Forest gaps, edge, and interior support different ant communities in a tropical peat-swamp forest in Borneo

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ABSTRACT. Southeast Asia's tropical peat-swamp forests (TPSF) are globally important for carbon storage and biodiversity conservation, but are at risk from multiple threats and urgently require improved management. Ants are often used as ecological indicators in monitoring programmes to guide adaptive management, but data on TPSF ants are scarce. We conducted a twelve-month study on ants in the Sabangau TPSF in Indonesian Borneo using baited traps, to compare community composition across three disturbance categories (forest gaps, forest edge and relatively undisturbed interior forest) and between dry and wet season. The three disturbance categories supported distinct ant communities across seasons. Differences in canopy cover likely underlie these changes in ant community composition. Surveying was more effective in the dry season, because ant capture rates were higher and more indicator taxa were identified than in the wet season, but overall ant community composition did not differ significantly between seasons. These findings suggest a potentially useful role of ants as ecological indicators in TPSF. Further surveys should be conducted in Sabangau and other TPSFs to test the transferability of our findings.

ABSTRACT – INDONESIAN TRANSLATION
Hutan Rawa Gambut Tropis (HRGT) yang berada di Asia Tenggara memiliki peran yang sangat penting dalam penyimpanan karbon serta pelestarian keanekaragaman hayati secara global, tetapi beresiko mengalami berbagai ancaman dan karena itu memerlukan perbaikan pengelolaan yang sangat

2   Stijn J. J. Schreven, Eric D. Perlett, Benjamin J. M. Jarrett, Nicholas C. Marchant, Fransiskus Agus Harsanto, Ari Purwanto, K. V. Sýkora & Mark E. Harrison

mendesak. Terkait hal tersebut, semut seringkali digunakan sebagai indikator ekologis untuk program pemantauan (monitoring) yang dapat menjembatani pengelolaan adaptif, walau demikian sangat disayangkan bahwa data tentang semut masih sangat langka di HRGT. Untuk itu, kami telah melakukan penelitian selama 12 bulan terhadap semut di kawasan HRGT Sabangau yang berlokasi di Kalimantan Tengah dengan menggunakan perangkap umpan yang bertujuan untuk membandingkan komposisi dari kelompok semut pada tiga kategori wilayah gangguan (hutan terbuka, tepian hutan, serta hutan interior yang relatif tidak terganggu), serta antara musim kemarau dan hujan. Ketiga kategori gangguan tersebut membantu kelompok semut yang berbeda di segala musim. Terkait hal tersebut, adanya perbedaan tutupan kanopi kemungkinan mendasari adanya perubahan pada komposisi kelompok semut. Selain itu, survei semut dianggap lebih efektif dilakukan pada musim kemarau karena tangkapan semut pada musim tersebut relatif lebih tinggi dan taksa indikator lebih banyak teridentifikasi jika dibandingkan musim penghujan, walau demikian secara keseluruhan komposisi kelompok semut tidak mengalami perbedaan yang signifikan antar musim. Temuan ini menunjukkan potensi penting dari peran semut sebagai indikator ekologis di kawasan HRGT. Survei lebih lanjut hendaknya dilakukan di kawasan Sabangau atau kawasan (HRGT) lainnya untuk menguji transferabilitas temuan kami.

Keywords: ecological indicator, Formicidae, baits, disturbance, seasonality, Kalimantan

INTRODUCTION

Southeast Asia's tropical peat-swamp forests (TPSF) are receiving increasing recognition for the vital ecosystem services they provide (Yule 2010, Page et al. 2011). Indonesia contains the second-largest area of global tropical peatlands (Gumbricht et al. 2017), of which a large part is located on Borneo. TPSF comprises some of Borneo's last strongholds of lowland forest and associated biodiversity (Posa et al. 2011, Nowak 2013), yet deforestation and conversion of peatlands into mainly industrial plantations continue at a rapid rate (Miettinen et al. 2016). Furthermore, while intact TPSF accumulates several metres of organic peat over thousands of years (Page et al. 2011), degraded peatlands are prone to decomposition and fires. This leads to extremely high carbon dioxide emissions (Page et al. 2002, Moore et al. 2013), soil subsidence (Hooijer et al. 2012), thick haze clouds and consequently high premature human mortalities (Crippa et al. 2016), besides negative impacts on biodiversity (Harrison et al 2016). For these reasons, there is an urgent need for improved conservation management and restoration of TPSF.

