However, the impacts of multiple rounds of selective logging on canopy ants remain unexplored. We studied the ant assemblages across a habitat gradient comprising old growth forest, twice-logged forest and oil palm plantation in Sabah, Malaysian Borneo. Canopy ants were collected using insecticide fogging across 36 sampling sites. Old growth forest and twice-logged forest had similar species richness and Shannon species diversity. These two forest habitats were significantly higher in species richness and Shannon diversity than oil palm plantation. Abundance of canopy ants was similar across all three habitats. There was a significant difference in species composition between all pairs of habitats. Leaf litter depth on the ground was positively related to ant species richness, while canopy cover was positively related to ant abundance. Hence, multiple rounds of logging cause shifts in ant species composition, while forest conversion to oil palm additionally causes reductions in ant diversity. This is of concern, since forests in Sabah and elsewhere are becoming increasingly degraded. Our results indicate that both old growth and twice-logged rain forests can be useful for conservation of canopy ants.

Keywords: Formicidae, SAFE Project, land-use change, canopy ants

Introduction

A major threat to rainforest biodiversity is logging and forest conversion to agriculture (Gibson et al., 2011). Southeast Asia is a global biodiversity hotspot, and is also under threat from habitat change, with a reduction in forest cover of 12% during the decade of 2000-2010 (Stibig et al., 2014). Malaysia in particular has seen reductions of 23% in the period between 2011-2016 (www.globalforestwatch.org), due to expansion of agricultural and agro forests. Malaysia is the second highest producer of palm oil in the world, after Indonesia, and increases in area planted with oil palm often results in loss of forested habitats (Koh & Wilcove, 2008). As tropical forests are increasingly vulnerable to such conversion, it is important to study the effects of these land use changes.

Rain forest canopies are highly diverse habitats, yet are relatively poorly known (Nakamura et al., 2017). The direct impact of logging of tropical forest is the alteration of canopy layers and the loss of the closed canopy (Whitmore, 1998). Specifically, this involves reduction in canopy height, canopy surface area, and crown sizes for individual trees (Okuda et al., 2003). Despite these changes, logged forests still support reasonable numbers of species of a range of groups from primary forest (Edwards et al., 2010). However, it is unlikely that all species could be conserved using this approach (Gibson et al., 2011). Oil palm primarily has a less complex physical structure than natural forest, with many fewer plant species, a hotter and drier microclimate, and experiences other direct human impacts, such as application of pesticides (Foster et al., 2011). Hence it supports substantially lower biodiversity than forested habitats (even those that have been heavily logged) for many groups (Fitzherbert et al., 2008; Foster et al., 2011).

Ants are dominant insects in tropical lowland forest (Turner & Foster, 2009). Approximately 50% of all ant species are at least partially reliant on the canopy in the tropics, making them ideal insects to study effects of changing forest landscapes in relation to arthropod assemblages (Floren, Wetzel & Staab, 2014). Compared to leaf litter on the ground, as a three-dimensional arboreal space the canopy supports a different composition of ant species (Hashimoto et al., 2006), and the species present are usually highly adapted to arboreal life with specialization of diet and other niches. Ants are also a useful focal group (Philpott et al., 2010) due to their high total biomass (Folgarait, 1998). They may influence the whole ecosystem as they play various important roles in terms of ecosystem services, as decomposers (McGlynn & Poirson, 2012), biological control agents (Hölldobler & Wilson, 1990; Navarrete et al., 2013), seed dispersers, mutualists (Hashimoto et al., 1999), soil engineers, scavengers or

predators, and drivers of nutrient re-distribution (Fayle et al., 2011; Folgarait 1998; Philpott et al., 2010).

