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Functional structure of ant and termite assemblages in old growth forest, logged forest and oil palm plantation in Malaysian Borneo

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Abstract Forested tropical landscapes around the world are being extensively logged and converted to agriculture, with serious consequences for biodiversity and potentially ecosystem functioning. Here we investigate associations between habitat disturbance and functional diversity of ants and termites—two numerically dominant and functionally important taxa in tropical rain forests that perform key roles in predation, decomposition, nutrient cycling and seed dispersal. We compared ant and termite occurrence and composition within standardised volumes of soil and dead wood in old growth forest, logged forest and oil palm plantation in Sabah, Malaysian Borneo. Termites occurred substantially less frequently in converted habitats than in old growth forest, whereas ant occurrences were highest in logged forest and lowest in old growth forest. All termite feeding groups had low occurrence in disturbed habitats, with soil feeders occurring even less frequently

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than wood feeders. Ant functional groups showed more variable associations, with some opportunist and behaviourally dominant groups being more abundant in degraded habitats. The importance of ants and termites in tropical ecosystems and such differing patterns of assemblage variation suggest that ecosystem functioning may be significantly altered in converted habitats.

Introduction

SE Asia contains many threatened biodiversity 'hotspots' (e.g. Myers et al. 2000; Koh 2008), with loss of up to three quarters of the original forest projected by 2100 (Sodhi et al. 2004). Global demands for timber and palm oil (e.g. Fitzherbert et al. 2008, Danielsen et al. 2009, Sodhi et al. 2009) mean that increasing areas of habitat are being converted—nearly 80 % of Malaysian Borneo was affected by logging and clearing operations between 1990 and 2009 (Bryan et al. 2013), with areas typically following a succession from old growth to logged forest, through to oil palm plantation (McMorrow and Talip 2001; Koh and Wilcove 2008; Bryan et al. 2013). Logged forest and oil palm plantations now dominate the landscape of Malaysian Borneo (Bryan et al. 2013).

Although selectively logged forests retain many species (e.g. Berry et al. 2010; Edwards et al. 2011) many taxa are strongly affected by disturbance. For example, a review of bird responses to tropical forest disturbance (Gray et al. 2007) found significant declines in richness and abundance of insectivores, omnivores and frugivores, although increases in granivores. Also, a review of tropical forest dung beetle communities showed similar diversity declines with increasing habitat disturbance, along with a reduction in the number of forest species (Nichols et al. 2007). A range of taxa including birds (Peh et al. 2006; Koh and Wilcove 2008), butterflies (Koh and Wilcove 2008) and dung beetles (Edwards et al. 2013; Gray et al. 2014) show substantial losses of biodiversity when forest is converted to oil palm plantation (see also review by Fitzherbert et al. 2008). Changes in assemblages, and particularly the loss of functionally important species, can have significant impacts on ecosystem functioning (Hooper et al. 2005).

Termites and ants are among the most important insect groups in tropical forest ecosystems. Termites feed on plant material in varying stages of decay (e.g. dead wood, leaf litter and soil). They play major roles in processes such as decomposition, and nutrient and carbon cycling (Eggleton et al. 1997; Jones and Eggleton 2000; Donovan et al. 2001). Ants disperse seeds, assist soil processing and nutrient cycling, and are mutualists with a range of species (e.g. Huxley 1980; Hölldobler and Wilson 1994). Ants can be omnivorous, opportunistic feeders; or herbivores, but many are specialist or generalist predators of invertebrates (Hölldobler and Wilson 1994). As both of these social insect groups play substantial ecological roles, the potential for interaction between them is important. Many ants feed on termites, and some ant species are specialised termite feeders (e.g. Maschwitz and Schönegge 1983; Mill 1984; Dejean and Fénéron 1999). Mutualistic interactions between ants and termites, such as nest-sharing, have also been observed (Jaffe et al. 1995; Diehl et al. 2005). In addition to direct predatory and mutualistic interactions, ants and termites may interact indirectly through changes they make to their environments. Both

groups are major ecosystem engineers (Jones et al. 1994) and affect soil properties and resource availability by their nest building, feeding and foraging (e.g. Folgarait 1998; Lavelle and Spain 2001; Jouquet et al. 2006). Given the major roles of ants and termites in ecosystem function it is likely that functioning and resilience of both rain forest and oil palm plantation ecosystems will be affected by the abundance and composition of ant and termite assemblages (Naeem et al. 1994, Bihn et al. 2010).

