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Forests on ultramafic-derived soils in Borneo have very depauperate termite assemblages

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Abstract: Previous studies in Sundaland (Borneo, Sumatra, Java and Peninsular Malaysia) have shown that termite assemblages in natural forests have a characteristic structure. These typical forest assemblages contain many soil-feeding species. However, this study investigated four natural forest sites in Borneo with depauperate termite assemblages, and compared their soils with soils from four other sites that have typical termite assemblages. In contrast to the typical assemblages, the four depauperate assemblages all have low species density (<35%), low relative abundance (<30%), a virtual absence of soil-feeders, significantly fewer wood-feeders, and a near-absence of species of Rhinotermitidae, *Amitermes*-group, *Termes*-group, *Pericapritermes*-group and *Oriensubulitermes*-group. The depauperate sites are on ultramafic-derived soils and have significantly higher concentrations of calcium, magnesium, nickel, chromium, cobalt, copper and zinc compared with the non-ultramafic soils at sites with typical assemblages. In addition, soil pH at the depauperate sites is significantly higher (>pH 5.4) compared with soils at the typical sites (which are all below pH 4.7). Possible mechanisms to explain the depauperate termite assemblages on ultramafic soils include metal toxicity, high pH disrupting gut physiology, and microbial interactions with metals.

Key Words: Isoptera, metal toxicity, Mount Kinabalu, Sabah, serpentine soils, soil-feeding, soil pH, South Kalimantan, Sundaland, ultisols

INTRODUCTION

Termites are intimately associated with soils through their nesting, tunnelling and feeding activities. Most species build subterranean or epigeal nests, and most wood-nesting species maintain some contact with the soil substratum. While many termites feed on dead wood, and some forage on grass or leaf litter, around 50% of species feed directly on mineral soil or humus (Brauman *et al.* 2000). Termites can achieve very high population densities in tropical soils (Bignell & Eggleton 2000), and are known to have a major influence over decomposition, mineralization, the redistribution of organic matter, soil structure and soil quality (Brauman 2000, Holt & Lepage 2000, Ji & Brune 2006, Lee & Wood 1971, Mando *et al.* 1996).

In contrast to the considerable amount of research investigating how termites affect soils and soil processes, there has been surprisingly little research on the extent to which soil type and soil properties influence termite distribution and ecology. Many studies have assessed termite assemblages (Bignell & Eggleton 2000) but most of these have not characterized the local soil. Only a few studies have shown that termites avoid soils with particular physical or chemical properties. Wild (1975) reported that termites are mainly absent from grassland on ultramafic (also known as serpentine) soils in Zimbabwe, where only two species were found, in stark contrast to neighbouring areas on non-ultramafic soils where termites were much more abundant and diverse. Harris (1963) compared eight woodland and savanna sites in Congo, and found relatively high species richness and frequency of termites in soils at all sites, with the exception of one site on sandy soil in which termites were absent. Very sandy soils may have insufficient cementing agents, such as clay and other fine colloid material, to allow termites to build mounds and subterranean galleries (Lee & Wood 1971). Ratcliffe *et al.* (1952) reported termites as virtually absent from the heavy clay soils of inland north-eastern Australia.

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The physical characteristics of these soils, which crack deeply and widely in dry periods and become waterlogged in wet periods, are thought to preclude termite survival, although this has been partly refuted by Holt & Coventry (1982). Finally, in habitats that have a high water table or are regularly inundated, such as peat swamp forest (Salick & Tho 1984) and flooded forest (Martius 1994), soil-nesting and soil-feeding termites can be absent or rare.

As termites are considered one of the principal biotic agents in tropical soil formation and conditioning, it is important to identify the circumstances where such a role may be limited. Jones & Eggleton (2000) developed a sampling protocol for assessing the species density of termites in a single transect (100 m × 2 m) of tropical forest. These transect samples have been shown to accurately represent the taxonomic and functional structure of the local termite assemblage (Jones & Eggleton 2000, Jones *et al.* 2006). To date, over 110 transects have been sampled from more than 50 localities around the world, and soil samples have been collected from a few transects.

Transects from Sundaland (Peninsular Malaysia, Borneo, Sumatra, Java and their associated islands) that were available during earlier analyses (Davies *et al.* 2003, Gathorne-Hardy *et al.* 2002) suggested that lowland forests have a rich and abundant termite assemblage with a characteristic taxonomic and functional structure. However, a new analysis using all transects that are now available uncovers a surprising result. A box-and-whisker plot of the 28 transects run in primary and selectively logged lowland forests in Sundaland reveals four transects from Borneo to be distinct outliers, with much lower species densities (Figure 1). The species density of these four transects (range: 7–10 species) is below the minimum non-outlier range (16 species), and well below the median (28 species) of the 'typical' transects in Sundaland lowland forest.

In this study we present an analysis of soil samples and termite assemblages from these four outlier transects (hereafter called the depauperate transects). These depauperate transects are found to be in forests on ultramafic-derived soils. We compare them with the only other transects used in Figure 1 from which we also have soil samples: these four transects, on non-ultramafic soils, have relatively high species densities and are close to the median value for Sundaland (hereafter called the typical transects). This is the first study to show that depauperate termite assemblages are associated with ultramafic-derived soils.

