

## THE SPECIES RICHNESS AND COMPOSITION OF TERMITES (ISOPTERA) IN PRIMARY AND REGENERATING LOWLAND DIPTEROCARP FOREST IN SABAH, EAST MALAYSIA

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*Abstract.* Termite assemblage data are presented from 100 m transects (a standardised method consisting of 20 sections, each 5 x 2 m) conducted through three forest types (undisturbed "Primary", 17 year old "Old Secondary" and 3 year old "Young Secondary", with two transects per type) in Sabah, east Malaysia. Overall species richness was similar across the three sites, although soil feeding termites were most species rich in primary forest and wood feeders were most species rich in mature regenerating forest (Old Secondary sites). Primary and Young Secondary sites are more similar to each other in species composition than to the Old Secondary site, suggesting that, if the observed differences are due to ecological succession, there may be a lag time before compositional changes are detectable after disturbance. These results are strikingly similar to those found, using the same sampling methods, across a forest disturbance gradient in southern Cameroon. Accepted 28 December 1997.

*Key words:* species diversity, assemblage structure, tropical rainforest, selective logging, Borneo.

### INTRODUCTION

Termites are the dominant decomposer insects in tropical ecosystems (Wood & Sands 1978, Eggleton & Bignell 1995). Their major role in: maintaining soil fertility (Lee & Wood 1971, Wood 1988), decomposition processes (Peakins & Josens 1978, Wood & Johnson 1986) and the carbon cycle (Lawton *et al.* 1996, Bignell *et al.* 1997) and nitrogen cycle (Higashi *et al.* 1992, Tayasu *et al.* 1994) is just beginning to be appreciated fully. However, comparative data on the diversity of termites are scarce, and, given their ecological importance, there is a pressing need to characterise termite assemblage structure within and between forest types (Eggleton & Bignell 1995).

In recent papers Eggleton *et al.* (1995, 1996) presented termite assemblage data from sites subjected to varying degrees of forest disturbance in the Mbalmayo Forest Reserve (MFR), southern Cameroon. The conclusions of these studies were that complete clearance had a very strong impact on termite diversity, but that conversion to secondary forest (or single indigenous-species plantation) had little effect on termite species richness, but had clear

effects on termite assemblage composition (Eggleton *et al.* 1995, 1996). Disturbance affected soil-feeding termites most strongly, with a lesser effect on wood-feeders.

There are several reasons, however, why the results of the MFR study may not be applicable in other tropical forests. Differences in forest type, climate, soil structure and biogeographical history are important determinants of termite assemblage structure at a wide range of spatial scales (Eggleton *et al.* 1994). Therefore, studies in other tropical forests are needed (Bignell *et al.* 1997).

Relatively little is known about the community ecology of south-east Asian termites (but see, for instance, Matsumoto & Abe 1979; Abe & Matsumoto 1979; Abe 1978, 1979; Collins 1983, 1984, Jones *et al.* in press; Jones & Brendell in press), and, in that region there has also been only one study which examined differences in assemblages across varying levels of forest disturbance (Collins 1980). Here, we describe the termite assemblages of three forest types in lowland dipterocarp forest in Sabah, north Borneo, using the same (standardised) transect technique as used in the MFR study.

## METHODS

*Study area.* Three study sites were chosen in and around the Danum Valley Conservation Area (DVCA), Sabah, Malaysia (4°58'N and 117°48'E). The conservation area consists of lowland primary dipterocarp forest classified as tropical moist forest in the Holdridge life zone system (Holdridge *et al.* 1971). Mean rainfall is 2,700 mm per year, with mean daily temperatures of 26.7°C (Danum Valley Field Centre Records). Soils are generally Ultisols (Pinard & Putz 1996).

Outside the Conservation Area there are forest blocks that have been selectively logged at different times during the last 20 years and then left to regenerate. For this study we chose three different forest types to represent differing levels of forest disturbance.

1. *Primary forest (PF).* An area of forest was selected 1.3–1.5 km along the West Trail within the DVCA. This site was far enough from the river to remove any edge effects (see Didham 1997).

