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A SURVEY OF THE TERMITES (INSECTA: ISOPTERA) OF TABALONG DISTRICT, SOUTH KALIMANTAN, INDONESIA

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ABSTRACT. - The aim of this project was to survey the termite fauna in different forest types in the Tabalong District of South Kalimantan, Indonesia. Termites were collected from six sites, at four of which a standardised transect sampling protocol was used. One transect was run in each of the following habitats: two selectively logged dipterocarp forest sites, a primary forest dominated by the endemic tree *Endertia spectabilis,* and a monoculture plantation of *Gmelina arborea.* A total of 64 species were recorded, representing the most significant collection of termites from Kalimantan to date. A new genus of soil-feeding Nasutitermitinae was found, and *Ancistrotermes pakistanicus* was recorded from Borneo for the first time. The two logged forest transects recorded 29 and 31 species, while only 5 and 7 species were found in the *Gmelina* plantation and the *Endertia* forest respectively. The Tabalong logged forest transect samples were similar to samples collected at Danum Valley, Sabah, using the same protocol. The drastic reduction in termite species richness, and the elimination of soil-feeding termites in the *Gmelina* plantation, is thought to be due to the burning of the site after forest clearance, the more arid microclimate caused by the loss of the forest canopy, and the reduction of dead wood and structural complexity compared with primary and selectively logged forests. The low species richness in the *Endertia* forest is probably caused by the higher pH of the soil, or naturally occurring toxic concentrations of elements in the soil.

KEY WORDS. - Borneo; *Endertia spectabilis; Gmelina arborea;* Kalotermitidae; Rhinotermitidae; Termitidae; Species composition.

INTRODUCTION

Termites are the dominant arthropod decomposers in lowland tropical forests (Wood & Sands, 1978; Matsumoto & Abe, 1979; Collins, 1983) and play a central role in nutrient fluxes (Lawton et al., 1996; Bignell et al., 1997; Tayasu et al., 1997; Eggleton et al., 1999). Termite activity, such as mound-building, subterranean tunnelling and soil-feeding, improves soil structure and quality (Lee & Wood, 1971; Black & Okwakol, 1997; Holt & Lepage, 2000; Donovan et al., 2001a). The impact of termites on ecosystem processes at any site is governed by the species composition and abundance of the local assemblage. Striking differences are observed in the species richness, number of clades, and functional diversity of termite assemblages between biogeographical regions (Eggleton et al., 1994; Eggleton, 2000; Davies, 2001). Therefore, to compare the ecological influence of termites among regions requires an accurate assessment of the structure of these assemblages. Unfortunately, species distributions and range sizes are poorly known for most regional faunas (with the exception of Australia; see Watson & Abbey, 1993), thus limiting the opportunities for ecological and biogeographical analyses. Within Southeast Asia, historical patterns of termite dispersal across the archipelago cannot be understood without adequate knowledge of species composition on the mainland and the major islands.

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The most comprehensive investigation of the structure of termite assemblages in mainland Southeast Asia has been conducted at Pasoh Forest Reserve in Peninsular Malaysia (Matsumoto, 1976; Abe, 1978; Abe & Matsumoto, 1979; Matsumoto & Abe, 1979; Jones & Brendell, 1998), but detailed studies have also been undertaken at sites in Thailand (Davies, 1997; Inoue et al., 2001). Across the archipelago, there have been studies of termite assemblages in northern Sumatra (Gathorne-Hardy et al., 2001), southern Sumatra, western Java, the Krakatau islands (Gathorne-Hardy et al., 2000a), and Borneo (see review below). There has been some collecting in New Guinea (Roonwal & Maiti, 1966; Roisin & Pasteels, 1996), and only two, very limited collections made in Sulawesi (Kemner, 1934; Gathorne-Hardy et al., 2000b).

Borneo is the world's third largest island, and is divided politically among Kalimantan (Indonesia), Brunei Darussalam, and the Malaysian states of Sabah and Sarawak (Fig. 1). However, our current understanding of Bornean termite assemblages is based on studies conducted at four sites in the north of the island (Fig. 1). Danum Valley, in southeast Sabah, has arguably the most intensively studied termite fauna on Borneo (Eggleton et al., 1997, 1999; Homathevi, 1999). To date, a total of 93 species have been recorded from Danum, the highest known termite species richness of any site in Southeast Asia (Jones & Eggleton, 2000). The other significant assemblage-level studies have been conducted at Mulu, northern Sarawak (Collins, 1980, 1983, 1984), Maliau Basin, south-central Sabah (Jones et al., 1998; Jones, 2000) and Belalong, Brunei (Jones, 1996). The taxonomic literature has a similar geographical bias, with most species descriptions and locality records originating from collections made in Sarawak (e.g. Haviland, 1898; Ahmad, 1968) and Sabah (Thapa, 1981; Chey, 1989). Kalimantan covers 73% of the island, yet the present study is the first assessment of the species composition of its termite fauna.

Fig. 1. Map of Borneo showing political boundaries, the locality of the Tabalong sampling area in South Kalimantan (Indonesia), and the four other sites in Borneo where major ecological studies of termite assemblages have been conducted.

This study aimed to examine termite assemblage structure in different forest types in Tabalong, South Kalimantan, using a standardized sampling protocol. The Tabalong assemblages were then compared with other sites in Borneo where this protocol has been used. A wider analysis of biogeographical patterns across Southeast Asia will be published elsewhere.

MATERIALS AND METHODS

Study sites. - The project was undertaken in the Sungai Tabalong Kiwa area, in the Tabalong District of South Kalimantan Province, Indonesia (Fig. 1). Sampling was carried out in an extensive zone of forest managed for timber production, known locally as "production forest". Geologically, the area is a mosaic of siltstones, mudstones, quartz sandstones, limestone, basalt and granite, and the soils are predominantly clay-rich red-yellow podsolics of the ultisol group. Annual rainfall is about 2200 mm in the district administrative town of Tanjung, but is probably nearer to 3000 mm in the survey area. The natural forest of the survey area is lowland and hill dipterocarp forest. Timber has been extracted from this area since the mid 1970s, and the only undisturbed forests to have survived logging activity are patches on very steep slopes or with low natural densities of commercial timber trees. Termites were collected from six sites during March 2000. At the first four sites the local assemblage was assessed using a standardized transect sampling protocol (one transect per site). Only casual collecting was undertaken at sites 5 and 6, with additional casual collecting from the other four sites when time allowed.

