Termite diversity and species composition in heath forests, mixed dipterocarp forests, and pristine and selectively logged tropical peat swamp forests in Brunei

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Abstract

Since the 1970s Southeast Asian peat swamp forests have been increasingly threatened by anthropogenic disturbance. Peat swamps act as refuge for many endangered species, and they may turn into a net producer of CO_2 and greatly contribute to climate change if cleared and drained. As one of the main invertebrate decomposers in the tropics, termites are likely to play a major role in peat forests. In this paper, we used a grid-based sampling plot protocol to sample termites in Brunei. We sampled termite communities in pristine and selectively logged peat swamp forests, that we compared with termite communities sampled in heat and dipterocarp forests. More precisely, we determined: (i) termite species diversity in peat swamp forests, and (ii) how termites respond to peat swamp logging. We found that species richness was the highest in the mixed dipterocarp forest. Selective logging had limited impact on species richness in peat swamp forest, suggesting that termite communities are resilient to limited amount of perturbations. Further data are needed in order to better understand the impact peat swamp clearance has on termite populations and their contribution to climate change.

Keywords Biodiversity, Brunei, Conservation biology, Community ecology, Southeast Asia, Species richness

Introduction

Tropical peat swamp forests originally covered an area of about 440,000 km^2 globally, 250,000 km^2 of which occurred in Southeast Asia and New Guinea (Page et al. 2011). Peat swamp forests have experienced minor disturbances in the past, mainly due to wood and food harvesting from local populations (Miettinen et al. 2012). However, since the 1970s, peat swamp forests have been increasingly threatened by deforestation (Miettinen et al. 2011, 2012), drainage (Hirano et al. 2009), fire (Langner and Siegert 2009; Page et al. 2009), and conversion of land to plantation (Hansen et al. 2009). Human degradation has reduced the Southeast Asian peat swamp forest cover to half of its original size, of which only a small fraction is protected (Yule 2010; Posa et al. 2011; Miettinen et al. 2011). Pressure from deforestation at its current rate is such that Southeast Asian peat swamps are predicted to vanish by 2030 (Miettinen et al. 2012).

Peat swamp forests generally have lower species richness than mixed dipterocarp forests, but they contain many endemic species. While no known terrestrial vertebrates are endemic to peat swamp, 80 endemic species of fish and 172 endemic species of plants have been recorded (Posa et al. 2011). Additionally, as lowland forests have already been largely deforested in many parts of Southeast Asia, peat swamps provide refuge for many species that can use a wide range of forest types (Posa et al. 2011). For instance, peat swamp forests are the most important remaining habitat for the iconic orangutan (Yule 2010).

Tropical peat swamp forests store a large amount of carbon, mainly in the peat belowground, which may contain up to 18 times the quantity of carbon stored in the aboveground vegetation (Jaenicke et al. 2008). Indonesian peatlands alone store an estimated 55 Gt of Carbon (Jaenicke et al. 2008), representing about four times the global carbon dioxide emission in 2016 (Olivier et al. 2017). Decomposition of organic matter is low in peat swamp forests due to abiotic and biotic factors. The acidic and anaerobic nature of peat (Moore 1989; Page et al. 1999) impedes bacterial activity (Jackson et al. 2009; Kanokratana et al. 2011), and the sclerophyllous plant species, common in peat swamp forests, are rich in tannins and toxins, deterring decomposers (Yule and Gomez 2009; Yule 2010). As a consequence, soil respiration and CO_2 emissions are reduced in peat swamps, although these increase with a seasonally low water table or when drained (Furukawa et al. 2005; Jauhiainen et al. 2005; Hirano et al. 2007, 2012).

Termites are one of the main invertebrate decomposers in tropical and sub-tropical forests (Martius, 1994; Eggleton et al. 1996; Cornwell et al. 2009; Dahlsjö et al. 2014a) where their abundance and biomass are high (Fittkau and Klinge 1973; Ellwood and Foster 2004). They feed on a range of dead organic matter from wood to leaf litter and mineralised soil (Donovan et al. 2001; Bourguignon et al. 2011a), which they break down with the help of symbiotic gut microorganisms (Bignell 2011; Ohkuma and Brune 2011). Termite diversity has been shown to be low in near-pristine peat swamp forests (Vaessen et al. 2011; Neoh et al. 2016, 2017) with further reductions in cleared peat swamps that experience regular fires (Neoh et al. 2016, 2017).

While termite community data are available for peat swamp fragments and selectively logged peat swamp forests, data for untouched peat swamps are lacking probably due to the very few truly untouched remaining peat swamp forests. In this study, we examine termite species richness and composition in pristine and selectively logged peat swamp forests, and compare them to that of heath forests and mixed dipterocarp forests. Specifically, we aim to examine:

(1) Termite species richness, diversity and composition in peat swamp forests.
(2) The effect of selective logging on termite species and feeding-group richness, diversity and composition in peat swamp forests.

Methods

Study sites

Brunei's climate is tropical equatorial with annual average temperature of 27°C, ranging between 18°C and 38°C. Air humidity ranges between 70 % and 100 % while the annual average rainfall is 3000 mm, with the period October - January being wetter, and the period February - March being dryer, than the period April - September. Four different habitats were examined in this study using ten sampling plots: pristine (4 plots) and selectively logged (2 plots) peat swamps, as well as heath (2 plots) and mixed dipterocarp (2 plots) forests.