Previous studies have shown that both ant and termite diversity usually decrease following habitat conversion (Jones et al. 2003; Brühl and Eltz 2009). Logging of old growth forest reduces the total number of termite species by 64 % (14 species cf. 39 species; Donovan et al. 2007), although it is not known how many termite species persist when forest is cleared for oil palm plantation. Ant species richness is also reduced by logging, although to a lesser extent, with 31 % of species being lost (Brühl 2001). Conversion to oil palm plantation has a more extreme effect, with ant species richness being reduced by 64-80 % (Brühl and Eltz 2009; Fayle et al. 2010). Termites and ants also show shifts in assemblage structure with habitat disturbance. Soil feeding termites are vulnerable to loss of old growth forest, although wood feeders may have more species in mature regenerating forest (Eggleton et al. 1997). Invasive and generalist species dominate ant assemblages in oil palm plantation (Brühl et al. 2003; Fayle et al. 2010). We know of no studies that have either, (a) sampled ants and termites simultaneously across a forest disturbance gradient or, (b) considered termite community composition in oil palm plantation. Here we assess the co-variation in functional and feeding group composition of ants and termites along a habitat disturbance gradient comprising sites in old growth forest, logged forest and oil palm plantation converted from logged forest, in Sabah, Malaysian Borneo.

Methods

Study site

All sampling was conducted in Sabah, Malaysian Borneo, at an average of 450 m asl. Survey habitats were: old growth lowland dipterocarp rain forest (OG) in the Maliau Basin Conservation Area (4°49′N, 116°54′E); twice-logged rain forest (LF); and oil palm plantation (OP) managed by Benta Wawasan (a subsidiary company of the state government body, Yayasan Sabah) (4°43′N, 117°35′E). Old growth forest survey points at Maliau were in forest that has never been logged commercially, although half of the survey points were in forest that has been lightly logged once. Stand basal area in this lightly-logged area remains similar to undisturbed sites (Hamzah Tangki, unpublished data) and substantially different from the commercially logged forest (Ewers et al. 2011). Tree communities were deemed not to have changed significantly (Ewers et al. 2011). Logged forest survey points were in forest that has been selectively logged twice: once during the 1970s and again from the late 1990s-2000s. Oil palm plantation survey points were in areas of *Elaeis guineensis* monocultures, planted in 2000 (10 years old at time of survey), with a low, open canopy and sparse understory vegetation. Further details are provided in Ewers et al. (2011).

We used survey points established as part of a large-scale, long-term experiment investigating the effects of forest fragmentation: the "Stability of Altered Forest Ecosystems (SAFE) Project" (Ewers et al. 2011). Fifty-nine survey points were sampled in our study: 18 in old growth forest, 32 in logged forest of varying forest quality, and nine in oil palm plantation (Online Resource, Fig. S1). A larger number of survey points were sampled in logged forest and old growth forest because we expected these habitats to be

more heterogeneous and we wanted our points to span a gradient of habitat disturbance across all the habitats. Neighbouring survey points were 178 m apart. Selection of these survey points was made with future repeat-surveys in mind once clearance of logged forest for oil palm plantation has resulted in the creation of forest fragments. There are no areas of continuous, unfragmented old growth forest near to the SAFE project sites and hence the study design does not allow separation of the effects of location from those of habitat disturbance. We are therefore cautious in our interpretation of the results, particularly about assigning causal relationships between treatments and assemblage composition.

Ant and termite collection

Survey work was conducted in April and May 2010 during the dry season, between 0800 h and 1700 h. This coincided with the end of an El Nino-related drought between February and April that year (see http://www.searrp.org/danum-valley/the-conservation-area/climate/). None of the sites was affected by fire during the drought period, however.

At each survey point a 4×4 m^2 quadrat was placed, with sixteen soil pits dug (1,131 cm^3 per pit: 12 cm diameter by 10 cm deep) centred within each square metre of the quadrat. Soil was removed from each pit and hand-searched for ants and termites using a white tray for 10 person-minutes. Large dead wood (diam > 5 cm) within the quadrat (up to a height of 2 m) was also searched for ants and termites, once per metre of dead wood (following Davies et al. 2003). Bark was removed and holes in the wood were examined. These methods only sample the fauna living within the soil and dead wood, and do not sample the leaf litter community.

Ants and termites were sorted to genus using the collections of the Natural History Museum, London, and relevant literature (Ahmed and Akhtar 1981; Tho and Kirton 1992; Bolton 1994; Gathorne-Hardy 2001; Hashimoto 2003). Ant and termite reproductives were excluded from counts to avoid including vagrants, and immature termites could not be identified. Ants and termites show niche conservatism within genera (Andersen 2000; Donovan et al. 2001) and so genus-level identification of both taxa was suitable for functional group assignment. Number of encounters of each ant and termite genus within a quadrat, defined as the sum of the number of pits and number of examinations of dead wood ('hits') containing that genus, was used as a surrogate measure of occurrence (referred to henceforth simply as "occurrence") (following Davies et al. 2003). Our approach is somewhat conservative, because species-rich genera, such as *Pheidole* and *Strumigenys*, are only counted as one occurrence per pit, despite being likely to be present as many species.