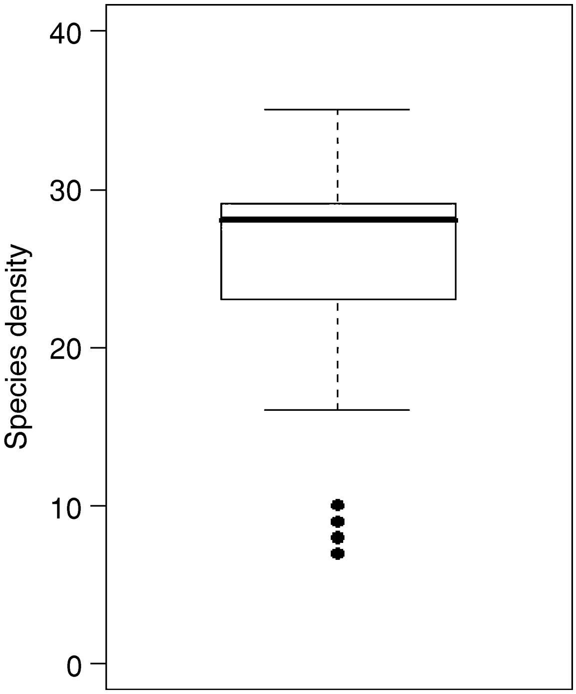

Figure 1. Box-and-whisker plot showing the median number of species (heavy black horizontal line in the box) in 28 standardized transects run in primary and selectively logged lowland forest sites (up to 630 m altitude) across Borneo (18 transects), Sumatra (8), Java (1) and Peninsular Malaysia (1). The upper and lower edges of the box represent the 1st and 3rd quartiles, and the non-outlier range (the outer bars) is 1.5× the inter-quartile range. The four outliers are the depauperate transects discussed in the text.

STUDY SITES

A single transect was run at each of eight sites, distributed across three areas of Borneo. All transects were run on gently undulating terrain. Two transects were run near the village of Serinsim, within the northern boundary of Mount Kinabalu National Park (116°42′E, 6°16′N), north-west Sabah in November 1997. The first transect (altitude *c.* 250 m) was in undisturbed primary forest (site code SePF). The second (*c.* 2 km from the first; altitude *c.* 200 m) was in forest that had been selectively logged at least a decade earlier (code SeOF), and at the time of sampling the site had a full canopy and many large-diameter trees. Both transects were in an area of ultramafic parent material consisting mainly of serpentinized peridotite. Although no data have been published on the soils or vegetation of these sites, aerial photographs from 1977 show this area as having a 'normal' lowland mixed dipterocarp forest with large crowns (K. Kitayama pers. comm.). Annual rainfall (at Kota Marudu) averages 2290 mm.

Three transects were run in the vicinity of Danum Valley Field Centre (4°57′N, 117°36′E), south-east Sabah. The parent material consists of sandstones, mudstones, siltstones, cherts and shale, overlying a crystalline basement that includes ultramafic and mafic intrusions (Douglas *et al.* 1999). Mean annual rainfall at the field station was 2700 mm (Eggleton *et al.* 1999). The first transect was in primary forest in the conservation area at W15 on the West Trail (code DaPF; altitude *c.*

100 m). This site consisted of mudstones and sandstones (Leong 1974), with Haplic Alisol soil (Chappell *et al.* 1999), which is equivalent to the USDA Ultisol order. The second was in logged forest (code DaOF; altitude 130 m) in the coupe 1978 concession, approximately 10 km east of the field centre. This site had been selectively logged 17 y earlier, and at the time of sampling the forest had a full canopy (Eggleton *et al.* 1997). The soils are primarily Ultisols (Eggleton *et al.* 1997) and include Acrisols-Alisols, Ferralsols and Luvisols in the FAO-UNESCO classification (ODA 1974). The first two Danum transects were run in May 1995. The third Danum transect, run in October 2000, was in primary forest adjacent to the Tembaling Trail (code DaTm; altitude 120 m), approximately 2 km south of the field centre. Soils in this area have not been surveyed but the ODA (1974) map suggests the soils are adjacent to areas of Luvisols and Acrisol-Alisols.

Three transects were run in the Sungai Tabalong Kiwa area, Tabalong District, South Kalimantan (south-east Borneo) in March 2000. Annual rainfall is about 2200 mm in the town of Tanjung, but is probably nearer 3000 mm at the sampling sites (J. Payne pers. comm.). The area has been managed for timber production since the 1970s, and most of the area has been selectively logged. The first transect (code TaOF; 1°35′05″S, 115°31′14″E; altitude *c.* 630 m) was at a site that had been selectively logged about 17 y earlier, and the forest had a full canopy at the time of sampling. The second was in a site (code TaLF; 1°36′44″S, 115°30′05″E; altitude *c.* 450 m) that had been selectively logged 2 y before sampling, and extensive damage to the canopy was still evident. These first two sites have mudstone, siltstone and quartz sandstone parent material. The soils are predominantly clay-rich red-yellow podzols (Boden 2001), which is equivalent to the USDA Spodosol order. The third transect was in a large patch of undisturbed forest (code TaEn; 1°36′0″S, 115°31′27″E; altitude *c.* 350 m) dominated by an endemic leguminous tree, *Endertia spectabilis*. This large tree has no commercial value, and where it is present tree diversity is relatively low and dipterocarps are rare or absent, and therefore these forests are not logged. The canopy was about 40 m high, and the physical structure of the forest was very similar to undisturbed mixed dipterocarp forest. This site is in an area which has granite, basalt and limestone intrusions in the mudstones and siltstones (Boden 2001).

METHODS

Termite sampling and identification

Termites were sampled using the Jones & Eggleton (2000) transect protocol. Transects were placed in visually homogeneous forest, avoiding running along topographical contours or through open areas and streams. Each transect (100 m × 2 m) was divided into 20 contiguous sections (5 m × 2 m) to ensure the equal distribution of sampling effort. Each section was sampled by two experienced collectors for 30 min (i.e. 1 h of manual sampling per section). The 20 sections are not treated as independent quadrats: instead each transect is treated as a single quadrat. In each section the following microhabitats were searched: 12 samples of surface soil (each 12 × 12 cm to 10 cm depth); accumulations of litter and humus at the base of trees and between buttress roots; the inside of tree stumps, dead logs, branches and twigs; the soil within and beneath very rotten logs; subterranean nests, mounds, carton sheeting and runways on vegetation, and arboreal nests up to a height of 2 m. Specimens from every termite population encountered were preserved in 80% ethanol. Mounds were sampled destructively to search for inquiline species (Eggleton & Bignell 1997). The sampling protocol gives a measure of termite relative abundance based on the number of encounters with each species in a transect (Jones *et al.* 2003). The number of encounters per transect can be used to compare the relative abundance of termites among transects. It gives no measure of the absolute abundance per unit area.