Monitoring of indicator taxa can be a cost-effective way to evaluate and improve conservation measures (Gardner 2010). Ants (Hymenoptera: Formicidae) are frequently used as ecological indicators in terrestrial ecosystems (Underwood & Fisher 2006, Gerlach et al. 2013), including tropical forests (e.g. Schmidt et al. 2013). Besides their sensitivity to environmental change, they are diverse and abundant in most terrestrial systems, and occupy many different trophic levels, contributing to important ecosystem processes such as nutrient cycling (Underwood & Fisher 2006, Griffiths et al. 2018).

So far, ant research in Borneo has been concentrated in the rainforests of Sabah and Sarawak, and hardly anything is known on the ant fauna of Kalimantan and TPSF (Pfeiffer et al. 2011). From these studies, however, it is clear that forest disturbances can impact Bornean ant communities. Different Bornean forest types support their own distinct ground ant communities owing to differences in environmental factors, possibly in combination with stochastic processes (Mezger & Pfeiffer 2011). Similarly, forest disturbance can impact ant communities by altering the structure and microclimate of the

forest strata. Since almost 50% of the known ant species of Borneo are arboreal (Floren et al. 2014), logging has the potential to severely alter forest ant communities. Selective logging shifts arboreal and ground ant community composition from forest specialists to open habitat specialists and opportunists (Widodo et al. 2004, Luke et al. 2014). The more drastic disturbance of forest clear-cutting and conversion into oil-palm plantations results in less even, species-poorer arboreal and ground-dwelling ant communities with fewer forest species and more non-native species (Brühl & Eltz 2010, Fayle et al. 2010).

When monitoring ant responses to forest disturbance, it is important to assess if the effects are consistent year-round. Tropical forest ant communities can display seasonal patterns in species richness, abundance and composition that differ among habitats (Barrow & Parr 2008, Neves et al. 2010) or disturbance conditions (Silveira et al. 2012). Such seasonal differences can also be expected in TPSF. A number of peat-swamp forest trees start flowering and fruiting in response to seasonal triggers (Harrison et al. 2010), which may cause subsequent variation in the availability of ant food resources (Kato et al. 1995). Because of the naturally high water table, large parts of the forest floor of TPSF are submerged during the wet season (Wösten et al. 2008). Such periodic flooding can decrease ant nest abundance and species richness and change species composition (Mertl et al. 2009).

In this study, we compared ant communities in three different forest disturbance categories (i.e. forest gaps, forest edge and relatively undisturbed interior forest) using honey-baited traps in Sabangau TPSF, Indonesian Borneo, over a twelve-month period that incorporated one wet and one dry season. Sabangau TPSF has important conservation value, as it harbours significant populations of felines (Cheyne & MacDonald 2011) and primates, such as the Bornean orangutan, Bornean white-bearded gibbon and red langur (Morrogh-Bernard et al. 2003, Cheyne et al. 2008, Ehlers-Smith & Ehlers-Smith 2013). Since 1999, ecological monitoring programmes have been set up in the area, including surveys on mammals, birds and butterflies (Harrison et al. 2012). Among others, these surveys have shown that forest disturbance reduces nymphalid butter-

fly diversity and favours more generalist species (Houlihan et al. 2013).

To the best of our knowledge, this is the first study to characterise the ant fauna of a Bornean TPSF. We aimed to investigate the utility of ants as indicators of ecological disturbance in Bornean TPSF by answering the following questions: 1) do ant communities differ in relation to TPSF disturbance? And 2) does ant community composition differ between dry and wet seasons?

MATERIAL AND METHODS

Study site and survey locations

Fieldwork was conducted in the mixed-swamp forest habitat sub-type in the 500-km^2 Natural Laboratory of Peat-swamp Forest (NLPSF, 2°19' S and 113°54' E), part of the 6,000 km^2 Sabangau Forest in Central Kalimantan, Indonesia (Figure 1; Page et al. 1999). The NLPSF was selectively logged under concession until 1997 and then illegally logged until 2004, after which logging in this part of Sabangau ceased. Past illegal logging was accompanied by swamp drainage, as canals were dug to float out timber, which has caused hydrological disturbance and placed the forest at increased risk of peat degradation and fire. The forest has suffered additional disturbance through hunting of large flying foxes (*Pteropus vampyrus*), in which hunters cleared the forest around a focal tree to create "bat gaps" and capture bats using nets (Struebig et al. 2007).