2. *Old secondary forest (OSF);* (The Coupe 1978 logging concession). An area of forest selectively logged in 1978 (i.e., 17 years before the sampling period). This area has been partially replanted with trees (FACE project), but these were only small saplings less than 2 m high during the sampling period. However, a small amount of disturbance had been caused by clearance of planting lines. This site was roughly 10 km east of the PF site.

3. *Young secondary (YSF);* (The Coupe 1992 logging concession). An area of forest selectively logged in 1992 (i.e., 3 years before the sampling period). This has extensive logging trails alongside patches of forest at different levels of disturbance. The logging trails have highly compacted soil with very little vegetation cover. The site was roughly 5 km east of the PF site.

In Sabah selective logging involves removing all mature trees (> 60 cm DBH) of commercial species (8–15 trees per ha). Typically, logs are removed to the road or storage areas by bulldozer, with as much as 30–40% of the area disturbed by the bulldozers (and thus left as skid trails), and 40–70% of remaining unlogged trees incurring damage (Pinard & Putz 1996). These represent extremely high levels of disturbance.

Soil characteristics of the forest types are given in Table 1. No data documenting the exact nature of the forests before disturbance were available, although all the sites were within about 10 km of each other, and were probably all originally mature lowland dipterocarp forest.

*Sampling methods and analyses.* (i) *Transect sampling.* We sampled along two 100 m belt transects of 2 m width in each site during a four week period, April–May 1995, giving us a total of six transects. Each transect was divided into twenty sections, each 5 m long and 2 m wide and sampled sequentially. Transect lines were placed to run through visually homogeneous habitats, except in YSF where the transects were chosen to run across representative parts of both forest and logging trails. Each section was sampled for a total of one person hour (30 minutes each for two workers experienced in termite transect sampling). The following microsites were investigated in detail: surface soil and litter down to a depth of about 5 cm, deep accumulations of litter and soil between large buttress roots, dead wood at all stages of decay, termite carton runways on tree trunks and other vegetation, and subterranean, epigeal and arboreal termite nests and mounds up to 2 m above ground level. This method does not sample termites that nest and feed exclusively below 5 cm, or termites nesting and feeding in arboreal dead wood. For full details of the methods see Davies (1997).

TABLE 1. Summary of soil parameters across the three forest types. Figures are means of 18 soil samples per forest type taken in August 1996. The figures are indicative of the forest types as a whole and are not specifically centred on the transect sites.

Site	pH (H <sub>2</sub> O)	Moisture	Organic C	Total N	C:N ratio
PF	3.9 ± 0.16	3.1 ± 0.75	3.7 ± 0.87	0.33 ± 0.11	11.2
OSF	3.6 ± 0.23	2.6 ± 0.68	3.4 ± 1.35	0.25 ± 0.07	13.6
YSF	4.5 ± 0.40	2.4 ± 1.14	3.0 ± 2.00	0.22 ± 0.12	13.6

Each pair of transects was in the same (roughly 5 ha) area and run at random angles to each other (no transects came closer than 100 m to each other). The transects were treated as replicates within each forest type for statistical purposes.

(ii) *Termite functional groups.* Accurate information on the natural history of many termite species is scarce, especially for soil feeders. However, we can recognise five broad feeding groups (see De Souza & Brown 1994; Eggleton & Bignell 1995; Eggleton *et al.* 1995, 1996):

1. *Soil feeders.* Termites distributed in the soil profile, surface litter (leaves and twigs), and/or epigeal mounds, feeding on mineral soil. There are at least three separate evolutionary acquisitions of the soil-feeding habit among the species collected during this study: in the Termitinae (the *Capritermes*-group and *Labritermes*), the Nasutitermitinae (the *Subulitermes*-group), and the Apicotermitinae (The *Anoplotermes*-group).

2. *Soil-wood interface feeders.* Termites feeding only or predominantly within soil under or plastered within logs, or feeding within highly decayed wood that has become friable and soil-like. This group is synonymous with "intermediate feeders" *sensu* De Souza & Brown (1994).