Specimens were identified at the Natural History Museum (BMNH), and deposited at Universiti Malaysia Sabah, Bogor Zoological Museum (Indonesia), and BMNH. Most specimens were identified to named species. Remaining taxa were identified to genus and assigned to morphospecies applied consistently across regional voucher collections (Eggleton *et al.* 1999, Gathorne-Hardy *et al.* 2002, Jones & Brendell 1998, Jones & Prasetyo 2002, Jones *et al.* 2003).

Termites were assigned to one of four feeding groups following the classification of Donovan *et al.* (2001). These groupings reflect feeding preferences along a humification gradient of the dietary substrate, and correlate with the amount of plant tissue fragments and silica in the gut. Feeding groups were then subdivided into Functional Taxonomic Groups (FTG) by assigning species to putative clades based on the phylogenetic framework of Inward *et al.* (2007). Species from eleven FTG (Appendix 1) were collected in this study.

Soil analyses

Six or eight soil samples (*c.* 100 g) were collected at 12-m or 15-m intervals along the length of each transect. After removing loose leaf litter and woody debris at the surface, samples were taken from the top 10 cm of the soil profile, which is where most subterranean termites forage in Sundaland (Jones *et al.* 2003). In the laboratory pH was measured in a mixture of 10 g soil with 25 ml of deionized water. Samples were dried, ground and digested in a mixture of HF + HNO_3 + $HClO_4$ (at

150 °C) and concentrations of calcium, magnesium and chromium were measured by induction coupled plasma atomic emission spectroscopy (Varian Vista-Pro Axial). The same solutions were diluted and the concentrations of nickel, cobalt, copper and zinc were measured by ICP mass spectroscopy (Thermo PQ3). Standard reference materials were analysed at the same time to check the accuracy of the results. Organic carbon (after removal of CO_3^{2-} with HNO_3) and total nitrogen were measured using a CNH analyser.

Data analyses

The eight transects were classified into two groups, based on Figure 1: the four depauperate transects (outliers with low species densities), and the four typical transects (relatively high species densities close to the median value for Sundaland). Metal concentrations across the soil samples were not distributed normally, so they were $\log_{10}$-transformed before statistical analyses. Soil properties were compared between the two groups using ANOVA of the means of each transect.

The use of FTG retains a high level of taxonomic resolution and has been shown to detect significant changes in the structure of local termite assemblages within and between regions (Davies *et al.* 2003, Gathorne-Hardy *et al.* 2002). Redundancy Analysis (RDA) was used to reveal patterns of FTG among transects using the CANOCO program (ter Braak & Smilauer 1998). Data were analysed as the number of species per FTG per transect. Soil properties, altitude and level of forest disturbance (primary or logged) were included as environmental variables.

RESULTS

The species density in the four depauperate transects (7–10 species) was considerably lower than the species density in the four typical transects (29–33 species) (Appendix 1). The four depauperate transects all had an absence, or near-absence, of Rhinotermitidae, *Amitermes*-group, *Termes*-group, *Pericapritermes*-group and *Oriensubulitermes*-group (Appendix 1). The biggest difference was in the *Pericapritermes*-group, which had from 10 to 14 species in the typical transects but zero or one species in the depauperate transects. The number of encounters in each transect followed the species density pattern, with the depauperate transects having far fewer (range: 18–23 encounters) compared with the four typical transects which all had at least three times as many encounters (range: 77–105) (Appendix 1).

In terms of feeding group composition, the assemblages in the depauperate transects were very different from those in the typical transects. The number of encounters with wood-feeding termites (group I + group II) was significantly lower in the depauprate transects ($F = 18.5$, df = 1, 6, $P < 0.01$) compared with the numbers in the typical transects (Figure 2). Furthermore, the number of encounters with soil-feeders (group III + group IV) was also significantly lower in the depauperate transects ($F = 155$, df = 1, 6, $P < 0.001$). The pattern for the number of species (not shown) was very similar to Figure 2, with both the number of wood-feeding species ($F = 40.0$, df = 1, 6, $P < 0.001$) and the number of soil-feeding species ($F = 177$, df = 1, 6, $P < 0.001$) being significantly lower in the depauperate transects.

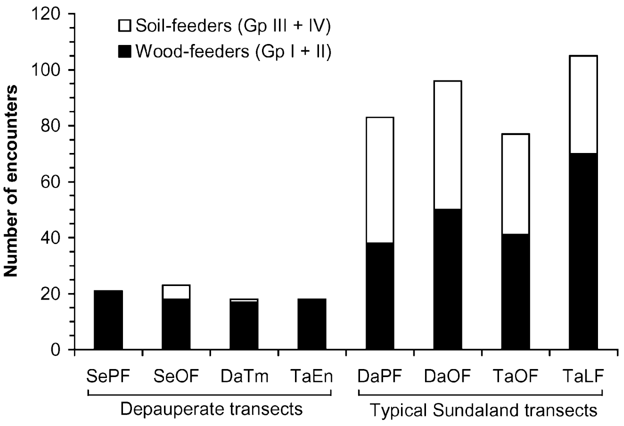

Figure 2. The number of encounters with wood-feeding and soil-feeding termites, collected from eight forest sites in Borneo using a standardized sampling protocol. See text for explanation of site abbreviations.