The forest in the NLPSF thus represents a mosaic of relatively undisturbed and disturbed/regenerating forest, with a distinct edge bordering non-forested sedge, which forms the floodplain of the Sabangau River, has experienced various fire events and is at varying stages of regeneration. Ants were sampled within the main NLPSF research grid using five plots in three forest conditions of differing disturbance histories and environmental characteristics (Figure 1, Electronic Supplementary Material Table S1):

– "Disturbed bat gaps" (grid plots G and H in Figure 1): these previously clear-cut patches of about 30-50 m diameter are found within the otherwise relatively undisturbed interior forest. The gaps have been regenerating since last used by hunt-

ers around 5 years prior to this study and have a dense regrowth of pioneer tree species to a height of around 1-2 m.

– "Disturbed forest edge" (line transect plot E): this 5 x 300 m plot runs parallel to and within 5 m of the edge between the forest and the deforested sedge swamp. Tree species composition along this edge differs markedly from that in the interior forest (Frank 2013).

– "Relatively undisturbed forest interior" (line transects A and B): these two 5 x 300 m plots are situated in relatively undisturbed mixed-swamp forest at 900 m and 1,900 m from the forest edge, respectively. They are believed to have suffered relatively light logging disturbance and have been regenerating since the cessation of logging in the area in 2004.

Sampling

In total 30 traps were positioned within each transect plot and 15 within each of the bat gap plots, with a 10 m distance between each trap. Since foraging range of ant species can exceed this distance (e.g. Pfeiffer & Linsenmair 1998, Maschwitz et al. 1989), we statistically tested the independence of traps (see below). Traps were baited on around the same days of each month from May 2011 to April 2012. Traps consisted of a yellow transparent plastic milkshake cup (10 cm high, top diameter 6 cm) with the convex lid turned upside-down on top and attached using tape (Figure 2). The lid had a central hole of 1 cm diameter through which ants could enter. Although some ants were able to escape through this entry hole, most were trapped in the bait solution. Each cup was tied to the stem of a sapling, shrub or tree, with the bottom touching the litter or ground and the top touching the stem, so that ants could access the trap from both the ground and higher forest strata. Traps were baited with 40 ml honey bait solution (95.33% water, 3.33% honey and 1.33% ethanol (70% alcohol by volume)) (cf. Yamane et al. 1996). Traps were emptied after 48 hours, and all ants present were collected and stored in 70% ethanol. We hereafter refer to each 48-hour trapping period as a "trapping unit". From a total 1,440 trapping units, 44 were lost owing to trap disruption (usually by wild pigs or primates), weather and other causes (Table 1).

Ant identification

Worker caste ants were identified under a microscope, using guides for world subfamilies and genera (Bolton 1994), supplemented with recent genus-group revisions (LaPolla et al. 2010) and online ant databases (Antweb.org, Antbase.net). For identification of species and classification of morpho-species, regional genus-level taxonomic reviews were used where available, and otherwise revisions of other geographical regions were used to derive diagnostic features for distinction of morpho-species (see Schreven et al. 2014 for a full list of identification literature used). Identification was performed by three of the authors (EP, BJ, SS), the last of which revised the reference collection and detected splitting and lumping errors in the (morpho-)species identifications before processing the samples of the final three months. Unfortunately, the original samples of the first nine months had been discarded by that time and could not be revised. Hence, we analysed our data at genus level only (excluding *Ochetellus* from the analyses as it contained a lumping error), except for the indicator species analysis (see below) that was conducted for each species independently, using only those for which we were confident there were no identification errors. The reference collection is available at the Borneo Nature Foundation, Palangka Raya, Indonesia.

Statistical analyses

Worker ant abundance was analysed at the level of individual traps and the level of plots. The trap-level analyses provided a higher data resolution than the plots and allowed for more community analyses than our plot-level data, but suffered from pseudo-replication. At the individual trap level, species abundance (i.e. total workers captured per trap across months) was classified into six abundance classes, hereafter referred to as scaled abundance: "0" for none, "1" for one individual, "2" for 2-5, "3" for 6-20, "4" for 21-50 and "5" for > 50 individuals (Hoffmann et al. 2000). At the plot level, species counts (i.e. the number of traps in which a species was captured) were standardized to percentages of traps per plot, since trap sample size varied between transects and bat gaps.