3. *Wood feeders.* Termites feeding on wood and excavating galleries in larger items of woody litter, which in some cases become colony centres. This group also includes termites having arboreal nests, and others having subterranean or epigeal nests in which fungus gardens are cultivated (*Macrotermite*-group).

4. *Litter foragers.* Termites that forage for leaf litter and small woody litter. This includes some subterranean and other mound building *Macrotermite*-group with fungal associates, as well as certain *Nasutitermitinae* that forage on the surface of the litter layer (e.g., *Longipeditermes* and some species of *Odontotermes*).

5. *Lichen feeders.* Termites that forage for lichens, mosses and algae on the bark of trees (*Hospitalitermes* only). There are no grass feeding species in the Danum Valley area.

(iii) *Statistical treatments.* Species accumulation curves were calculated using the SPPAREA program of the PC-ORD program (McCune 1987). This calculates the average richness of all possible species richness combinations of a single section, then all possible combinations of two sections and so on up to 20 sections.

An estimate of the actual number of species in each transect area was obtained by using the first-order jackknife estimator. The first order jackknife was chosen as it is the most precise nonparametric estimator of species richness (Palmer 1991). The necessary assumption that the transect sections were randomly sampled quadrats was supported by species richness autocorrelation levels (i.e., between successive transect sections), which were not above those expected by chance (analysis using SERIES module of SYSTAT, Wilkinson *et al.* 1992) even though the sections were contiguous.

Similarities in species composition between transects was examined by Two Way Indicator Species Analysis (TWINSPAN, Gauch 1982) using the PC-ORD program. A classification was established using this method, and expressed as a tree diagram.

## RESULTS

A total of 66 species were collected in the six transects (Table 2). Of these, 57 were described species, implying that roughly 14% of the species collected were new to science (a smaller proportion than the c. 30% found in Cameroon, Eggleton *et al.* 1995, 1996). The assemblage as a whole (as recorded from all transects) is dominated by Termitinae (42% of the total assemblage, with the soil-feeding *Capritermes*-group making up 30% of the total assemblage) and *Nasutitermitinae* (30% of the total assemblage, with wood- and litter-feeding species as 24% of the total assemblage). All other taxonomic elements are present at less than 11% of the total assemblage. Epigeal and arboreal nesting forms are relatively rare (less than 20% of the total assemblage), with wood and hypogeal nesting species most common (Table 2). The two *Euhamitermes* (*Apicotermitinae*) species recorded here are the first known records of the subfamily in Borneo.

There was no significant difference in species richness between transects as estimated by the first-order jackknife (Table 3). Fig. 1 shows the species accumulation curves for the six transects, again showing no obvious differences between the transects. The species richness differences between the forest types were insignificant (one-way ANOVA,  $F_{2,3} = 0.76$ ,  $P > 0.5$ ).

Species composition differed between forest types (Fig. 2). In all cases replicated transects within a forest type were more similar in termite species composition to each other than to other transects.

TABLE 2. Termite species collected across the six transects. Feed gp = feeding group; nest gp = nesting group. For feeding groups, l = litter feeders, lic = lichen feeders, s = soil feeders, s/w = soil/wood interface feeders, w = wood feeding, (f) = fungus growers. For nesting groups, a = arboreal, e = epigeal, h = hypogeal, w = in dead wood. Assignment to groups are based on our own observations and Collins (1984).