Ants were assigned to functional groups following Andersen (2000) and Brown (2000) and termites to feeding groups following Donovan et al. (2001) (Table 1). Ants were grouped according to differences in behaviour, dominance and temperature preferences in addition to feeding strategy, whereas termite groups were based only on feeding differences (position along the humification gradient) and associated morphological (mandibular and gut structural) characters (Donovan et al. 2001). Differences in these ant and termite functional groups between treatments are therefore likely to be associated with differences in the rate of decomposition, the type of material being decomposed (by termites) and the extent and type of predation (by ants). The termite feeding group assignments represent the only widely-used functional classification system for this group. For ants, although morphological classifications (Bihn et al. 2010) and classifications based on field observations of diet and nesting preference (Ryder Wilkie et al. 2010) are becoming more popular, the functional groupings implemented here are still the most widely used (Andersen 2010;

Wiezik et al. 2010; So and Chu 2010; Mustafa et al. 2011; Bharti et al. 2013). Full details of genera within functional groups are listed in Tables 2 and 3.

Environmental variation

We measured the following environmental variables in each quadrat to assess habitat type and degree of disturbance: slope using a clinometer; percentage cover of leaf litter, bare ground, low vegetation, trees, dead wood, and grass (following Cleary et al. 2005); the number of small saplings (dbh < 5 cm, and height < 5 m), tall saplings (dbh < 5 cm, and height > 5 m), small poles (dbh 5-10 cm, and height < 10 m), tall poles (dbh 5-10 cm, and height > 10 m) and trees (dbh > 10 cm) were counted; the number of lianas/vines, epiphytes and low vegetation was recorded using a four point scale; 0 = absent, 1 = one or a few (up to three occurrences), 2 = moderately abundant (occupying ≤ 25 % of the quadrat area), 3 = very abundant (occupying > 25 % of the quadrat area); and forest quality was scaled from very poor (zero) to very good (five) based on vegetation and canopy cover in the visible area around the survey point (Online Resources, Table S1). At each pit, leaf litter depth and humus depth were measured before digging. Humus depth was defined as depth (mm) of the dark, uppermost layer of soil between the decomposing leaf litter and lighter, more compact soil below.

Statistical methods

Statistical analyses were conducted using R 2.7.0 statistics package (R Core Development Team, http://www.r-project.org/, 2011). Trends in genus richness and genus occurrence were consistent across soil and dead wood samples (Online Resources, Table S2), so data from both microhabitats were combined for use in all analyses. We tested differences in both total and functional group occurrence across different habitat types using Kruskal–Wallis tests because occurrence data were not normally distributed and could not be normalised by transformation. For comparisons of total occurrence across different habitat types, number of 'hits' containing any ants and termites (including unidentifiable worker termites found without soldiers) were used. For functional group analyses we excluded 'hits' that only contained unidentifiable workers. Pairwise Wilcoxon rank sum tests with critical p-values reduced to account for multiple tests (following Sokal and Rohlf 1995, p 240) were used to determine which habitats showed significant differences in occurrences.

Ordination analyses were conducted in CANOCO (version 4.5) to test the association of environmental variables with functional group composition. Data on occurrence of ant and termite functional groups were first entered into a Detrended Correspondence Analysis (DCA) to assess gradient lengths. In both cases gradient lengths were short (<3) indicating linear responses of ant and termite functional groups to underlying environmental gradients and therefore that Redundancy Analysis (RDA) was the appropriate direct gradient analysis (Lepš and Šmilauer 2003). The significance of the association between each environmental variable (with readings averaged for each quadrat and habitat type included as a dummy binary variables) and variation in community functional structure were tested using Monte Carlo permutation tests with 999 randomisations. Forward selection was used to rank variables in order of importance in terms of their association with differences in species composition. This procedure selects the variable with the highest marginal eigenvalue followed, stepwise, by those with the highest eigenvalues conditional on the variance explained by all the previous steps (Ter Braak and Verdonschot 1995). Both marginal effects (explanatory effect of each variable when considered singly) and conditional effects (additional explanatory effect of each

Table 1 Ant functional group and termite feeding group definitions, following Andersen (2000), Brown (2000) and Donovan et al. (2001)

