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Termite assemblages, forest disturbance and greenhouse gas fluxes in Sabah, East Malaysia

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A synthesis is presented of sampling work conducted under a UK government-funded Darwin Initiative grant undertaken predominantly within the Danum Valley Conservation Area (DVCA), Sabah, East Malaysia. The project concerned the assemblage structure, gas physiology and landscape gas fluxes of termites in pristine and two ages of secondary, dipterocarp forest. The DVCA termite fauna is typical of the Sunda region, dominated by *Termes*-group soil-feeders and Nasutitermitinae. Selective logging appears to have relatively little effect on termite assemblages, although soil-feeding termites may be moderately affected by this level of disturbance. Species composition changes, but to a small extent when considered against the background level of compositional differences within the Sunda region. Physiologically the assemblage is very like others that have been studied, although there are some species that do not fit on the expected body size–metabolic rate curve. As elsewhere, soil-feeders and soil–wood interface-feeders tend to produce more methane. As with the termite assemblage characteristics, gross gas and energy fluxes do not differ significantly between logged and unlogged sites. Although gross methane fluxes are high, all the soils at DVCA were methane sinks, suggesting that methane oxidation by methanotrophic bacteria was a more important process than methane production by gut archaea. This implies that methane production by termites in South-East Asia is not contributing significantly to the observed increase in levels of methane production worldwide. Biomass density, species richness, clade complement and energy flow were much lower at DVCA than at a directly comparable site in southern Cameroon. This is probably due to the different biogeographical histories of the areas.

Keywords: biodiversity; Isoptera; landscape gas fluxes; dipterocarp forest; energy flows

1. INTRODUCTION

Termites dominate tropical forest soils. Their role in decomposition processes is well known (Bignell & Eggleton 1999; Wood & Sands 1978), while their contributions to gas exchanges (Bignell *et al*. 1997), nitrogen fixation (Tayasu *et al*. 1997), and soil stability and quality (Wood 1988; Bignell *et al*. 1997) are just beginning to be revealed. However, there are still relatively few comprehensive studies of termites in tropical forests. A particularly uncertain area is methane fluxes, where termites have been implicated as possibly significant global sources of methane (e.g. Zimmerman *et al*. 1982; Bignell *et al*. 1997), although this has been vigorously contested (Khalil *et al*. 1990).

The Sunda region (defined here as Peninsular Malaysia, Sumatra, Borneo, Java and associated islands to the east) is probably the best known area for tropical termites in the world (Eggleton 1999). Good taxonomic accounts exist for Peninsular Malaysia (Tho 1992) and Sabah (Thapa 1981). There have also been a number of ecological studies within west Malaysia and Thailand, using forms of randomized sampling (Abe 1978, 1979; Abe & Matsumoto 1979). Within

Borneo, the most comprehensive quantitative sampling remains Collins's (1984) work on Gunung Mulu.

This paper represents a synthesis of the termite ecological, physiological and systematic work undertaken within the Danum Valley Conservation Area (DVCA) under a UK government, Department of the Environment-funded Darwin Initiative grant, 1994–1996.

(a) *The Darwin Initiative project*

This project grew out of discussions regarding collaborative work between the Universiti Malaysia Sabah (UMS) and the Termite Research Group of the Natural History Museum, London. In Sabah it is recognized as a priority to document and explore the effects of forest disturbance on biodiversity and ecosystem processes, integrating the results into the improvement of forestry and environmental management practices, and the promotion of biodiversity conservation. Termites and (associated) methane fluxes were chosen, respectively, as models in a project on the termites of Sabah.