- <u>Pristine peat swamp forest (PSF1, PSF2, PSF3, PSF4)</u>

  The pristine peat swamp forest site has been exposed to little anthropogenic disturbance and was dominated by *Shorea albida* (see Anderson 1961 for description of similar peat swamps). Two sampling plots, PSF1 (N 04.375°, E 114.357°) and PSF2 (N 04.372°, E 114.355°), were conducted on the edge of the peat swamp domed structure. PSF1 was located 400 m from the main river, and PSF2 was located 900 m from the main river. Both sampling plots were located in a zone known as *alan batu*, characterised by large trees reaching over 40 m in height (Anderson 1961; Momose and Shimamura 2002). Another two sampling plots, PSF3 (N 04.361° E 114.353°) and PSF4 (N 04.361° E 114.354°), were conducted in the centre of the peat swamp, in the *pandang alan* zone, where trees are lower than 30 m in height (Anderson 1961; Momose and Shimamura 2002). The PSF3 and PSF4 sampling plots were located further away from the main river at 1900 m.

- Selectively logged peat swamp forest (SLF1, SLF2)

  Two sampling plots were conducted in the site: SLF1 (N 04.404°, E 114.362°) and SLF2 (N 04.404°, E 114.360°). The selectively logged peat swamp forest was originally comprised of vegetation similar in composition to the pristine peat swamp forest (PSF) and was selectively logged, but not drained, between 1980 and 2010. When sampling was conducted, the peat swamp forest comprised low stature secondary forest species and lacked larger trees that are characteristic of pristine forests. The two sampling plots were located in the centre of the peat dome at a distance of 2600 m from the main river.

- Heath forests (HTF1, HTF2)

  Heath forests grow on acidic, nutrient poor and well-drained soil and tree species diversity is low compared with mixed dipterocarp forests (see Davies and Becker, 1996). Two sampling plots were conducted in two different heath forests: HTF1, located in Bandas (N 4.567°, E 114.417°) and *Agathis borneensis*-dominated; and HTF2, located in Bukit Sawat (N 4.576°, E 114.506°) and selectively logged in the 1960s.

- Mixed dipterocarp forests (MDF1, MDF2)

Two sampling plots were conducted in two pristine mixed dipterocarp forests: MDF1 located in Andulau (N, 4.656°, E 114.519°); and MDF2, located in the Temburong National Park (N 4.541°, E 115.151°). The forests were historically and visibly undisturbed (no signs of logging or tree stumps were seen) except for selective logging that may have taken place prior to the 1960s. Floristic composition was characteristic of Western Borneo mixed dipterocarp forests with high species richness (see Davies and Becker 1996).

Sampling methods

Termites were sampled using the standard sampling plot method described in Bourguignon et al. (2017). Each sampling plot comprised 25 quadrats of 5 m^2 (2.24 m x 2.24 m) placed in a grid. Each quadrat was located 10 m apart. Representatives of termite species from a range of microhabitats (mounds, dead wood, leaf litter, runways, decomposed matter at the base of plants and in the soil) were collected in each quadrat over a period of 0.5 person-hours (active searching for termites by one person for 30 minutes). Once collected, termites were stored in 80% alcohol.

Identification

All samples were grouped into morphospecies based on the morphology of soldiers and workers. Morphospecies were identified at the genus and species level using monographic revisions (Thapa 1982; Tho 1992). Samples of termite incipient colonies comprising dealates and larvae only were discarded as they did not represent established colonies. Species were separated into epiphyte-feeders, wood-feeders and soil-feeders, according to the substrate on which they feed (Table S1). We used previous termite survey to determine feeding-groups (Eggleton et al. 1999).

Data analysis

In order to compare species richness among forest types we produced species rarefaction curves and computed 95 % confidence interval using the Mao-Tau method implemented in EstimateS 9 (Colwell et al. 2004, 2013). Rarefaction curves were compared pairwise and considered significantly different when 95 % confidence interval did not overlap. We pooled the following sampling plots: PSF1 + PSF2 (referred as PSF1 + PSF2) located near the river, PSF3 + PSF4 located near the centre of the peat swamp dome, and SLF1 + SLF2 (hereafter: SLF). Pooled sampling plots were located in the same habitat and geographic locations. These sampling plots were pooled to increase the sampling effort for habitats with low termite abundance.

Nonmetric multidimensional scaling (NMDS) was conducted using Morisita distance to compare differences in species composition among sites. The significant difference among sites was tested with ANOSIM in the software PAST 2.14 (Hammer et al. 2001). We conducted the ANOSIM with species density data, using Morisita distance and 9999 permutations. Bonferroni corrections were used to adjust *P*-values significance level.

Results

In this study, a total of 26 genera, comprising 69 termite species, were recorded (Table S1). The Mao-Tau 95% confidence intervals of species rarefaction curves show that HTF2 significantly differed from SLF1 + SLF2 (SLF) and MDF2 (Fig. 1). Other rarefaction curves did not significantly differ. The highest termite species richness was found in the MDF forest type (MDF1 + MDF2), with 41 species recorded in both sites combined. SLF had the second highest species richness with 30 species. The lowest species richness was found in PSF1 + PSF2 with a total number of 17 species.