Site 1. *Gmelina* plantation (Gmel). (1°48'44"S, 115°20'12"E; altitude c. 100 m.a.s.l.). Formerly lowland mixed dipterocarp forest that was logged in 1990, and then cleared, burnt and planted with hill rice. In 1993 the site was designated as an industrial tree plantation and young trees of *Gmelina arborea* were planted in a grid with 4 m x 2 m spacing. The site was weeded in 1994, 1995 and 1997. At the time of sampling the trees were about 4 m in height and the canopy was very open. The herbaceous layer was dominated by Gramineae and *Eupatoria* and there were a few rotting tree stumps left from the original forest. The transect was placed at 63° to the rows of trees. The land was gently undulating.

Site 2. Recently logged forest (RLF). (1°36'44"S, 115°30'0.5"E; altitude c. 450 m.a.s.l.). Mixed dipterocarp forest that was logged in 1998 (two years before sampling). The site was a ridge spur of about 5 ha in area, enclosed on three sides by a logging road. Logs were removed using D8 caterpillar bulldozers. The logging was very severe in places causing open areas. The transect crossed two skid trails, and these areas had little canopy cover.

Site 3. Old logged forest (OLF). (1°35'0.5"S, 115°31'14"E; altitude c. 630 m.a.s.l.). Hill dipterocarp forest that was thought to have been selectively logged in c. 1983 (17 years before sampling). However, disturbance appears to have been minimal, with only a few old cut tree stumps in the vicinity of the transect. The sampling area was on a slope with a logging road at the top, and a large area of essentially undisturbed forest below.

Site 4. *Endertia* forest (End). (1°36'0"S, 115°31'27"E; altitude c. 350 m.a.s.l.). This was the only unlogged forest site surveyed in the project. The area was dominated by an endemic leguminous tree, *Endertia spectabilis.* This large tree has no commercial value, and where it is present dipterocarps are rare or absent and tree diversity is relatively low. The canopy was at about 40 m in height, and the physical structure of the forest was very similar to undisturbed mixed dipterocarp forest. The transect ran across a gentle ridge, and was well above the nearest logging road.

Site 5. Logged forest. (1°36'0"S, 115°31'27"E; altitude c. 600 m.a.s.l.). Mixed dipterocarp forest that was selectively logged in 1983. The site was a ridge spur of about 8 ha in area, enclosed on three sides by a logging road.

Site 6. Upper Lou River valley area. (1°44'S, 115°28'E; altitude c. 200 m.a.s.l.). Samples collected from a large area of selectively logged mixed dipterocarp forest.

The standardised sampling protocol. - The standardised sampling protocol was based on a belt transect of 100 m length by 2 m width, divided into 20 contiguous sections of 5 x 2 m (Jones & Eggleton, 2000). In order to standardise sampling effort, each section was sampled by two trained people for 30 minutes (a total of one hour of sampling per section). In each section the following microhabitats were searched: 12 samples of surface soil (each about 12 x 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 above ground level. Workers and soldiers (if present) from every termite population encountered were sampled and placed in 80% ethanol. Care was taken to search termite mounds because they are known to harbour inquiline species (Eggleton & Bignell, 1997).

The transect protocol provides a measure of the relative abundance of termites based on the number of encounters with each species in a transect (Jones 2000). An encounter is defined as the presence of a species in one section. Therefore, if a species was present in every section of a transect it would have a relative abundance score of 20. The number of encounters per transect can then be used to compare the relative abundance of termites among transects. It gives no measure of the absolute abundance per unit area.

Identification of material. - Species-level identifications were made using the taxonomic works of Thapa (1981), Tho (1982, 1992), Ahmad & Akhtar (1981), Gathorne-Hardy (2001) and other relevant publications. Identifications were based initially on the external characters of the soldier caste, and the mandible, gut and enteric valve characters of the worker caste. The Tabalong specimens were compared with voucher collections (held at BMNH) from Danum Valley, Maliau Basin, Pasoh, and numerous sites in Java and Sumatra. Several groups are in need of taxonomic revision, resulting in the use of open nomenclature. However, taxa assigned to morphospecies were cross-referenced against the voucher collections to ensure taxonomic consistency. This provided for accurate species composition analyses among sites.

Functional groups. - Termites were assigned to one of four feeding groups following the classification of Donovan et al. (2001b). This classification is based on morphological characters of the worker gut and mandibles, which relate to feeding preferences along a humification gradient of the dietary substrate. This correlates with the relative amounts of plant tissue fragments and silica in the gut content (Donovan et al., 2001b). The feeding groups are:

Group I: All lower termites. These feed on living and dead plant material. Most species feed on woody matter but some harvest grass (although grass-harvesters do not occur in Borneo).

Group II: Members of the Termitidae that have a range of feeding habits. Most are wood-feeders, but the group also includes grass-feeders, litter-feeders, and micro-epiphyte-feeders.

Group III: Members of the Termitidae that feed on soil with a high organic content, and highly decayed wood that has lost its structure and become soil-like. These termites can be considered "organic-rich soil-feeders".

Group IV: Members of the Termitidae that feed on mineral soil with a lower organic content. These termites can be considered "true soil-feeders".

Hospitalitermes feed on micro-epiphytes such as lichens, algae and hepatics, and other free living non-vascular plants which they graze from the surface of tree trunks (Collins, 1979; Jones & Gathorne-Hardy, 1995). *Hospitalitermes* was included in Group II because analysis of the gut content clustered it within the Group II wood-feeders on the humification gradient (Donovan et al., 2001b). Termites that feed predominantly on leaf-litter and small items of woody debris, such as *Longipeditermes longipes* (see Hoare & Jones, 1998) also cluster within Group II.

Comparisons of species composition. - The structure of the termite assemblages in the four Tabalong transects were compared with six transects run at Danum Valley (Eggleton et al., 1997) and four at Maliau Basin (Jones, 2000) in Borneo (see Fig. 1 for site locations). The Danum transects were all run in lowland mixed dipterocarp forest (at about 100 m altitude): two in primary forest, two in recently logged forest and two in old logged forest. In contrast, the Maliau sites were all primary forest at 1000 m elevation, with two transects run in lower montane forest and two transects run in upper montane forest.

Similarities in species composition among the 14 transects were examined using detrended correspondence analysis (DCA) (Hill & Gauch, 1980). In the ordination plot the closer the transects are in ordination space, the more similar they are in composition.