The project also had an important training element. In early 1995, there was relatively little expertise in termite taxonomy, community ecology and physiology in Malaysia. However, a consortium of UK scientists with

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appropriate skills had been formed concurrently under the Terrestrial Initiative in Global Environmental Research (TIGER) programme (funded through the Natural Environment Research Council) to work in comparable rainforest ecosystems in Cameroon, West Africa. This consortium was therefore allocated an advisory and supervisory role in the Sabah project. This had the advantage of allowing the most recent termite sampling protocols to be employed in Malaysia, very soon after their development in Africa (see Eggleton *et al.* 1995, 1996; Eggleton & Bignell 1995). It also permitted a major training element to be introduced into the project, using the large and actively curated termite collections of the Natural History Museum, London. The project therefore incorporated the twin aims of re-establishing indigenous Malaysian taxonomic expertise on termites and laying the foundations for the establishment of good reference collections within the country (at UMS). A major additional benefit to all participants would be the acquisition of two directly comparable data sets on the responses of rainforest ecosystems to disturbance in two biogeographically separated sites: in Sabah and Cameroon.

Studies of biodiversity and large-scale ecological processes in tropical ecosystems had been undertaken predominantly by scientists from developed countries. Studies conducted by scientists of the host country were long overdue, and the information gained would, hopefully, be more easily integrated into forestry practice and environmental management policies because of direct host country participation. Also, there is a great need for the training of taxonomists and building good reference collections within developing countries, in order to acquire accurate baseline data for conservation. The link between current ecological questions and the development of basic taxonomic skills was seen as doubly empowering for the Malaysian scientists involved.

The project had the following objectives:

1. To conduct a faunistic and taxonomic survey of the termites of a typical Bornean dipterocarp forest.
2. To examine the effects of typical logging disturbance on termite assemblage structure and associated ecophysiological processes, especially energy and methane fluxes.
3. To characterize the assemblage functionally and physiologically (mainly through gas exchanges).
4. To scale up predicted gas exchanges to ecosystem levels and make measurements of actual gas fluxes from mounds and soil.
5. To compare and contrast all these data with those from a parallel system from southern Cameroon.

In this paper we present a summary of the results of studies (points 1–4 above) published in detail elsewhere (Eggleton *et al.* 1997; Jeeva *et al.* 1999; MacDonald *et al.* 1999; R. Homathevi, unpublished data), and focus on the synthesis and comparison (point 5 above).

2. METHODS

(a) *Study sites*

Three study sites were chosen in and around the DVCA, Sabah, Malaysia ($4°58'$ N, $117°48'$ 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 $2700\,mm\,yr^{-1}$, with mean daily temperatures of $26.7\,°C$ (DVFC Records). Soils are generally Ultisols (Pinard & Putz 1996).

DVCA offers a large but generally well-documented study area, hosting numerous other scientific projects designed to address rainforest processes and conservation, and with good records of historical land uses, including logging.

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

(i) *Primary forest (PF)*

An area of pristine, high dipterocarp forest, located along the West Trail at 1.3–1.5 km distance from the Segama River and free of edge effects from the river and associated roads (see Didham *et al.* 1998).

(ii) *Old secondary forest (OSF)*

An area of forest selectively logged in 1978 (i.e. 17 years before the sampling period) (the Coupe 1978 logging concession). This area has been partially replanted with trees (FACE project), but these were only small saplings less than 1 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.

(iii) *Young secondary forest (YSF)*

An area of forest selectively logged in 1992 (i.e. three years before the sampling period) (the Coupe 1992 logging concession). This has extensive logging trails alongside patches of secondary forest at different levels of disturbance. The logging trails have highly compacted soil with very little vegetation cover. However, the secondary forest areas generally had complete or almost complete canopy cover. The plots were roughly 5 km east of the PF site.

In Sabah selective logging involves removing all mature trees (>60 cm diameter at breast height (dbh)) of commercial species (8–15 trees ha^{-1}). 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.

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.

We used these three study sites in all the ecological, physiological and atmospheric chemistry work.

(b) *Sampling protocols*

Two discrete standardized sampling protocols were employed. The first was a 100 m belt transect and the second was a quantitative sampling regime consisting of a 50 m × 50 m plot. Within each forest type two transects and three plots were sampled. The transects were run close to but not inside the plots.

