# Ant community composition in relation to forest disturbance in a Bornean tropical peat swamp forest



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## Abstract

Restoration and conservation of Borneo's peat swamp forests is urgently needed to sustain vital ecosystem services. This requires feedback from ecological monitoring to guide effective management. Ants are reliable indicators of ecological disturbance elsewhere, but they are poorly known from tropical peat swamp forest. Ant community composition was studied in the Sabangau tropical peat swamp forest (Central Kalimantan, Indonesia) in relation to forest disturbance, to provide a baseline for monitoring of this ecosystem. In addition, temporal variation in ant composition and taxonomic sufficiency were investigated.

Five plots were sampled monthly using honey-baited traps from May 2011 to April 2012, and a number of environmental variables were measured. Indirect gradient and clustering analyses, as well as nonparametric MRPP, IndVal analyses and diversity and similarity statistics were performed.

Different ant communities were discriminated in cleared forest gaps, near the forest edge and in interior forest. Behaviourally dominant ants characterized the disturbed habitats of gaps and edge, whereas opportunists and inhabitants of undisturbed forest characterized the interior forest. Although these patterns were subject to temporal variation, ant communities remained different between habitats. Taxonomic sufficiency seems to apply for genera, offering the opportunity to increase cost-effectiveness of future monitoring programmes.

This is the first study to describe ant communities in a Bornean peat swamp forest in relation to disturbance. Sampling design could be further improved and findings are therefore preliminary. Further baseline surveys are needed to test the robustness of these findings and extend research within Sabangau and to other peat swamp forests in order to make general statements on the use of ants as ecological indicators in peat swamp forest.

## Introduction

Only since several decades, scientists are gaining insight in the ecosystem services of tropical peat swamp forests, initiated by the concerns on their rapid loss due to logging, land conversion, drainage and fires (Page et al. 1999). They not only store massive carbon stocks (Page et al. 2011), but also contribute among others to air and water quality, water safety, economically important forest products and biodiversity conservation (Page et al. 1999, Harrison 2013). Indonesia possesses the largest extent of tropical peatlands, i.e. 20.7 million hectares, which store 65% of all tropical peat carbon (Page et al. 2011). Most of Indonesia's peatlands used to be covered by peat swamp forest, and largest areas are found on Sumatra, Borneo and Irian Jaya (Indonesian Papua) (Rieley et al. 1996).

Tropical peat swamp forests form on permanently waterlogged organic matter that accumulates as ombrogenous peat to a layer of up to 20 m thick (Page et al. 2011). The peat swamp follows a dome shape, with mixed swamp forest at the outer zone, a low pole forest more interiorly and a tall interior forest on the top of the dome, all different in forest structure and peat characteristics (Page et al. 1999). Unlike other Southeast-Asian rainforest types, peat swamps have been avoided by naturalists until recently. They have long been assumed to be species-poor and the physical conditions were seen as an impediment to field research (Page et al. 1997, Posa et al. 2011). They support, however, a considerable proportion of the region's wildlife (Page et al. 1997, Posa et al. 2011). Due to the destruction of other forest types like heath forests and dipterocarp forests, peat swamp forest are becoming increasingly important as a refuge for threatened and regionally endemic fauna (Posa et al. 2011, Nowak 2013). At present, the largest remaining wild populations of Bornean orang-utan (*Pongo pygmaeus*) and Bornean agile gibbon (*Hylobates albilabris*) are found in the protected Sabangau peat swamp forest (Morrogh-Bernard et al. 2003, Cheyne et al. 2008). Besides, there is a number of stenotopic species of peat swamp forest, especially among trees (Posa et al. 2011) and freshwater fish (Giam et al. 2012).

Since the 1980s, however, these forests have been increasingly degraded due to logging practices, drainage and fires, or converted into industrial plantations (Miettinen et al. 2012). Borneo annually loses 2.2% of its peat swamp forests, and over 40% of Southeast-Asia's original peatlands have already been lost (Page et al. 2011). Owing to the rapid loss of forest and associated vital ecosystem services, the concern for urgent conservation and restoration of remaining and degraded peatlands has grown considerably (Page et al. 2009).

In order for restoration to be effective, the quality of the ecosystem should be monitored to provide feedback on management (Kremen et al. 1994). However, surveying an entire tropical forest ecosystem is hardly ever possible, while monitoring indicator taxa instead greatly reduces costs and efforts (Maleque et al. 2009). A particular taxon can serve as an ecological indicator if its response to a certain environmental stressor is representative of the response of the ecosystem (McGeoch 1998). Target species of peat swamp forest, such as orang-utans, show responses to habitat disturbance, but these may be delayed for several years due to dietary flexibility (Husson et al. 2009) and hence may not represent the actual ecological integrity of the forest.

Arthropods, however, have many characteristics that potentially make them highly suitable as ecological indicators: they comprise the majority of species and biomass in most terrestrial ecosystems, contribute variedly to ecological interactions and ecosystem functioning, have short lifecycles, and are very sensitive to changes in temperature and moisture (McGeoch 1998, Maleque et al. 2009). Whether or not a certain taxonomic group is indeed reliably indicative, requires rigorous testing, starting with baseline surveys to test the relation of the response (e.g. species composition) of the particular group to the disturbance of interest, the consistency of this response over time and in different areas, and its representation of responses of other related and unrelated taxa (McGeoch 1998).

One of the main problems with insects in tropical ecosystems is the fact that the majority of species is undescribed, an impediment termed the Linnaean shortfall (Brown & Lomolino 1998 in Landeiro et al. 2012). Since the rate of biodiversity loss exceeds the rate of description of new species, conservationists need to find alternatives to study insect diversity (Landeiro et al. 2012). Often, species are identified to genus and subsequently classified according to morphological differences, resulting in so-called morphospecies. This enables people that are non-expert on the taxonomic group to process samples (parataxonomy). Another approach is to determine if supraspecific taxa can

reproduce the same results as the findings using species data, i.e. taxonomic sufficiency. If yes, this can facilitate analyses and increase the rate of knowledge acquisition (Landeiro et al. 2012).

Ants have already frequently been used for ecological monitoring and shown to respond to different forest disturbances (Underwood & Fisher 2006). Besides their occurrence in most terrestrial ecosystems and high diversity, they are numerous and fulfil many ecosystem services at various trophic positions (Alonso & Agosti 2000). Furthermore, the presence of workers directly indicates the presence of a reproductive unit, i.e. a nest with a queen, in or near the habitat.

This study investigates the potential of ants (Hymenoptera: Formicidae) as ecological indicators of tropical peat swamp forest in Borneo, in this case limited to the forest of the Sabangau catchment, Central Kalimantan. It aims to identify differences in ant community composition in relation to environmental disturbances and seasonal variation.

At present, most research on Bornean ants comes from only a handful of sites in the Malaysian states of Sabah and Sarawak, mainly from dipterocarp forests (Pfeiffer et al. 2011). Very little, if anything, is known about the ants of the island's peat swamp forests (Pfeiffer et al. 2011). The same can be said about the ant fauna of Kalimantan (Indonesian Borneo). Thus, the present study contributes not only to the knowledge on ants in bioindication, but also more fundamentally to the natural history of ants of tropical peat swamp forests in Borneo.

With regard to the aims and background stated above, the following research questions have been formulated (the term 'ant community composition' refers to species, genera, functional groups and indicator taxa):

- 1. To what extent do different habitats of peat swamp forest differ in their ant community composition? And which environmental factors can best explain these differences?
- 2. Which spatial scale is best to analyse these compositional differences?
- 3. Does ant community composition vary between seasons?
- 4. Are the findings consistent at taxonomic level of both species and genera?

# **Material and methods**

#### **Study site**

The fieldwork was conducted in the mixed peat swamp forest of the 500-km<sup>2</sup> National Laboratory for Peat Swamp Forest (NLPSF), situated in the largest remaining Bornean lowland forest, in the Sabangau catchment, Central Kalimantan, Indonesia (Page et al. 1999). Between 1970 and 1997 the majority of the area has been selectively logged under the Setia Alam logging concession, and several parts (near the river and along the logging railways) have been intensively logged. The riverine forests have been clear-felled and replaced by sedge swamp (Page et al. 1999). Illegal logging occurred between 1997 and 2004, but became negligible after 2004.

The NLPSF research site is divided into a grid by N-S and W-E transects (**Figure 1**). For the present study, five plots were surveyed on ant fauna. They comprise three 0.15-ha plots (5 m x 300 m) along transects and two plots that contain sampling grids of different shape. These five plots represent three habitats: forest gaps, forest edge and forest interior.

- Forest gaps (G and H, 2 grid plots): the gaps are previously clear-felled patches of about 50 m diameter within the interior forest, which have been used by local community to hunt for fruit-bats (Struebig et al. 2007). They have been regenerating for 5 years, and are covered with saplings of about 1-2 m tall. Two former bat hunting gaps have been sampled, one is situated along transect T1.3 (G), the other along transect T0.8 (H).
- Forest edge (E, 1 line transect): this transect runs parallel to and within 5 m from the forest edge bordering the sedge swamp of the Sabangau river. This edge has moved approximately 50 m into the sedge swamp as a result of natural regeneration. The tree composition is strikingly different from the interior forest, with dominance of several pioneer species (Frank 2013).
- Forest interior (A and B, 2 line transects): these two plots are situated in relatively undisturbed mixed-swamp forest at 900 m (A) and 1900 m (B) from the edge of the forest. They are

located at least 500 m away from the logging railways, and are believed to be regenerating following selective logging prior to 2004.