RESULTS

The Tabalong collection. - A total of 380 series of termites were collected from the six sites in the Tabalong area. The collection contained 39 genera and 64 species (Table 1). The four families of termites known to occur in Southeast Asia were found in Tabalong. In addition, all four subfamilies of Termitidae were represented in the collection, including the Apicotermitinae (*Euhamitermes* sp.) which is rare in the Sunda region. *Ancistrotermes pakistanicus* was recorded for the first time in Borneo,

Table 1. Checklist of the 64 species of termites collected from six sites in Tabalong District, South Kalimantan, in March and April 2000. Feeding groups (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 groups are: 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 sites are: *Gmelina* plantation (Gmel); recently logged forest (RLF); old logged forest (OLF); *Endertia* forest (End); logged forest (sites 5 and 6). The number of series collected at each site is given. This represents all species records from each site, and therefore combines series collected using the standardised transect sampling protocol as well as casual samples.

KALOTERMITIDAE	Feeding group	Nesting group	Gmel	RLF	OLF	End	Site 5	Site 6
Glyptotermes brevicaudatus (Haviland, 1898)	I	w	-	-	-	1	-	-
Cryptotermes sp.	I	w	-	-	-	-	1	-
RHINOTERMITIDAE								
Coptotermes curvignathus Holmgren, 1913	I	w	-	-	-	-	-	1
Coptotermes kalshoveni Kemner, 1934	I	w	-	-	-	-	-	1
Coptotermes sepangensis Krishna, 1956	I	w	-	-	8	-	1	-
Heterotermes tenuior (Haviland, 1898)	I	w	-	1	-	-	-	-
Parrhinotermes minor Thapa, 1981	I	w	-	-	1	-	1	-
Schedorhinotermes brevialatus (Haviland, 1898)	I	w	1	1	2	-	-	-
Schedorhinotermes medioobscurus (Holmgren, 1913-14)	I	w	23	17	1	1	2	-
Schedorhinotermes sarawakensis (Holmgren, 1913)	I	w	2	-	1	-	-	-
TERMITIDAE								
Macrotermitinae								
Macrotermes gilvus (Hagen, 1858)	II(f)	e	-	4	2	8	2	2
Macrotermes malaccensis (Haviland, 1898)	II(f)	s	-	7	9	11	1	2
Odontotermes denticulatus Holmgren, 1913	II(f)	s	-	1	-	-	-	-
Odontotermes neodenticulatus Thapa, 1981	II(f)	s	-	-	2	-	-	-
Odontotermes sarawakensis Holmgren, 1913	II(f)	s	-	17	5	-	1	-
Hypotermes xenotermitis (Wasmann, 1896)	II(f)	s	-	-	1	1	-	-
Ancistrotermes pakistanicus (Ahmad, 1955)	II(f)	s	9	-	-	-	-	-
Apicotermitinae								
Euhamitermes sp.	III	s	-	-	2	-	-	-
Termitinae								
Labritermes buttelreepeni Holmgren, 1914	III	s	-	-	-	-	4	-
Prohamitermes hosei (Desneux, 1906)	II	s	-	-	-	-	2	-
Prohamitermes mirabilis (Haviland, 1898)	II	s	-	12	7	-	-	-
Protohamitermes globiceps Holmgren, 1912	II	s	-	-	2	-	1	-
Globitermes globosus (Haviland 1898)	II	s/w?	-	6	7	-	2	1
Microcerotermes dubius (Haviland, 1898)	II	w	-	9	7	-	1	1
Microcerotermes serrula (Desneux, 1904)	II	w	-	6	7	-	1	-
Termes borneensis Thapa, 1981	III	a/w	-	-	-	-	1	-
Termes comis Haviland, 1898	III	w/i/a	-	-	1	-	1	1
Termes laticornis Haviland, 1898	III	w/i	-	-	1	-	-	-
Termes propinquus (Holmgren, 1914)	III	w/i	-	6	-	-	-	-
Mirocapritermes connectens Holmgren, 1914	III	s	-	3	1	-	-	-
Homallotermes eleanorae Krishna, 1972	III	w	-	2	-	-	1	1
Malaysiocapritermes prosetiger (Ahmad, 1965)	III	s	-	20	11	-	1	-
Pseudocapritermes silvaticus Kemner, 1934	III	s	-	-	3	-	-	-
Coxocapritermes orientalis Ahmad & Akhtar, 1981	III	s	-	3	2	-	-	-
Coxocapritermes sp. C	III	s	-	-	1	-	-	-
Procapritermes atypus Holmgren, 1912	III	s	-	1	1	-	-	-
Procapritermes minutus Haviland, 1898	III	s	-	-	-	-	1	-
Procapritermes neosetiger Thapa, 1981	III	s	-	-	3	-	-	-
Procapritermes sp. F	III	s	-	-	1	-	-	-
?*Coxocapritermes* near *P. atypus*	III	s	-	-	-	-	1	-
Oriencapritermes kluangensis Ahmad & Akhtar, 1981	IV	s	-	2	4	-	-	-
Syncapritermes greeni (John, 1925)	IV	s	-	-	-	-	1	-
Kemneritermes sarawakensis Ahmad & Akhtar, 1981	IV	s	-	1	-	-	-	-
Pericapritermes latignathus (Holmgren, 1914)	III	s	-	-	7	-	-	-
Pericapritermes mohri (Kemner, 1934)	III	s	-	-	1	-	-	-
Pericapritermes semarangi (Holmgren, 1913)	III	s	-	2	-	-	-	-
Pericapritermes speciosus (Haviland, 1898)	III	s	-	-	9	-	-	-
Dicuspiditermes nemorosus (Haviland, 1898)	III	e	-	5	-	-	2	-
Dicuspiditermes santschii (Silvestri, 1922)	III	e	-	1	-	-	-	-

Nasutitermitinae								
Havilanditermes atripennis (Haviland, 1898)	II	s?	-	-	-	4	-	1
Nasutitermes longinasus (Holmgren, 1913)	II	a/w	-	7	-	-	1	-
Nasutitermes longirostris (Holmgren, 1913)	II	w	1	-	-	-	-	-
Nasutitermes matangensis (Haviland, 1898)	II	a	-	1	-	-	2	-
Nasutitermes neoparvus Thapa, 1981	II	a	-	-	-	-	-	1
Bulbitermes sp. A	II	a	-	-	-	2	-	-
Hospitalitermes hospitalis (Haviland, 1898)	II(e)	a	-	9	2	-	1	2
Hospitalitermes lividiceps (Holmgren, 1913)	II(e)	a	-	-	-	-	-	1
Hospitalitermes new species	II(e)	a	-	-	-	-	1	-
Longipeditermes longipes (Haviland, 1898)	II	s	-	2	-	-	-	1
Leucopitermes leucops (Holmgren, 1914)	III	s	-	1	1	-	1	-
Oriensubulitermes inanis (Haviland, 1898)	III	s	-	-	-	-	1	-
Aciculitermes sp.	III	s	-	-	1	-	-	-
Malaysiotermes sp. 1A	III	s	-	1	-	-	-	-
New genus near *Oriensubulitermes*	III	s	-	1	-	-	-	-

from the *Gmelina arborea* plantation. This termite was formerly recorded from the Indian subcontinent, across Burma and Thailand, and into Peninsular Malaysia, Sumatra and Java. A new genus of Nasutitermitinae, and a new species of *Hospitalitermes* were found. The new genus appears to be close to the soil-feeding (group III) genus *Oriensubulitermes.*