This sampling programme represented a trade-off between the competing needs of the project. The set-up was not ideal statistically for some comparisons, as pseudoreplication within each sampling area in effect reduced sample sizes to $n = 3$ for

plots and $n = 2$ for transects (thus leading to possible type II statistical errors—accepting null hypotheses when they are false). This was despite the large number (20, see below) of quadrats per sampling area. However, for the atmospheric chemistry and biomass density work a plot-based approach constituted a self-contained arena within which we could investigate soil, wood and mounds in a strictly comparable way. As with much tropical ecology, the statistical rigour that is possible in planned experiments in temperate regions was not achieved. This was because of habitat heterogeneity, a lack of time and the conflicting demands on it, and the physical difficulties of working in tropical environments.

(i) *Transect surveys (TS)*

These are intended to give a rapid but robust assessment of species richness within a given area (see Jones & Eggleton (1999) for the statistical rationale for this claim). However, they provide only approximate information concerning the relative abundances of particular species.

Sampling was conducted along 100 m belt transects. Each transect was divided into 20 sections, each 5 m long and 2 m wide, and sampled sequentially. Transect lines were placed to run through visually homogeneous habitats. Each section was sampled for a total of one person-hour (30 min 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 5–10 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. Representative samples of termites were preserved in 80% alcohol. The number of termite 'encounters' gave a rough measure of termite abundance. 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 Eggleton *et al.* (1997) and Davies (1997). We ran two transects per site in June–July 1995.

(ii) *Quantitative density surveys (QDS)*

These give population and biomass density estimates for termites within a defined sampling area, including rarer mound building species. However, they have proven to be less effective for estimating species richness (Jones & Eggleton 1999). QDS is very labour intensive.

Each plot consisted of a 50 m × 50 m area (0.25 ha) with an internal grid (10 m separation) marked out with string to facilitate quadrat placement and mapping. Within each plot three sampling methods were employed:

1. Randomly generated coordinates were used to locate 20 quadrats, each 2 m × 2 m. Quadrats falling on standing trees or other obstacles were reassigned new random coordinates. Within each quadrat, all dead wood and litter was removed to a work area outside the plot and hand-sorted on site by trained assistants. The woody material was opened and all termites extracted and preserved in 90% alcohol. Subsampling was sometimes necessary when woody litter was highly abundant within a quadrat.
2. After removing the wood and litter, a single soil pit of 30 cm × 30 cm × 25 (depth) cm was dug from the centre of the quadrat and hand-sorted on site.
3. Finally, a systematic survey of mounds and nests was carried out over the entire area of the plot, making use of the

existing grid system. Each mound was mapped and destructively sampled. Termite numbers were obtained by direct counting or by a subsampling procedure (Eggleton & Bignell 1995; Eggleton *et al.* 1996).

(iii) *Analysis of data*

Here we summarize the results of TS and QDS for species richness, abundance and biomass density. Full statistical results have been, or will be, published elsewhere (Eggleton *et al.* 1997; R. Homathevi, unpublished data). In addition, we analyse species diversity and relative abundance (broadly characterized here as 'assemblage composition') across a broader geographical scale. For this, termite encounter data from the QDS (the wood quadrats, soil pits and mound mapping) were combined with the TS to form a single pooled set for the following samples: the 18 DVCA samples (nine QDS, six transects, three 'training' transects); two transects from two habitat types (lower montane and upper montane forest; *sensu* Jones *et al.* 1998) in the Maliau Basin; a mid-altitude (1000 m) site in central Sabah (Jones *et al.* 1998; Jones 1999); one transect in a primary forest site at the Pasoh Forest Reserve, Peninsular Malaysia (Jones & Brendell 1998); and one transect in a primary forest site in Jambi, Central Sumatra (D. T. Jones, unpublished data). We hoped thereby to put the Danum work into a broader context.