Two-dimension NMDS had a stress (loss function) of 0.11. MDF and HTF had low scores along the first axis while PSF and SLF had high scores (Fig. 2). All sampling plots in the PSF forest type clustered together and did not markedly differ from the sampling plots in the SLF forest type. Species composition differed significantly among sites (ANOSIM: global R = 0.153, $p < 0.001$). All paired comparisons were significantly different from each other, except for the comparison between PSF and SLF, although SLF1 differed significantly from PSF3 and PSF4 (Table 1). The main driver of the difference in species composition was the absence of Macrotermitinae from PSF and SLF.

Discussion

(1) Termite species richness and composition in peat swamp forests

Although the extreme hydrological and chemical conditions of peat swamps are generally believed to reduce animal species diversity, few studies have made direct observations of species diversity and endemism in peat swamp forests (Posa et al. 2011). Termite species richness, abundance and composition vary naturally among different types of primary forests (e.g. Jones et al. 2010; Bourguignon et al. 2011b; Dahlsjö et al. 2014b), and recent studies suggest that termite communities are strongly depauperate in peat swamp forests (Vaessen et al. 2011; Neoh et al. 2016, 2017). However, the termite diversity of truly pristine peat swamps is yet to be studied, and has never been directly compared with other forest types (Vaessen et al. 2011; Neoh et al. 2016, 2017).

Rarefaction curves did not plateau for any forest type, and therefore the sampling was incomplete. Termite species richness in PSF was similar to that of HTF and consistently lower than that of MDF, although these differences were not significant. The termite diversity patterns shown in this study are consistent with previous termite surveys of peat swamp forests in Sarawak (Malaysian Borneo) and Sumatra (Indonesia) (Vaessen et al. 2011; Neoh et al. 2016, 2017).

Amazonian floodplains are periodically flooded and have been shown to harbour fewer termite species, while supporting similar abundances, as *terra firme* (Martius 1997). While some soil-feeding termites are abundant in the Amazonian floodplains, they avoid flooding by nesting in trees (Martius 1997). However, as no tree-nesting soil-feeding termites exist in Brunei, termites may only avoid flooding by living in soil patches that are raised above the flood line, preventing many species from establishing viable colonies. The preference for well-drained soil has been clearly demonstrated in flood prone areas in South African savannahs where the density of termite mounds was highest on raised crests (Davies et al. 2014). Our study confirms the results of Vaessen et al. (2011) and Neoh et al. (2016, 2017), and show that the diversity of Nasutitermitinae is high in peat swamp forests while Macrotermitinae are absent. These results largely contributed to the distinctive position of PSF on the NMDS graph, and suggest that some termite groups are predisposed to living in the waterlogged conditions that peat swamps provide. Unlike Macrotermitinae, species of Nasutitermitinae often build arboreal nests that are protected from flooding, probably contributing to their success in peat swamp forests.

Although peat swamp forests appear to support a lower number of termite species than mixed dipterocarp forests, a few species, such as *Bulbitermes constrictus*, *Nasutitermes matangensis* and *Nasutitermes longirostris*, were consistently found in peat swamps while they were absent in other forest types. However, *B. constrictus* and *N. matangensis* have been recorded in other habitats (Inoue et al. 2006; Gathorne-Hardy et al. 2006), suggesting that very few termite species are truly endemic to peat swamps and that the value of peat swamp conservation may lie elsewhere.

(2) Termites and peat swamp disturbance

We sampled termites in the centre of the pristine peat swamp site (sampling plots PSF3 and PSF4) as well as in the centre of the selectively logged peat swamp forest (sampling plots SLF1 and SLF2). Termite species richness slightly increased from the pristine peat swamp forest to the selectively logged peat swamp site, although not significantly. One possible explanation for the slight increase in termite species richness in SLF is a possible increase in available organic matter, including wood and dry peat. However, this hypothesis remains to be tested.

Termite species composition did not differ significantly between the pristine peat swamp forest and the selectively logged peat swamp forest, except for two paired comparisons (Table 1). Macrotermitinae and *Procapritermes*, comprising ten species found in this study, were absent from the pristine peat swamp, selectively logged peat swamp and heath forest. Both the selectively logged peat swamp forest and the heath forest shared similarities with the pristine peat swamp forest (Davies and Becker 1996), although neither of the SLF and HTF sites were waterlogged.

(4) Conclusion

Our results show that few species are likely to be unique to peat swamp forests and several taxa are absent, including the subfamily Macrotermitinae and species of the genus *Procapritermes*. We also found that selective logging has limited impact on termite communities in peat swamp forests in the short term. Termites are one of the main decomposers of organic matter in tropical rainforests, and as such potentially play a role in the accumulation of peat in peat swamp forests. Future studies quantifying termite abundance and biomass, and its relation to peat decomposition, may provide broader insights into the CO_2 emissions following peat swamp clearance.

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References

Anderson JAR (1961) The ecology and forest types of the peat swamp forests of Sarawak and Brunei in relation to their silviculture. University of Edinburgh.

Bignell DE (2011) Morphology, physiology, biochemistry and functional design of the termite gut: an evolutionary wonderland. In: DE Bignell, Y Roisin, N Lo (eds) Biology of termites: A modern synthesis. Springer, Dordrecht, pp 375–412.

Bourguignon T, Šobotník J, Lepoint G, Martin JM, Hardy OJ, Dejean A, Roisin Y (2011a) Feeding ecology and phylogenetic structure of a complex neotropical termite assemblage, revealed by nitrogen stable isotope ratios. Ecol Entomol 36:261–269.

Bourguignon T, Leponce M, Roisin Y (2011b) Beta-diversity of termite assemblages among primary French Guiana rain forests. Biotropica 43:473–479.