In Malaysian Borneo, the impacts of logging and conversion to oil palm vary widely both between taxonomic groups (Foster et al., 2011) and as a result of differences in logging intensity (Edwards et al., 2014). Although oil palm clearly supports fewer canopy ant species and different communities than primary forest (Fayle et al., 2010), the situation regarding logged forest is less clear. Previous work has shown in a forest that was selectively logged only once in Danum Valley, canopy ant species richness and abundance did not differ from the nearby primary forest (Widodo et al., 2004). Furthermore, although species diversity metrics were higher in primary forest than in one once-logged forest area, they did not differ between primary forest and a second area of once-logged forest. Elsewhere, in Papua New Guinea, primary forest supports a higher species richness of canopy ants than secondary forests that have regrown following complete clearance (Klimes et al., 2012). Hence, the importance of degraded forest as a habitat for ant species depends greatly on the particular management that the forest has undergone. In Sabah, the majority of logged forests have now been logged more than once, and so the results of Widodo et al. (2004) are not representative of the value of logged forest in the area more broadly. Furthermore, work on leaf litter ants has shown that twice-logged forest supports fewer species than primary forest at small scales, but that the total number of species remains the same (Woodcock et al., 2011). Here we look at species richness, diversity, abundance and species composition of canopy ants using fogging in a primary forest, a twice-logged forest and an oil palm plantation in Sabah, Malaysia. We also record environmental variables to see how they affect the ant assemblages.

Materials and Methods
Study site
Sampling took place in lowland tropical rain forest and oil palm plantation in Sabah, Malaysia, located in north-east Borneo. Average annual temperature in the area (recorded in nearby primary forest in Danum Valley) is 26.7°C, while average annual rainfall is 2669 mm (Walsh & Newbery, 1999). Sampling was conducted from January 28, 2015 until November 6, 2015. Three survey habitats were selected: old growth forest in Maliau Basin Conservation Area, twice-logged forest and oil palm plantation. In each habitat, 12 survey sites were
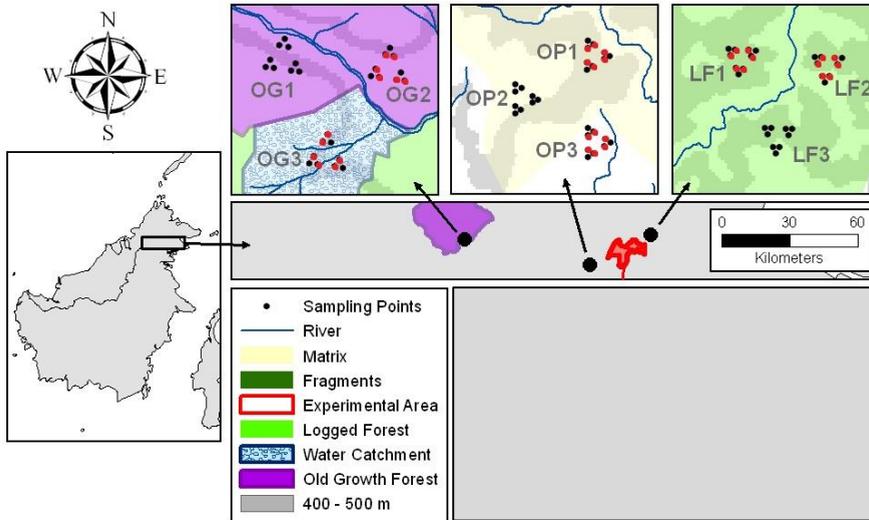
Figure S1. Map of sampling points in Malaysian Borneo (denoted in red). Adapted from the SAFE project website (www.safeproject.net). Note that the SAFE experimental area was not sampled, and so is not presented in this map.

established as part of the Stability of Altered Forest Ecosystems (SAFE) Project (Figure S1) and were used with collections being conducted at "second order" (referring to the fractal sampling design) SAFE survey sites (Ewers et al., 2011). Old growth forest (4º 41'-4º65'N 116º4'-117 º4'E) comprised six sites that have never been logged, and six sites that experienced very low intensity logging in the 1970s and 1990s around the field centre area for construction purposes. However, these low intensity logged sites retained a structure similar to that of pristine primary forest (Ewers et al., 2011). Twice-logged forest was situated to the north of the experimental area of SAFE Project. It is a continuous forest but has been selectively logged twice, once during the 1970s and again from the late 1990s to 2000s (Hardwick et al., 2015). Oil palm plantation (4º33'E, 117º28'24.41"E) was a monoculture of *Elaeis guineensis* with sites planted in either 2000 or 2006 (Ewers et al., 2011). Although the sampling sites for different habitat types were not spatially interspersed (Figure S1), they were representative in terms of these kinds of habitats in Sabah.