**Figure 1.** Top picture: location of Sabangau National Park (red border) and the 500-km<sup>2</sup> NLPSF (blue border); grey area represents forest cover; bottom: detailed map of transect grid in NLPSF, with sampling locations.

## Sampling

A total of 120 traps were used in this survey, and set out monthly from May 2011 to April 2012, for two consecutive days each month. Traps were spaced 10 m apart. Thirty traps were positioned in each transect plot, 15 in each of the forest gaps.

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. The lid had a central hole of 1 cm diameter through which ants could enter the trap. Thus, traps emulated the design of the local pitcher plants (*Nepenthes spp.*). 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 both from the ground and from the higher forest strata. Each trap was baited with 40 ml of honeybait solution, prepared from 50 ml honey, 20 ml alcohol (70%) and 1430 ml water (honeybaits: e.g. Yamane et al. 1996, King et al. 1998, Dias & Perera 2011). After 48 hours in the field, traps were emptied and ants were collected from the bait solution and stored on 70% alcohol.

### **Environmental variables**

For all plots, basal circumference and diameter at breast height (DBH) were recorded for each tree with DBH larger than 6 cm (Harrison 2009). In the grid plots of forest gaps, trees did not exceed this threshold and therefore mean DBH and basal area (BA) for these plots were set to zero.

At the trap level, the relative ground cover of dead wood (DW), living plant material (LP) and bare ground (GR) were estimated visually for the area directly around the trap between the observer and the ground, and scored in four classes: 0-25, 25-50, 50-75 and 75-100%. Furthermore, using a densitometer, percentage canopy cover directly above the trap was estimated at 10 m (CCa), 20 m (CCb) and > 20 m height (CCc) (Harrison & Perlett 2011).

#### Ant identification

Ants of the worker caste were identified under the microscope, using literature for the world subfamilies and genera (Bolton 1994) supplemented with recent genus-group revisions (LaPolla *et al.* 2010, Baroni Urbani & De Andrada 2007). For the identification of species and classification of morphospecies, 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 morphospecies. Online ant databases (Antweb.org, Antbase.net) were also consulted. A list of identification literature can be found in **Appendix 2**.

Workers have been identified by three OuTrop Interns of varying expertise and with different quality of equipment. Specimens collected from February to April 2012 have been identified with greater accuracy, using the microscopes of the University of Palangkaraya and literature as mentioned previously. Morphospecies of earlier months have been revised, but complete revision of samples was impossible since most specimens had been discarded. As a compromise, the morphospecies from February to April 2012 were matched to those from May 2011 to January 2012, so that some accuracy was lost but species composition remained comparable and the data could be analysed as a whole.

#### **Statistical analyses**

For statistical analyses, only records from the worker caste were included since these directly indicate the presence of an established colony in the habitat. Reproductives (gynes and males) and unidentified specimens were excluded.

Data were analysed at three spatial scales: individual traps, clusters of five adjacent traps and plots. At the level of individual traps, the total abundance of species (summed per trap across months) was transformed into a scaled abundance using 5 abundance classes: 1 = 1 individual, 2 = 2-5 individuals, 3 = 6-20 individuals, 4 = 21-50 individuals and 5 = more than 50 individuals) (cf. Hoffmann et al. 2000). Especially with pitfall traps and baited traps, such transformation is needed to avoid distortion by captures of extremely high numbers of workers (Longino 2000, Bestelmeyer et al. 2000). Autocorrelation of distance and Bray-Curtis dissimilarity in species composition of individual traps was tested using Mantel's Monte Carlo test in PC-ORD 4.25 (McCune & Mefford 1999). Lumping individual traps into 5-trap clusters resulted in six sampling units for the transect plots. For each grid plot, only one cluster of five traps in adjacent linear position was possible. A species presence count was used ranging from 0 (species absent from all five traps of the cluster) to 5 (species present in all five traps) for each cluster. At the plot level, species incidences (traps across months) were standardized to percentages since sample size of plots varied.

In order to determine the saturation of sampled ant communities in the survey, sampling completeness was calculated based on species richness estimators (ICE or Chao2) using EstimateS version 9.0.0 (Colwell 2013). In this analysis, the number of incidences (months) per trap for a species were analysed per plot, using the traps as sampling units.

Scaled abundance data of ants of individual traps were tested for significant differences in ant community composition (Euclidean distance) among plots using nonparametric multiple response permutation analyses (MRPP, Zimmerman et al. 1985, Villa-Castillo & Wagner 2002) in PC-ORD 4.25 (McCune & Mefford 1999). Species overlap between plots was quantified using the Chao Adjusted Jaccard Index (CAJI, Chao et al. 2005) from the Shared Species statistics of EstimateS version 8.2.0 (Colwell 2006).

Indirect gradient analysis of ant community composition at the different spatial scales was conducted using Principal Components Analysis (PCA). In the ordination plots, envelopes were drawn around samples (traps or 5-trap clusters) based on TWINSPAN clustering analysis. Multivariate analyses were run using the software package of Canoco version 4.55 (Ter Braak & Smilauer, 2006).

Indicator species analyses were performed for the trap-level scaled abundance values, using the IndVal method (Dufrene & Legendre 1997) in PC-ORD 4.25 (McCune & Mefford 1999) at four typologies: disturbed versus interior forest, forest gaps versus edge versus interior, forest gaps versus the separate transect plots, and all plots separate.

To identify seasonal shifts in ant community composition, PCA was performed for plots separated for dry and wet season. Furthermore, indicator species analysis was run for plots in dry (May-Oct) and wet season (Nov-Apr) separately, to find out seasonal differences.

All analyses described above (except diversity estimation) were performed at the taxonomic level of both (morpho)species and genera, in order to discuss the generic surrogacy of species in the main results of this study. To reveal differences in ecological nature of the different habitats, an additional IndVal analysis was done for functional groups (*sensu* Andersen 1995, Brown 2000), using functional group scaled abundance for individual traps grouped into different typologies. In all analyses, significance level was  $\alpha = 0.05$ .



**Figure 2.** Rarefied species accumulation curves for the individual plots. All plots level off and have tendency to asymptote except plot B, which is increasing steadily and has highest species richness. Forest gaps (G and H) have lowest species richness, and forest edge (E) intermediate.

# **Results**

A total of 3051 worker ants were collected, of which 2918 were used in the analyses, belonging to 47 (morpho)species, 24 genera and five subfamilies. The remaining 134 specimens were damaged and impossible to identify. Out of 1080 trap days, 42 were lost in the field due to predation, weather and other causes. The species list including codes used in the analyses can be found in **Appendix 1**.

Species richness was lowest in forest gaps, intermediate near the forest edge and highest in the interior forest plots. Sampling completeness followed the opposite order, with sampled ant community saturated most in the gaps and least in the interior forest (**Table 1**). Rarefied species accumulation curves approached an asymptote for four out of five plots (**Figure 2**), indicating sampling was efficient at most sites.

The Mantel test showed a significant positive correlation between distance and compositional dissimilarity of individual traps in one of the forest gap plots (H) (r = 0.310, P = 0.008) and weakly in forest edge plot (E) (r = 0.109, P = 0.08). In these plots, traps display spatial autocorrelation and may not be independent sampling units. In all others, no significant relationship between matrices was found.

plot	N			capture	S	ICE 3,4	Chao2 <sup>4,5</sup>		completeness
	traps	trap days <sup>1</sup>	individuals	rate <sup>2</sup>			mean	95% C.I. limits	(%) <sup>6</sup>
G	15	180	411	2.28	20	25.39	21.75	20.27 - 31.37	91.95
н	15	180	308	1.71	16	19.12	17.12	16.13 - 25.83	93.46
E	30	360	456	1.27	27	33.25	30.38	27.62 - 45.35	88.87
А	30	360	815	2.26	29	36.31	35.40	30.37 - 58.90	79.87
В	30	360	928	2.58	31	46.49	43.00	34.18 - 76.31	66.68
Total	120	1440	2918	2.03	47	58.50	59.00	50.18 - 92.31	79.66

 Table 1. Observed and estimated species richness and sampling completeness.

<sup>1</sup> a trap day is the replicated unit of 48 hours in which a trap is active per survey (i.e. month), N(trap days) = N(traps) x 12. <sup>2</sup> capture rate = N(individuals) / N(trap days).

<sup>3</sup> ICE = incidence coverage-based estimator.

<sup>4</sup> for species richness estimation in EstimateS, traps have been used as sampling units.

<sup>5</sup> Classic Chao2 has been used for A, B and Total, bias-corrected Chao2 for G, H and E.

<sup>6</sup> recommended richness estimator for G, H, E and Total is Chao2, for A and B ICE. These values were used to calculate completeness.

#### Habitat differences in ant community composition

Nonparametric MRPP showed that scaled abundance varied significantly more between predefined groups (plots) than within groups, both on a species level (T = -21.419, A = 0.078, P < 0.001) and generic level (T = -19.966, A = 0.091, P < 0.001). In other words, there are significant differences in composition of species and genera between plots.

Compositional similarity was calculated using the Chao incidence-based Jaccard estimator (CAJI, Chao et al. 2005) (**Table 2**). Similarity was highest between forest gaps and between interior forest plots, but also between forest edge and forest interior. Gaps and edge were least similar. This was true at both species and genus level, and the CAJI matrices of both taxonomic levels showed a significant positive correlation (Mantel's Monte Carlo test: r = 0.939, P = 0.009).