	PF1	PF2	OSF1	OSF2	YSF1	YSF2	Feed gp	Nest gp
<b>KALOTERMITIDAE</b>								
<i>Glyptotermes paracaudomunitus</i>			X				w	w(a)
<i>Glyptotermes brevicaudatus</i>			X				w	w(a)
<i>Glyptotermes</i> sp. B	X						w	w(a)
<b>RHINOTERMITIDAE</b>								
<i>Heterotermes tenuior</i>	X	X	X	X	X	X	w	h
<i>Coptotermes curvignathus</i>	X						w	w
<i>Coptotermes sepangensis</i>			X	X			w	w
<i>Parrhinotermes aequalis</i>			X			X	w	w
<i>Schedorhinotermes brevialetus</i>			X	X	X	X	w	w
<i>Schedorhinotermes javanicus</i>		X	X	X	X	X	w	w
<i>Schedorhinotermes sarawakensis</i>	X	X				X	w	w
<b>TERMITIDAE</b>								
<b>MACROTERTMITINAE</b>								
<i>Hypotermes xenotermis</i>			X	X	X	X	w(f)	h
<i>Macrotermes gilvus</i>			X	X			w/l(f)	e
<i>Macrotermes malaccensis</i>	X	X		X	X	X	w/l(f)	h
<i>Odontotermes oblongatus</i>	X			X	X	X	w(f)	h
<i>Odontotermes sarawakensis</i>	X	X	X	X	X		w(f)	h
<i>Odontotermes</i> sp. C			X	X			w(f)	h
<b>APICOTERMITINAE</b>								
<i>Euhamitermes</i> sp. 1	X				X		s	h
<i>Euhamitermes</i> sp. 2		X			X	X	s	h
<b>TERMITINAE</b>								
<i>Microcerotermes dubius</i>		X	X	X			w	e
<i>Microcerotermes serrula</i>	X	X	X	X	X	X	w	w
<i>Protophamitermes</i> sp. n. 1		X					s/w	h
<i>Globitermes globosus</i>	X	X		X	X		w	h
<i>Prohamitermes mirabilis</i>		X	X	X	X	X	s/w	h
<i>Termes borneensis</i>				X		X	s/w	e/w
<i>Termes popiniquus</i>		X					s/w	e/w
<b>Capritermes-group:</b>								
<i>Mirocapritermes connectens</i>	X	X	X	X	X	X	s	h
<i>Homalotermes exiguus</i>	X						s/w	w
<i>Dicuspiditermes nenorosus</i>			X				s	e
<i>Dicuspiditermes santschii</i>				X			s	e
<i>Coxocapritermes</i> sp. A	X	X					s	h
<i>Pericapritermes</i> sp. A	X	X		X		X	s	h
<i>Pericapritermes nr. dolichocephalus</i>		X	X		X	X	s	h
<i>Pericapritermes nr. nitobei</i>	X	X	X	X	X		s	h
<i>Pericapritermes ?semarangi</i>	X	X	X	X	X	X	s	h
<i>Oriencapritermes</i> sp. A	X	X	X	X	X	X	s	h
<i>Syncapritermes</i> sp. A					X		s	h

TABLE 2. Continued.

	PF1	PF2	OSF1	OSF2	YSF1	YSF2	Feed gp	Nest gp
<i>Procapritermes neosetiger</i>	X	X	X	X	X	X	s	h
<i>Procapritermes</i> sp. A	X	X		X	X	X	s	h
<i>Procapritermes</i> sp. B	X	X		X			s	h
<i>Procapritermes</i> sp. C	X	X	X				s	h
<i>Procapritermes minutus</i>	X	X		X		X	s	h
<i>Procapritermes</i> nr. <i>sandakanensis</i>	X	X	X	X	X	X	s	h
<i>Malaysiocapritermes prosetiger</i>	X	X		X			s	h
<i>Capritermes</i> -group gen. et sp. nov.						X	s	h
<i>Labritermes emersoni</i>				X			s	h
<i>Labritermes kistneri</i>		X					s	h
NASUTITERMITINAE								
<i>Subulitermes</i> -group:							s	h
<i>Aciculoiditermes</i> sp A		X	X				s	h
<i>Proaciculitermes</i> sp. A	X	X		X	X	X	s	h
<i>Proaciculitermes</i> sp.B	X	X					s	h
<i>Proaciculitermes</i> sp. C			X				s	h
<i>Subuloiditermes</i> sp A					X		s	h
<i>Nasutitermes</i> -group:								
<i>Nasutitermes</i> sp A						X	w	a
<i>Nasutitermes</i> sp. B					X		w	a
<i>Nasutitermes longinatus</i>		X	X		X		w	a/w
<i>Nasutitermes matangensisformis</i>						X	w	a
<i>Nasutitermes neoparvus</i>			X	X			w	a
<i>Bulbitermes flavicans</i>			X	X	X	X	w	a
<i>Bulbitermes</i> sp. A	X	X		X	X	X	w	a
<i>Bulbitermes</i> sp. C		X		X			w	a
<i>Hirtitermes spinocephalus</i>			X				w	w
<i>Longipeditermes longipes</i>	X				X		l	h
<i>Havilanditermes atripennis</i>	X					X	l	h
<i>Hospitalitermes hospitalis</i>					X		lic	a
TOTALS	29	33	29	33	29	28		