Sampling methods
Fogging was used to sample the canopy ants with synthetic pyrethrum insecticide (active compound: alphacypermethrin with synergist 2.27%) diluted in diesel by a ratio of 15:1 (Yusah et al., 2012). Four circular 1 m^2 area collecting

trays were laid out and suspended using ropes tied to trees or oil palm trunks at each site (a total of 144 m^2 of sampled canopy area across 36 samplings sites). In plantations, the only large trees at the sites were oil palm. Trays were placed as close as possible to the pre-designated sampling point, regardless of the presence of vegetation. Fogging was carried out around 06:00 am to avoid strong lateral drift of insecticide fog. Days with wind or rain were avoided. The fogging machine was run for four minutes and then the site was left for two hours for the insecticide to act before collection of ants, which were brushed into pots of 70% ethanol suspended from apertures at the centre of the trays. Ants were identified to genus (Fayle et al., 2011), sorted to morphospecies, and then species names assigned where possible. Voucher specimens were deposited at the Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah. We excluded reproductive individuals, major workers and callow ants from counts to avoid misidentification and subsequent inflation of species counts. In each habitat, four environmental variables were recorded: leaf litter depth, canopy cover, dead wood coverage and climber coverage. These variables are potentially important for ant communities (Wilkie, Mertl & Traniello, 2010). Climbers are important for providing a three-dimensional structure in the forest canopy, allowing spatial partitioning of canopy ant communities (Tanaka, Yamane & Itioka, 2010) and also providing connectivity between different canopy strata (Powell et al., 2011). The average leaf litter depth was obtained from three readings within a 1 m^2 quadrat. The canopy cover, dead wood and climber coverage measures were based on the standard scale used for SAFE project vegetation plots, ranging from very poor or few (one) to very good or abundant (five): 1 = up to 20% canopy cover, absent dead wood or lianas; 2 = up to 40% canopy cover, one or a few occurrences of dead wood and lianas; 3 = up to 60% of canopy cover, moderately abundant dead wood or lianas; 4 = up to 80% of canopy cover, abundant dead wood or lianas; 5 = full coverage of canopy, very abundant dead wood or lianas. These variables were estimated within a 20 m by 20 m area, centred on the sampling point, with one estimate made per variable per sampling point.

Statistical analyses
A series of linear models were run to test for differences in species diversity (Shannon diversity index), species richness and ant abundance along the habitat gradient using the *lm* function in the R 3.3.0. Data from the four fogging trays were pooled prior to analysis. We used a $log_{10}(x)$ data transformation for abundance to normalize the data. To determine the relationship between the environmental variables and the species diversity we ran models twice: once with only the habitat as a predictor, and a second time with all environmental

variables as predictors as well. Full models were included first, and then simplified by stepwise removal of predictors (using the *drop1* function in R 3.3.0), such that AIC was minimised. Post-hoc tests for differences between habitats were conducted where a significant effect of habitat was found using the linear models, using Tukey honest significant differences (*TukeyHSD* function in R 3.3.0). A non-metric multidimensional scaling (NMDS) ordination was used to illustrate differences in species composition between habitat types, with pairwise ANOSIM tests being conducted to test statistically for differences between all habitat pairs (*metaMDS* and *anosim* functions run on presence-absence data in the R vegan package). The analyses for species composition were conducted on ant presence/absence data.