        Dissimilarity of ant community composition between traps or plots was calculated us-

Table 1. Plot size, sampling effort and capture rates for each plot. [1] Capture rate = No. individuals captured / (No. trapping units – no. units lost).

Condition	Plot	Plot size (m²)	Trap arrangement	No. traps	No. trapping units (no. units lost)	No. individuals captured	Capture rate [1]
Gap	G	1500	Grid	15	180 (2)	424	2.38
	H	1500	Grid	15	180 (2)	329	1.85
Edge	E	1500	Transect	30	360 (11)	481	1.38
Interior	A	1500	Transect	30	360 (14)	855	2.47
	B	1500	Transect	30	360 (15)	962	2.79
Total				120	1440 (44)	3051	2.19

ing the Morisita-Horn index (Wolda 1981) in the *vegdist* function of the vegan package of R (Oksanen et al. 2018). Autocorrelation of inter-trap distance and Morisita-Horn dissimilarity in genus composition of individual traps was tested using Mantel's Monte Carlo test (1000 permutations) in the *mantel* function of the vegan package of R.

Differences among disturbance categories in ant community composition (Morisita-Horn dissimilarity) of individual traps were tested by means of the permutational multivariate analysis of variance (PERMANOVA) using the *adonis* function (Anderson 2017) in the vegan package of R. Indirect gradient analysis of ant genus community composition at the different spatial scales was conducted using Principal Components Analysis (PCA) in the software package CANOCO version 4.55.

Indicator species analyses were performed for the trap-level presence-absence data to compare the three disturbance categories, using the IndVal method (Dufrêne & Legendre 1997) in PC-ORD 4.25. The indicator value (IV) is a product of the specificity of a taxon (i.e. in our case, the frequency of the taxon in a given group relative to its mean frequency in all groups) and its fidelity (i.e. the relative frequency of the taxon in a given group). Perfect indication (IV = 100%) means that a taxon is only present in one group (specificity = 100%) and occurs in all samples within that group (fidelity = 100%). Indicator taxa were identified as those with an indicator value that is both significant (P < 0.05, Mantel's Monte Carlo test, 1000 permutations) and larger than 25%.

To identify seasonal variations in ant community composition, PCA, PERMANOVA and IndVal analyses were performed on dry and wet season data, comparing the four months of dry season (June-September 2011) to the four central months of the wet season (December 2011-March 2012). Seasonal differences in log-transformed ant abundances (y = log(x+1)) per trap per month were analysed in a generalized least squares (GLS) regression model with disturbance category and season as fixed factors, and accounting for heterogeneity of variances in the disturbance category x season combinations, using the *gls* function of the nlme package in R (Pinheiro et al. 2018). Model selection was based on Akaike's Information Criterion (AIC) (Akaike 1974). Tukey-adjusted post-hoc comparisons were made using the *lsmeans* function of the lsmeans package in R (Lenth 2016). For all statistical analyses in R, version 3.4.2 was used (R Core Team, 2017).

RESULTS

Species richness and independence of traps

A total 3,051 worker ants were collected, of which 2,933 were undamaged and included in the analyses (Table 1). These were identified to six subfamilies, 25 genera and 47 (morpho-)species (Table S2). From these 47 morphospecies, 38 did not contain lumping errors after revision.

Inter-trap distance and Morisita-Horn dissimilarity of traps were positively correlated in the bat gap plot H (Mantel test, 1000 permu-

tations, r = 0.314, P = 0.016), but no significant correlations were found for the other four plots, indicating that for the latter plots individual traps can be treated as statistically independent sampling units.

Differences in community composition among forest disturbance categories
Ant community composition of traps varied significantly more between than within disturbance categories (PERMANOVA, 1000 permutations, $F_{1,118}$ = 27.91, P = 0.001). The first and second axes of the PCA of the individual traps together explained 43.7% of total variance and distinguished the gaps from the edge and interior forest, whereas the latter two categories overlapped (Figure 3A). The third PCA axis did not distinguish these latter two groups either. At the level of plots, all three groups were more separated and the first and second PCA axes together explained 90.3% of the variance (Figure 3B).

Indicator taxa of the three forest disturbance categories
IndVal analysis showed similarity between species and genera (Table 2). Most indicator genera included an indicator species for the same disturbance category. In these cases, the species was often the only abundant species in the genus. There are two exceptions: *Pheidole* was not an indicator genus, but *Pheidole rugifera* was an indicator species of interior forest, and the genus *Crematogaster* was an indicator of the forest edge, but contained no significant indicator species.