The YSF and PF transects are in turn more similar to each other than to the OSF transects.

Feeding group composition of the three sites is shown in Fig. 3. The proportions of soil and wood feeders differed between the forest types, with soil feeders having their highest species richness in the PF site and lower species richness in the OSF and YSF site (this difference was not statistically significant; one-way ANOVA,  $F_{2,3} = 5.26$ ,  $P = 0.1$ ). Conversely, wood feeders were most species rich in the OSF site and less species rich in the other two sites (one-way ANOVA,  $F_{2,3} = 63.5$ ,  $P < 0.01$ ) Soil/wood interface feeders, litter feeders and lichen feeders

TABLE 3. Actual species richness and jackknife ( $\pm 95\%$  confidence limits) estimates of species richness for the six forest sites.

Site	actual spp. richness	estimated spp. richness (1st order jackknife)
PF1	29	38 $\pm$ 7
PF2	33	48 $\pm$ 7
OSF1	29	42 $\pm$ 9
OSF2	33	43 $\pm$ 7
YSF1	29	37 $\pm$ 5
YSF2	28	36 $\pm$ 6

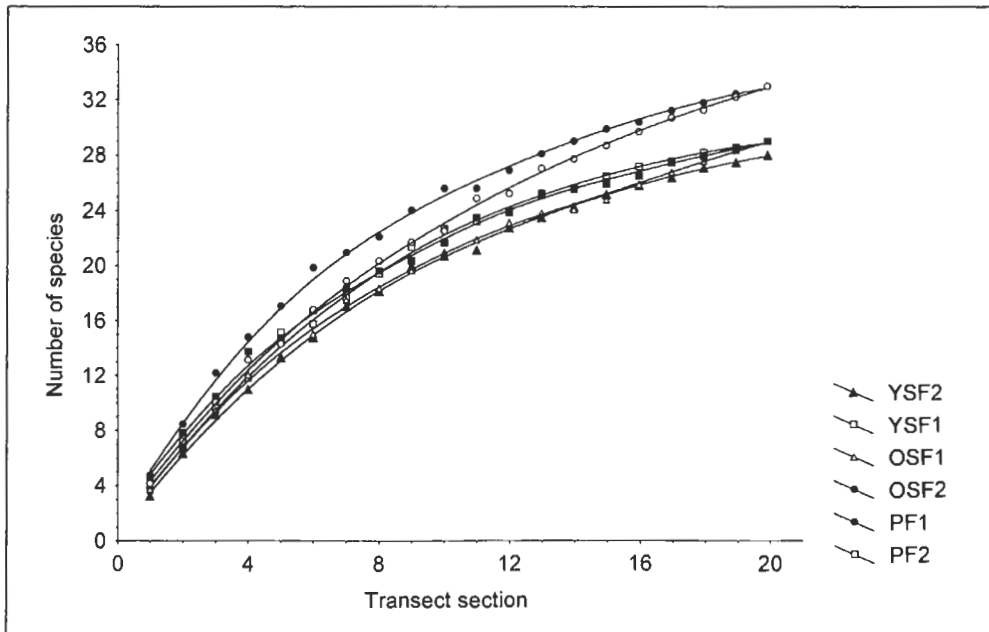


FIG. 1. Species accumulation curves for the six forest sites. The curves, for illustrative purposes only has been fitted using Distance Weighted Least Squares by the SYSTAT statistical package.