Table 2	. Compositional	similarity	(CAJI)	between	plots	for	species	(white	background)	and	genera	(grey
backgro	und). Standard de	eviation of	the est	timator in	parent	thes	es.					

	G	н	E	А	В
G		0.910 (0.060)	0.723 (0.147)	0.823 (0.108)	0.849 (0.096)
Н	0.943 (0.046)		0.739 (0.127)	0.789 (0.108)	0.773 (0.105)
E	0.739 (0.133)	0.788 (0.117)		0.854 (0.068)	0.945 (0.059)
А	0.869 (0.114)	0.860 (0.079)	0.908 (0.067)		0.955 (0.048)
В	0.829 (0.104)	0.838 (0.093)	0.950 (0.053)	1.000 (0.031)	

Indirect gradient analysis (PCA) resulted in three distinct groups at plot and 5-trap cluster scales (**Figure 3**), corresponding well with the distinction of forest gaps, edge and interior. In the ordination of individual traps, TWINSPAN clusters largely overlapped in plots of both  $1^{st}$  and  $2^{nd}$  ordination axes and  $1^{st}$  and  $3^{rd}$  axes. The 5-trap clusters provide both a clear distinction between habitats and some detail within plots, a combination that is lacking at the ordinations of plots and traps. These patterns are largely consistent at the species and genus level.

Triplots show the species and environmental variables in relation to the ordinated samples (**Figure 4**). Among the species at trap ordination, especially *Nylanderia Ny1*, *Pheidole rugifera (Per)* and *Monomorium cf. floricola (Mmf)* associate strongly with the variation among samples, but apart from the latter, they do not seem to be distinctive for any one cluster at this spatial scale. At the taxonomic level of genera, the clusters are more distinctive but still overlapping, with genera corresponding with the previously mentioned species showing strongest association, as well as *Crematogaster (Cre)* and *Tetramorium (Ttm)*.

At a higher spatial scale (5-trap clusters), the samples are more clearly clustered and more species are associated with the groups. *Monomorium cf. floricola (Mmf)* is clearly associated with forest gaps, as is *Oecophylla smaragdina (Oes)* to a lesser extent. *Polyrhachis PrM, Crematogaster Cr1, Tetramorium Tm1* and *TmT, Pheidole Peo* all associate with samples from forest edge. The interior forest cluster appears to be more characterized by the association with *Pheidole Per* and *Pes, Tetramorium TmL, Technomyrmex Tck, Nylanderia Ny1* and *Camponotus gigas (Cmg)*.

On a generic level, similar separation of sample groups can be seen. The association of genera with samples is a resultant of the separate species within the genus, and therefore their arrows point mainly towards the samples in which the species are most abundant. *Monomorium* and *Oecophylla* clearly associate with forest gaps, whereas *Polyrhachis, Tetramorium* and *Crematogaster* associate with the forest edge. *Pheidole* has association with both forest edge and interior, and *Camponotus, Technomyrmex* and *Nylanderia* appear associated with interior forest. At a plot level, more or less the same associations are visible as at the 5-trap cluster level.



**Figure 3.** PCA scatter plots of samples for ant community composition of species (**a-c**) and genera (**d-f**) at trap (**a, d**), five-trap cluster (**b, e**) and plot scale (**c, f**). X- and Y-axis correspond to 1<sup>st</sup> and 2<sup>nd</sup> PCA axis, respectively. TWINSPAN groups are displayed for gaps (black circles), edge (purple squares) and interior forest (green diamonds). In case of trap-scale PCA, the TWINSPAN group of "edge" (purple squares) contains a mix of samples from edge and interior forest plot. Sample labels are displayed except in **a** and **d**.



**Figure 4.** PCA triplots of samples, species (black arrows) and environmental variables (red arrows) for ant community composition of species (**a-c**) and genera (**d-f**) at trap (**a**, **d**), five-trap cluster (**b**, **e**) and plot scale (**c**, **f**). X- and Y-axis correspond to  $1^{st}$  and  $2^{nd}$  PCA axis, respectively. TWINSPAN groups of samples are indicated by envelopes for gaps (black), edge (purple) and interior forest habitat (green); individual samples are not displayed. For definition of species codes see **Appendix 1**.

The cumulative percentage variance explained by environmental variables decreases with the spatial scale, i.e. going from plots to trap clusters to individual traps (**Table 3 and 4**). At the plot level, the first PCA axis is explained most by variables of tree composition: mean DBH, basal area and canopy cover at 10 m. The second axis is explained best by variables of ground composition: bare ground cover (species) or dead wood (genera). At intermediate spatial scale (trap clusters), percentages cover of dead wood (species) and living plant material (genera) correlate most positively with the 1<sup>st</sup> PCA axis and canopy cover at 20 m correlates most negatively with the 2<sup>nd</sup> axis. At the smallest level, both 1<sup>st</sup> and 2<sup>nd</sup> axis correlate best with canopy cover variables, i.e. with canopy cover at 10 m and 20 m respectively for both species and genus level.

Understandably, the variables of tree composition show high correlations at the plot level (**Appendix 6**): high values of canopy cover correlate with high values of mean DBH and basal area. Canopy cover at the stratum above 20 m correlates least with the other tree variables, but shows high correlation with bare ground cover. At smaller spatial scales, tree variables (canopy cover) show lower correlation, and correlation between ground cover variables is higher. At trap level, correlations are lowest: only canopy cover at and above 20 m, and percentage cover of bare ground and dead wood have moderate correlation.

**Table 3.** Correlations of PCA axes for species with environmental variables at different spatial scales. Highest correlation coefficients (r) are highlighted in grey. Total env. = total variance of species axis explained by corresponding environmental axis; CCa = canopy cover at 10 m, CCb = canopy cover at 20 m, CCc = canopy cover above 20 m height, LP = ground cover of living plant material, DW = ground cover of dead wood, GR = ground cover of bare ground, mDBH = mean DBH, BA = total basal area of plot, cum. % = cumulative percentage variance of species-environment relation.

	plots			5-trap clu	isters		traps			
variable	1st axis	2nd axis	3rd axis	1st axis	2nd axis	3rd axis	1st axis	2nd axis	3rd axis	
total env.	<b>?</b> ª	? <sup>a</sup>	? <sup>a</sup>	0.8769	0.8427	0.6165	0.6879	0.4517	0.3639	
CCa	-0.9085	-0.3997	-0.0483	0.0295	-0.5323	0.1152	-0.4897	0.1761	0.0254	
CCb	-0.8476	-0.5181	-0.0598	-0.1375	-0.7984	-0.0103	-0.4202	0.3639	0.0961	
CCc	-0.4479	-0.8594	-0.1882	-0.4364	-0.4119	-0.0372	-0.1311	0.2246	0.0087	
LP	0.6927	-0.1458	-0.2953	-0.4221	0.4194	-0.2389	0.4509	0.0321	-0.0743	
DW	-0.2633	0.9610	0.0724	0.8313	0.1506	-0.1071	-0.1552	-0.1762	-0.2820	
GR	-0.0128	-0.8019	0.5026	-0.7061	-0.0884	0.0314	0.1060	0.1633	0.3383	
mDBH	-0.9207	-0.3762	-0.0635							
ВА	-0.9119	-0.3985	-0.0948							
cum.%	60.5	84.5	94.7	39.8	67.7	75.8	48.7	68.5	75.2	

<sup>a</sup> Spurious zero-values were given in the log-file, cause unknown but perhaps overparameterization and collinearity of variables. These could not be corrected timely for the present report and interpretations should be with caution.

	plots			5-trap clu	sters		traps			
variable	1st axis	2nd axis	3rd axis	1st axis	2nd axis	3rd axis	1st axis	2nd axis	3rd axis	
total env.	? <sup>a</sup>	?ª	<b>?</b> <sup>a</sup>	0.8112	0.8760	0.5985	0.7188	0.3004	0.2046	
CCa	-0.9432	-0.2791	-0.1444	-0.3623	-0.4028	-0.0672	-0.5227	-0.0644	-0.0717	
CCb	-0.8938	-0.4009	-0.1724	-0.3681	-0.7280	0.1209	-0.4852	0.1947	-0.1054	
CCc	-0.5199	-0.7804	-0.3245	0.0842	-0.5870	0.0496	-0.2180	0.0604	0.0283	
LP	0.7000	-0.2287	-0.2472	0.6251	0.1841	0.0517	0.4388	0.1041	-0.0261	
DW	-0.1692	0.9607	0.2179	-0.5095	0.6108	0.2385	-0.0773	-0.1581	0.1592	
GR	-0.1088	-0.8898	0.3878	0.3831	-0.5732	-0.2029	0.0266	0.1323	-0.1600	
mDBH	-0.9516	-0.2552	-0.1537							
BA	-0.9426	-0.2785	-0.1835							
cum.%	72.9	90.9	97.9	44.9	74.4	83.7	64.9	75.3	77.8	

**Table 4.** Correlations of PCA axes for genera with environmental variables at different spatial scales. Highest correlation coefficients (r) are highlighted in grey. For explanation of variables see Table 3.

<sup>a</sup> Spurious zero-values were given in the log-file, cause unknown but perhaps overparameterization and collinearity of variables. These could not be corrected timely for the present report and interpretations should be with caution.

#### **Indicator taxa**

Indicator species and genera were calculated at the two lower spatial scales, for different predefined groups of samples (**Table 5**). Both spatial scales show much agreement in indicative taxa, though there are some differences.