$\log_{10}$ concentrations of calcium, magnesium, nickel, chromium, cobalt, copper and zinc in soils were all significantly higher in the depauperate transects compared with the typical transects (Figures 3a–g). In addition, the pH of the soils (Figure 3h) in the depauperate transects were also significantly higher (all having means above pH 5.4) compared with the typical transects (all having means below pH 4.7). However, the percentage of both organic carbon and total nitrogen in soils were not significantly different between the depauperate and the typical transects (Figures 3i, j).

In the RDA forward selection the $\log_{10}$ concentration of the seven metals and the soil pH all showed significant marginal effects. However, the percentage of organic carbon and total nitrogen in soils, altitude, and the level of forest disturbance had no significant marginal effects. In the forward selection the only environmental variables to show significant conditional effects were $\log_{10}$ calcium concentration and percentage organic carbon. The RDA was then rerun, with only $\log_{10}$ calcium and percentage organic carbon in the analysis. The four depauperate transects are strongly associated with the $\log_{10}$ calcium vector, and are clearly separated from the typical transects on axis 1 (Figure 4). The *Pericapritermes*-group, the

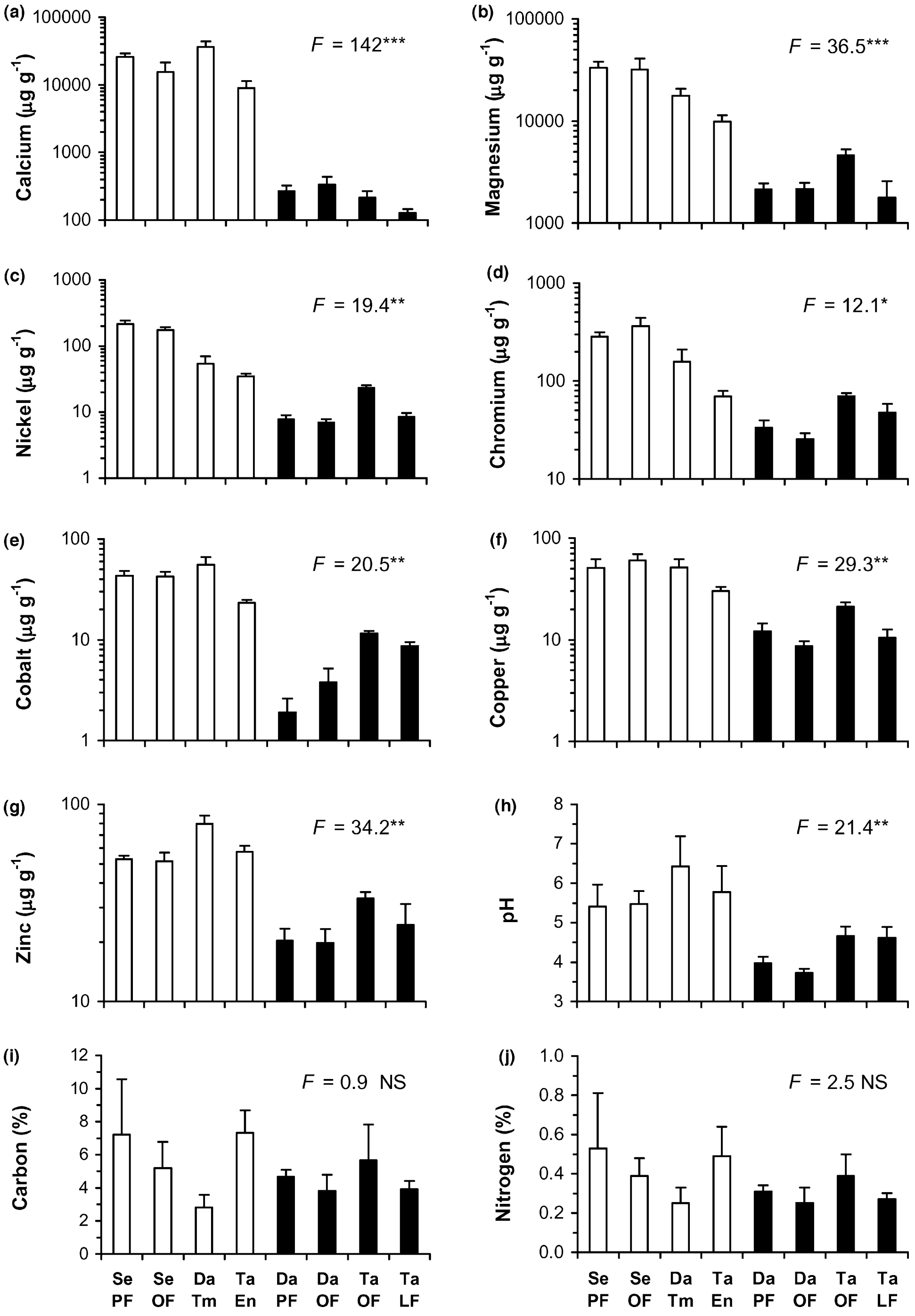

Figure 3. Bar charts of mean soil properties (+ 1 SD) in surface soils from transects collected at eight sites in Borneo. Concentrations (μg g^{-1}) of calcium (a), magnesium (b), nickel (c), chromium (d), cobalt (e), copper (f) and zinc (g) in soils are plotted on a logarithmic scale. Also shown are soil pH (h), soil organic carbon% (i) and soil total nitrogen% (j). The four sites with depauperate termite assemblages have open bars. The four sites with relatively high species densities have black bars.