Results

We sampled a total of 9,002 individual ants, 199 morphospecies and 44 genera from all habitats across the 36 sampling sites. The total number of subfamilies, genera and morphospecies recorded was highest in the old growth forest, followed by twice-logged forest and then oil palm plantation (Table 1). Across all the habitats combined, *Polyrhachis* was the most species-rich genus (33 species) followed by *Camponotus* and *Crematogaster,* both with 23 species each. Myrmicinae was the most diverse subfamily representing 42.4% of the total species sampled. Mean species richness in old growth forest and twice-logged forest was significantly higher than in oil palm plantation (Linear model: F=10.29, df=2,33, p<0.001; Tukey HSD: old growth-oil palm, p<0.001; twice logged-oil palm, p=0.037) but not different between old growth forest and twice-logged forest (Tukey HSD, old growth-twice logged, p=0.144). The mean species richness in old growth forest was five times higher than in oil palm plantation (Figure 1a).

Table 1. Composition of canopy ants in old growth forest, twice-logged forest and oil palm plantation.

Subfamily	Old growth		Twice-logged forest		Oil palm	
	Genera	Species	Genera	Species	Genera	Species
Formicinae	10	54	10	41	7	13
Myrmicinae	19	61	13	32	8	11
Dolichoderinae	3	16	3	8	2	2
Ponerinae	8	8	1	2	0	0
Pseudomyrmecinae	1	3	1	4	0	0
Ectatomminae	1	1	1	1	0	0
Proceratiinae	1	1	0	0	0	0
TOTAL	43	144	29	88	17	26
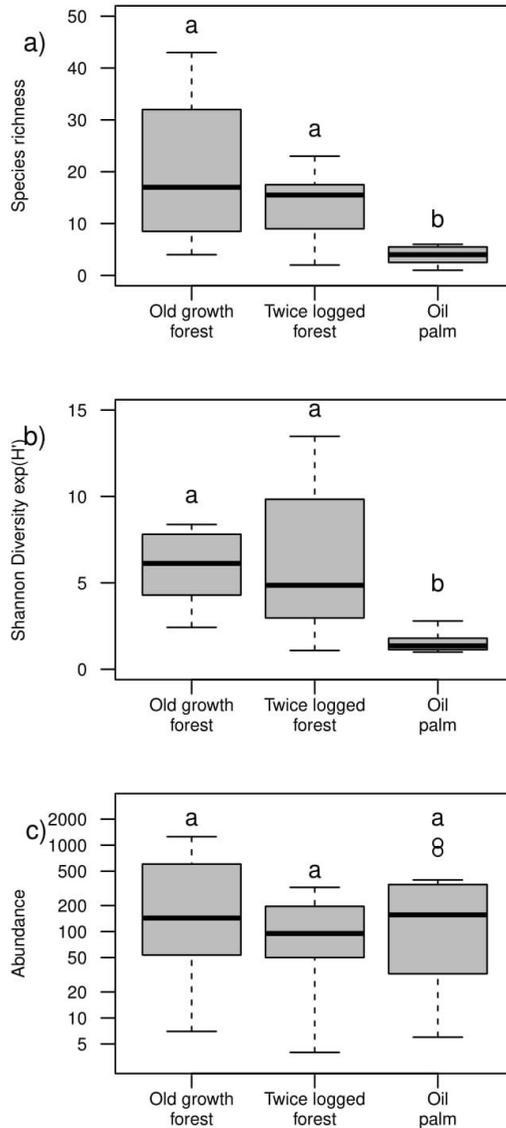
Figure 1. a) Species richness, **b)** Shannon diversity and **c)** abundance (note logarithmic scale on y-axis) per sampling point in old growth forest, twice-logged forest and oil palm plantation. Different letters indicate statistically significant differences between habitats when only habitat type is included in the linear model. Boxplots show medians (thick horizontal line), interquartile ranges (grey boxes), and full ranges (whiskers). Outliers more than 1.5 times the interquartile range from the 25th or 75th percentiles denoted as unfilled circular points.

Similarly, old growth forest and twice-logged forest had a significantly higher Shannon species diversity than oil palm plantation but there was no difference between old growth forest and twice-logged forest (Linear model, F=10.6, df=2,33, p<0.001; Tukey HSD: old growth-twice-logged, p=0.776; old growth-oil palm, p<0.001; twice-logged-oil palm, p<0.001). Species diversity was highest in old growth forest followed by twice-logged forest, with oil palm plantation having lowest diversity. There was no significant difference in mean ant abundance between the three habitats (Linear model, F=1.70, df=2,33, p=0.198).