Influence of season
Log-transformed ant capture rates were significantly higher in the dry season than in the wet season, whereas no significant effect was found of the disturbance category (Figure 4; GLS regression, factor "season" $F_{1,236}$ = 36.819, P < 0.001; factor "disturbance", $F_{2,236}$ = 1.783, P = 0.170). The model accounting for heterogeneity of variances in disturbance categories and seasons was the best fit compared to the null model and models with heteroscedasticity in only one factor (model$_{null}$ df = 5, AIC = 253.54; model$_{season}$ df = 6, AIC = 247.99; model$_{disturbance}$ df = 7, AIC = 241.88; model$_{season*disturbance}$ df = 10, AIC = 240.86).

Ant community composition of plots differed significantly among disturbance categories but not between dry and wet season (PERMANOVA, 1000 permutations, factor "disturbance": $F_{1,7}$ = 20.100, P = 0.005; factor "season": $F_{1,7}$ = 1.124, P = 0.369). A similar picture resulted from the PCA ordination of the dry and wet season ant communities of plots. The first PCA axis distinguished the gaps from the edge and interior and explained most variation (66.4%, Figure S1). The second PCA axis explained a much smaller part of the variation, which appeared to be due to seasonal differences (13.9%, Figure S1A), whereas the third PCA axis (8.7%, Figure S1B) separated the edge and interior plots. Thus, the seasonal differences in community composition appeared secondary to the differences among disturbance categories. Nonetheless, the indicator values of individual taxa varied between seasons (Table 2). None of the indicator taxa in the dry

Table 2. Indicator species and genera associated with forest disturbance categories in Sabangau, overall and in dry and wet season separately. For each indicator genus, the number of recorded species is in parentheses. Perfect indication (IV = 100%) means a taxon is only present in that group and occurs in all samples within that group. Only taxa with significant indicator values (IV ≥ 25% and P < 0.05) are displayed.