Oriensubulitermes-group and the *Termes*-group (all soil-feeders) are strongly negatively correlated with axis 1 and associated with the typical transects. In contrast, the percentage organic carbon was not associated with the main soil-feeding groups. The first canonical axis explained 79.6% of the variation in the species data (F = 19.5, P = 0.022), with the second explaining a further 5.9%. Soil pH and log$_{10}$ nickel were plotted on Figure 4 as passive variables (i.e. they were not used in the RDA analysis) to show the direction of their vectors. The other metals (log$_{10}$ magnesium, chromium, cobalt, copper and zinc) all fall between the soil pH and log$_{10}$

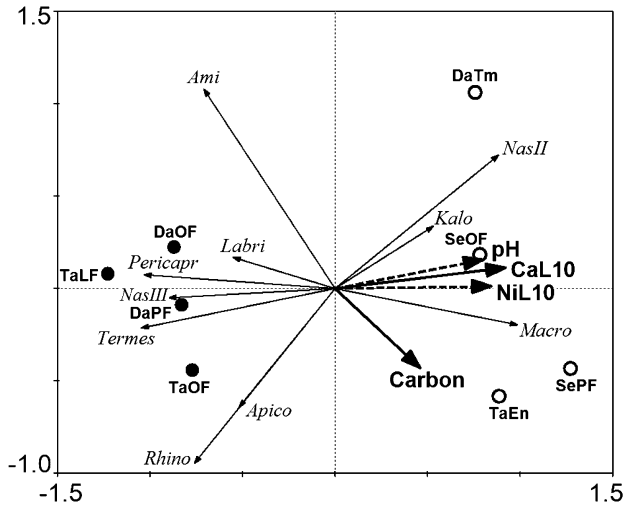

Figure 4. Redundancy Analysis of the number of termite species in each of ten Functional Taxonomic Groups (FTG) from transects sampled in eight natural forest sites in Borneo. The four closed circles are the sites with species-rich assemblages, the four open circles are sites with depauperate assemblages. See text and Appendix 1 for site and FTG abbreviations. Log_{10} calcium concentration (CaL10) and percentage organic carbon in soil were the only environmental variables in the analysis. Log_{10} nickel concentrations (NiL10) and pH in soils were mapped as passive variables.

nickel vectors because they are all highly correlated with $\log_{10}$ calcium.

DISCUSSION

The four typical transects have species densities, relative abundances, taxonomic and functional structures that are very similar to those documented in other relatively undisturbed lowland forests in Sundaland (Abe 1978, Collins 1984, Davies *et al.* 2003, Gathorne-Hardy *et al.* 2002). It is therefore valid to call them 'typical' assemblages. In sharp contrast, the four depauperate assemblages all have low species density, low relative abundance, and an absence or near-absence of species of Rhinotermitidae, *Amitermes*-group, *Termes*-group, *Pericapritermes*-group and *Oriensubulitermes*-group. The functional composition of these depauperate assemblages is also different, having significantly fewer wood-feeders, and a near-absence of soil-feeders compared with the typical assemblages.

The environmental factors that were strongly associated with the depauperate sites are the significantly higher concentrations of calcium, magnesium, nickel, chromium, cobalt, copper and zinc, plus significantly higher pH of the surface soils. Although termite species density is known to decline with increasing altitude (Gathorne-Hardy *et al.* 2001) and disturbance (Davies *et al.* 2003, Jones *et al.* 2003), these factors were not significant in this study as all the sites were relatively undisturbed and at relatively low altitudes.

Soils derived from ultramafic rocks are variable in their mineral composition but usually have a high concentration of magnesium and iron, a high Mg/Ca quotient (above 10), and are often rich in nickel, chromium and cobalt, which can cause metal toxicity to plants (Proctor 1999). Some ultramafic soils are associated with distinct and/or stunted vegetation, while others support species-rich large-stature forests (Proctor 1992). The pH of the A horizon in ultramafic soils is usually between 5.0 and 7.0 (Proctor 1992), which is high for most tropical lowland forests. Two of the depauperate sites in the present study are known to have ultramafic parent material, while the remaining two have soils with similar high concentrations of metals and pH above 5.7 (Figure 3), and are therefore probably ultramafic-derived soils (W. Dubbin pers. comm.). However, in all four depauperate sites calcium concentrations are higher, the Mg/Ca quotient is less than 10, and nickel, chromium and cobalt concentrations are lower than are often found in ultramafic soils, suggesting they have a less-extreme ultramafic metals profile.

The present results are compared with data from another 15 South-East Asian forest sites where details of soil type and pH are available (Table 1). Ten of these sites have the typical species-rich assemblage (transects with at least 26 species), and where recorded, relatively high termite abundance (range: 257–2290 m^{-2} in soil). A common feature of these typical sites is relatively acid soil (range: 3.1–5.0), of which seven are classified as Ultisols. Ultisol is the most common soil order in South-East Asia, and is dominant across most of Borneo. The soils at the other sites with typical assemblages are Spodosols, Entisol or Andisol (Table 1). The four typical sites examined in the present study are Ultisols and Spodosols. The four depauperate sites are very unlikely to be Ultisols or Spodosols because the soil pH is too high (W. Dubbin pers. comm.).

Table 1 includes five sites on ultramafic soils classified as Inceptisols. These five sites have less-acid soils (pH range 5.0–6.1) compared with the other ten non-ultramafic sites. Four of these ultramafic sites have low termite abundances (range: 16–98 m^{-2}) compared with the non-ultramafic sites (Table 1). Moreover, considering all sites from Table 1 with termite abundance data ($n = 13$), there is a significant negative correlation ($r^2 = 0.44$, $P < 0.02$) between $\log_{10}$ abundance and soil pH (Figure 5). If the termite assemblages in these ultramafic sites are under the same constraints as those in the four depauperate sites, then we can expect them to have a similarly low species density. The abundance at the fifth ultramafic site in Table 1 (738 m^{-2}) falls within the range of typical Sundaland abundances. This relatively

Table 1. Termite species density in transects, and/or abundance in soil at other forest sites in South-East Asia which fall within the altitudinal range of the eight sites reported in this study. Transects were sampled using the Jones & Eggleton (2000) protocol. Only studies where the soil pH and the soil type and/or parent material could be found have been included. Note the higher pH of the five ultramafic sites at the bottom of the table. MDF = mixed dipterocarp forest. LMF = lower montane forest.