When environmental variables were also included in starting models, for species richness, leaf litter depth was the only variable remaining in the final model and was positively related to richness (linear model: t=5.71, p<0.001, Figure 2a). Habitat was not included in this final model, and leaf litter depth was a significant predictor of species richness even when habitat and leaf litter were included in the same model. For species diversity, no environmental variables were present in the final model, with habitat being the only predictor remaining (see model in paragraph above). For ant abundance, the final model included both habitat and canopy cover (linear models: habitat: old growth-twice logged t=-1.15, p=0.259, old growth-oil palm t=1.07, p=0.293, twice logged-oil palm t=2.23, p=0.032, canopy cover: t=2.09, p=0.053, Figure 2b).
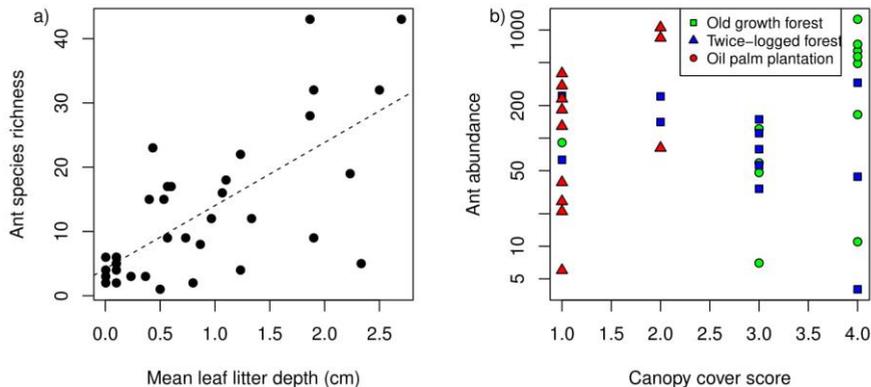

Figure 2. Statistically significant relationships between environmental variables and aspects of canopy ant community structure. **a)** Relationship between leaf litter depth and ant species richness. **b)** Relationship between canopy cover/habitat and ant abundance.

Canopy cover had a positive relationship with ant abundance, and twice-logged forest had lower ant abundance than oil palm plantation, when also accounting for differences in canopy cover. All of the environmental variables varied between the habitats (Figure 3).
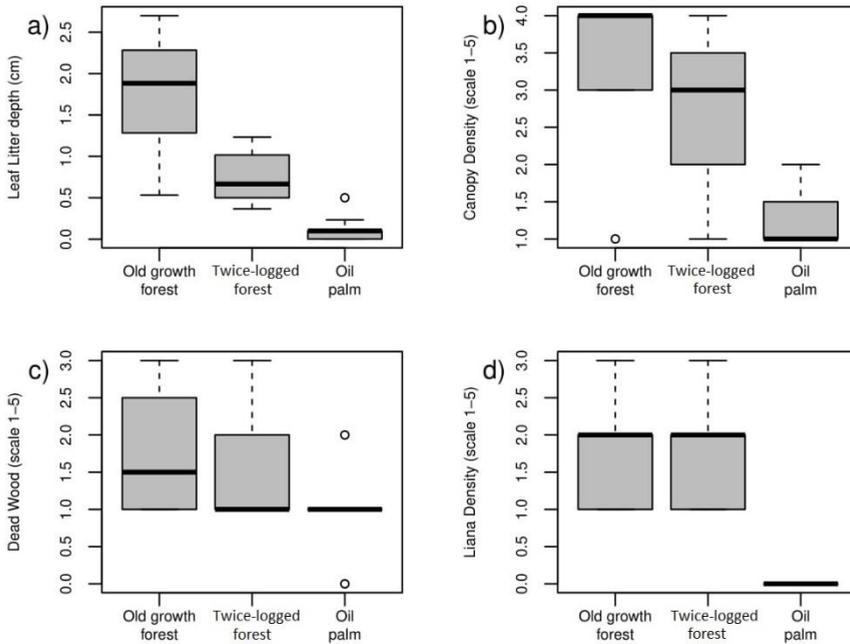
Figure 3. Boxplots for all environmental variables measured across the three different habitats. **a)** Leaf litter depth. **b)** Canopy density. **c)** Dead wood. **d)** Liana density.