The Tabalong transects. - The old logged forest transect (OLF) had the highest species richness with 31 species, while the recently logged forest transect (RLF) had 29 species (Fig. 2). The *Endertia* forest transect had only seven species, far fewer than expected for a primary forest at relatively low elevation. The lowest richness was recorded in the *Gmelina* plantation transect where only five species were found. In the two logged forest sites, species of Termitinae constituted the largest taxonomic group (Fig. 2). In contrast, the Termitinae were absent from the *Endertia* forest and the *Gmelina* plantation.

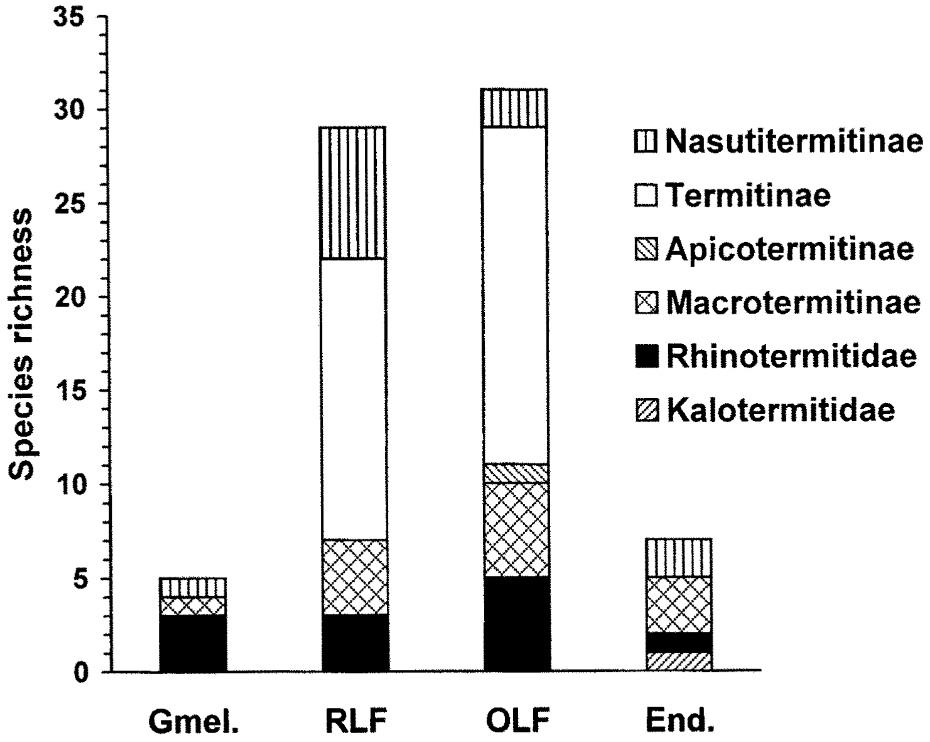

Fig. 2. The gray shading for the Macrotermitinae is difficult to distinguish from the black shading of the Rhinotermitidae. I enclose a new hard copy version of Figure 2, with the Macrotermitinae marked with cross-hatching. This makes it much easier to distinguish the six different taxonomic groups.

The most striking feature related to the relative abundance of the four feeding groups is the absence of soil-feeding termites (groups III and IV) from both the *Gmelina* plantation and the *Endertia* forest (Fig. 3). In addition, both these transects had a lower relative abundance of wood-feeding termites (groups I and II) compared with the two logged forest transects. Of the 25 encounters recorded in the *Gmelina* transect, 17 were of *Schedorhinotermes* (group I) and seven were *Ancistrotermes* (group II). By contrast, of the 18 encounters in the *Endertia* transect, 13 were species of Macrotermitinae, while only one was *Schedorhinotermes*.

Comparison of termite assemblages in Borneo. - In terms of species composition, the lowland transects were separated from the Maliau transects (all at 1000 m altitude) along axis 1 of the DCA, while the Tabalong transects were separated from the Danum transects along axis 2 (Fig. 4). All the lowland mixed dipterocarp forest transects at Tabalong and Danum had a higher species richness than the montane forest transects at Maliau (Table 2). This was expected because termite species richness is known to decline with elevation (Jones, 2000). A significant change in assemblage composition, similar to that observed at Maliau, was found along an altitudinal transect in the mountains of the Leuser Ecosystem, northern Sumatra (Gathorne-Hardy et al., 2001).

Despite its low elevation, the *Gmelina* transect was closer in composition to the Maliau transects than to the other lowland transects (Fig. 4). This is probably due to the absence of soil-feeding species (which are also rare at Maliau), and the high relative abundance of *Schedorhinotermes medioobscurus* (a species that is also common in Maliau). The Macrotermitinae (fungus-growing, group II wood-feeders) are the dominant group in the Endertia forest, and this may account for the position of the transect between the