At both scales, *Polyrhachis PrM* is an indicator species of disturbed forest, and has maximum indication for the forest edge. Another indicator of disturbed forest is *Monomorium cf. floricola* (*Mmf*), which is most characteristic of forest gaps, together with *Oecophylla smaragdina* (*Oes*). *Pheidole Peo* is a third indicator for disturbed forest; its indication for the forest edge is only relevant at the trap scale. Distinctive for the opposite group, i.e. intact (or interior) forest, are Nylanderia Nyl and Pheidole rugifera (Per).

*Crematogaster Cr1* is an additional indicator of the forest edge, in both spatial scales. *Leptogenys Lg1* is a forest edge indicator only at the cluster scale. Further, there are two species of *Tetramorium*, *TmT* and *TmL*, indicative of forest edge (at trap scale) and intact forest (at cluster scale), respectively. Only at the cluster scale are there indicator species differentiating the two plots of interior forest: *Pheidologeton cf. affinis (Poa)* and *Technomyrmex Tck*, both for plot A.

At a higher taxonomic level, the genera largely agree with the patterns at species level. Few differences occur. *Camponotus (Cam)* is indicative of intact forest at both trap and cluster level, though no indicator species of this genus met the criteria for display in the species tables (IV > 25% and P-value < 0.1). The genus *Pheidole* contained indicator species of both intact and disturbed forest, which is why it is lacking as an indicator genus for either group. *Tetraponera (Ttp)* distinguishes plot B from plot A within the interior forest only at cluster level.

**Tables 5.** Predefined sample groups (vertical) and associated indicator species (a,c) and genera (b,d). Table a-b have traps as samples; c-d have 5-trap clusters as samples. Species are displayed with an indicator value above 25% and a P-value smaller than 0.1 (italic) or 0.05 (normal), until the typology where they reach maximum indicator value (bold) (*cf.* Dufrene & Legendre 1997). The number of predefined groups in each typology is indicated in the top row.

2		3		4		5			2	
	PrM (29)	sd	Mmf (79)			g	Oes (37)			,
<del>a</del>	Mmf (45)	ga	Oes (30)			Т	-		ed	
rbe	Peo (28)		PrM (60)						turb	
istu		e (E)	Cr1 (46)						dist	
p		edge	TmT (33)							
		Ť	Peo (29)						t	
act	Ny1 (56)			٩	-			]	Itac	
inta	Per (38)			В	-				Ξ.	

a. Species (based on traps)

b. Genera (based on traps)

2		3		4		5	
	Mon (49)	sd	Mon (76)			ט	Oec (37)
bed	Pol (29)	ga	Oec (30)			Т	-
turb		(E)	Cre (45)				
dis		lge (	Pol (60)				
		eo	Ttm (36)				
act	Nyl (56)			A	-		
int	Cam (37)			Ð	-		

c. Species (based on clusters)

2		3		4	
	Ta2 (63)	sd	Oes (100)		
bed	Mm1 (55)	eß	Mmf (78)		
disturb	PrM (57)	(E)	Cr1 (50)		
	Lg1 (38)	lge (	PrM (65)		
	Peo (59)	еq	Lg1 (43)		
t	TmL (59)			٢	Poa (60)
ntaci	Per (65)			1	Tck (41)
. <b>=</b>	Ny1 (53)	В	-		

d. Genera (based on clusters)

2		3		4	
	Pol (57)	sd	Oec (100)		
bed	Mon (63)	ga	Mon (71)		
turk	д Цер (38)		Cre (49)		
dis		ge (	Pol (77)		
		ed	Lep (50)		
act	Cam (60)			A	-
int	Nyl (54)			В	Ttp (50)

#### **Functional groups**

Functional groups differed significantly at the division of gaps, edge and interior forest (T = -8.796, A = 0.039, P = 5E-7). At the higher division of disturbed versus intact forest, no significant differences in composition were found (MRPP: T = -1.027, A = 0.003, P = 0.142). Figure 5 shows the distribution of functional groups of the three habitats, with significance of indicator values displayed based on indicator species analyses of scaled abundance in traps.

At the typology of three habitats, Generalist Myrmicinae (GM) are dominant in and indicative of forest gaps, whereas the forest edge is dominated by Opportunists (O) and furthermore characterized by Subordinate Camponotini (SC) and Specialist predators (SP). No significant indicators were found for interior forest, though Tropical climate specialists (TCS) have highest relative abundance in this habitat.



**Figure 5.** Relative abundance of functional groups per sample group, with significant indicator values displayed on bars (\* = P-value < 0.05; • = P-value < 0.1). TCS = tropical climate specialists, SP = specialist predators, SC = subordinate Camponotini, O = opportunists, HCS = hot climate specialists, GM = generalist Myrmicinae, DD = dominant Dolichoderinae, C = cryptic species.



**Figure 6.** PCA scatter plot of samples (plots) separated for dry (-d) and wet season (-w) for ant community composition of species (**a**) and genera (**b**). X- and Y-axis correspond to 1<sup>st</sup> and 2<sup>nd</sup> PCA axis, respectively. Arrows indicate shifts of community composition from dry to wet season per plot. TWINSPAN groups are indicated by symbols as in **Figure 3-4**.

#### Temporal variation of community composition and indicator taxa

When plotting similarity measures (CAJI) of species compositions of plots in dry season against those of plots in wet season, it can be seen that compositional similarity is higher in the dry season than in the wet season (**Figure 6**). Similarity values of both seasons are not significantly correlated (Mantel test: r = -0.069, P = 0.450). The same can be seen for genus composition of plots in dry and wet season (Mantel test: r = -0.300, P = 0.295).

Despite similarity being higher in dry than in wet season, in both seasons community composition of traps differed significantly between the predefined groups of disturbed and intact (interior) forest, and between forest gaps, forest edge and forest interior (MRPP, all P-values < 0.0001). Plots, separated for dry and wet season, were also grouped according to the division of forest gaps, edge and interior in the TWINSPAN clustering analysis.

However, individual species did not show consistent patterns in defining these three habitats in both seasons. Plots showed distinct shifts in species composition from dry to wet season in the PCA ordination (**Figure 7**). As an additional support, indicator species analysis showed that the compositional differences found in MRPP were not ascribable to the same species in both seasons (**Table 6**). Most species only had a significant indicator value above 25% in one season; only *Monomorium cf. floricola (Mmf)* and *Crematogaster Cr1* were reliable indicators (i.e. P < 0.05 and IV  $\geq 25\%$ ) of respectively forest gaps and forest edge in both seasons, as were their corresponding genera. Additionally, the genus of *Polyrhachis* was consistently indicative of forest edge year-round.



**Figure 7.** Compositional similarity (CAJI) between plots in wet (x-axis) and dry (y-axis) season, for species (**a**) and genera (**b**). At both taxonomic levels, between-plot similarity is higher in the dry season than in the wet season for the majority of plots. Blue line is y = x.

Tables	6.	Predefined	sample	groups	(vertical)	and	associated	indicator	species	(a,c)	and	genera	(b,d)	in d	Iry
season	(a,	<b>b</b> ) and wet	season (	c <b>,d</b> ). Disp	lay and f	forma	atting same	as in Tabl	e 5.						

a. Sp	a. Species - dry season									
2		3								
st.	Mmf (36)	ъ.	Mmf (75)							
di		e.	Cr1 (36)							
act	Per (25)			٨	-					
int				В	-					

c. Sp	becies - wet s	easor	า		
2		3		4	
	Mmf (32)	g.	Mmf (53)		
dist.	PrM (26)	ge	PrM (52)		
-		ed	Cr1 (25)		
act	Ny1 (54)			A	-
int	Per (28)			В	-

#### b. Genus - dry season

2		3		4	
р	Mon (38)	·8	Mon (73)		
rbe		0	Cre (35)		
istu		edge	Ttm (28)		
р		Э	Pol (27)		
act	-			A	-
int				В	-

. G	enus - wet se	ason			
2		3		4	
	Mon (36)	·8	Mon (53)		
dist.	Pol (26)	ge	Pol (52)		
		еq	Cre (25)		
act	Nyl (53)			٨	-
I	Phe (39)			В	-

## **Discussion**

### **Ant species richness**

Although sampling efficiency appeared generally high, ant species richness of Sabangau peat swamp forest is undoubtedly higher than reported in this survey. First of all, species richness may have been higher in the survey, since not all specimens had been identified with equal accuracy and similar-looking species are likely to have been lumped for the first nine months. The morphospecies used in the analyses are a compromise of the low- and high-accuracy identifications (**Appendix 1**), resulting in lower species richness than in reality. Minor underestimation may be caused by lost data (3.9% of trap days, 4.4% of specimens).

Second, the sampling design is selective. Ants will only be sampled if they encounter a trap and are attracted to the bait. Because of the position of the traps on the ground and attached to a living stem, only ants foraging on litter, ground or in the higher forest strata are likely to pass the spot where the trap touches the stem or the ground. This position combined with the honeybait, samples mainly dietary generalist ground- and litter-dwelling ants (Longino 2000) or ants that nest on the ground and forage in higher strata or vice versa (Hashimoto et al. 2010, Tanaka et al. 2010). Subterraneous and arboreal ants are undersampled, as well as solitary foragers and dietary specialists (Longino 2000, Bestelmeyer et al. 2000). Honeybaits in dipterocarp forest only sampled 22% of the known species richness, but this survey was conducted only in January (Yamane et al. 1996).

Third, the present survey only sampled at five locations, comprising three habitats of peat swamp forest. All habitats studied so far were located in the mixed swamp forest subtype. Since tall interior forest and low pole forest are very different habitats within PSF (Page et al. 1999), it is likely that their ant communities and corresponding species have not yet been discovered with the current study.