Bourguignon T, Dahlsjö CAL, Jacquemin J, Gang L, Wijedasa LS, Evans TA (2017) Ant and termite communities in isolated and continuous forest fragments in Singapore. Insect Soc 64:505–514.

Colwell RK (2013) EstimateS: Statistical estimation of species richness and shared species from samples. User's guide and application.

Colwell RK, Mao CX, Chang J (2004) Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecology 85:2717–2727.

Cornwell WK, Cornelissen JHC, Allison SD, Bauhus J, Eggleton P, Preston CM, Scarff F, Weedon JT, Wirth C, Zanne, AE (2009) Plant traits and wood fates across the globe: rotted, burned, or consumed? Glob Chang Biol 15:2431–2449.

Dahlsjö CAL, Parr CL, Malhi Y, Meir P, Chevarria OVC, Eggleton P (2014a) Termites promote soil carbon and nitrogen depletion: Results from an in situ macrofauna exclusion experiment, Peru. Soil Biol Biochem 77:109–111.

Dahlsjö, CAL, Parr CL, Malhi Y, Rahman H, Meir P, Jones D, Eggleton P (2014b) First comparison of quantitative estimates of termite biomass and abundance reveals strong intercontinental differences. J Trop Ecol 30:143-152.

Davies SJ, Becker P (1996) Floristic composition and stand structure of mixed dipterocarp and heath forests in Brunei Darussalam. J Trop For Sci 8:542–569.

Davies AB, Levick AR, Asner GP, Robertson MP, van Rensburg BJ, Parr CL (2014) Spatial variability and abiotic determinants of termite mounds throughout a savanna catchment. Ecography 37:852-862.

Donovan SE, Eggleton P, Bignell DE (2001) Gut content analysis and a new feeding group classification of termites. Ecol Entomol 26:356–366.

Eggleton P, Bignell DE, Sands WA, Mawdsley NA, Lawton JH, Wood TG, Bignell NC (1996) The diversity, abundance and biomass of termites under differing levels of disturbance in the Mbalmayo Forest Reserve, southern Cameroon. Philos Trans R Soc Lond B Biol Sci 351:51–68.

Eggleton P, Homathevi R, Jones DT, MacDonald JA, Jeeva D, Bignell DE, Davies RG, Maryati M (1999) Termite assemblages, forest disturbance and greenhouse gas fluxes in Sabah, East Malaysia. Philos Trans R Soc Lond B Biol Sci 354:1791–1802.

Ellwood MDF, Foster WA (2004) Doubling the estimate of invertebrate biomass in a rainforest canopy. Nature 429:549–551.

Fittkau EJ, Klinge H (1973) On biomass and trophic structure of the Central Amazonian rain forest ecosystem. Biotropica 5:2–14.

Furukawa Y, Inubushi K, Ali M, Itang AM, Tsuruta H (2005) Effect of changing groundwater levels caused by land-use changes on greenhouse gas fluxes from tropical peat lands. Nut Cyc Agro 71:81–91.

Gathorne-Hardy FJ, Syaukani, Inward DJG (2006) Recovery of termite (Isoptera) assemblage structure from shifting cultivation in Barito Ulu, Kalimantan, Indonesia. J Trop Ecol 22:605–608.

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: Paleontological statistics software package for education and data analysis. Palaeontol Electron 4:9.

Hansen MC, Stehman SV, Potapov PV, Arunarwati B, Stolle F, Pittman K (2009) Quantifying changes in the rates of forest clearing in Indonesia from 1990 to 2005 using remotely sensed data sets. Environ Res Lett 4:034001.

Hirano T, Jauhiainen J, Inoue T, Takahashi H (2009) Controls on the Carbon balance of tropical peatlands. Ecosystems 12:873–887.

Hirano T, Segah H, Harada T, Limin S, June T, Hirata R, Osaki M (2007) Carbon dioxide balance of a tropical peat swamp forest in Kalimantan, Indonesia. Glob Chang Biol 13:412–425.

Hirano T, Segah H, Kusin K, Limin S, Takahashi H, Osaki M (2012) Effects of disturbances on the carbon balance of tropical peat swamp forests. Glob Chang Biol 18:3410–3422.

Inoue T, Takematsu Y, Yamada A, Hongoh Y, Johjima T, Moriya S, Sornnuwat Y, Vongkaluang C, Ohkuma M, Kudo T (2006) Diversity and abundance of termites along an altitudinal gradient in Khao Kitchagoot National Park, Thailand. J Trop Ecol 22:609–612.

Jackson CR, Liew KC, Yule CM (2009) Structural and functional changes with depth in microbial communities in a tropical Malaysian peat swamp forest. Microbial Ecology 57:402–412.

Jaenicke J, Rieley JO, Mott C, Kimman P, Siegert F (2008) Determination of the amount of carbon stored in Indonesian peatlands. Geoderma 147:151–158.

Jauhiainen J, Takahashi H, Heikkinen JEP, Martikainen PJ, Vasander H (2005) Carbon fluxes from a tropical peat swamp forest floor. Glob Chang Biol 11:1788–1797.

Jones DT, Rahman H, Bignell DE, Prasetyo AH (2010) Forests on ultramafic-derived soils in Borneo have very depauperate termite assemblages. J Trop Ecol 26:103–114.