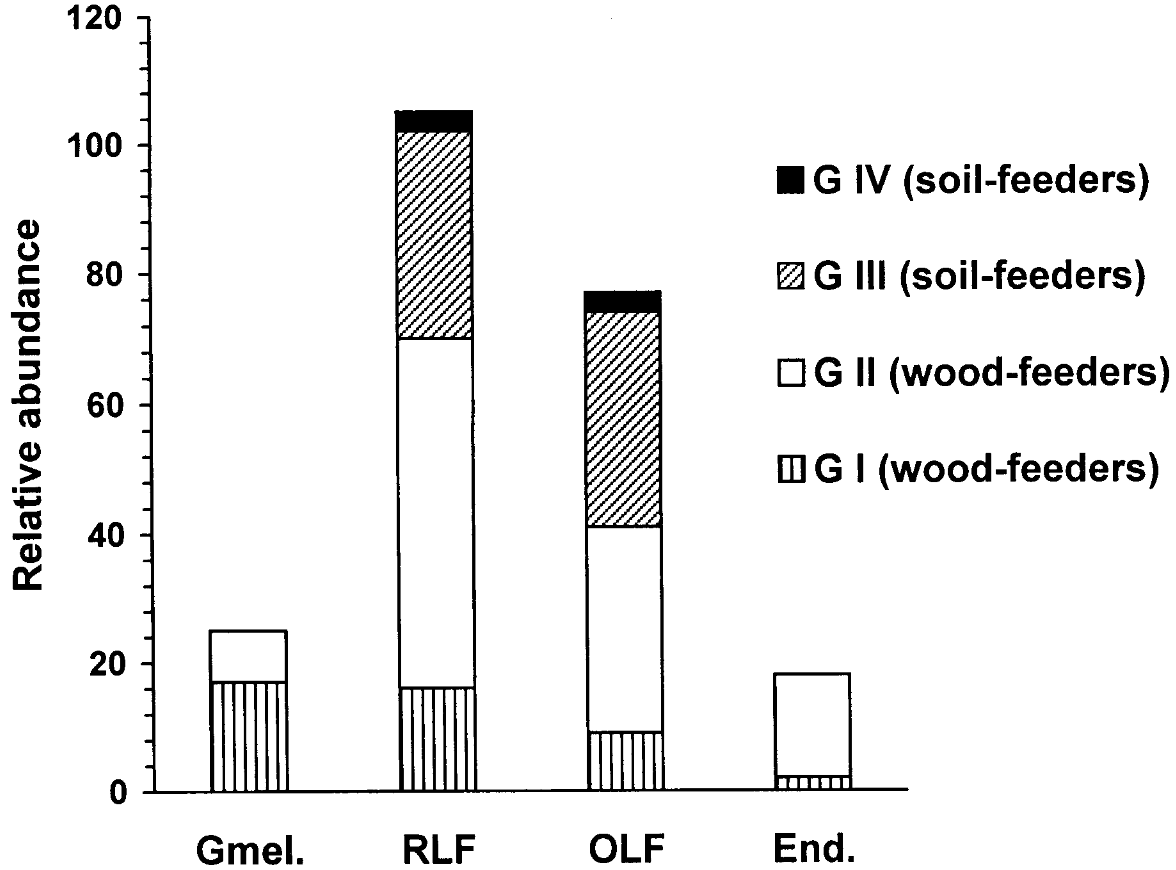

Fig. 3. The relative abundance of termites collected using standardised transects run in four habitat types at Tabalong, South Kalimantan. The relative abundance is the number of encounters with each species in a transect. The habitat types were; *Gmelina arborea* plantation (Gmel.), recently logged dipterocarp forest (RLF), old logged dipterocarp forest (OLF), and *Endertia spectabilis* forest (End.). Each species was assigned to one of four feeding groups.

Danum transects and the two Tabalong logged forest transects (Fig. 4). In Southeast Asia the Macrotermitinae are restricted to lowland forests, and do not occur at Maliau (Jones, 2000). Although *Ancistrotermes,* a genus of Macrotermitinae, occurred in the *Gmelina* transect, because this taxon was not recorded at any other site, its presence could not increase the compositional similarity to other transects.

DISCUSSION

The Tabalong termite fauna. - The Tabalong survey recorded 64 species of termites, including the first record of *Ancistrotermes pakistanicus* from Borneo. *Ancistrotermes* nests in soil, and it is extremely unlikely that it was introduced to Borneo by human activity. Despite being a common and widespread species in Java and Sumatra, *A. pakistanicus* has not colonized the neighbouring island of Krakatau. In the 118 years since the volcanic eruption, only wood-nesting termites have colonized Krakatau by rafting (Gathorne-Hardy et al., 2000a). Moreover, there have never been any records of Macrotermitinae being transported between land masses by humans (Gay, 1969).

Apart from *A. pakistanicus* and the new genus of Nasutitermitinae, the Tabalong collection does not contain any species that would not be expected in samples from lowland mixed dipterocarp forests in Borneo. Furthermore, there are no taxonomic groups that are obviously missing from the Tabalong collection that are found elsewhere in Borneo. The two logged forest transects at Tabalong are very similar to the six Danum transects in species richness and in overall taxonomic and functional group structure (Eggleton et al., 1997). Therefore, taking the collection as a whole (as given in Table 1) the Tabalong fauna appears to be a typical Bornean lowland forest fauna. The highly anomalous structure of the termite assemblage in the *Endertia* forest is discussed below.

The impact of forest clearance. - The most dramatic effect of disturbance was seen in the *Gmelina* plantation, where complete clearance of the forest and replacement with a tree monoculture resulted in the elimination of all soil-feeding termites, and a drastic reduction in overall species richness. Four factors may explain these effects:

First, after the original forest was cleared, the site was burnt in preparation for growing hill rice. Subterranean termites in tropical lowland forests usually occur in the organic layer of the soil (Collins, 1989). At Pasoh, Peninsular Malaysia, Abe & Matsumoto (1979) found that termites occurred mainly in the top 15 cm of the soil and were rare below 25 cm. Therefore, many subterranean termite colonies in the *Gmelina* site may not have escaped intense fires at the soil surface. The *Gmelina* plantation is no longer surrounded by natural forest, so soil-feeding species cannot recolonise from adjacent areas.

Second, it is possible that the low, open canopy of the *Gmelina* plantation allows greater fluctuations in temperature and moisture levels compared with the closed canopy of undisturbed forest. Studies in Cameroon suggest that a closed or very dense canopy in a tropical forest system is one of the key factors favouring high termite species richness and

Table 2. The species richness of termites in standardised transect samples from three sites in Borneo. Four transects were run at Tabalong, Kalimantan (present study), six transects at Danum Valley (Eggleton et al., 1997), and four at Maliau Basin (Jones, 2000).

Site	Habitat type	Species richness
Tabalong	*Gmelina arborea* plantation	5
Tabalong	Recently logged dipterocarp forest	29
Tabalong	Old logged dipterocarp forest	31
Tabalong	Primary *Endertia spectabilis* forest	7
Danum Valley	Primary dipterocarp forest (two transects)	28 and 32
Danum Valley	Recently logged dipterocarp forest (two transects)	29 and 28
Danum Valley	Old logged dipterocarp forest (two transects)	29 and 33
Maliau Basin	Primary lower montane forest (two transects)	19 and 15
Maliau Basin	Primary upper montane forest (two transects)	12 and 10

abundance (Dibog et al., 1999; Eggleton et al., 1995, 1996). Recent work conducted along a land-use intensification gradient in lowland central Sumatra shows that the adverse conditions found under an open canopy, or following canopy removal and replacement with commercial plantations, leads to a considerable drop in termite species richness and relative abundance (D.T. Jones, unpublished data). Moreover, these impacts are thought to be significantly greater on soil-feeders than wood-feeders due to the energetic limitations imposed by their feeding habit (Bignell, 1994; Eggleton et al., 1998).