Functional/feeding group definitions	
Ants	Termites
Dominant Dolichoderinae (DD): Dominate numerically and behaviourally in hot and open environments	Group I: Dead wood and grass feeders. The only group with flagellate protists in their guts
Subordinate Camponotini (SC): Often diverse and abundant in species-rich ant communities. Avoid competition with Dominant Dolichoderinae by occupying different ecological niches	Group II: Feed on grass, dead wood and leaf litter
Tropical-climate Specialists (TCS): Biogeographically based within the tropics. Few specialised adaptations	Group IIF: Feed on grass, dead wood and leaf litter, with the help of fungal symbionts grown inside the nest ("Fungus-growing termites")
Hot-climate Specialists (HCS): Biogeographically based within arid regions, often with adaptations to forage in extreme heat	Group III: Feed in the organically rich upper soil layers ("Humus feeders")
Cryptic species (C): Small species that are either subterranean, or nest in leaf litter or rotting logs. They are abundant and diverse in forests	Group IV: Feed on organically very poor soil ("True soil feeders")
Opportunists (O): Unspecialised and poorly competitive with a widespread distribution. Particularly abundant where species richness is low and/or there are few behaviourally dominant ants	
Generalised Myrmicinae (GM): Widespread genera that can dominate resources with chemical defences. Often dominant in the absence of Dominant Dolichoderinae	
Specialist Predators (SP): Species adapted to prey on particular arthropods. Generally found at low densities in all habitats	

successive new variable when added by forward selection) were calculated. We focus on RDA results generated using environmental variables with significant marginal effects ($p < 0.05$), rather than conditionally significant variables, although the latter are also presented in Table 4. We chose to present the marginal effects rather than conditional effects since it cannot be assumed that the latter will select those variables with ecologically meaningful correlations with assemblage structure. Instead, displaying marginal effects allows a number of candidate explanatory variables to be visualised in relation to the major gradients of assemblage variation.

Results

Overall occurrence across habitats

A total of 4,931 ants and 1,392 termites were sampled across 944 soil pits and 128 dead wood examinations. Ants were found in every quadrat, in 75 % of soil pits and 51 % of dead wood examinations. Termites were found in 71 % of quadrats, 16 % of soil pits and 16 % of dead wood examinations. Ant occurrences were significantly greater in logged forest than in old

Table 2 Classification of the ant genera into functional groups (Andersen 2000, Brown 2000)

Functional group	Ant genera
Dominant Dolichoderinae (DD)	*Iridomyrmex*
Subordinate Camponotini (SC)	*Camponotus, Echinopla, Polyrhachis*
Tropical-climate Specialists (TCS)	*Pseudolasius, Loweriella, Euprenolepis, Proatta, Gnamptogenys, Aenictus, Lordomyrma, Dorylus, Lophomyrmex, Cladomyrma, Tetraponera, Myrmecina, Solenopsis, Dolichoderus, Myrmicaria, Vollenhovia, Epelysidris, Acanthomyrmex, Pristomyrmex, Anoplolepis, Acropyga*
Hot-climate Specialists (HCS)	*Meranoplus*
Opportunists (O)	*Tetramorium, Paratrechina, Paraparatrechina, Nylanderia, Cardiocondyla, Technomyrmex, Tapinoma, Aphaenogaster, Ochetellus*
Generalised Myrmicinae (GM)	*Pheidole, Crematogaster, Monomorium*
Specialist Predators (SP)	*Pachycondyla, Odontoponera, Anochetus, Leptogenys, Platythyrea*
Cryptic species (C)	*Mayriella, Ponera, Carebara, Hypoponera, Pheidologeton, Plagiolepis, Mystrium, Dacetinops, Calyptomyrmex, Amblyopone, Strumigenys, Proceratium, Probolomyrmex, Eurhopalothrix, Centromyrmex, Cryptopone, Discothyrea, Protanilla, Cerapachys*

Table 3 Classification of the termite genera found in this study into feeding groups (Donovan et al. 2001)

Feeding group	Termite genera
Group I	*Schedorhinotermes, Rhinotermes, Heterotermes, Parrhinotermes*
Group II	*Microcerotermes, Globitermes, Lacessititermes, Prohamitermes, Nasutitermes, Bulbitermes*
Group IIF	*Hypotermes, Macrotermes, Odontotermes*
Group III	*Euhamitermes, Discuspiditermes, Malaysiotermes, Mirocapritermes, Procapritermes, 'Homatermes'* (undescribed genus), *Termes, Syncapritermes, Pericapritermes, Homallotermes, Oriensublitermes, Aciculitermes, Labritermes*
Group IV	*Oriencapritermes*

growth forest (Kruskal–Wallis $\chi^2 = 10.72$, df $= 2$, $p = 0.005$; Wilcoxon rank sum OG-LF, $W = 134.5$, $p = 0.002$), but not different between other habitats (Wilcoxon rank sum OG-OP, $W = 71.0$, $p = 0.623$; LF-OP, $W = 202.5$, $p = 0.067$). Termite occurrence was significantly higher in old growth forest than in logged forest or oil palm plantation (Kruskal–Wallis $\chi^2 = 17.66$, df $= 2$, $p < 0.001$; Wilcoxon rank sum OG-LF, $W = 465.5$, $p < 0.001$; OG-OP, $W = 142.5$, $p = 0.001$). Encounters with ants were approximately three times more frequent than encounters with termites in old growth forest, 10 times more frequent in logged forest, and 25 times more frequent in oil palm plantation.