Kanokratana P, Uengwetwanit T, Rattanachomsri U, Bunterngsook B, Nimchua T, Tangphatsornruang S, Plengvidhya V, Champreda V, Eurwilaichitr L (2011) Insights into the phylogeny and metabolic potential of a primary tropical peat swamp forest microbial community by metagenomic analysis. Microbial ecology 61:518–28.

Langner A, Siegert F (2009) Spatiotemporal fire occurrence in Borneo over a period of 10 years. Glob Chang Biol 15:48–62.

Martius C (1994) Diversity and ecology of termites in Amazonian forests. Pedobiologia 38:407–428.

Martius C (1997) The termites. In: WJ Junk (Ed) The Central-Amazon Floodplain: Ecology of a Pulsing System. Springer Verlag, Berlin, Germany, pp 361–371.

Miettinen J, Shi C, Liew S (2011) Deforestation rates in insular Southeast Asia between 2000 and 2010. Glob Chang Biol 17:2261–2270.

Miettinen J, Shi C, Liew SC (2012) Two decades of destruction in Southeast Asia's peat swamp forests. Front Ecol Environ 10:124–128.

Momose K, Shimamura T (2002) Environments and people of Sumatran peat swamp forests I: Distribution and typology of vegetation. Southeast Asia Stud 40:74–86.

Moore PD (1989) The ecology of peat-forming processes: a review. Int J Coal Geol 12:89–103.

Neoh KB, Bong LJ, Muhammad A, Itoh M, Kozan O, Takematsu Y, Yoshimura T (2016) The Impact of tropical peat fire on termite assemblage in Sumatra, Indonesia: Reduced complexity of community structure and survival strategies. Environ Entomol 45:1170–1177.

Neoh KB, Bong LJ, Muhammad A, Itoh M, Kozan O, Takematsu Y, Yoshimura T (2017) The effect of remnant forest on insect successional response in tropical fire impacted peatland: A bi-taxa comparison. PLOS ONE 12:e0174388.

Ohkuma M, Brune A (2011) Diversity, structure, and evolution of the termite gut microbial community. In: DE Bignell, Y Roisin, N Lo (eds) Biology of termites: A modern synthesis. Springer, Dordrecht, pp 413–438.

Olivier JGJ, Schure KM, Peters JAHW (2017) Trends in global CO2 and total greenhouse gas emissions: 2017 report.

Page SE, Rieley JO, Shotyk W, Weiss D (1999) Interdependence of peat and vegetation in a tropical peat swamp forest. Philos Trans R Soc Lond B Biol Sci 354:1885–1897.

Page S, Hoscilo A, Wösten H, Jauhiainen J, Silvius M, Rieley J, Ritzema H, Tansey K, Graham L, Vasander H, Limin S (2009) Restoration ecology of lowland tropical peatlands in Southeast Asia: Current knowledge and future research directions. Ecosystems 12:888–905.

Page SE, Rieley JO, Banks CJ (2011) Global and regional importance of the tropical peatland carbon pool. Glob Chang Biol 17:798–818.

Posa MRC, Wijedasa LS, Corlett RT (2011) Biodiversity and conservation of tropical peat swamp forests. BioScience 61:49–57.

Thapa, RS (1982) Termites of Sabah (East Malaysia). Sabah Forest Department, Sandakan, Malaysia.

Tho YP (1992) Termites of Peninsular Malaysia. Malayan Forest Records 36:1–224.

Vaessen, T, Verwer, C, Demies, M, Kaliang, H. & van der Meer, P. (2011) Comparison of termite assemblages along a landuse gradient on peat areas in Sarawak, Malaysia. J Trop For Sci 23:196–203.

Yule CM (2010) Loss of biodiversity and ecosystem functioning in Indo-Malayan peat swamp forests. Biodiv Cons 19:393–409.

Yule CM, Gomez LN (2009) Leaf litter decomposition in a tropical peat swamp forest in Peninsular Malaysia. Wetl Ecol Manag 17:231–241.

Table 1. Differences in species composition between sites for termite communities. Values indicated are *p*-values and were obtained with ANOSIM. Significant differences among paired sites after Bonferroni correction are indicated in italic (p < 0.05) or in bold (p < 0.01).

	PSF1	PSF2	PSF3	PSF4	SLF1	SLF2	HTF1	HTF2	MDF1
PSF2	0.1664								
PSF3	0.1412	0.5186							
PSF4	0.1172	0.3388	0.7039						
SLF1	0.0673	0.0078	*0.001*	**0.0001**					
SLF2	0.3845	0.2354	0.2870	0.0381	0.2922				
HTF1	**0.0001**	**0.0001**	**0.0002**	**0.0001**	**0.0001**	**0.0001**			
HTF2	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	0.0142		
MDF1	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	0.0014	
MDF2	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**