Third, the *Gmelina* plantation had relatively little dead wood lying on the ground compared with undisturbed and selectively logged forests. The limited food resources and wood-nesting microsites may have contributed to the lower abundance of wood-feeding termites.

Finally, compared with the plantation site, undisturbed forest has greater structural complexity (e.g. larger trees, greater plant diversity, and more dead wood), thus providing a greater array of nesting and feeding sites for termites. Of particular importance are existing termite mounds, since they are favoured nesting sites for other termites in addition to the mound-building species (Dejean & Ruelle, 1995; Eggleton & Bignell, 1997). No epigeal mound-building species occurred in the *Gmelina* plantation, whereas epigeal mounds of *Macrotermes, Dicuspiditermes* and *Hospitalitermes* (plus subterranean nests of *Prohamitermes* in the surface soil layer) were common in logged forest sites and may have contributed to their higher diversity.

The impact of selective logging. - The impact of selective logging on the termite assemblage can only be quantified by comparison with the assemblage in local primary forest. Unfortunately, this was not possible in the present study because the termite assemblage in the undisturbed *Endertia* forest is not typical of lowland mixed dipterocarp forest. However, data from Danum Valley (Eggleton et al., 1997, 1999) suggest that selective logging has much less impact on the termite assemblage than complete forest clearance. The impact of logging depends, to a

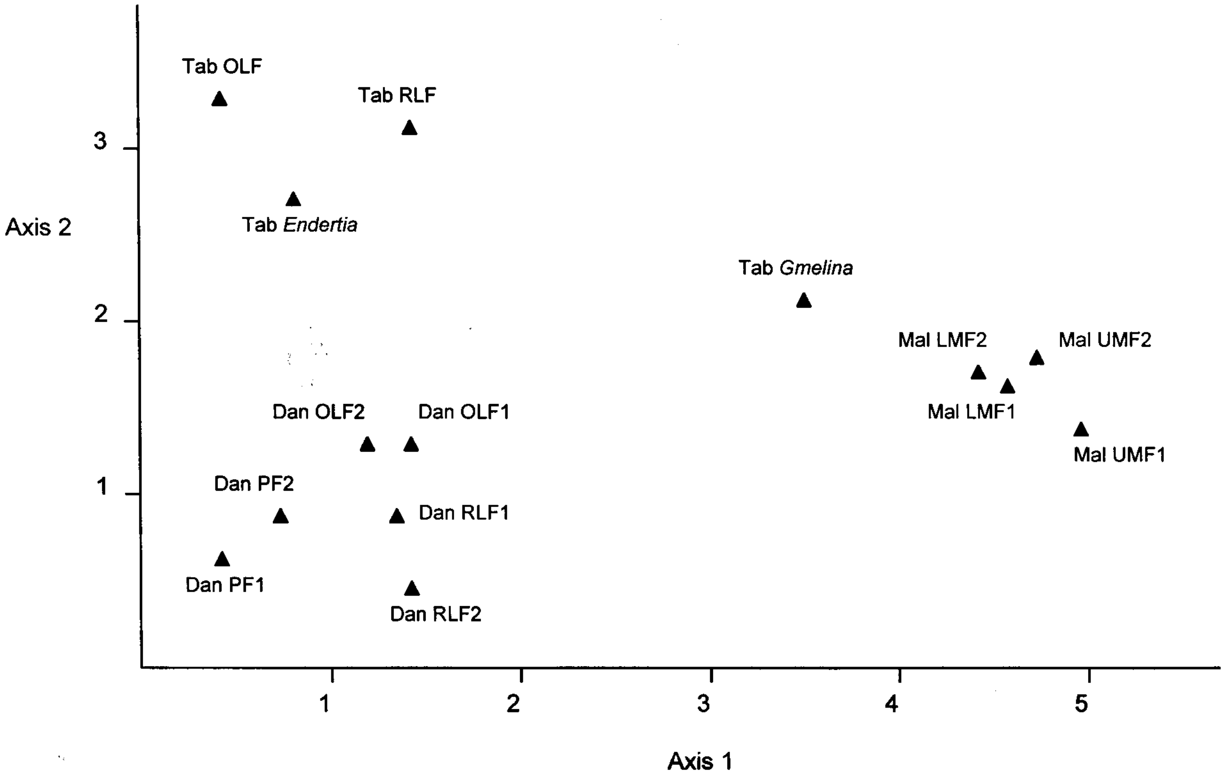

Fig. 4. Results of DCA ordination comparing termite species composition among 14 standardised transects at three locations in Borneo. Tab = Tabalong, South Kalimantan; Dan = Danum Valley, Sabah; Mal = Maliau Basin, Sabah. PF = primary dipterocarp forest; RLF = recently logged dipterocarp forest; OLF = old logged dipterocarp forest; LMF = lower montane forest; UMF = upper montane forest. Axis 1 eigenvalue = 0.715; axis 2 eigenvalue = 0.421.

large extent, on the severity of damage to the physical structure of the forest and its canopy (D.T. Jones, unpublished data). The more canopy cover a logged forest retains, the greater will be its capacity to buffer microclimate.

***The Endertia* forest.** - The termite assemblage in the *Endertia* forest is highly depauperate compared with primary and logged mixed dipterocarp forest, with an absence of soil-feeders, and a lower species richness and relative abundance of wood-feeders. We can speculate that the environmental conditions that cause the dominance of *Endertia spectabilis* may inhibit termites and dipterocarp species. It is thought that *E. spectabilis* favours damp and rocky areas (J. Payne pers. comm.), although the transect was run across the upper slopes of a gentle spur and appeared to be well drained and not unusually rocky, suggesting that other factors are responsible.

The most likely explanation is that soil properties are responsible for this forest type. It is known that the soils in *Endertia* forest often have a higher pH than mixed dipterocarp forest soils. For example, the pH of the A horizon from dipterocarp forest at Tabalong (with no *Endertia* trees present) ranged from 4.3 to 5.6 (mean = 4.7; n = 14), while the pH of soils from the *Endertia* forest ranged from 4.6 to 6.9 (mean = 5.8; n = 12) (J. Payne pers. comm.). Recent data from Sabah has revealed very low abundance and diversity of termites in a forest with elevated pH (Jones unpublished data). Alternatively, the underlying rock type may contain high concentrations of elements that are toxic to soil-feeding termites. It is clear that this unusual habitat warrants further research.

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LITERATURE CITED

Abe, T., 1978. Studies on the distribution and ecological role of termites in a lowland rain forest of west Malaysia. 1. Faunal composition, size, colouration and nest of termites in Pasoh Forest Reserve. *Kontyu*, **46**: 273-290.