Initial data analysis of this extended data set was by detrended correspondence analysis (Ter Braak 1987). Subsequently we used Monte Carlo tests within a canonical correspondence analysis (CCA; Ter Braak 1987) to assess the statistical significance of environmental variables on species composition. These variables were nested as follows to give a series of comparisons at different spatial–habitat scales: forest–regional type (primary dipterocarp Sabah, primary dipterocarp Sumatra, primary dipterocarp Peninsular Malaysia, young secondary dipterocarp Sabah, old secondary dipterocarp Sabah, lower montane Sabah, lower montane heath forest Sabah), altitude (lowland, montane) and region (Sabah, Peninsular Malaysia, Central Sumatra). Environmental variables were treated as three sets of nominal variables as they could not easily be measured along a linear or rank scale. Method of collecting (TS, QDS) was treated as a covariable (i.e. its effect was 'partialled out', that is, removed statistically), on the assumption that its effect was of no biological interest. Only the results of the partial CCA are shown, as both DCA and CCA give essentially similar axes of variation in the same order of statistical importance.

(c) *Physiological measurements*

O_2 uptake and CO_2 release (abbreviated as xO_2 and xCO_2 below) at 28 °C were determined (in the worker caste) in 26 species from the DVCA assemblage, using classic Warburg manometry (Umbreit *et al.* 1964). The species selected constituted approximately 30% of the assemblage and represented all five of the major feeding groups encountered. CH_4 fluxes (at 26 °C) were determined simultaneously by incubating additional batches of the same termites (20 species) in closed containers and analysing the headspace composition by gas chromatography, after transporting sealed subsamples to the UK. The incubations were generally considered satisfactory, except that gas fluxes during the first 30 min of confinement were irregular.

The main purpose of these assemblage-wide gas flux measurements was to combine estimates of actual gas emissions by termites with accurate biomass data, to produce locality and landscape-level budgets for termite-mediated energy use

(cf. Eggleton *et al.* 1998) and carbon mineralization as both CO_2 and CH_4 (cf. Bignell *et al.* 1997). This approach represents an important advance on earlier studies where calculations have been based on estimates of the consumption rate of organic matter, with the application of arbitrary conversion ratios for gas production (reviewed in Sanderson 1996). However, it has also been possible to compare the gas exchanges and metabolic rate characteristics of DVCA termites in a range of feeding groups and taxa with an equivalent but phylogenetically unrelated assemblage in the Mbalmayo Forest Reserve, Cameroon, which was examined by the same methods (Eggleton *et al.* 1996; Bignell *et al.* 1997). A final application of the laboratory data is the prediction of gross CH_4 emissions in termite mound populations (as point sources in the landscape), for comparison with the actual effluxes observed from nests (MacDonald *et al.* 1999). As almost all existing information on termite respiration and gas exchanges (especially CH_4 emissions) has come from tropicopolitan species or assemblages outside South-East Asia, the DVCA results are a significant addition to our knowledge of termite physiology, characterizing the large oriental forest region.

Warburg manometry for O_2 and CO_2, and headspace gas analysis for CH_4, are convenient for determining gas exchanges under field conditions or in field laboratories, as the apparatus is indefinitely serviceable with simple maintenance and power is required only for a single water bath. The data produced are reciprocal in the sense that determinations of CH_4 efflux are necessary as correction factors for manometric volume changes (Nunes *et al.* 1997), and because methanogenesis can then be assessed across a range of termite species with different feeding habits, with varying body sizes and metabolic rates. The disadvantage of the methods is that H_2, another minor gaseous product of termite intestinal fermentation (Slaytor *et al.* 1997), cannot be reliably measured without sophisticated equipment, and was therefore excluded from the determinations.

(d) *Atmospheric chemistry*

For methane measurements, we examined the actual fluxes from soil and mounds using static chambers. Measurements were made over the 20 soil pit quadrats (as described above) before they were dug so that termite biomass could be related to methane fluxes. For full technical details see MacDonald *et al.* (1999). Twenty flux measurements were made at each site.