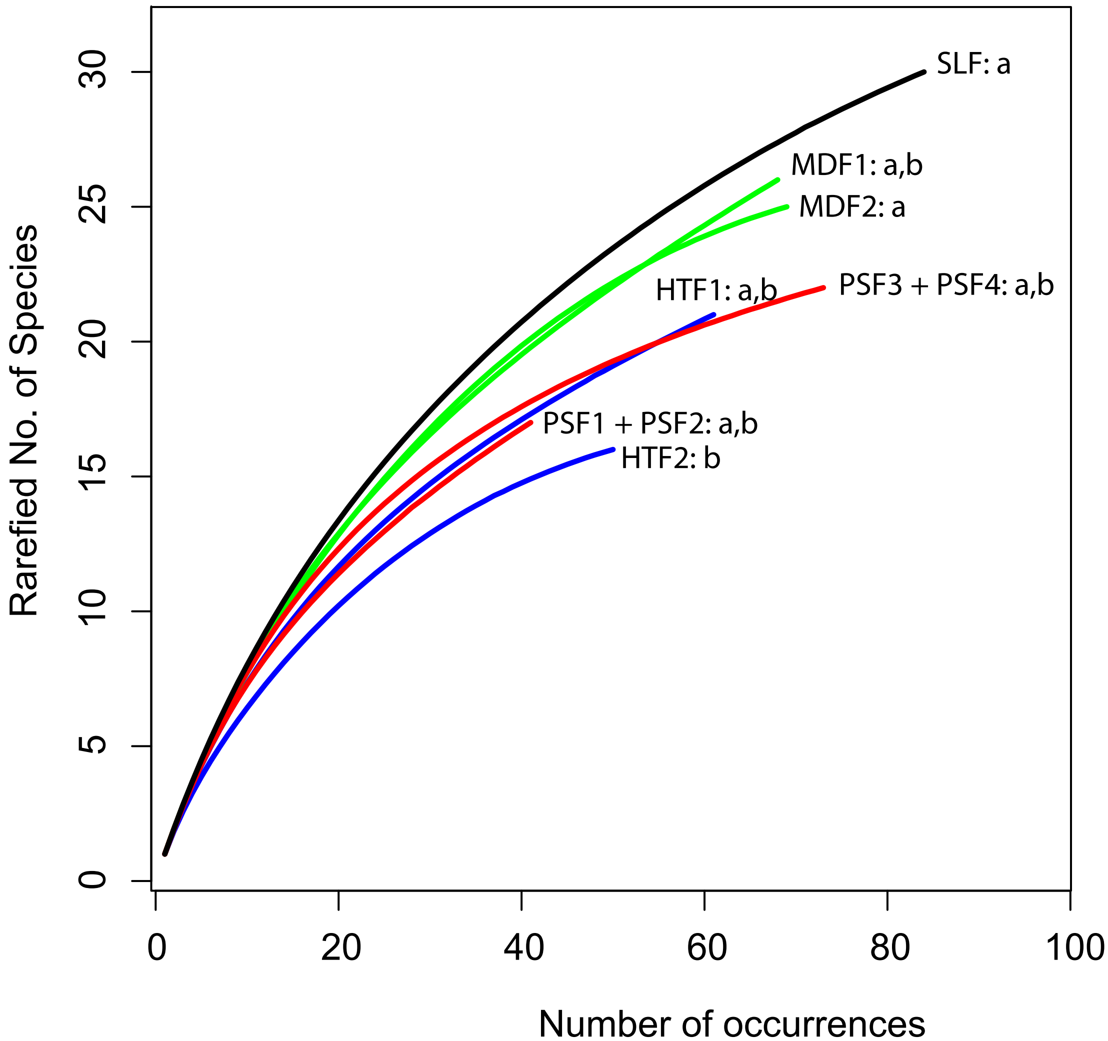

Fig. 1. Termite species rarefaction curves. Curve colours indicate forest types: black: SLF; blue: HTF; green: MDF; red: PSF. *PSF1+PSF2*: pristine peat swamp forest near river; *PSF3+ PSF4*: pristine peat swamp forest away from river; *SLF*: selectively logged peat swamp forest; *HTF1* and *HTF2*: pristine heath forest; *MDF1* and *MDF2*: pristine mixed dipterocarp forest. Rarefaction curves which do not share lower case letters are significantly different. Significance levels were assessed using non-overlapping 95 % confidence interval calculated with Mao-Tau method (Colwell et al. 2004).