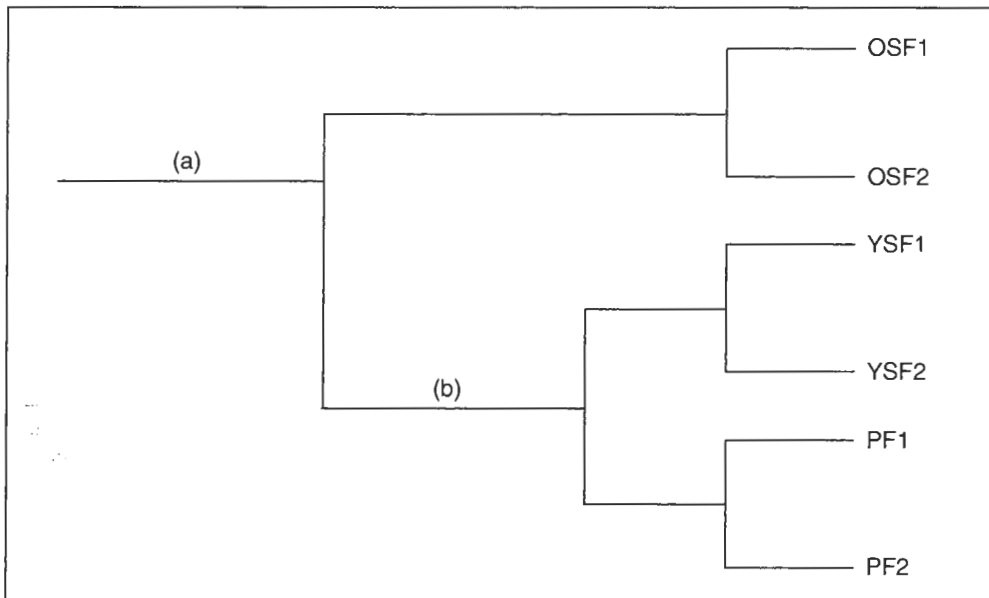


FIG. 2. TWINSPAN classification of sites presented as a tree diagram. Branch lengths are arbitrary. Species preferentials are given in Table 4.

make up a relatively small proportion of the assemblage and do not differ greatly across the forest types.

These conclusions are supported by the TWINSPAN analysis (Fig. 2, Table 4) where the species preferentials are predominantly soil + soil-wood interface feeders on the YSF + PF side of the first division (6:1) and predominantly wood + litter feeders on the OSF side of the first division (9:5). In turn there are more soil/soil-wood interface feeders on the PF side of the subsequent (second) division (8:3), than on the YSF side, and the same number of wood/litter feeders (5:5) on both sides of the second

division. The difference between PF and YSF is due predominantly to the loss of the soil-feeding *Capritermes*-group species in YSF (50% of the preferentials on the PF side of the division).

## DISCUSSION

Clear differences were observed in the termite species composition of the three forest types. These differences are similar to those described by Collins (1980) in Sarawak, although his sites were more disturbed and his sampling methods are not strictly

TABLE 4 a, b. Species preferentials for each split of the TWINSPAN analysis (Fig. 2). Soil feeders include soil/wood interface feeders; wood feeders include litter feeders.