From 199 morphospecies sampled, 94, 39 and 12 species were found only in old growth forest, twice-logged forest and oil palm plantation respectively. Only seven species were present across all habitats, while 38 species appeared in both old growth and twice-logged forest. There were significant differences in species composition between all habitats (ANOSIM: old growth -twice logged, R=0.270, p=0.001; old growth -oil palm, R=0.531, p=0.001; twice-logged -oil palm, R=0.549, p=0.001; Figure 4).
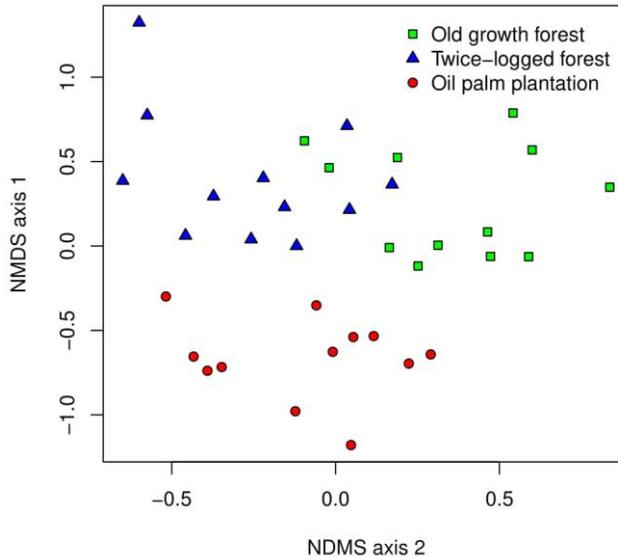
Figure 4. NMDS ordination plot showing the species composition according to habitat type (stress = 0.145) There were significant differences in species composition between all three habitat types (see text for details).

Discussion

Old growth forest and twice-logged forest did not differ in terms of mean species richness and Shannon diversity of ants. This broadly follows findings from other biogeographic regions (e.g. Schulz & Wagner, 2002), and from other microhabitats in Sabah (Woodcock et al., 2011). The results suggest that at the scale of a single sampling site, the two different forest types provide similar amounts of habitat for ants, and can hence support similar numbers at these smaller scales. Depending on the age of forest regeneration, a logged forest may provide intermediate conditions for nesting and niches for ants (Luke et al., 2014). The continuous (unfragmented) nature of old growth and twice-logged forest in the present study sites allow ants to move at a larger scale without restriction. Types of trees may also affect the distribution of canopy ants (Foster et al., 2011; Schulz & Wagner, 2002) especially trees with extra-floral nectaries available (Blüthgen, Verhaagh & Goitía, 2000). Hence, it might be expected that tree community changes due to logging would impact ant communities. However, ant-plant interactions take place on myrmecophytes such as *Macaranga* sp. that have higher abundance in secondary forest than in old growth forest (Tanaka et al., 2008), which may help to offset any effects of vegetation simplification due to logging. The presence of epiphytes such as ferns on trees provide an additional niche for canopy arthropods, including ants, in the tropics

(Fayle et al., 2009; Turner & Foster, 2009). However, the majority of ant-plant interactions are not particularly specific at the level of entire forests (Klimes et al., 2012), and hence the impacts of tree community composition on ant species persistence are likely to be complex. Furthermore, old growth forests are mostly occupied by large trees and thus have a non-uniform canopy layer. Although the larger trees have a different composition of ant species, at least within old growth forest in the region (Yusah & Foster, 2016), impacts of tree size on local ant species richness can be moderated if there are high levels of connectivity via lianas (Adams et al., 2016).