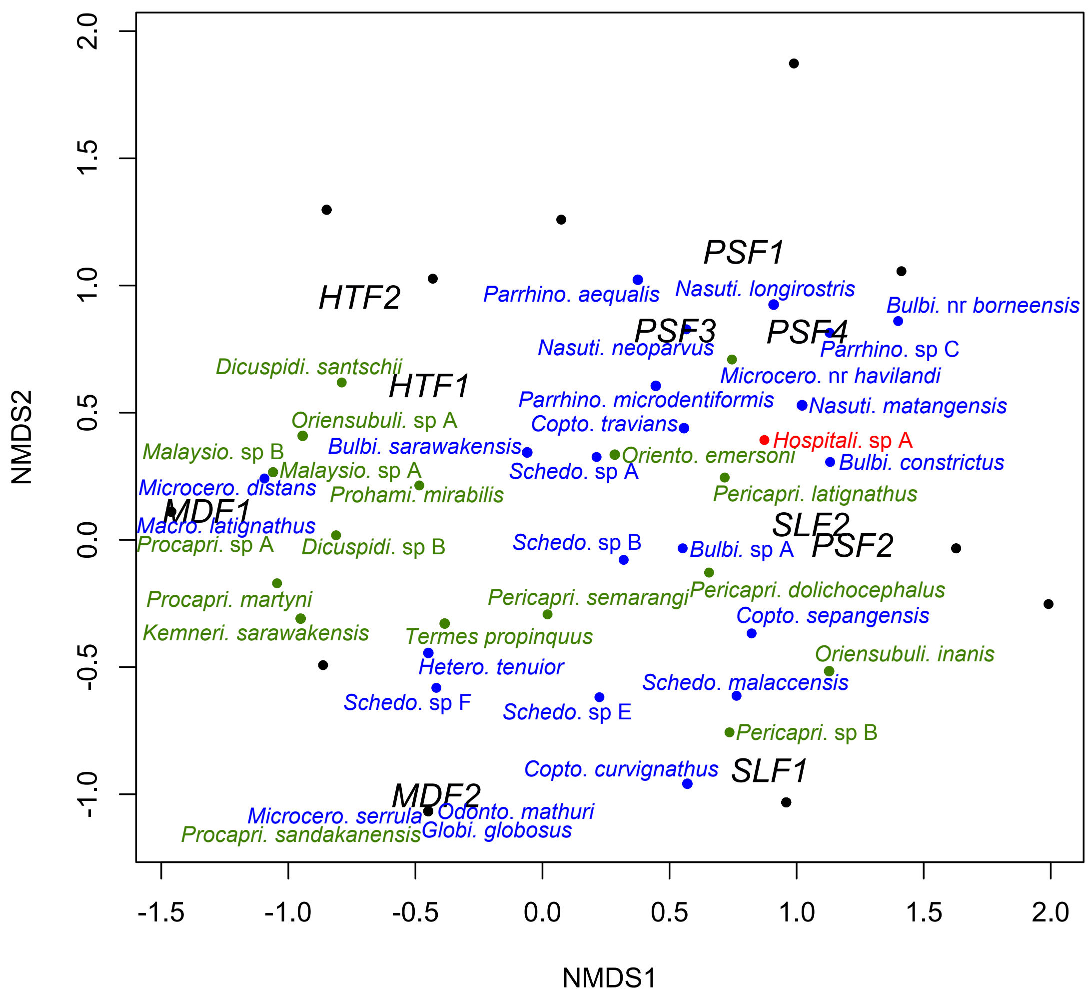

Fig. 2. Nonmetric multidimensional scaling (NMDS) of termite assemblages. The names of species recorded less than three times were not included, as their placement in the NMDS plot is highly uncertain. *PSF1, PSF2, PSF3* and *PSF4*: pristine peat swamp forests; *SLF1* and *SLF2*: selectively logged peat swamp forests; *HTF1* and *HTF2*: pristine heath forests; *MDF1* and *MDF2*: pristine mixed dipterocarp forests. Blue labels: wood-feeders; green labels: soil-feeders; red labels: Epiphyte-feeders; black dots: species with less than three occurrences.

	Feeding group	PSF1	PSF2	PSF3	PSF4	SLF1	SLF2	HTF1	MDF1	MDF2	HTF2	Tot
Kalotermitidae												
Kalotermitidae sp A	wood-feeder	0	0	0	0	0	0	1	0	0	0	**1**
Glyptotermes ? paracaudomunitus	wood-feeder	0	0	0	0	1	0	0	0	0	0	**1**
Glyptotermes sp B	wood-feeder	0	0	0	0	0	0	0	0	0	1	**1**
Rhinotermitidae												
Coptotermes sepangensis	wood-feeder	0	2	0	1	4	0	0	0	1	0	**8**
Coptotermes travians	wood-feeder	3	4	7	4	2	5	6	0	0	2	**33**
Coptotermes curvignathus	wood-feeder	0	0	0	0	2	0	0	0	1	0	**3**
Heterotermes tenuior	wood-feeder	0	0	0	0	0	0	3	2	6	3	**14**
Parrhinotermes microdentiformis	wood-feeder	1	0	1	1	0	2	2	0	0	2	**9**
Parrhinotermes aequalis	wood-feeder	2	0	3	1	0	0	1	0	0	1	**8**
Parrhinotermes sp C	wood-feeder	0	0	1	2	0	1	0	0	0	0	**4**
Parrhinotermes sp D	wood-feeder	0	0	0	0	0	0	0	0	0	2	**2**
Schedorhinotermes sp A	wood-feeder	1	0	1	1	0	2	0	2	1	0	**8**
Schedorhinotermes sp B	wood-feeder	0	3	3	0	4	4	1	4	0	0	**19**
Schedorhinotermes malaccensis	wood-feeder	0	1	0	0	2	0	0	0	1	0	**4**
Schedorhinotermes sp D	wood-feeder	0	0	0	0	1	0	0	0	0	0	**1**
Schedorhinotermes sp E	wood-feeder	0	0	0	0	1	1	0	0	2	0	**4**
Schedorhinotermes sp F	wood-feeder	0	0	0	0	0	0	1	1	4	2	**8**
Termitidae												
Macrotermitinae												
Macrotermes sp A	wood-feeder	0	0	0	0	0	0	0	0	2	0	**2**
Macrotermes latignathus	wood-feeder	0	0	0	0	0	0	0	3	0	0	**3**
Odontotermes sarawakensis	wood-feeder	0	0	0	0	0	0	0	2	0	0	**2**
Odontotermes denticulatus	wood-feeder	0	0	0	0	0	0	0	1	0	0	**1**
Odontotermes mathuri	wood-feeder	0	0	0	0	0	0	0	0	11	0	**11**
Foraminitermitinae												
Labritermes buttelreepeni	soil-feeder	0	0	0	0	0	0	0	1	0	0	**1**
Termitinae												
Dicuspiditermes santschii	soil-feeder	0	0	0	0	0	0	2	2	0	3	**7**