Abe, T. & T. Matsumoto, 1979. Studies on the distribution and ecological role of termites in a lowland rain forest of West Malaysia. 3. Distribution and abundance of termites in Pasoh Forest Reserve. *Japanese Journal of Ecology*, **29**: 337-351.

Ahmad, M., 1968. Termites of Malaysia. I. Nasute genera related to *Subulitermes* (Isoptera, Termitidae, Nasutitermitinae). *Bulletin of the Department of Zoology, University of Panjab*, **3**: 1-34.

Ahmad, M. & M. S. Akhtar, 1981. New termite genera of the *Capritermes* complex from Malaysia, with a note on the status of *Pseudocapritermes* (Isoptera: Termitidae). *Pakistan Journal of Zoology*, **13**: 1-21.

Bignell, D. E., 1994. Soil-feeding and gut morphology in higher termites. In: Hunt, J. H. & C. A. Nalepa (eds.), *Nourishment and Evolution in Insect Societies*. Westview Press, Oxford. pp. 131-157.

Bignell, D. E., P. Eggleton, L. Nunes & K. L. Thomas, 1997. Termites as mediators of carbon fluxes in tropical forest: budgets for carbon dioxide and methane emissions. In: Watt, A. D., N. E. Stork & M. D. Hunter (eds.), *Forests and Insects*. Chapman and Hall, London. pp. 109-134.

Black, H. I. J. & M. J. N. Okwakol, 1997. Agricultural intensification, soil biodiversity and agroecosystem function in the tropics: the role of termites. *Applied Soil Ecology*, **6**: 37-53.

Chey, V. K., 1989. *A survey of termites in Sabah forests*. Forest Research Centre, Sandakan, Malaysia. 144 pp.

Collins, N. M., 1979. Observations on the foraging activity of *Hospitalitermes umbrinus* (Haviland), (Isoptera: Termitidae) in the Gunung Mulu National Park, Sarawak. *Ecological Entomology*, **4**: 231-238.

Collins, N. M., 1980. The distribution of soil macrofauna on the West Ridge of Gunung (Mount) Mulu, Sarawak. *Oecologia*, **44**: 263-275.

Collins, N. M., 1983. Termite populations and their role in litter removal in Malaysian rain forests. In: Sutton, S. L., T. C. Whitmore & A. C. Chadwick (eds.), *Tropical rain forest: Ecology and management*. Blackwell Scientific Publications, Oxford. pp. 311-325.

Collins, N. M., 1984. The termites (Isoptera) of the Gunung Mulu National Park, with a key to the genera known from Sarawak. *Sarawak Museum Journal*, **30**: 65-87.

Collins, N. M., 1989. Termites. In: Lieth, H. & M. J. A. Werger (eds.), *Tropical Rain Forest Ecosystems. Biogeographical and ecological studies*. Elsevier, Amsterdam. pp. 455-471.

Davies, R. G., 1997. Termite species richness in fire-prone and fire-protected dry deciduous dipterocarp forest in Doi Suthep-Pui National Park, northern Thailand. *Journal of Tropical Ecology*, **13**: 153-160.

Davies, R. G. 2001. *Patterns of termite functional diversity: from local ecology to continental history*. Ph.D.

Thesis. University of London. 238.

Dejean, A. & J. E. Ruelle, 1995. Importance of *Cubitermes* termitaries as shelter for alien incipient termite societies. *Insectes Sociaux*, **42**: 129-136.

Dibog, L., P. Eggleton, L. Norgrove, D. E. Bignell & S. Hauser, 1999. Impacts of canopy cover on soil termite assemblages in an agrisilvicultural system in southern Cameroon. *Bulletin of Entomological Research*, **89**: 125-132.

Donovan, S. E., P. Eggleton & D. E. Bignell, 2001b. Gut content analysis and a new feeding group classification of termites (Isoptera). *Ecological Entomology*, **26**: 356-366.

Donovan, S. E., P. Eggleton, W. Dubbin, M. Batchelder & L. Dibog, 2001a. The effect of a soil-feeding termite, *Cubitermes fungifaber* (Isoptera: Termitidae) on soil properties: termites may be an important source of soil microhabitat heterogeneity in tropical forests. *Pedobiologia*, **45**: 1-11.

Eggleton, P., 2000. Global patterns of termite diversity. In: Abe, T., D. E. Bignell & M. Higashi (eds.), *Termites: evolution, sociality, symbiosis, ecology*. Kluwer Academic Publications, Dordrecht, The Netherlands. Pp 25-51.

Eggleton, P. & D. E. Bignell, 1997. Secondary occupation of epigeal termite (Isoptera) mounds by other termites in the Mbalmayo Forest Reserve, southern Cameroon, and its biological significance. *Journal of African Zoology*, **111**: 489-498.

Eggleton, P., D. E. Bignell, W. A. Sands, N. A. Mawdsley, J. H. Lawton, T. G. Wood & N. C. Bignell, 1996. The diversity, abundance, and biomass of termites under differing levels of disturbance in the Mbalmayo Forest Reserve, southern Cameroon. *Philosophical Transactions of the Royal Society*, **351**: 51-68.

Eggleton, P., D. E. Bignell, W. A. Sands, B. Waite, T. G. Wood & J. H. Lawton, 1995. The species richness of termites (Isoptera) under differing levels of forest disturbance in the Mbalmayo Forest Reserve, southern Cameroon. *Journal of Tropical Ecology*, **11**: 85-98.

Eggleton, P., R. G. Davies & D. E. Bignell, 1998. Body size and energy use in termites (Isoptera): the responses of soil feeders and wood feeders differ in a tropical forest assemblage. *Oikos*, **81**: 525-530.

Eggleton, P., R. Homathevi, D. Jeeva, D. T. Jones, R. G. Davies & M. Maryati, 1997. The species richness and composition of termites (Isoptera) in primary and regenerating lowland dipterocarp forest in Sabah, east Malaysia. *Ecotropica*, **3**: 119-128.

Eggleton, P., R. Homathevi, D. T. Jones, J. MacDonald, D. Jeeva, D. E. Bignell, R. G. Davies & M. Maryati, 1999. Termite assemblages, forest disturbance and greenhouse gas fluxes in Sabah, East Malaysia. *Philosophical Transactions of the Royal Society*, **354**: 1791-1802.

Eggleton, P. E., P. H. Williams & K. J. Gaston, 1994. Explaining global termite diversity: productivity or history? *Biodiversity and Conservation*, **3**: 318-330.