Peat swamp forests may pose serious challenges that allow only few ant species to establish, for instance because of supposedly harsh conditions of wet peaty soil (for kerangas, Mezger & Pfeiffer 2010) and an extensive litter layer (Clay et al. 2010). Unfortunately, the selective sampling design of the present study does not allow for comparison of species richness estimates with those of other forest types in Borneo and SE-Asia that use more complete sampling techniques (Mezger & Pfeiffer 2011, Mustafa et al. 2011). Comparison of species richness between habitats within this survey is problematic as well, since spatial sampling design has not been consistent. The forest gaps have lowest numbers of species, but also sample a much smaller area than the transects. Thus, it could be the result of a difference in sampled area, in habitat, or both. For a valid comparison of forest gaps with the other habitats, sampling grids of identical size and shape should be used.

#### Forest gaps, edge and interior support distinct ant communities

Different ant communities were clearly distinguished corresponding with the three habitats, at both five-trap cluster and plot level. This implies that the ant community of interior mixed swamp forest is altered drastically by small-scale disturbances within the forest (gaps), and edge effects can be found in proximity to the sedge swamp. In Borneo, ant community composition of the forest floor has previously been shown to differ in four different rainforest types (dipterocarp, alluvial, limestone and kerangas) with characteristic species per forest type (Mezger & Pfeiffer 2011). The present findings suggest that different habitats within a single forest type (peat swamp forest) can also be distinguished based on differences in ant community composition.

Some caution in interpreting the results should be taken, since sampling was done using only a selective method. Species identified as indicators in this study should only be viewed as indicators using the here-described baiting method. Besides, capture rates may not directly represent actual ant community composition or habitat preference but also be influenced by variations in ant species attraction to the bait, species-specific foraging ranges and proximity of a trap to a nest (Longino 2000). More complete sampling techniques should be employed to find out whether true distribution differences underlie differences in community composition resulting from baiting.

Although Andersen's classification (1995) of ant functional groups is based on genera and therefore coarse and generalized, it may provide preliminary understanding of functional diversity of ant communities of the three habitats. The classification is grounded on competitive interactions, habitat

requirements and responses to stress or disturbance (i.e. decreased productivity or biomass of ants) and it reasons that ants compete for warmer and more open sites (Andersen 1995, 2000). Competitively dominant ant species can dominate such a spot and they determine the distribution of other species. Dominant Dolichoderinae (DD) aggressively occupy resources, whereas Generalist Myrmicinae can occupy and defend a resource by rapid recruitment and competitive strength. Subordinate Camponotini avoid competition with DD, but can dominate sites where DD are absent. Opportunists are poor competitors that can only thrive at sites where stress (e.g. shade, water-logged soil or low temperature) limits the stronger functional groups. Tropical climate specialists are specific to certain climates, but can be dominant in the absence of DD. All these groups are generalist foragers; specialist predators and cryptic species have little competition with other groups due to their specific niches (Andersen 1995).

The interior forest habitat within Sabangau was characterized by *Pheidole rugifera* and *Nylanderia Ny1*, belonging to respectively Generalist Myrmicinae and Opportunists. *Pheidole rugifera* is known from well-developed lowland forest (Eguchi 2001). It was found in all habitats of peat swamp forest, but clearly more abundant in interior forest. This suggests that, in peat swamp forest, the species prefers undisturbed forest. The same can be said for *Nylanderia Ny1*, which was common throughout the survey but most abundant in the interior. *Nylanderia* species are common and often very abundant in tropical forests (LaPolla et al. 2011), and its indication for interior forest in the present study may indicate it is adapted to shaded environments.

The functional group structure of interior forest corresponds with previous studies on tropical rainforests. Generalist Myrmicinae and Opportunists dominated the habitat, and Tropical climate specialists are well-represented. This shows similarity to the community structure of Australian monsoon rainforest (Andersen 2000) but with more Tropical climate specialists as suggested by Andersen (1995) for humid tropical rainforest. Whether this composition is general for peat swamp or lowland forests on Borneo remains unknown. The fact that there are very few Dominant Dolichoderinae (only some *Philidris sp.*) in the ground ant community of the interior may be an indication that forest structure is intact (Mustafa et al. 2011), since this group prefers hot and open habitats (Andersen 1995). In forests, such conditions can be found in the canopy or in forest clearings (Mustafa et al. 2011).

The fact that some of the traps or five-trap clusters from the interior forest plots were grouped together with samples of the edge or gap habitats in the PCA, indicates that heterogeneity occurred to some extent within the interior forest habitat. This may be because of natural tree falls that cause small-scale disturbances within the forest, enabling species of gap and edge communities to establish or increase in numbers. Furthermore, the two interior forest plots seem to be different to a slight degree. Future more detailed surveys could investigate if distinct ant communities occur within the interior forest, and by what biotic and abiotic factors these different communities are explained.

The ant community composition of the forest gaps is very different from the surrounding interior, which is likely caused by the absence of large trees resulting in a hotter, more exposed habitat. Nest temperature has been identified as a key determinant of niches of ant species in other Bornean forest types (Mezger & Pfeiffer 2010), and it is likely that the temperature near the forest floor is higher in the gap than in the closed interior forest. As the surrounding interior forest would mainly harbour species adapted to shade and lower temperatures, only few species from the interior forest would be able to colonize the gap. This may explain why the sampled species richness is considerably lower in the gaps than in the interior, although the lower sampling effort in the gaps could also influence this.

The sampled ant community of the gaps is dominated by *Monomorium cf. floricola* and an additional indicator species is *Oecophylla smaragdina*. Assuming the identification is correct, *M. floricola* would not only be a generalist myrmicine but also a tramp species, that is, a species with worldwide distribution due to human commerce, mainly confined to anthropogenically altered environments (Pfeiffer et al. 2008). Generalist Myrmicinae recruit rapidly to baits and defend it from other species (Andersen 1995). Such competitively dominant behaviour could be an alternative explanation why fewer species have been captured at the baits than in the surrounding interior. The arboreal *Oecophylla smaragdina*, too, can be behaviourally dominant (Andersen 1995), and its presence in the gaps may result from the fact that the open, hot climate of the shrub and sapling canopy was very close to the ground.

In a study on forest conversion in Southeast-Asia, Senior and colleagues (2013) found a dominance of smaller species of lower trophic level in oil-palm plantations, that occurred in low abundance in forest, for ants, birds and beetles. Such a similar mechanism could be in play for *Monomorium cf. floricola*, which was found occasionally in the forest interior, but reached dominance in the forest gaps.

The absence of cryptic and specialized predatory ant species from the gaps may be an additional result of disturbance, though these functional groups are generally undersampled in baited traps (Longino 2000) and dominant ants (discussed above) may have prevented other species to enter the traps (Bestelmeyer et al. 2000).

What is apparent is that the ant community of the forest gaps is still different from the intact surrounding forest after five years of natural regeneration. It is likely that the ant communities of former gaps and interior forest become increasingly alike as succession proceeds. Especially since the clearing borders to a continuous intact forest, it can be expected that recolonisation of the gap by interior forest species will not be constrained by effects of habitat fragmentation, which is the case for many other degraded forests. These forest gaps would therefore provide a valuable opportunity to study natural recovery of a disturbed environment (in this case clear-felled) in peat swamp forest over time.

The forest edge of Sabangau has a lower and more uniform canopy than the interior forest (Frank 2013), and it is therefore understandable that more arboreal species (*Polyrhachis* and *Crematogaster*) turn up in the sampled community. Both *Crematogaster* and *Polyrhachis* contain mainly arboreal species that can be dominant in tropical forest (Andersen 1995). *Crematogaster* as well as another edge indicator *Pheidole (Peo)*, are Generalist Myrmicinae that can recruit and occupy a resource rapidly. Both morphospecies, however, comprised multiple species after revision (*Crematogaster (Cr1)*: 4 morphospecies; *Pheidole (Peo)*: *Pheidole orophila*, *P. aglae* and *P. plagiaria*), and it is unclear which of these species contributes most to the indicator values.

The *Polyrhachis (Myrma)* species that was found as an indicator of the forest edge was the same species that visited the lower pitchers of *Nepenthes sp.*, suggesting that there is at least some similarity between attraction of ants by the baited traps and by pitcher plants. The pitcher plants *N. rafflesiana* and *N. gracilis* are also more abundant near the forest edge than in the interior (Frank 2013). Only few *Polyrhachis* were captured in the interior, although *Polyrhachis ypsilon* was regularly encountered in the field. The attraction of *Polyrhachis (Myrma) sp.* to the baited traps may therefore be related to the occurrence of pitcher plants near the edge, and the visitation behaviour of this ant to pitchers.

What can be concluded from these findings, is that the disturbed habitats of forest gaps and forest edge both are characterized by the high abundance of behaviourally dominant ant species. This can be expected because in both habitats the disturbance was manifested in an alteration of the canopy structure and height. The more open canopy exposed the forest ground to sunlight, which enables dominant species to compete for light in the lower forest stratum. The identities of the dominant species, however, were different between both disturbed habitats. Compositional similarity was higher between forest gaps and interior and between forest edge and interior, than between forest gaps and forest edge. Differences in local forest structure and surrounding landscape might play a role in this.