Dicuspiditermes sp B	soil-feeder	0	0	0	0	0	0	1	13	4	6	**24**
Globitermes globosus	wood-feeder	0	0	0	0	0	0	0	0	5	0	**5**
Kemneritermes sarawakensis	soil-feeder	0	0	0	0	0	0	0	2	1	0	**3**
Microcerotermes nr *havilandi*	wood-feeder	0	0	2	2	1	0	0	0	0	1	**6**
Microcerotermes distans	wood-feeder	0	0	0	0	0	0	1	3	0	0	**4**
Microcerotermes serrula	wood-feeder	0	0	0	0	0	0	0	0	4	0	**4**
Pericapritermes sp A	soil-feeder	1	0	0	0	0	0	0	0	0	0	**1**
Pericapritermes sp B	soil-feeder	1	0	0	0	3	0	0	0	1	0	**5**
Pericapritermes dolichocephalus	soil-feeder	0	1	1	0	1	2	0	0	1	0	**6**
Pericapritermes semarangi	soil-feeder	0	0	1	0	4	3	6	1	8	3	**26**
Pericapritermes latignathus	soil-feeder	0	0	0	1	0	1	0	0	1	0	**3**
Pericapritermes sp F	soil-feeder	0	0	0	0	0	1	0	0	0	0	**1**
Pericapritermes sp G	soil-feeder	0	0	0	0	1	0	0	0	0	0	**1**
Procapritermes sandakanensis	soil-feeder	0	0	0	0	0	0	0	0	3	0	**3**
Procapritermes sp A	soil-feeder	0	0	0	0	0	0	0	3	0	0	**3**
Procapritermes sp B	soil-feeder	0	0	0	0	0	0	0	1	0	0	**1**
Procapritermes sp C	soil-feeder	0	0	0	0	0	0	0	2	0	0	**2**
Procapritermes sp D	soil-feeder	0	0	0	0	0	0	0	0	2	0	**2**
Procapritermes martyni	soil-feeder	0	0	0	0	0	0	0	3	1	0	**4**
Prohamitermes mirabilis	soil-feeder	0	0	0	0	1	0	14	11	3	18	**47**
Orientotermes emersoni	soil-feeder	2	3	5	2	1	1	3	2	1	1	**21**
Termes propinquus	soil-feeder	0	0	0	0	0	0	0	0	1	2	**3**
Nasutitermitinae												
Bulbitermes constrictus	wood-feeder	0	1	1	1	0	2	0	0	0	0	**5**
Bulbitermes nr *borneensis*	wood-feeder	0	1	0	3	0	0	0	0	0	0	**4**
Bulbitermes sarawakensis	wood-feeder	0	0	2	0	1	1	4	2	0	0	**10**
Bulbitermes sp A	wood-feeder	6	1	2	1	8	6	4	0	0	0	**28**
Hirtitermes sp A	wood-feeder	0	0	0	0	0	1	0	0	0	0	**1**
Hirtitermes sp B	wood-feeder	0	0	0	0	0	0	0	1	0	0	**1**
Hospitalitermes sp A	epiphyte-feeder	0	0	0	1	1	0	1	0	0	0	**3**
Hospitalitermes umbrinus	epiphyte-feeder	0	0	0	0	1	0	0	0	0	0	**1**

Leucopitermes leucops	soil-feeder	0	1	0	0	0	0	0	0	0	0	**1**
Longipeditermes longipes	wood-feeder	0	0	0	0	0	0	0	1	1	0	**2**
Malaysiotermes sp A	soil-feeder	0	0	0	0	0	0	1	2	0	0	**3**
Malaysiotermes sp B	soil-feeder	0	0	0	0	0	0	1	2	0	0	**3**
Nasutitermes atripennis	wood-feeder	0	0	1	0	0	0	1	0	0	0	**2**
Nasutitermes longinasus	wood-feeder	0	0	0	0	0	0	0	0	1	0	**1**
Nasutitermes longirostris	wood-feeder	0	0	3	3	0	1	0	0	0	0	**7**
Nasutitermes matangensis	wood-feeder	2	2	2	4	1	2	0	0	0	0	**13**
Nasutitermes neoparvus	wood-feeder	1	1	4	4	0	0	5	0	0	2	**17**
Nasutitermes nr *longinasus*	wood-feeder	0	0	0	0	0	0	0	0	1	0	**1**
Nasutitermes rectangularis?	wood-feeder	0	0	0	0	0	0	0	0	0	1	**1**
Nasutitermes regularis?	wood-feeder	0	0	0	0	2	0	0	0	0	0	**2**
Nasutitermes sp A	soil-feeder	0	0	0	1	0	0	0	0	0	0	**1**
Oriensubulitermes inanis	soil-feeder	0	0	0	0	3	2	0	0	0	0	**5**
Oriensubulitermes sp A	soil-feeder	0	0	0	0	0	0	2	2	0	0	**4**
Total		**20**	**21**	**40**	**33**	**46**	**38**	**61**	**69**	**68**	**50**	**446**
Number of species		**10**	**12**	**17**	**17**	**22**	**18**	**21**	**25**	**26**	**16**	**69**

Table S1. Termite occurrences, and their feeding-groups, recorded in the 10 sampling plots. *PSF1* and *PSF2*: pristine peat swamp forests located nearby the river; *PSF3* and *PSF4*: pristine peat swamp forests located nearby the centre of the dome; *SLF1* and *SLF2*: selectively logged peat swamp forests; *HTF1* and *HTF2*: pristine heath forests; *MDF1* and *MDF2*: pristine mixed dipterocarp forests.