| Disturbance category	Species	Indicator value (%)			Genus	Indicator value (%)		
		overall	dry	wet		overall	dry	wet
Bat gaps	*Monomorium cf. floricola*	72	69	50	*Monomorium* (2 spp.)	65	66	48
	Oecophylla smaragdina	30			*Oecophylla* (1 sp.)	30		
Edge	*Polyrhachis (Myrma) sp.*	59			*Polyrhachis* (3 spp.)	57	27	
	Tetramorium sp. cf. "Triglyphothrix"	34			*Crematogaster* (9 spp.)	42	36	
					Tetramorium (6 spp.)	32	25	
Interior	*Pheidole rugifera*	27			*Nylanderia* (3 spp.)	37		
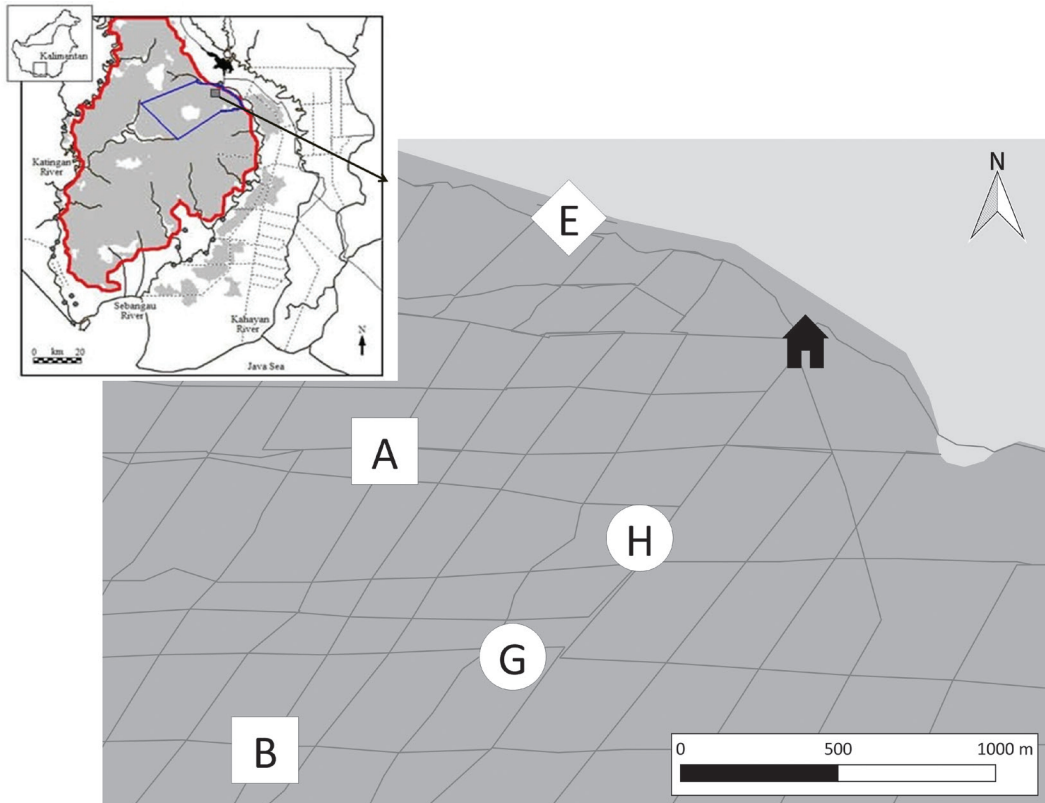
Fig. 1. Location of Sabangau Forest and survey transects. Inset: red border indicates the Sabangau Forest, blue border indicates the 500-km2 NLPSF and grey shading indicates forest cover. Main image: map of transect grid in the NLPSF, with letters for sampling locations corresponding to those used in the text: G+H = bat gaps, A+B = interior forest, E = edge. G and H are grid plots, A, B and E are line transect plots.
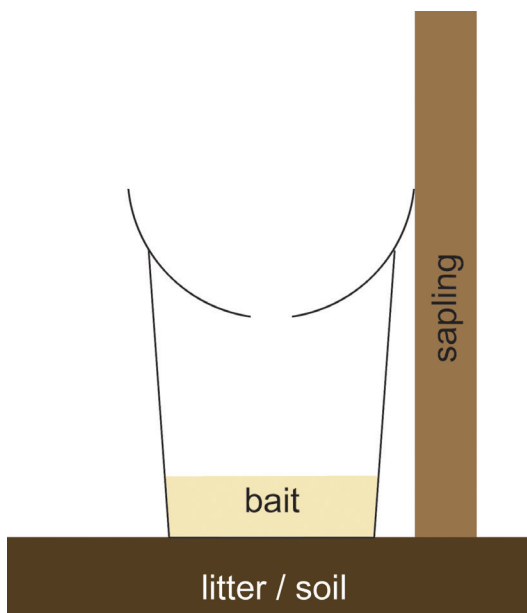