Functional group occurrence across habitat types

Functional group structure of both taxa varied with habitat type (Fig. 1). For the ants (Fig. 1a), significantly more Cryptic and Tropical-climate Specialist ants were found in

Table 4 Results of redundancy analysis (RDA) forward selection to test the effects of environmental variables on ant functional group and termite feeding group structure across habitat types, listing all marginally significant ($p < 0.05$) environmental variables included in the final models

Ants/termites	Environmental variables	Conditional effects, λ_2	Conditional effects, p	Marginal effects, λ_1	Marginal effects, p
a. Ants	Leaf litter cover	0.11	0.001	0.11	0.001
	Logged forest (LF)			0.08	0.007
	Old growth forest (OG)	0.09	0.001	0.08	0.003
	Slope			0.07	0.006
	Forest quality	0.05	0.016	0.06	0.011
	Small saplings cover	0.04	0.042	0.06	0.009
	Humus depth			0.05	0.018
	Bare ground cover			0.04	0.045
	Grass cover			0.04	0.042
	Leaf litter depth	0.03	0.038		
b. Termites	Old growth forest (OG)	0.33		0.33	0.001
	Forest quality			0.26	0.001
	Tall poles cover			0.16	0.001
	Logged forest (LF)			0.15	0.003
	Bare ground cover			0.09	0.022
	Slope			0.08	0.033
	Leaf litter cover			0.07	0.048
	Rocks cover	0.06	0.028		
	Humus depth	0.05	0.04		

Conditional effects (λ_2) show the variation explained, and associated significance, for each variable as it was included into the model by forward selection. Marginal effects (λ_1) show the variation explained by a variable and associated significance level (p), when no other variables are included in the model. Significance of each environmental variable was calculated using Monte Carlo permutation tests with 999 random permutations

logged forest than in old growth forest (C: Kruskal–Wallis $\chi^2 = 7.17$, df = 2, $p = 0.028$; Wilcoxon rank sum OG-LF, $W = 155.5$, $p = 0.007$; TCS: Kruskal–Wallis $\chi^2 = 8.38$, df = 2, $p = 0.015$; Wilcoxon rank sum, OG-LF, $W = 166.0$, $p = 0.014$). Dominant Dolichoderinae were only found in oil palm plantation (Kruskal–Wallis $\chi^2 = 11.31$, df = 2, $p = 0.004$). Opportunist ants were significantly more abundant in oil palm plantation than in old growth forest (Kruskal–Wallis $\chi^2 = 7.24$, df = 2, $p = 0.027$; Wilcoxon rank sum OG-OP, $W = 31.0$, $p = 0.010$; LF-OP, $W = 73.0$, $p = 0.025$) (Fig. 1a).

Group I dead wood feeding termites showed no significant difference in occurrence patterns across the three habitat types, whereas Group II wood and leaf litter feeders, showed significant overall differences in occurrence (Kruskal–Wallis $\chi^2 = 7.77$, df = 2, $p = 0.021$). They were most abundant in old growth forest (Wilcoxon rank sum OG-LF, $W = 381$, $p = 0.036$; OG-OP, $W = 121$, $p = 0.022$) although pairwise comparisons were non-significant following reduction of critical p-values to account for multiple tests (Fig. 1b). Fungus-growing termites (Group IIF) were more abundant in old growth forest than logged forest (Kruskal–Wallis $\chi^2 = 6.45$, df = 2, $p = 0.040$; Wilcoxon rank sum OG-LF, $W = 385.5$, $p = 0.013$) but their occurrence in oil palm plantation was higher than in logged forest and not significantly different from in old growth forest (Fig. 1b). Group III, that feed in the upper organic soil, were more
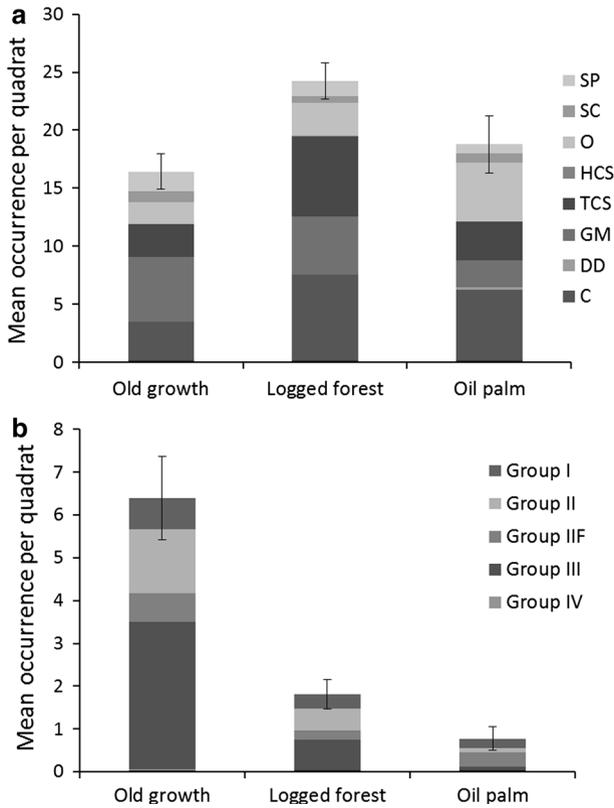
Fig. 1 Mean occurrence of ants (**a**) and termites (**b**) per quadrat in old growth forest, logged forest and oil palm plantation. *Shading* indicates mean occurrence per group (see legend). Ant functional groups: DD dominant Dolichoderinae, SC subordinate Camponotini, TCS tropical-climate Specialists, HCS hot-climate Specialists, C cryptic species, O opportunists, GM generalised Myrmicinae, SP specialist predators. Termite feeding groups: Group I—feed on dead wood and grass; Group II—feed on grass, dead wood and leaf litter; Group IIF—feed on grass, dead wood and leaf litter with the help of fungal symbionts; Group III—feed on organic rich upper soil layers; Group IV—feed on organically poor soil. *Error bars* show ± 1SE of the mean total occurrence