Location (altitude) and forest type	Soil type (USDA soil order) and/or parent material; pH of surface soil	Number of termite species per transect, or abundance (m^{-2}) in surface soil (m^{-2})
Belalong, Brunei (200 m), primary MDF	Ultisol; 3.3–3.6 (Pendry & Proctor 1997)	1 transect = 26 species (Jones 1996), 592 (Jones 1996)
Danum, Sabah (*c.* 100 m), primary MDF	Ultisol (Chappell *et al.* 1999); 3.9 ± 0.16 (Eggleton *et al.* 1997)	1 transect = 29 species (Eggleton *et al.* 1997), 544 (Homathevi 1999)
Danum, Sabah (*c.* 100 m), 17-y-old selectively logged MDF	Ultisol; 3.6 ± 0.23 (Eggleton *et al.* 1997)	1 transect = 29 species (Eggleton *et al.* 1997), 617 (Homathevi 1999)
Danum, Sabah (*c.* 100 m), 3-y-old selectively logged MDF	Ultisol; 4.5 ± 0.40 (Eggleton *et al.* 1997)	2 transects = 28 and 29 species (Eggleton *et al.* 1997), 257 (Homathevi 1999)
Barito Ulu, Kalimantan (c. 150 m), primary MDF	Ultisol; 3.1–3.2 (Brearley *et al.* 2004)	1 transect = 26 species (Gathorne-Hardy *et al.* 2006)
Pasoh, Peninsular Malaysia (*c.* 100 m), primary MDF	Ultisol; 4.16–4.21 (Yamashita & Takeda 2003)	1 transect = 29 species (Jones & Brendell 1998), 2290 (Abe & Matsumoto 1979)
Mulu, Sarawak (130 m), primary MDF	Entisol; 4.5–5.0 (Collins 1980)	1604 (Collins 1980)
Mulu, Sarawak (220 m), primary MDF	Spodosol; 3.5–4.5 (Proctor *et al.* 1982)	1125 ± 585 (Collins 1979)
Mulu, Sarawak (500 m), primary MDF	Spodosol; 3.5–4.5 (Collins 1980)	779 (Collins 1980)
Jambi, Sumatra, (*c.* 50 m), primary MDF	Ultisol (Gillison *et al.* 2003); 4.0 (Jones *et al.* 2003)	1 transect = 34 species (Jones *et al.* 2003)
Gunung Silam, Sabah (280 m), primary MDF	Inceptisol on ultramafic rock; 5.7 (Proctor *et al.* 1988)	738 (Leakey & Proctor 1987)
Gunung Silam, Sabah (330 m), primary MDF	Inceptisol on ultramafic rock; 5.8 (Proctor *et al.* 1988)	16 (Leakey & Proctor 1987)
Gunung Silam, Sabah (480 m), primary MDF	Inceptisol on ultramafic rock; 6.1 (Proctor *et al.* 1988)	76 (Leakey & Proctor 1987)
Gunung Silam, Sabah (610 m), primary MDF	Inceptisol on ultramafic rock; 6.0 (Proctor *et al.* 1988)	98 (Leakey & Proctor 1987)
Mount Giting-Giting, Philippines (*c.* 350 m), primary LMF	Inceptisol on ultramafic rock; 5.0–5.5 (Thomas & Proctor 1997)	31 (Thomas & Proctor 1997)

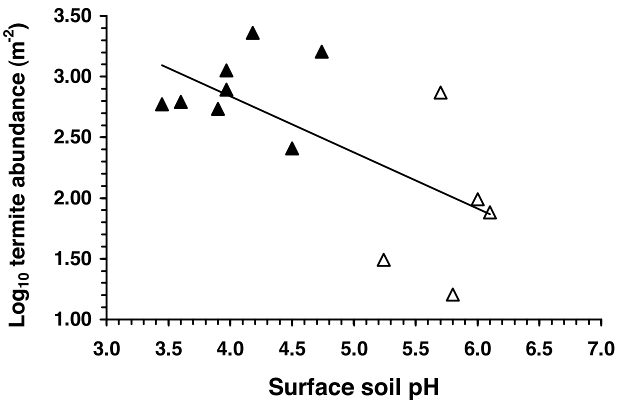

Figure 5. The relationship between $\log_{10}$ abundance (m^{-2}) of termites in soil samples against the pH of the soil, taken at 13 lowland forest sites in South-East Asia (the sites are listed in Table 1). Where a range of values was given, the geometric mean was used. The open triangles are those sites with ultramafic soils, the closed triangles are those sites with non-ultramafic soils.

high abundance may be associated with the fact that the calcium concentration in the parent material at this site is less than one-tenth of those at the other ultramafic sites (Proctor *et al.* 1988).

Several hypotheses may explain the depauperate assemblages on ultramafic-derived soils. The first assumes metal toxicity in food. The toxicity of a number of heavy metals to arthropods, annelids and molluscs is now well established (reviewed by Fountain & Hopkin 2004, Hopkin 1989, Wilson 2001), whereas systematic toxicological studies with termites appear to be absent. Several authors have shown that cobalt, copper and zinc are micronutrients, and that excess concentrations in the diet may saturate and therefore inactivate the metallothioneins that are secreted to facilitate their uptake. Other metals that are not part of normal metabolism may use the same uptake pathways, but bind irreversibly (Braeckman *et al.* 1997, Nichol *et al.* 2002). Soil-feeding termites on ultramafic soils may not have evolved mechanisms to limit the absorption or ensure the detoxification of high concentrations of potentially harmful metals such as nickel. However, this needs to be tested because the most appropriate comparative data for insects show that the concentrations of nickel, copper and zinc found in the soils at the four depauperate sites are below the levels at which significant harmful effects are observed in Collembola (Fountain & Hopkin 2004).