Fig. 2. Schematic drawing of the baited trap. The upside-down lid with central hole acts as a funnel through which ants fall into the bait solution. Ants can enter the trap by climbing up the side of the cup to the lid from the ground, or by walking from the stem of a sapling onto the lid.
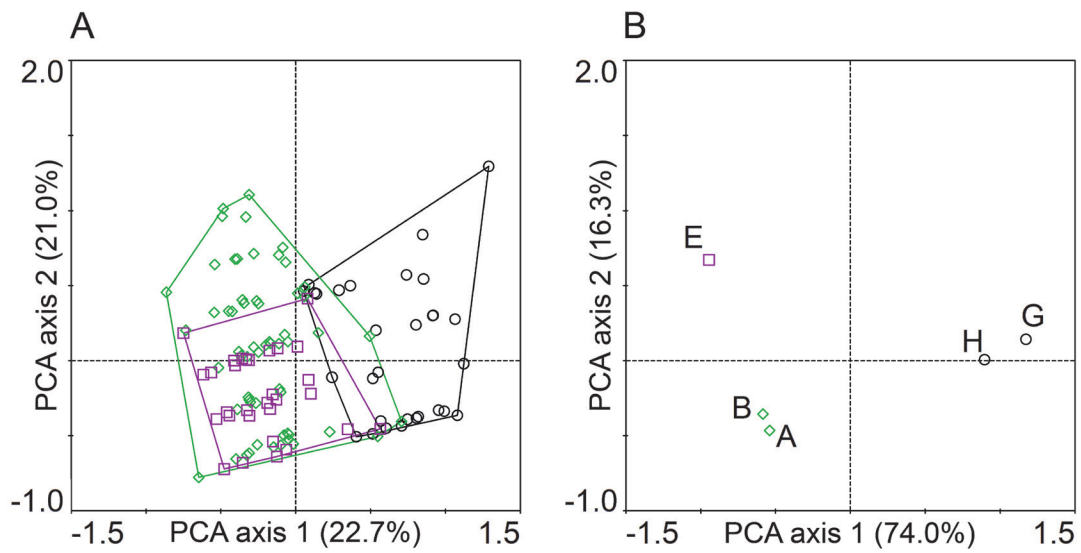
Fig. 3. PCA samples for ant community composition of genera at trap (A) and plot scale (B). Percentage of explained variance is in parentheses. Different colours and symbols represent the different disturbance categories: bat gaps (black circles), edge (purple squares) and interior forest (green diamonds). Capital letters in B indicate the plots as in Figure 1 (G+H = gaps, A+B = interior forest, E = edge). Percentage explained variance for all four PCA axes per PCA scatter plot is in Table S3.
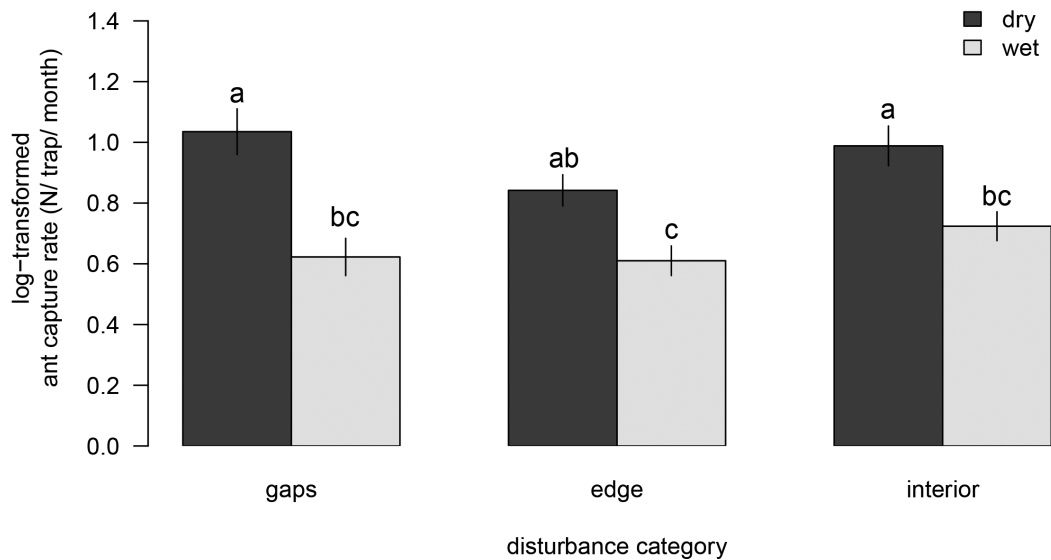

Fig. 4. Log-transformed ant capture rate (number of workers captured per trap per month), means ± SE, for the three disturbance categories separated for dry (dark grey) and wet season (light grey). Different letters indicate significantly different means.

season also exhibited a significant indicator value above 25% in the wet season, except *Monomorium cf. floricola* and its corresponding genus.

DISCUSSION

Ant community composition differed among disturbance categories

We report differences in ant community composition among three different disturbance categories in a tropical peat-swamp forest (TPSF) in Borneo. We show that ant capture rates are higher in the dry than in the wet season, but this did not translate into significant seasonal differences in ant community composition.

Our baited traps likely biased sampling towards generalist ant species foraging on the ground and/or lower canopy strata that are attracted to honey, undersampling those species that have narrower diets or are confined to the arboreal or subterraneous strata (Bestelmeyer et al. 2000). Thus, our data do not provide a complete or representative sample of the entire TPSF ant community. Nonetheless, survey methods with inherent systematic sampling biases can still be useful for ecological monitoring purposes, provided that such biases are understood and acknowledged, and that sampling methods remain consistent over space and time (Gardner, 2010). We believe our samples provide a reliable reflection of a subset of ants, but it would be inappropriate to attempt to generalise these findings beyond this subset of the TPSF ant community.