abundant in old growth forest than in both logged forest and oil palm plantation (Kruskal–Wallis $\chi^2 = 21.56$, df = 2, $p < 0.001$; Wilcoxon rank sum OG-LF, $W = 473.5$, $p < 0.001$; OG-OP, $W = 146$, $p < 0.001$), which did not differ from each other. The 'true' soil feeding termites (Group IV) were only present in old growth forest (Fig. 1b). See Online Resources, Table S3 for all statistical results.

Associations between functional groups and environmental variables

For ants, the strongest associations with functional group composition were: forest quality, humus depth, slope, cover of leaf litter, small saplings, grass and bare ground cover (Table 4a). These variables were included in the final RDA (Fig. 2a). Logged forest and grass cover were more strongly associated with axis 1 which largely comprises a gradient of occurrence of Tropical-climate Specialists and Subordinate Camponotini, both being found more commonly in logged forest with high grass cover (Fig. 2a). The remaining

significant environmental variables (old growth forest, humus depth, leaf litter depth, forest quality, slope, small saplings cover, and bare ground cover) were associated with axis 2 (Fig. 2a; Table 5a). In the latter case, all variables were positively associated, except for bare ground cover which was negatively associated. Ant functional groups were variable in their associations with this disturbance gradient (Fig. 2a) with some functional groups positively correlated with axis 2 and therefore low disturbance sites (Generalised Myrm- icinae; Specialist Predators; and to a lesser extent, Hot-climate Specialists), and some negatively correlated with axis 2 and therefore associated with high disturbance sites (Opportunists; Cryptic species; and to a lesser extent Dominant Dolichoderinae).

For termites, forest quality, slope, cover of tall poles, leaf litter and bare ground were strongly associated with feeding group structure (Table 4) and were the variables included in the final RDA (Fig. 2b). Old growth forest, forest quality, slope, tall poles and leaf litter cover were positively associated with axis 1, while logged forest and bare ground cover had negative axis 1 scores (Fig. 2b; Table 5b). Axis 1 of the RDA largely reflected associations with forest quality and a habitat disturbance gradient. All termite feeding groups were positively associated with axis 1 (i.e. with low disturbance levels), with dead wood/leaf litter feeders (Group II) and organic soil feeders (Group III) being strongly so, dead wood/feeders (Group I) and fungus-growing termites (Group IIF) being more weakly associated, and true soil feeders (Group IV) having the weakest association of all (note, there were very few Group IV occurrences) (Fig. 2b). Axis 2 accounted for only 2.5 % of assemblage variation. Group IIF and Group I showed stronger associations with axis 2 than axis 1, being positively and negatively associated with bare ground cover, respectively (Fig. 2b).

Discussion

Both ants and termites inhabiting soil and dead wood varied in occurrence and functional group composition with habitat disturbance. However, the results differed greatly between the two taxa. All termite feeding groups showed fewer occurrences in more disturbed sites, whereas ant functional groups showed more idiosyncratic patterns. Variation in functional group occurrence was related to habitat treatment for both ants and termites, but the strength of associations with other variables differed between the taxa.