Two groups of wood-feeders (Rhinotermitidae and *Amitermes*-group) are virtually absent from the depauperate sites. In contrast, two other wood-feeding groups, the Macrotermitinae and the *Nasuititermes*-group are relatively diverse and abundant in these sites. Interestingly it is two species from these latter two groups, *Odontotermes transvaalensis* and *Trinervitermes dispar* that occur on ultramafic soils in Zimbabwe (Wild 1975). Workers of both species contained concentrations of nickel and chromium that were between five and 15 times higher than the concentrations in soldiers and a queen of *O. transvaalensis*. Workers feed directly on dead plant material whereas soldiers and the royal pair are fed by trophallaxis (liquid secretions regurgitated by the workers), suggesting that these species may have evolved mechanisms that allow workers to reduce the concentrations of these metals in their food. The extent to which plants on ultramafic soils accumulate metals to concentrations that may be toxic to termites is unknown. However, foliar analyses of plants growing on ultramafic soils in Borneo (Gunung Silam) suggest that metal hyperaccumulation is less frequent and less extreme compared with the ultramafic vegetation of New Caledonia (Proctor 1992).

A second hypothesis involves disruptive pH levels, and may explain the absence of soil-feeding termites. All termites have a slightly acid to slightly alkaline (pH 6.0 to 8.0) midgut and mixed segment, and slightly to strongly alkaline (pH 7.5 to 12.5) P1 and P3 gut chambers (Bignell & Eggleton 1995, Brune & Kühl 1996). However, despite this pH range in the gut, in most tropical forest locations termites are adapted to ingesting soil with a more acid pH (e.g. pH of between 3.1 and 4.5 in Ultisols, Table 1). Most groups of soil-feeding termites evolved in African forests (Aanen & Eggleton 2005) on highly weathered soils which probably had a low pH. Therefore, the gut physiology of soil-feeders may be disrupted if they ingest soil of a pH above the optimal range, thereby reducing their nutritional efficiency and their survival. Another possibility is that the relatively high pH of the material ingested by soil-feeders may cause shortages of available calcium and iron.

Third, several hypotheses relate to different interactions between metals and micro-organisms. The Macrotermitinae cultivate *Termitomyces* (Basidomycotina) fungus gardens in their nests (Aanen & Eggleton 2005). The fungus decomposes plant material collected by the termites, and it may detoxify the food before it is consumed by the workers. Other interactions are possible, for example the poisoning of essential microbiota in the termite gut, or bioaccumulation by those microbes with subsequent poisoning of the termite host (Vu *et al.* 2004). In the case of free-living microbes, recent research suggests that the activity of some microflora in ultramafic soils may release nickel and cobalt (Amir & Pineau 2003), thereby possibly making them more available to termites.

In conclusion, more research is required to explain why termite assemblages are so depauperate on ultramafic soils. Furthermore, studies of termites in forests on limestone soils would be an interesting comparison as limestone soils also have high pH and high calcium concentrations.

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Appendix. Termite species found in the eight transects collected from three areas of Borneo. Site names: Se = Serinsim, northwest Sabah; Da = Danum, southeast Sabah; DaTm = Tembaling Trail (primary forest), Danum; Ta = Tabalong, southeast Kalimantan; TaEn = *Endertia* forest (primary forest), Tabalong. Forest status: PF = primary forest; OF = old logged forest; LF = recently logged forest. Functional Taxonomic Groups (FTG; see text for definitions) are: I and II = wood-feeders; III = humus soil-feeders; IV = mineral soil-feeders. Additional feeding classifications: f = fungus-growers; e = micro epiphyte-feeders. Nesting classification (NC) is: w = nesting in wood; s = subterranean nest; e = epigeal mound; a = arboreal nest; i = inquiline (sharing the nest built by another species of termite). The numbers in each column represent the number of encounters with each species in that transect.