#### **Community composition varies with season, but habitats remain distinct**

Our data suggest that ant species show seasonal differences in their attraction to the bait. Whether this is caused by seasonal patterns in population dynamics of ants or by indirect effects of seasonal variation in water level, rainfall or food availability is unclear. Bait attraction has been recorded previously to vary for the fire ant *Solenopsis invicta* in North America (Stein et al. 1990), which was suspected to be caused by temporal variation in temperature and associated resource needs for colony maintenance and brood production. Rainfall and water level in peat swamp forest vary considerably with season, the forest being flooded in the wet season (Page et al. 1999, Harrison et al. 2010). From Amazon rainforests, it has been shown that flooding caused lower diversity and density of ants (Mertl et al. 2009), presumably through reduced numbers of suitable nesting sites.

Overall, the wet season showed better distinction of ant communities than the dry season. More indicators could be identified in the wet season, and overall similarity of plots was consistently lower at the species level, and to a large extent at the genus level as well. Although this seems to agree with the study of Silveira and colleagues (2012) in the Amazon that found clearer ant community responses

in wet season, in this case the effect may also be contributed to different lengths of dry and wet season in the Sabangau tropical peat swamp forest, i.e. eight months wet season and four months dry season (Harrison et al. 2010), resulting in a sample size that is twice as large in the wet season compared to the dry season. Incidence frequencies in both seasons did not differ when correcting for sample size (**Appendix 7**), but the better distinction of habitats in wet season may be the result of a higher resolution (more detailed variation in species richness and abundance) due to a longer sampling period. It is therefore hard to tell if the wet season is a better time to conduct surveys than the dry season.

Despite the temporal variation in similarity and composition of sampled ant communities, habitats remained clearly distinct at the plot level, and a number of species and genera were consistent habitat indicators in both dry and wet season. *Monomorium cf. floricola, Crematogaster Cr1* and *Pheidole rugifera* each indicated the same out of three habitats year-round as described above. At the genus level, this was true for *Monomorium* and *Crematogaster*, and for *Polyrhachis*. For the interior forest, robust indicator genera were only found in the wet season, not in the dry season.

#### **Appropriate spatial scale**

Ideally, the spatial scale to analyse compositional differences should have samples that each contain the complete ant community at the site and show sufficient detail to identify differences in community composition. For individual traps, there is detailed variation in the abundance data, but communities per trap are likely to be undersampled. Distinction of ant communities was problematic, as was shown in the overlap of TWINSPAN clusters and in the PCA plots at this spatial scale.

Besides, it is questionable whether individual traps can be considered independent sampling units, as spatial autocorrelation occurred between traps of one of the forest gaps and of the forest edge. Traps were spaced 10 m apart, which should be sufficient for most species (Eguchi et al. 2004; personal communication Tom Fayle). However, foragers of species with larger foraging ranges could be encountered in multiple traps even though they come from the same nest. Additionally, ants can use twigs, stems or other linear substrates to facilitate foraging (Clay et al. 2010), which may increase their foraging range.

The plots would not have the problem of spatial autocorrelation and present the most complete overview of ant community composition. However, since replication of plots is very limited, analyses at this level would have low resolution. Additionally, sampling design and sampling effort are different in forest gaps (grids) than in the other habitats (transects), making comparison difficult. Foraging behaviour of ants could be influenced by the spatial arrangement of traps and species with large foraging ranges – e.g. *Leptogenys sp.* (Maschwitz et al. 1989) and *Camponotus gigas* (Pfeiffer & Linsenmair 1998) – may be sampled more stochastically in the grid plots, since these grids attract ants from a smaller area than the transects.

The five-trap clusters are a useful compromise: they have more complete communities per sampling unit than the individual traps, yet retain more detailed information and more replication than the plots. Although this can be regarded as pseudoreplication of sampling units since the clusters are subsamples of the same plots, it allows for analyses of variation within and between habitats at a higher resolution than at plot level, and better distinction of ant communities than at trap level. The spatial autocorrelation is expected to be lower as well, since sampling units now comprise larger areas. In anticipation of improved baseline surveys in peat swamp forest, this can be a useful way to find preliminary differences in community compositions. Additionally, the spatial relations between traps were kept equal, by using only one cluster of five adjacent traps in a linear arrangement for each forest gap, making them comparable to the five-trap clusters in the line transects, as opposed to the level of plots.

## **Taxonomic sufficiency**

Although some resolution is lost, the main findings of this study are conserved when analysing the data on a generic instead of a specific level. The analyses at genus level have both advantages and disadvantages. It improves the data quality in this study since most ants have been accurately identified to genus by three students, but splitting and lumping errors occurred at the morphospecies

level, as became clear after revision. Only one genus (*Ochetellus*) contained a misidentified specimen at genus level (*Camponotus*), and as a consequence findings on this genus should be interpreted with caution. The more practical benefit of analysis at this taxonomic scale is that it would require a lower skill set for accurate identification, which can be a more cost-effective, timesaving approach, especially for long-term monitoring (Timms et al. 2012).

There is, however, also an apparent drawback of genus-level analysis, i.e. losing the resolution of the species level. Species responses to habitat or disturbance cannot always be generalised to the generic level, and doing so would mean losing information. An example in the present study is *Pheidole*, a genus in which two valuable indicator species, *P. rugifera* and *P. ("Peo")*, are found. Since both indicate different habitats (i.e. interior forest and forest edge, respectively), the genus itself loses the indicator value for either habitat. Thus, an analysis at generic level would not have discovered *Pheidole* as a diagnostic genus, even though the genus contains species that are very indicative of different habitats and therefore could be of great importance for ecological monitoring programmes.

The generality of taxonomic sufficiency is still subject of much scientific debate (Bertrand et al. 2006, Timms et al. 2012). There are myrmecological studies reporting that genera and functional groups can suffice for certain ecological monitoring studies (e.g. Pik et al. 1999), but also some that recommend species identification for discrimination of habitats (e.g. Piper et al. 2009). It could be dependent on the scale and type of habitats studied, whether genera would suffice for discrimination of disturbance gradients.

Bertrand and colleagues (2006) provide a critical review of taxonomic surrogacy for biodiversity and ecological monitoring, arguing that supraspecific taxa are subjective and horizontal comparison (diversity of genera within families or families within orders) is therefore meaningless. The use of taxonomic sufficiency should be assessed for each individual case, by performing baseline studies to validate generalisation of species at generic level (Bertrand et al. 2006). The present study can be regarded as such a baseline survey, and the preliminary results suggest that generalisation is to a large extent valid. Continued monitoring on a species level should however be recommended, since the data set only spans one year, and further data collection would make a more robust support for correlation of species and genus responses. Current results are limited to three habitats in the Sabangau NLPSF only, so it is unclear whether the preliminary taxonomic sufficiency also holds for other Bornean peat swamp forests and other habitats within.

## Towards an ecological monitoring programme for ants in Bornean peat swamp forests

The present study shows distinct ant communities in three habitats of peat swamp forest in the Sabangau catchment, characterized by several indicator species of which a number is reliable yearround. It shows that ants can be sensitive to anthropogenic disturbance in peat swamp forest, and gives insights in the way in which ant communities may respond to such disturbances. The conclusions from this study should be used with caution, however, and it is strongly recommended to continue baseline surveys to improve and further support the premature findings reported in this study.

The sampling design had several limitations that constrained quality of statistical analyses. The limited replication of plots does not justify extrapolation of the present findings of ant community responses to Bornean peat swamp forests in general, and even generalisation to habitats within the Sabangau should be done with caution. Additionally, the different spatial arrangement of traps in either sampling grids or along transects makes interpretation of compositional differences problematic. For future consistent sampling design, it is therefore recommended to use sampling grids of identical size, shape and arrangement, so that both small-scale disturbances and large-scale habitats can be sampled and replicated in comparable ways.

The varied accuracy of identifications should be avoided in future surveys. In the present study, some species may have been missed by splitting and lumping errors during the first nine sampling months, and some compromised morphospecies likely contain species of different habitat preference (e.g. in *Pheidole*). With accurate identification, it is expected that additional indicator species will be found, and a more precise characterisation of ant communities be formed.

The baited trapping method successfully discriminates among habitats and efficiently samples the ant communities, but baiting is known to be a very selective sampling method (Longino 2000, Bestelmeyer et al. 2000). A more complete sampling would be valued not only to provide an overview of overall ant diversity in peat swamp forests and assess the effectiveness of baited trapping, but also because precisely those specialists missed by baiting could be more characteristic of particular habitats. The use of complementary sampling techniques therefore deserves consideration. Pitfall traps did not appear effective in peat swamp forest (OuTrop, unpublished data). Berlese funnels, Winkler traps (Bestelmeyer et al. 2000) and fogging (e.g. Longino & Colwell 1997) are generally more effective and less selective methods than baiting, but are more expensive. A simple, less selective technique is the use of sticky traps to sample arboreal ants (Majer 1990). Besides, the baiting method itself may be improved, e.g. by testing higher concentrations of bait or by positioning the traps both attached to tree trunks and free on the ground in order to attract complementary portions of the ant community (Yamane et al. 1996).

Although environmental variables explained large parts of variance in the ordinations, some important microclimatic variables have not been measured or have been measured with limited precision. The following measurements are recommended for future surveys: tree species composition around the trap or in the sampling grid, plant composition of the undergrowth, identity and DBH of the tree, sapling or shrub to which a trap is tied, total canopy cover, more detailed values for ground cover, litter volume and depth, presence of logs and tree trunks. For each trapping day, microclimate (e.g. soil surface) and ambient temperature, relative humidity, and rainfall should be recorded, since these not only characterize the microclimate but can also influence foraging activity of ants and resulting capture rates.