### (a) PF + YSF versus OSF

PF + YSF	OSF
<i>Schedorhinotermes sarawakensis</i>	<i>Coptotermes sepangensis</i>
<i>Macrotermes malaccensis</i>	<i>Schedorhinotermes breviaulatus</i>
<i>Eubamitermes</i> sp. 1	<i>Hypotermes xenotermitis</i>
<i>Eubamitermes</i> sp. 2	<i>Macrotermes gilvus</i>
<i>Coxocapritermes</i> sp. A	<i>Odontotermes</i> sp. C
<i>Procapritermes</i> sp. A	<i>Microcerotermes dubius</i>
<i>Procapritermes</i> sp. B	<i>Aciculioiditermes</i> sp. A
<i>Procapritermes</i> sp. C	<i>Nasutitermes neoparvus</i>
<i>Longipeditermes longipes</i>	<i>Bulbitermes flavicans</i>
<i>Havilanditermes atripennis</i>	<i>Bulbitermes</i> sp. C
<i>Bulbitermes</i> sp. A	
Soil 6: Wood 5	Soil 1: Wood 9

### (b) PF versus YSF

PF	YSF
<i>Schedorhinotermes sarawakensis</i>	<i>Schedorhinotermes breviaulatus</i>
<i>Odontotermes sarawakensis</i>	<i>Schedorhinotermes javanicus</i>
<i>Microcerotermes dubius</i>	<i>Hypotermes xenotermitis</i>
<i>Globitermes globosus</i>	<i>Odontotermes oblongatus</i>
<i>Coxocapritermes</i> sp. A	<i>Eubamitermes</i> sp. 2
<i>Pericapritermes</i> sp. A	<i>Prohamitermes mirabilis</i>
<i>Pericapritermes</i> nr. <i>nitobei</i>	<i>Pericapritermes</i> nr. <i>dolichocephalus</i>
<i>Malaysiocapritermes prosetiger</i>	<i>Bulbitermes flavicans</i>
<i>Procapritermes</i> sp. B	
<i>Procapritermes</i> sp. C	
<i>Procapritermes minutus</i>	
<i>Aciculioiditermes</i> sp. A	
<i>Bulbitermes</i> sp. C	
Soil 8: Wood 5	Soil 3: Wood 5

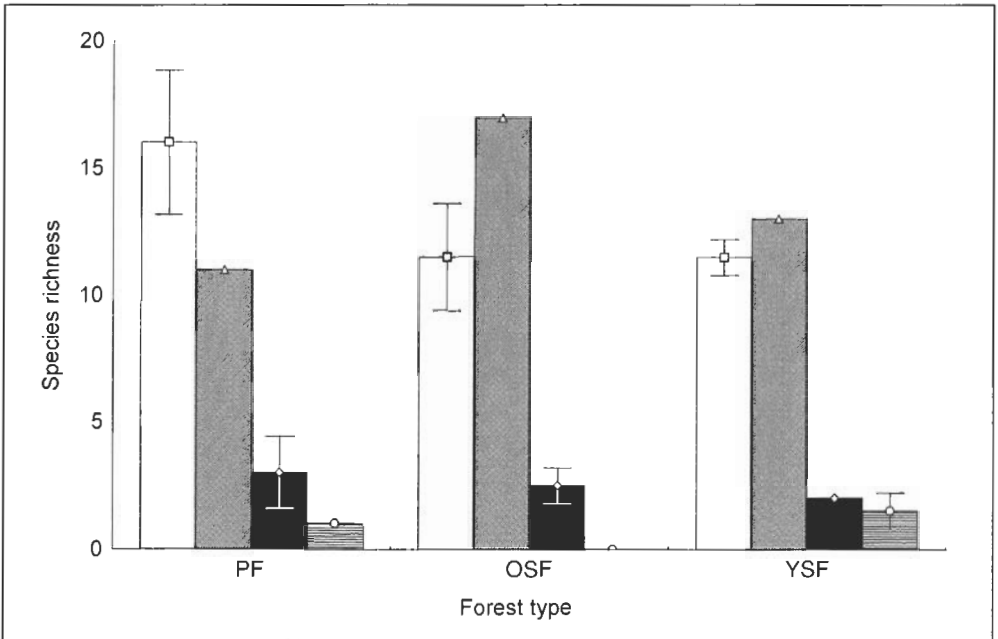


FIG. 3. Species richness of feeding groups in each of the three forest types. Totals are means of the two transects per forest type, with standard deviations as error bars. Soil-feeders – unhatched bar; wood-feeders – diagonal hatched, left low, right high; soil-wood feeders – black bar; litter-feeders – horizontal hatch. Lichen-feeders were found only in YSF1.

comparable with ours. They are more similar, however, to those found in the directly comparable Cameroon studies (Eggleton *et al.* 1995, 1996) especially when considering functional groupings and overall assemblage composition.