Ants were well represented in disturbed habitats, with occurrences highest in logged forest. Studies in Amazonia have also found high ant abundances in moderately disturbed habitats such as re-growth forest and fragment edges (Didham 1997; Vasconcelos 1999). Andersen (2000) considers low temperature, lack of nest sites (e.g. rotting logs), poor food supply, and high structural complexity of foraging surfaces to be the main stressors lim- iting ant populations. Logged forests may offer intermediate conditions that favour greater ant abundance, in which nest sites are available, but surfaces are not too complex to limit foraging, with temperatures slightly higher on average than in old growth forest. However, more highly disturbed forests, such as secondary regrowth following clearance, support fewer species due to differences in tree density, diversity and size distribution (Klimes et al. 2012). In contrast, termites were more common in old growth forest than in the other two habitats. Many termites require a closed canopy to buffer microclimate and avoid desiccation, as well as relatively clayey soils rich in organic material for colony building and food (Eggleton et al. 1997, Hassall et al. 2006). Logging, habitat clearance and conversion to oil palm plantation lead to hotter and drier microclimate (Turner and Foster 2006), and the disruption of soil structure by logging tracks (Malmer and Grip 1990).

Fig. 2 Ordination tri-plots showing redundancy analysis (RDA) of ant functional group occurrence (**a**) and termite feeding group occurrence (**b**) and marginally significant environmental variables in quadrats across all habitat types. For ants (**a**) axis 1 explained 17.6 % of assemblage variation and axis 2 explained an additional 11.1 % of the variation. For termites **b** axis 1 explained 36.3 % of the variation and axis 2 accounted for an additional 2.5 % of variation. Abbreviations for functional and feeding groups are as for Fig. 1, with Grp I–Grp IV representing termite Groups I–IV
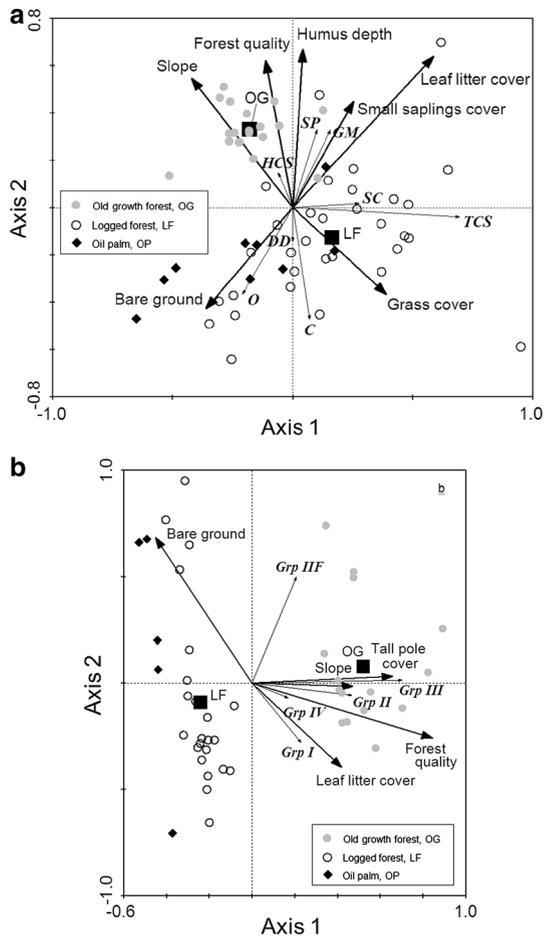
These differences may have been accentuated by a drought that was just ending during the sampling period (see http://www.searrp.org/danum-valley/the-conservation-area/climate/), because disturbed forests may be less able to buffer microclimate (Ewers and Banks-Leite 2013). Termite assemblages generally have lower abundances and species densities in disturbed habitats (e.g. Eggleton et al. 1997; Gathorne-Hardy et al. 2002; Donovan et al. 2007). Apart from *Macrotermes gilvus*, Borneo lacks termite species that are adapted to drier, disturbed conditions (Jones et al. 2003; Hassall et al. 2006) and so species are lost as habitat disturbance increases, but are not replaced by others.

We found that the functional group composition of ant communities varied with habitat degradation, in association with variables linked to disturbance. Of these, slope was positively associated with forest quality because steep slopes are less intensively logged. Overall, ant functional groups showed variable associations with habitat disturbance. Species within the functional groups of Opportunists and Dominant Dolichoderinae thrive in hot and open areas (Andersen 2000) and were most abundant in oil palm plantation—a very open and thermally favourable habitat. Cryptic species were more abundant in logged forest than old growth forest. This may be due to increased dead wood levels in logged

Table 5 Intraset correlation coefficients of marginally significant environmental variables for the first two axes of the RDA for functional and feeding group structure of ants and termites

Ants/termites	Environmental variables	Axis 1	Axis 2
a. Ants	Forest quality	−0.114	0.621
	Slope	−0.422	0.546
	Small saplings cover	0.254	0.449
	Leaf litter cover	0.587	0.639
	Bare ground cover	−0.362	−0.428
	Grass cover	0.390	−0.367
	Humus depth	0.043	0.667
b. Termites	Forest quality	0.868	−0.181
	Slope	0.593	0.011
	Tall poles cover	0.695	0.103
	Leaf litter cover	0.370	−0.353
	Bare ground cover	−0.384	0.692

Old growth forest (OG) and logged forest (LF) were omitted because they were nominal variables

forest compared with old growth forest (e.g. 50 % greater in Amazon forests; Palace et al. 2007) providing additional microhabitats.