Even though baiting likely samples a small fraction of the entire ant community, if it consistently samples this fraction it could be a cost-effective method for ecological monitoring. Evaluating ants as ecological indicators using McGeoch's review (1998), the ant communities in this study are sensitive to the disturbances of interest and can be explained by environmental variables that characterize the habitat. Their representativeness of responses of other taxa has not yet been investigated, but parallel ecological monitoring has been conducted on birds and butterflies (OuTrop, unpublished data). These could be compared for congruent patterns in the near future, which can answer the more general question whether ants are indicators of ecosystem responses to certain disturbances.

But before anything else, the ant monitoring programme needs a more robust and more detailed baseline. Future sampling should focus on the improvements mentioned above, and extend its research to more habitats in peat swamp forest, e.g. degraded forest, post-fire regrowth, and tall pole and low pole peat swamp forest. Scientifically interesting is that Sabangau NLPSF contains several types of disturbed forest within the relatively intact continuous forest. Recolonization of previously disturbed sites by ants is therefore not constrained by habitat fragmentation. This could serve as a reference for other fragmented and disturbed forests. Sites of different age after disturbance could serve as a chronosequence to study succession in ant community composition, and its indication for ecosystem recovery.

For these baseline surveys, it is recommended that plots be sampled in both dry and wet season, since community composition varies and different species are indicative. Temporal variations in ant responses are still preliminary, and become more robust with continued data collection. In later surveys, sampling can then focus on the season with strongest segregation of ant communities between habitats.

In short, the presented findings provide the first positive implications for the use of ants as ecological indicators in peat swamp forests of Borneo, but additional surveys are needed with improved design and sampling in more habitats or forests to support and generalize these results.

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# Appendices

				İ					
	Conus (codo)	Sp.		plot					
Subfamily	+ functional group	code	Species after revision	G	н	F	Δ	R	Total
Dolichoderinae	Ochetellus (Och) O	0c1	Ochetellus sn 1	2	15	2	2	2	23
Dononoucimue		001	Camponotus sp. 5 (1 specimen)	-	15	2	-	-	23
	Philidris (Phi) DD	Pi1	Philidris sp. 1				11	1	12
	Taninoma (Tan) O	Tam	Taninoma melanocenhalum	2			8	4	14
		Ta1	Tapinoma sp. 1	-		1	0		1
		Ta2	Taninoma sp. 2	1	1	11			13
	Technomyrmex (Tec) O	Tck	Technomyrmex kraenelini	-	1	6	18	1	26
		1 Cit	Technomyrmex lisae		-	Ũ	10	-	20
		Tc1	Technomyrmex sp. 1	1				1	2
Formicinae	Camponotus (Cam) SC	Cmg	Camponotus ajaas	1		6	16	8	31
		Cm1	Camponotus sp. 1	11	12	14	28	36	101
		Cm3	Camponotus sp. 3				1		1
		Cm4	Camponotus sp. 5			2	1	1	4
	Euprenolepis (Eup) TCS	Fup	Euprenolepis procera	2		1	- 77	105	185
	Nylanderia (Nyl) O	Nv1	Nylanderia sp. 1	35	32	153	154	236	610
		,=	Nylanderia sp. 2			200			010
			Nylanderia sp. 3						
	Oecophylla (Oec) TCS	Oes	Oecophylla smaraadina	16	3				19
	Polyrhachis (Pol) SC	PrM	Polyrhachis (Myrma) sp.			33	2	1	36
			Polyrhachis (Myrmhopla) sexspinosa-						
		PrS	group <i>sp</i> .					1	1
		Pry	Polyrhachis (Polyrhachis) ypsilon			1			1
	unknown	F1	Formicinae sp. 1 (cf. Lasius)			1			1
Myrmicinae	Cardiocondyla (Car) O	Cd1	Cardiocondyla sp. 1	1	1		1		3
			Cardiocondyla sp. 2						
			Cardiocondyla wroughtonii-group sp. 1						
			Cardiocondyla wroughtonii-group sp. 2						
	Crematogaster (Cre)	Cro	Crematogaster (Physocrema) cf. onusta				4		4
	GM		Crematogaster (Physocrema) sewardi						
			Crematogaster sp. 6						
		Cr1	Crematogaster sp. 1	10	6	65	23	38	142
			Crematogaster sp. 3						
			Crematogaster sp. 4						
			Crematogaster sp. 5				_		
		Cr2	Crematogaster sp. 2				6	1	7
		Cr7	Crematogaster sp. 7			2			2
	Mayriella (May) TCS	Ma1	Mayriella sp. 1				1		1
	Meranoplus (Mer) TCS	Mem	Meranoplus malaysianus			_	1		1
	Monomorium (Mon)	Mmf	Monomorium cf. floricola	193	158	8	29	9	397
	GM	Mm1	Monomorium sp. 1	2	2	8		1	13
	Pheidole (Phe) GM	Pex	Pheidole aristotelis	24	29	8	64	61	186
		Рео	Pheidole orophila	17	4	22	8	2	53
			Pheidole aglae						
		<u> </u>	Pheidole plagiaria	<u> </u>	-		_	<b>F</b> 2	=0
		Pes	Prietaole quadricuspis	4	/	6	3	59	79
		Der	Phelaole quadrensis	0.2	20	10	200	244	604
		Per	rneidole tugijeta	ŏΖ	30	19	300	244	100

Appendix 1. Species list (including codes) and total absolute abundance per plot.

	Pheidologeton (Pho)	1							
	TCS	Роа	Pheidologeton cf. affinis				4		4
		Рор	Pheidologeton cf. pygmaeus					10	10
	Rhopalomastix (Rho)								
	TCS	Rh1	Rhopalomastix sp.			1			1
	Solenopsis (Sol) TCS	So1	Solenopsis sp. 1			2			2
	Strumigenys (Str) C	Sg1	Strumigenys sp. 1					2	2
	Tetramorium (Ttm) O	Tm1	Tetramorium sp. 1 Tetramorium pacificum	3	5	42	23	11	84
		TmS	Tetramorium scabrosum-group sp.	2				3	5
		TmT	Tetramorium sp. cf. "Triglyphothrix"			26	3	72	101
			Tetramorium tonganum-group sp. (near						
		TmL	laparum)	2		1	5	9	17
		TmU	Tetramorium tortuosum-group sp.				2	4	6
	Vollenhovia (Vol) TCS	Vh1	Vollenhovia sp. 1				13		13
	Gnamptogenys (Gna)								
Ponerinae	TCS	Gng	Gnamptogenys gabata			5	1	1	7
	Leptogenys (Lep) SP	Lg1	Leptogenys sp. 1		2	10			12
Pseudomyr-									
mecinae	Tetraponera (Ttp) TCS	Тра	Tetraponera attenuata					1	1
		Тре	Tetraponera extenuata / T. modesta					1	1
		Tpn	Tetraponera nitida					2	2
	unidentified		Formicidae <i>indet</i> .	13	21	25	40	34	133

#### Appendix 2. Identification literature for ants.

Baroni Urbani, C. and M.L. de Andrada (2007) The ant tribe Dacetini: limits and constituent genera, with descriptions of new species (Hymenoptera, Formicidae). *Annali del Museo Civico di Storia Naturale "G. Doria"* 99: 1-191.

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Appendix 3. TWINSPAN settings

Maximum number of divisions:4Maximum number of indicators per division:4Minimum group size:2 (five-trap clusters, plots); 5 (traps)

Cut levels

For traps and five-trap clusters 5 cut levels were used, corresponding with scaled abundance in traps (0-5) and presence scores in clusters (0-5).

For plots, percentages were classified into 5 classes as follows:

Cut level	Percentage
1	0
2	10
3	25
4	50
5	100

Appendix 4. TWINSPAN clustering table output.

#### Traps

For the level of individual traps, TWINSPAN tables are not included in the appendix since they comprise large data sets. Instead, the classification of traps into TWINSPAN groups is given below. Codes refer to individual traps.

Species composition Cluster "gaps": G1-5, 7-14; H17-30; E4-5; A19, 21, 23-25; B15, 21. Cluster "edge-interior": H16; E2, 3, 7, 9-11, 13-30; A1-4, 13, 17, 18, 22, 26; B4, 6-10, 12, 14, 17, 19, 23-27, 30. Cluster "interior": G6, 15; E1, 6, 8, 12; A5-12, 14-16, 20, 27-30; B1-3, 5, 11, 13, 16, 18, 20, 22, 28, 29.

Genus composition Cluster "gaps": G1-5, 7-15; H17-30; E4-6, 8; A19, 21-25; B13. Cluster "edge-interior": E1-3, 9-30; A1-4, 8; B2-4, 6, 7, 9, 10, 12, 16, 17, 23-27, 30. Cluster "interior": G6; H16; E7; A5-7, 9, 10, 15, 16, 18, 26, 28-30; B1, 5, 8, 11, 14, 15, 18-20, 22, 28, 29.