			Depauperate transects				Typical Sundaland transects			
	FTG	NC	SePF	SeOF	DaTm	TaEn	DaPF	DaOF	TaOF	TaLF
Kalotermitidae										
Glyptotermes brevicaudatus (Haviland)	I	w	–	–	–	1	–	–	–	–
Neotermes sp.	I	w	–	–	1	–	–	–	–	–
Rhinotermitidae			–							
Coptotermes sepangensis Krishna	I	w	–	–	–	–	–	2	5	–
Heterotermes tenuior (Haviland)	I	s	–	–	–	–	5	3	–	1
Parrhinotermes minor Thapa	I	w	–	–	–	–	–	–	1	–
Schedorhinotermes brevialatus (Haviland)	I	s	–	–	–	–	–	2	1	1
Schedorhinotermes medioobscurus (Holmgren)	I	s	–	–	–	1	1	2	1	14
Schedorhinotermes sarawakensis (Holmgren)	I	s	–	–	–	–	3	–	1	–
Termitidae: Macrotermitinae										
Macrotermes gilvus (Hagen)	IIf	e	9	7	3	4	–	5	2	4
Macrotermes malaccensis (Haviland)	IIf	s	3	–	–	8	1	4	6	6
Odontotermes denticulatus Holmgren	IIf	s	–	–	–	–	–	–	–	1
Odontotermes javanicus Holmgren	IIf	s	3	1	–	–	–	–	–	–
Odontotermes grandiceps Holmgren	IIf	s	1	–	–	–	–	–	–	–
Odontotermes neodenticulatus Thapa	IIf	s	–	–	–	–	–	–	2	–
Odontotermes oblongatus Holmgren	IIf	s	–	1	–	–	–	1	–	–
Odontotermes sarawakensis Holmgren	IIf	s	–	3	5	–	4	4	4	13
Odontotermes sp. C	IIf	s	–	–	–	–	–	1	–	–
Hypotermes xenotermitis (Wasmann)	IIf	s	1	–	1	1	–	1	1	–
Apicotermitinae										
Euhamitermes sp.	III	s	–	–	–	–	1	–	2	–
Termitidae: *Foraminitermes* group										
Labritermes emersoni Krishna & Adams	III	s	–	–	–	–	–	1	–	–
Labritermes kistneri Krishna & Adams	III	s	–	–	–	–	3	–	–	–
Amitermes group										
Prohamitermes mirabilis (Haviland)	II	s	–	–	–	–	2	4	3	8
Protohamitermes globiceps Holmgren	II	s	–	–	–	–	1	–	1	–
Globitermes globosus (Haviland)	II	s/w?	–	–	2	–	11	4	4	3
Microcerotermes dubius (Haviland)	II	w	–	–	–	–	1	1	3	4
Microcerotermes serrula (Desneux)	II	w	–	–	1	–	1	5	5	4
Termes group										
Termes borneensis Thapa	III	a/w	–	–	–	–	–	1	–	–
Termes comis Haviland	III	w/i	–	–	–	–	–	–	1	–
Termes propinquus (Holmgren)	III	w/i	–	–	–	–	1	–	–	4
Pericapritermes group										
Mirocapritermes connectens Holmgren	III	s	–	–	–	–	4	6	1	2
Homallotermes eleanorae Krishna	III	w	–	–	–	–	–	–	–	2
Malaysiocapritermes prosetiger (Ahmad)	III	s	–	–	–	–	1	2	7	11
Procapritermes atypus Holmgren	III	s	–	–	–		–	–	1	1
Procapritermes minutus (Haviland)	III	s	–	–	–	–	2	1	–	–
Procapritermes neosetiger Thapa	III	s	–	–	–	–	6	7	3	–
Procapritermes near *sandakanensis*	III	s	–	–	–	–	1	3	–	–
Procapritermes sp. A	III	s	–	–	–	–	2	1	–	–
Procapritermes sp. B	III	s	–	–	–	–	3	2	–	–
Procapritermes sp. C	III	s	–	–	–	–	1	–	–	–
Procapritermes sp. F	III	s	–	–	–	–	–	–	1	–
Coxocapritermes orientalis Ahmad & Akhtar	III	s	–	–	–	–	–	–	1	3
Coxocapritermes sp. A	III	s	–	–	–	–	1	–	–	–
Coxocapritermes sp. C	III	s	–	–	–	–	–	–	1	–
Pseudocapritermes silvaticus Kemner	III	s	–	–	–	–	–	–	3	–
Pericapritermes dolichocephalus (John)	III	s	–	–	–	–	1	–	–	–
Pericapritermes latignathus (Holmgren)	III	s	–	5	–	–	–	–	5	–
Pericapritermes mohri (Kemner)	III	s	–	–	–	–	–	–	1	–

Appendix. Continued.

			Depauperate transects				Typical Sundaland transects			
	FTG	NC	SePF	SeOF	DaTm	TaEn	DaPF	DaOF	TaOF	TaLF
Pericapritermes nitobei (Shiraki)	III	s	–	–	–	–	2	9	–	–
Pericapritermes semarangi (Holmgren)	III	s	–	–	–	–	6	3	–	2
Pericapritermes speciosus (Haviland)	III	s	–	–	–	–	–	–	5	–
Pericapritermes sp. A	III	s	–	–	–	–	1	2	–	–
Pericapritermes sp. C	III	s	–	–	–	–	5	3	–	–
Dicuspiditermes nemorosus (Haviland)	III	e	–	–	–	–	–	–	–	3
Dicuspiditermes santschii (Silvestri)	III	e	–	–	–	–	–	1	–	1
Oriencapritermes kluangensis Ahmad & Akhtar	IV	s	–	–	–	–	–	–	3	2
Oriencapritermes sp.	IV	s	–	–	1	–	–	–	–	–
Kemneritermes sarawakensis Ahmad & Akhtar	IV	s	–	–	–	–	–	–	–	1
Nasutitermitinae: *Nasutitermes* group										
Havilanditermes atripennis (Haviland)	II	s/w?	–	–	–	2	–	–	–	–
Nasutitermes longinasus (Holmgren)	II	a/w	–	–	–	–	4	–	–	4
Nasutitermes matangensis (Haviland)	II	a	–	–	–	–	–	–	–	1
Nasutitermes neoparvus Thapa	II	a	2	–	–	–	–	2	–	–
Bulbitermes borneensis (Haviland)	II	a	1	1	–	–	–	–	–	–
Bulbitermes flavicans (Holmgren)	II	a	1	2	2	–	–	1	–	–
Bulbitermes sp. A	II	a	–	2	1	1	3	7	–	–
Bulbitermes sp. C	II	a	–	2	–	–	1	1	–	–
Hospitalitermes sp. 1	IIe	a	–	–	–	–	–	–	1	4
Longipeditermes longipes (Haviland)	II	s	–	1	1	–	–	–	–	2
Oriensubulitermes group										
Leucopitermes leucops (Holmgren)	III	s	–	–	–	–	–	–	1	1
Malaysiotermes spinocephalus Ahmad	III	s	–	–	–	–	2	4	–	–
Malaysiotermes sp. 1A	III	s	–	–	–	–	–	–	–	1
Aciculioiditermes sp. A	III	s	–	–	–	–	2	–	–	–
New genus near *Oriensubulitermes*	III	s	–	–	–	–	–	–	–	1
Number of species			8	9	10	7	32	33	31	29
Number of encounters			21	23	18	18	83	96	77	105