In both this study and the MFR study there was little overall difference in termite species richness between regenerating and primary forest types, but this seemed to be due to a roughly compensating balance between soil feeding and wood feeding termites across the forest types. In addition, in both studies the termite assemblages of the “young forest” plots (YSF in Sabah, YP in Cameroon) appear to be more similar in composition to mature primary forest (PF in Sabah, NP in Cameroon) than to those of older regenerating forest (OSF in Sabah, OSF in Cameroon) (Fig. 2).

It is tempting to interpret these clear parallel differences between forest types in both the Sabah and Cameroon studies as due to the effects of disturbance. However, we were not able to replicate sites properly in either case due to the limited number of accessible

forest sites and time constraints. This has meant that we have a limited idea of the variation within sites, and so measured differences between sites may be due to pre-logging differences in general forest structure, microclimate, or soil conditions rather than due to true effects of disturbance. In Sabah, PF and YSF sites were located closer to each other than they were to OSF, and this may partially explain the compositional characteristics of the forest types.

Disturbance is, however, an obvious plausible explanation for some of the differences between forest types, especially as the conditions are so similar in both the Cameroon and Sabah studies. Both the functional group differences and the taxonomic compositional differences are discussed in this context below.

Physical disturbance of the soil, in addition to the drying out caused by the opening of the canopy after disturbance, probably has an adverse effect on soil-feeding termites (Eggleton *et al.* 1995, 1996). Soil-feeders are poorly protected from desiccation and require a well structured, organic rich soil for colony development. (moreover, in Sabah skid trails within



regenerating forest represent areas of highly compacted soil that are extremely poor microhabitats for soil feeding termites). The soil characteristics of the forest types (Table 1) seem to support these general conclusions: PF had higher moisture, organic carbon and total nitrogen levels (and concomitant lower pH and C:N ratio levels) than YSF, while OSF had intermediate levels of these characteristics. Similar results are reported in Eggleton *et al.* (1996).

In contrast to soil feeders, wood feeders and litter feeders, which forage on the surface or inside logs may be less affected by disturbance, and may even benefit from the greater organic input from the disturbance. The two factors acting on feeding group composition (soil degradation and increased dead wood input) may be working in roughly equal opposition to each other.

The largest differences in soil-feeder richness between the PF and OSF plots is due to *Capritermes*-group species (PF1 = 14 species, PF2 = 15; OSF1 = 9, OSF2 = 13), although the total number collected in each of the two forest sites was the same (16). Species similarities (within the *Capritermes*-group) between paired transects were concomitantly higher in PF (Jaccard's similarity index  $S_j = 0.81$ ), than in OSF ( $S_j = 0.38$ ), suggesting that the OSF site may be more heterogenous than the PF site. This may be due to a mosaic of different decay rates of the dead wood within the regenerating forest, allowing a range of termite species to be present in a variety of small-scale microsites.

The compositional similarity between young and mature forest systems was discussed in Eggleton *et al.* (1996) where it was conjectured to be due to similarities between sites in the dynamics of soil feeder mound growth, senescence and recolonisation. In Sabah, however, soil-feeding mound builders make up a very small proportion of the termite species in the Danum Valley area and they are not represented as preferentials linking the YSF and PF plots together in the TWINSPLAN analysis. A more likely common explanation is that selective logging of primary forest, although having a long term detrimental effect on "deep forest" soil feeding termite colonies, does not immediately cause them all to die. There may, therefore, be a lag time (greater than three years) between logging and obvious changes in the termite assemblage structure. The related question of whether regenerating forest ever returns to a state allowing the original termite assemblage structure to be restored is clearly an important area for further research.

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