The sampled ant communities differed significantly between the three disturbance categories studied. The PCA plots suggested that the small-scale disturbances of the gaps altered local ant community composition to a greater degree than the disturbances along the forest edge. This difference could have been due to the absence of higher forest strata in the gaps compared to the edge and interior (Table S1). The dense regrowth of saplings in the gaps was only 1-2 m high. Here sunlight could reach the lower vegetation and ground, unlike in the edge and interior forest. This could increase temperature, which can drive competition of ant species (Mezger & Pfeiffer 2010) and may have allowed only a few

very competitive species to dominate the community. These findings are in line with previously reported effects of larger-scale disturbances such as selective logging and forest conversion to plantations, where lower habitat complexity, decreased canopy cover and more dense understorey vegetation led to decreased evenness and shifted ant communities towards ants of more open habitat (Widodo et al. 2004, Brühl & Eltz 2010, Fayle et al. 2010, Luke et al. 2014). The lower canopy of the forest edge compared to the interior forest could explain the collection of the more arboreal genera of *Polyrhachis* and *Crematogaster* in this disturbance category. In Sabangau TPSF, *Polyrhachis* ants are frequent visitors to *Nepenthes* pitcher plants (particularly *N. rafflesiana*; SS personal observations), which are more abundant at the forest edge (Frank 2013).

Genus responses do not necessarily represent underlying species responses (Timms et al. 2012), although ecological monitoring can be more cost-effective when identifying only genera (Souza et al. 2016). In line with Timms et al. (2012) for other arthropod groups, we suspect that taxonomic sufficiency of our genus-level IndVal analyses decreased with increasing taxonomic ratios, i.e. with more species per genus, but because of the lumping errors in some species identifications we cannot confirm this.

It must be said that the grid sampling design in the gaps may have emphasized local dominance of species whereas a similar local dominance may have been attenuated along the 300 m transects in the edge and interior forest plots. Another limitation of our study is that the data of individual traps are pseudo-replicates, with the true replicates being the five plots. Thus, the interpretation of the trap-level findings and comparison between the two spatial levels must be done cautiously. For instance, the PCA of plots explained more variance than the PCA of the traps, but this is a mathematical effect of pooling trap data in their corresponding plots. Nonetheless, the trap data enabled us to perform informative tests impossible otherwise and individual traps in most plots could be regarded statistically independent. Sampling of more plots, other forest subtypes (Page et al. 1999) and additional TPSF areas can verify the transferability of our findings.

Stijn J. J. Schreven, Eric D. Perlett, Benjamin J. M. Jarrett, Nicholas C. Marchant, Fransiskus Agus Harsanto, Ari Purwanto, K. V. Sýkora & Mark E. Harrison

Seasonal differences in ant capture rates, but not in community composition

Despite seasonal variation in ant capture rates and in individual responses of a number of indicator taxa, disturbance categories differed significantly in ant community composition regardless of season. Overall ant communities did not differ significantly between seasons. Although sampling in either season seems appropriate for monitoring forest disturbance, sampling appears more effective in the dry season, which exhibited higher ant capture rates and more indicator taxa. The higher capture rates may have resulted in the identification of more indicator taxa in the dry season, meaning that the same taxa may still be characteristic of a disturbance category in the wet season, but because of lower abundance the indicator value is low and not significant. Seasonal differences may also be caused by temporal variation in bait attraction, caused by fluctuations in food availability or changing food preferences related to brood production cycles (Stein et al. 1990). However, since the forest floor in Sabangau is annually flooded during the wet season (Wösten et al. 2008), the observed patterns likely represent real seasonal variation in forager density and activity on the forest floor and in the lower forest strata. A possible mechanism underlying the relation between wet-season flooding and low ant abundance could be that forest inundation during the wet season may reduce nesting site availability for leaf-litter ants (Mertl et al. 2009), while at the same time arboreal ants avoid foraging on the inundated forest floor (Adis & Schubart 1984). Despite the plausibility of such a mechanism, the seasonal differences in our study only cover one year, and ant communities can be in a long-term equilibrium but vary from year to year (Donoso 2017). Since the bat gaps had been abandoned only 5 years prior to our survey and forest regeneration is still in process, it is likely that local ant communities have not reached such a long-term equilibrium yet.

Our findings suggest that ants can be used successfully as ecological indicators of forest disturbance in TPSF and that sampling in the dry season is most effective, at least using our trapping method. Several taxonomic groups are being monitored in the Sabangau TPSF. Previous findings showed that fruit-feeding butterfly communities also responded to forest disturbance (Houlihan et al. 2013), even though their mobility is much higher (Marchant et al. 2015) than that of ant colonies. Future studies can compare the cost-effectiveness of these different taxonomic groups, e.g. in terms of proportions of indicator taxa and standardized survey costs (cf. Gardner et al. 2008).

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