Despite the robustness of the rainforest to two rounds of logging in terms of number of canopy ant species per sampling site, the total number of species collected was greater in the primary forest. The greater number of species at larger scales in old growth forest indicate some kind of habitat heterogeneity at these larger scales that is not present in twice-logged forest. This hypothesis is supported by the fact that twice-logged forest also differed from old growth forest in terms of ant species composition. This change in composition may have been driven by adaptation of dominant genera such as *Camponotus, Crematogaster* and *Polyrhachis* to particular types of nesting sites (Floren, Wetzel & Staab, 2014). Our results are important because they demonstrate that two rounds of selective logging can affect canopy ant species composition, whereas previous work on logged areas that had undergone one round of logging did not show major effects (Widodo et al., 2004). This is of concern because the majority of degraded forests in Sabah have been logged multiple times, and also because tropical forests more widely are becoming more degraded. Further research could study an even wider range of different degrees of logging intensity, over greater spatial ranges (to overcome any biases in our data introduced from lack of interspersion of sampling sites in different habitats), and with a more comprehensive range of canopy environmental measurements.

In contrast, in oil palm plantation, there were reductions in number of species, and changes in species composition relative to both old growth and twice-logged forest. This agrees with previous work comparing canopy ants from old growth forest with those in oil palm plantation (Fayle et al., 2010). In our study, most ant species in oil palm plantation could not be found in old growth forest or twice-logged forest and vice versa. This suggests that the ability to live under environmental conditions differs between ant species. In particular, the harsh microclimate in oil palm plantation (Turner & Foster, 2009) in combination with the low diversity of trees is likely to negatively affect ant communities. We also found a high abundance of non-native species in oil palm plantation, such as

Anoplolepis gracilipes, as has been previously noted by Brühl and Eltz (2010). Another species with high abundance in oil palm plantation recorded in this study was *Oecophylla smaragdina*, which is associated with human disturbance. Although fogging is efficient in sampling canopy arthropods, this method does not necessarily exclude all ground nesting but canopy foraging ant species (Weiser et al., 2010). However, this study focused on ants that use canopy in general (rather than only those that nest there), and hence we can still conclude that losing the canopy affects ant composition. The differences between forested habitats and oil palm plantation indicate that conversion of any kind of forest, even that which has undergone multiple rounds of logging, is likely to have negative impacts on ant biodiversity.

In terms of directly measured environmental variables, both ground leaf litter and canopy density affected ant communities. Depth of ground leaf litter was positively related to site ant species richness, both when accounting for overall differences in richness between habitats, and when analysed by itself. There are two possible explanations for this. First, that ground conditions are important because there is some movement of ants from ground to the canopy and vice versa. For example in Bornean forests, some ant species nest at ground level and forage into the canopy (e.g. *Dinomyrmex gigas*, the giant forest ant (Pfeiffer & Linsenmair, 2000)). Second, that the depth of leaf litter is an indicator of some aspect of canopy complexity that we did not measure. Ant abundance was positively related to canopy density, and once canopy density was accounted for, there were significantly lower ant abundances in twice-logged forest than in oil palm plantation. The overall relationship with canopy density suggests that, generally, more dense canopies provide a greater amount of habitat for canopy ants. However, because this effect is observed for overall ant abundance and not site species richness, this indicates that the average colony size is larger in less degraded habitats. The difference between twice-logged forest and oil palm plantation indicates that for a given amount of canopy cover, there are more ants in twice-logged forest. This may relate either to the change in microclimate, or simply to the fact that for any given canopy density in oil palm, the vast majority of that canopy will comprise only one plant species.

In summary, multiple rounds of logging changes canopy ant species composition, and conversion to oil palm causes further shifts in ant composition accompanied by reduction in species richness and species evenness, and increases in the occurrence of non-native ant species. These impacts on canopy ants may shift the ecological functioning of the whole canopy ecosystem. Our results suggest that twice-logged forest is likely to be of use for conserving canopy ant

biodiversity, but that some species are likely to require maintenance of areas of unlogged forest.

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