### *Clusters* Species composition

	E4	E5	E6	E3	E1	A5	G	н	A4	B6	A1	B5	B2	B1	B3	E2	A6	A3	A2	B4
Oc1	1	1	-	-	-	1	1	-	-	-	1	-	2	-	•	•	-	-	-	-
Cd1	-	-	-	-	-	-	1	-	1	-	-	-	-	-	•	-	-	-	-	-
Mmf	-	-	-	1	2	5	5	5	1	1	-	1	-	-	1	1	-	-	-	-
Oes	-	-	-	-	-	-	2	1	-	-	-	-	-	-	•	-	-	-	-	-
Ta1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cr7	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pry	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rh1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
So1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ta2	-	1	1	1	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
PrM	4	4	5	4	-	-	-	-	-	-	-	-	-	-	-	2	-	1	1	1
Mm1	-	1	1	-	1	-	1	-	-	-	-	-	-	-	1	1	-	-	-	-
Рео	3	2	4	4	2	2	2	-	1	-	1	1	-	1	-	-	-	-	1	-
Tm1	3	4	1	2	-	3	1	2	1	1	3	2	-	-	-	1	-	1	1	-
TmT	5	1	-	3	4	1	-	-	-	2	-	2	1	2	1	1	-	1	-	1
Gng	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1
Lg1	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
TmS	-	-	-	-	-	-	1	-	-	-	-	-	1	1	-	-	-	-	-	-
Роа	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	1	-	-
Cm1	1	1	2	3	1	2	1	3	3	2	3	3	2	2	2	2	1	-	3	-
Ny1	4	5	5	3	4	5	2	5	5	3	5	5	5	5	5	4	5	5	5	4
Cr1	4	5	5	4	3	2	2	1	1	3	3	4	4	4	2	5	1	3	3	2
Per	2	1	1	1	1	2	1	1	3	2	3	3	-	4	3	1	2	3	5	3
Pex	1	1	1	-	-	1	1	-	3	2	1	-	3	-	2	2	-	1	1	1
Pes	-	-	1	1	-	-	-	-	-	-	1	1	3	1	2	1	-	2	-	-
Cmg	-	-	-	2	-	1	-	-	-	-	-	1	-	3	-	2	2	3	4	1
Eup	1	-	-	-	-	-	1	-	-	-	1	-	3	2	-	-	-	-	-	-
Tc1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Тра	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Sg1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
PrS	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Cm3	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Tpn	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-
TmL	-	-	-	-	-	1	-	-	2	1	1	1	2	2	-	1	-	-	-	1
Tam	-	-	-	-	-	-	-	-	1	2	-	-	-	1	-	-	-	1	1	-
TmU	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	1	1
Pi1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-
Vh1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-
Ma1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Cro	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	-	-
Тре	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Cr2	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	3	-	-

Mem	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Cm4	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	2	1	-	-	-
F1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Рор	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1
Tck	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	2	3	1	1	-
	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	1	1	1	1	1
	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	0	0	1	1	1
	0	1	1	0	1	0	1		0	0	1	1	0	1	0	1	1	0	0	1
		0	1						0	1	0	1				0	1	0	1	

### Genus composition

	B2	A1	B5	A6	E2	A2	A3	A4	B1	B4	B6	E3	E1	E6	E5	E4	<b>B3</b>	A5	Н	G
Gna	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	2	-	-	-	-
Lep	-	-	-	-	2	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-
Pol	-	-	-	-	2	1	1	-	-	1	-	4	-	5	4	4	-	-	-	-
Rho	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Sol	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Тар	-	-	-	-	-	1	1	1	1	-	2	1	1	1	2	-	-	-	-	-
Phi	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Str	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ttp	1	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Vol	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
May	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mer	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Тес	-	-	-	2	2	1	1	-	2	-	-	-	-	-	-	-	-	-	1	-
Cre	4	3	4	2	4	4	5	2	4	2	3	4	3	5	5	5	2	2	1	2
Ttm	4	4	4	-	2	3	2	3	3	3	3	4	4	1	5	5	1	3	2	1
Cam	3	3	3	3	4	5	3	4	4	1	3	3	1	2	1	1	2	2	3	1
Nyl	5	5	5	5	4	5	5	5	5	4	3	3	4	5	5	4	5	5	5	2
Phe	3	4	3	2	4	5	5	5	4	3	3	5	3	5	3	3	4	3	1	3
Eup	3	1	-	-	-	-	-	-	2	-	-	-	-	-	-	1	-	-	-	1
Car	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1
Pho	-	-	-	-	-	-	1	1	-	1	-	-	-	-	-	-	1	1	-	-
Och	1	1	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	1	-	1
Mon	-	-	1	-	2	-	-	1	-	-	1	1	2	1	1	-	2	5	5	5
Oec	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	1
	0	0	0	1	1	1	1	1	1	1	1	0	0	0	1	1	0	0	1	
	0	1	1	0	1	1	1	1	1	1	1	0	1	1	0	1	0	1		

#### *Plots* Species composition

(continued	)
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•					
	Е	Н	G	В	Α
PrM	4	-	-	1	1
Pry	1	I	-	I	-
F1	1	I	-	I	-
Lg1	2	1	-	I	-
Ta2	2	1	1	-	-
So1	1	-	-	-	-
Cr7	1	I	-	I	-
Rh1	1	I	-	I	-
Ta1	1	I	-	I	-
Oes	1	2	3	I	-
Mm1	2	2	2	1	-
Oc1	1	3	2	1	1
Рео	4	2	3	1	2
TmS	-	-	2	1	-
Mmf	2	4	4	2	2
Cd1	-	1	1	-	1
Cm1	3	4	3	3	3
Ny1	4	4	4	4	5
Tm1	3	3	1	2	3
Cr1	4	3	3	4	3
Pes	2	2	2	2	2
Pex	2	3	2	3	2
Eup	1	-	2	2	1
Tc1	-	-	1	1	-
Per	2	3	3	4	4

	Е	Н	G	В	А
TmL	1	-	2	2	2
Tck	1	1	-	1	2
TmT	3	-	-	3	1
Gng	1	-	-	1	1
Cmg	2	-	1	2	3
Tam	-	-	1	2	2
Cm4	1	-	-	1	1
Рор	1	I	-	1	-
Vh1	-	-	-	-	1
Cr2	-	-	-	1	2
Тре	-	-	-	1	-
Cro	-	-	-	-	2
Tpn	1	1	-	1	-
Pi1	-	-	-	1	1
Cm3	1	1	-	I	1
Роа	-	-	-	-	2
PrS	-	-	-	1	-
TmU	-	I	-	1	1
Sg1	1	1	-	1	-
Mem	-	-	-	-	1
Тра	-	-	-	1	-
Ma1	-	-	-	-	1
	0	0	0	1	1
	0	1	1	0	1
		0	1		

Genus composition

	Е	В	А	G	Н	
May	-	-	1	-	-	
Mer	-	-	1	-	-	
Pho	-	1	2	-	-	
Phi	-	1	1	-	-	
Str	-	1	-	-	-	
Ttp	-	2	-	-	-	
Vol	-	-	1	-	-	
Gna	1	1	1	-	-	
Pol	4	1	1	-	-	
Rho	1	-	-	-	-	
Sol	1	-	-	-	-	
Тар	2	2	2	1	-	
Cam	3	4	4	3	4	
Cre	4	4	4	3	3	
Nyl	4	4	5	4	4	
Phe	4	4	4	4	4	
Ttm	4	4	4	3	3	
Eup	1	2	1	2	-	
Lep	2	-	-	-	1	
Тес	1	1	2	2	2	
Mon	2	2	2	4	4	
Och	1	1	1	2	3	
Car	-	-	1	1	1	
Oec	-	-	-	3	2	
	0	0	0	1	1	
	0	1	1	0	1	
		0	1			

Appendix 5. Maximum lengths of gradient from Detrended Correspondence Analysis.

	Length of gradient for data			
Spatial scale	Species	Genus		
traps	3.473	3.349		
clusters	2.353	1.675		
plots	1.566	1.317		

In all cases, maximum length of gradient is smaller than 4, so PCA is allowed.

Appendix 6. PCA posthoc correlations of environmental variables. Correlations were the same for species and genus composition.

	CCb	CCc	LP	DW	GR	mDBH
CCa	0.991	0.7416	-0.6288	-0.1433	0.2717	0.9991
CCb		0.8207	-0.5564	-0.2747	0.3649	0.9871
CCc			-0.0272	-0.7287	0.6518	0.7345
LP				-0.3727	0.1667	-0.6171
DW					-0.7454	-0.12

## Plot data

#### Cluster data

GR

mDBH

	CCb	CCc	LP	DW	GR
CCa	0.5346	0.1966	-0.2612	-0.1985	0.147
CCb		0.3893	-0.394	-0.3279	0.2328
CCc			-0.1201	-0.5602	0.2706
LP				-0.3495	0.0893
DW					-0.7501

#### Trap data

	CCb	CCc	LP	DW	GR
CCa	0.3447	0.0606	-0.2479	-0.0966	0.1354
CCb		0.0484	-0.1591	-0.1551	0.1364
CCc			-0.0983	-0.1704	0.0883
LP				-0.2339	-0.1221
DW					-0.6508

Appendix 7. Wilcoxon Signed Ranks Test for species capture rates in dry and wet season.

For this analysis, uniques and duplicates have been excluded, since seasonal effects in these species would be very imprecise. Data were tested using Wilcoxon signed rank test, because per species there is one pair of data (one value for dry season and one for wet season). Tests were performed in SPSS v19.

ΒA

0.2549

0.9952 0.9876

0.7646

-0.5623

-0.1486

0.2752

0.9976

#### Uncorrected data (number of species incidences)

	Ν	Mean rank	Sum of ranks	Test statistic Z	P-value (2-tailed)
Negative ranks	21	15.29	321.00	-2.242	0.025
Positive ranks	8	14.25	114.00		
Ties	0				
Total	29				

Corrected data (number of species incidences divided by sample size)

	Ν	Mean rank	Sum of ranks	Test statistic Z	P-value (2-tailed)
Negative ranks	12	10.92	131.00	-1.645	0.100
Positive ranks	16	17.19	275.00		
Ties	1				
Total	29				