In contrast, occurrence of Specialist Predators and Generalised Myrmicinae was correlated with variables associated with old growth forest, with Generalised Myrmicinae being numerically dominant in old growth forest. Generalised Myrmicinae are often outcompeted by Dominant Dolichoderinae in open areas. Greater shade tolerance may therefore allow Generalised Myrmicinae to escape competition inside forests (Andersen 2000). This pattern of loss of forest specialist canopy ants and replacement by open-habitat species when forests are logged has been observed by Widodo et al. (2004). Specialist Predators may decline in modified habitats because they feed on prey such as termites, which are lost with disturbance. The Specialist Predator genera, *Pachychondyla* and *Leptogenys,* are believed to predate termites, and had highest occurrence rates in old growth forest and logged forest respectively. However, although some studies have considered foraging behaviour that includes termite predation (Maschwitz and Schönegge 1983; Wilson and Brown 1984; Johnson et al. 2003), there are few quantitative data for termite predation by ants in forest systems.

Termite feeding group composition was strongly correlated with variation in habitat disturbance, with all groups being most abundant in old growth forest. The RDA analysis confirmed that factors associated with habitat disturbance were significantly associated with variation in feeding group structure. Degree of exoskeleton sclerotisation and therefore potential resistance to desiccation, decreases across feeding groups from groups I to IV, i.e. from dead wood to soil feeders (Eggleton et al. 1997). Humus feeders in Group III showed significant decreases in occurrence in disturbed habitats. Desiccation-prone soil feeders lack the energy resources to maintain their water balance in hot, variable habitats (Gathorne-Hardy et al. 2002). Compaction and changes in soil composition with disturbance (Nye and Greenland 1964) are also likely to affect termite nesting and feeding negatively (Eggleton et al. 1997).

Dead wood feeders and fungus-growing termites in Groups I and IIF did not show as much difference in occurrence in disturbed sites as soil feeders, and had weaker correlations with disturbance-associated variables in the RDA than Group III. Higher exoskeleton

sclerotisation of Group I/IIF termites provides resistance to desiccation in open habitats. Similarly, feeding on wood provides more energy per unit of substrate than soil, giving greater energetic resilience to a varying microclimate. Group II termites are also predominantly wood feeders, and are moderately sclerotised, perhaps explaining why their decline over the disturbance gradient was less dramatic than the poorly sclerotised soil feeders. Wood feeding termites have also been found to be more resilient to disturbance and habitat conversion than soil feeders in West Africa and Sumatra (Eggleton et al. 1995, 2002, Jones et al. 2003).

Changes in assemblage composition with habitat disturbance may disrupt ecosystem functions. The consistently strong negative response of all termite groups, may lead to a decline in decomposition rates. The only study to consider this to date (Foster et al. 2011), shows that leaf litter breakdown remains constant along a similar habitat disturbance gradient, and thus does not support this hypothesis. However, leaf litter may not be representative of the functioning of the whole system, because termites feed on a range of organic material, and leaves may only be a small part of that system (Eggleton et al. 1997). Furthermore, leaf litter is consumed by a wide range of other invertebrates. In addition, the majority of decomposition in oil palm plantations is conducted by only a single termite species (*Macrotermes gilvus*) (Foster et al. 2011) indicating low levels of functional redundancy, and high vulnerability of ecosystem functioning to species loss.

The differences in ant functional group occurrence were more varied, and so any changes in ecosystem functioning that might occur may be more subtle. Some Dominant Dolichoderinae are predators of invertebrate herbivores, so higher abundances of them in disturbed habitats may benefit plantations. However, other Dominant Dolichoderinae also tend phytophagous insects, which could be herbivores of oil palm (Wielgoss et al. 2014). Some non-native Tropical-climate Specialists (e.g. the yellow crazy ant *Anoplolepis gracilipes*), may supress herbivores (Blüthgen and Feldhaar 2010). Conversely, predation by Specialist Predators of specific groups (e.g. termites) may decline with disturbance. Other functions, such as soil turnover and scavenger mediated nutrient redistribution (Fayle et al. 2011) found in most functional groups, may track overall ant abundance, which does not change drastically with habitat disturbance.

Global agricultural expansion threatens the biodiversity and ecological functions of tropical forests. Here, we have identified significant differences in the overall encounter rates of ants and termites between old growth forest, logged forest and oil palm plantation, and showed that ant abundances appear more resilient to forest disturbance than termite abundances. This study demonstrates a dramatic difference in ant functional group and termite feeding group occurrence which suggests likely changes in the ecosystem functions that will be performed by these dominant taxa in disturbed habitats.

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