Gathorne-Hardy, F. J., 2001. A review of the South East Asian Nasutitermitinae (Isoptera: Termitidae) with descriptions of one new genus and a new species and including a key to the genera. *Journal of Natural History*, **35**: 1485-1506.

Gathorne-Hardy, F. J., N. M. Collins, R. D. Buxton & P. Eggleton, 2000b. A faunistic review of the termites (Insecta: Isoptera) of Sulawesi, including an updated checklist of the species. *Malayan Nature Journal*, **54**: 347-353.

Gathorne-Hardy, F. J., D. T. Jones & N. A. Mawdsley, 2000a. The recolonization of the Krakatau islands by termites (Isoptera), and their biogeographical origins. *Biological Journal of the Linnean Society*, **71**: 251-267.

Gathorne-Hardy, F., Syaukani & P. Eggleton, 2001. The effects of altitude and rainfall on the composition of the termites (Isoptera) of the Leuser Ecosystem (Sumatra, Indonesia). *Journal of Tropical Ecology*, **17**: 379-393.

Gay, F. J., 1969. Species introduced by man. In: Krishna, K. & F. M. Weesner (eds.), *Biology of termites*, vol. 1. Academic Press, New York. pp. 459-494.

Haviland, G. D., 1898. Observations on termites; with descriptions of new species. *The Journal of the Linnean Society, Zoology*, **26**: 358-442.

Hill, M. O. & H. G. Gauch, 1980. Detrended correspondence analysis, an improved ordination technique. *Vegetatio*, **42**: 47-58.

Hoare, A. & D. T. Jones, 1998. Notes on the foraging behaviour and taxonomy of the southeast Asian termite *Longipeditermes longipes* (Termitidae: Nasutitermitinae). *Journal of Natural History*, **32**: 1357-1366.

Holt, J. A. & M. Lepage, 2000. Termites and soil properties. In: Abe, T., D. E. Bignell & M. Higashi (eds.), *Termites: evolution, sociality, symbioses, ecology*. Kluwer Academic Publishers, Dordrecht. pp. 389-407.

Homathevi, R. 1999. *Diversity and ecology of forest termite (Isoptera) populations in Sabah, East Malaysia, with special reference to the* Termes-Capritermes *clade*. Ph.D. Thesis. University Malaysia Sabah, Kota Kinabalu. 334.

Inoue, T., Y. Takematsu, F. Hyodo, A. Sugimoto, A. Yamada, C. Klangkaew, N. Kirtibutr & T. Abe, 2001. The abundance and biomass of subterranean termites (Isoptera) in a dry evergreen forest of northeast Thailand. *Sociobiology*, **37**: 41-52.

Jones, D. T., 1996. A quantitative survey of the termite assemblage and its consumption of food in lowland mixed dipterocarp forest in Brunei Darussalam. In: Edwards, D. S., W. E. Booth & S. Choy (eds.), *Tropical Rainforest Research - Current issues*. Kluwer Academic Publishers, Dordrecht. pp. 297-305.

Jones, D. T., 2000. Termite assemblages in two distinct montane forest types at 1000 m elevation in Maliau Basin, Sabah. *Journal of Tropical Ecology*, **16**: 271-286.

Jones, D. T. & M. J. D. Brendell, 1998. The termite (Insecta: Isoptera) fauna of Pasoh Forest Reserve, Malaysia. *Raffles Bulletin of Zoology*, **46**: 79-91.

Jones, D. T. & P. Eggleton, 2000. Sampling termite assemblages in tropical forests: testing a rapid biodiversity assessment protocol. *Journal of Applied Ecology*, **37**: 191-203.

Jones, D. T. & F. Gathorne-Hardy, 1995. Foraging activity of the processional termite *Hospitalitermes hospitalis*

(Termitidae: Nasutitermitinae) in the rain forest of Brunei, north-west Borneo. *Insectes Sociaux*, **42**: 359-369.

Jones, D. T., J. Tan & Y. Bakhtiar, 1998. The termites (Insecta: Isoptera) of the Maliau Basin, Sabah. In: Maryati, M., W. Sinun, A. Anton, M. N. Dalimin & A. H. Ahmad (eds.), *Maliau Basin Scientific Expedition.* Universiti Malaysia Sabah, Kota Kinabalu. pp. 95-112.

Kemner, N. A., 1934. Systematische und biologische studien uber termiten Javas und Celebes. *Kongliga Svenska Vetenskaps Akademiens Handlingar,* **13**: 1-241.

Lawton, J. H., D. E. Bignell, G. F. Bloemers, P. Eggleton & M. E. Hodda, 1996. Carbon flux and diversity of nematodes and termites in Cameroon forest soils. *Biodiversity and Conservation,* **5**: 261-273.

Lee, K. E. & T. G. Wood, 1971. *Termites and soils.* Academic Press, London. 251pp.

Matsumoto, T., 1976. The role of termites in an equatorial rain forest ecosystem of west Malaysia. 1. Population density, biomass, carbon, nitrogen and calorific content and respiration rate. *Oecologia,* **22**: 153-178.

Matsumoto, T. & T. Abe, 1979. The role of termites in an equatorial rain forest ecosystem of west Malaysia. 2. Leaf litter consumption on the forest floor. *Oecologia,* **38**: 261-274.

Roisin, Y. & J. M. Pasteels, 1996. The nasute termites (Isoptera: Nasutitermitinae) of Papua New Guinea. *Invertebrate Taxonomy,* **10**: 507-616.

Roonwal, M. L. & P. K. Maiti, 1966. Termites from Indonesia including West Irian. *Treubia,* **27**: 63-140.

Tayasu, I., T. Abe, P. Eggleton & D. E. Bignell, 1997. Nitrogen and carbon isotope ratios in termites: an indicator of trophic habit along the gradient from wood-feeding to soil-feeding. *Ecological Entomology,* **22**: 343-351.

Thapa, R. S., 1981. Termites of Sabah. *Sabah Forest Record,* **12**: 1-374.

Tho, Y. P. 1982. *Studies on the taxonomy and biology of termites (Isoptera) of Peninsular Malaysia.* Ph.D. Thesis. University of Aberdeen. 685.

Tho, Y. P., 1992. Termites of Peninsular Malaysia. (Kirton, L.G. Ed.). *Malayan Forest Records*, No. **36**: 224 pp. Forest Research Institute Malaysia, Kepong.

Watson, J. A. L. & H. A. Abbey, 1993. *Atlas of Australian Termites.* CSIRO, Australia, Canberra. 155.

Wood, T. G. & W. A. Sands, 1978. The role of termites in ecosystems. In: Brian, M. V. (ed.), *Production ecology of ants and termites.* Cambridge University Press, Cambridge. pp. 245-292.