Mounds in each plot were mapped and CH_4 flux measurements made from a representative selection, with minimal disturbance. The mounds included: *Dicuspiditermes nemorosus*, *Dicuspiditermes santschii*, *Bulbitermes* sp. C and *Prohamitermes mirabilis*. The mounds were then destructively sampled (or subsampled) to obtain the numbers of termites they contained. In some cases, mounds were removed to the laboratory and further determinations of CH_4 fluxes made (also by static chambers) before destruction. In such cases, a seal at the base of the chambers was obtained by standing mounds on a large plastic sheet on a level concrete floor, before placing the static chamber over them and closing the base with Plasticine. Overall, the procedures enabled actual and predicted CH_4 fluxes from mounds to be compared.

Atmospheric methane concentration profiles were estimated by sampling ambient drawn through polypropylene tubing at heights above the ground of 50 cm, 2 m and 5 m. Litre samples were withdrawn using a gas-tight syringe (Hamilton) and stored in tedlar bags. Samples were analysed by tunable diode laser spectroscopy (TDL). Samples were taken at three intervals between 08.00 and 17.00. Samples were not taken in the young secondary forest.

Soil temperature, soil moisture and dry bulk density were all measured routinely during flux measurements.

3. RESULTS AND DISCUSSION

(a) *Faunistics*

A total of 93 species in 37 genera have been recorded from DVCA (table 1). This is only ten fewer species than recorded in a taxonomic survey of the whole of Sabah based on all available material (Thapa 1981). Two genera and species are definitely new to science, while there is an uncertain number of potentially new species to which we could not assign names (*ca.* 40 of which < 25 are probably new).

In biomass terms, the system is dominated by wood-feeders. However, the proportionally most species-rich group in the DVCA is the *Termes*-group Termitinae (table 1), soil and highly decayed wood inhabitants, all with highly characteristic snapping (generally more or less asymmetrical) soldier mandibles (Krishna 1968). About half of these species are present at low biomass densities ($< 10 \, \mathrm{mg \, m^{-2}}$). Species of this group appear not to be true soil feeders (S. E. Donovan, unpublished data), but probably feed on highly diluted, but still recognizable dead plant material. The group is found throughout the tropics, but has one of its highest richnesses in the Sunda region (Eggleton 1999). One species within this group is clearly of an undescribed genus and the clade within the Sunda region is presently being revised (R. Homathevi, unpublished data).

The other major group found at DVCA is the snouted termites (Nasutiterminae), which have the highest combined biomass density of any group. They show a wide range of feeding habits at DVCA, including wood-, litter-, microepiphyte-, soil–wood interface- and soil-feeding (although, again, they appear not to be feeding as far along the humification gradient as other termite clades). Among the Nasutitermitinae the wood-feeding *Bulbitermes* and *Nasutitermes* reach the highest biomass densities at DVCA. The oriental soil-feeding Nasutitermitinae have often been placed in a putative clade (the *Subulitermes*-group, see Ahmad (1968)) along with apparently similar forms in South America and Africa. However, our studies (and those of Sands (1965, 1998)) suggest that all of the soil-feeding Nasutitermitinae in DVCA are best placed in another genus group, close to the wood-feeding *Nasutitermes*.

The *Amitermes* group (Termitinae), although not particularly diverse (only seven species at DVCA; table 1), has four species (*Microcerotermes serrula*, *Microcerotermes dubius*, *Prohamitermes mirabilis* and *Globitermes globiceps*) that are very common wood- and wood–soil interface-feeders in all the forested habitats, and so add disproportionately to overall biomass density. *Microcerotermes dubius* is particularly interesting, as it is one of the few termites in tropical forests to feed on, and kill, living trees (Tho 1992).

Although probably of great functional importance, the fungus-growing termites (Macrotermitinae) are relatively poorly represented in the DVCA, with only three genera, *Macrotermes*, *Odontotermes* and *Hypotermes*. Of these, *Macrotermes gilvus* reaches high biomass densities only in the more disturbed areas.

Rhinotermitidae are commonly encountered in dead wood in the DVCA, but make up only a moderate

Table 1. *List of the 93 species collected during the Darwin project*

((*a*) Feeding group (W, wood-feeding; L, litter-feeding; E, epiphyte-feeding; I, soil–wood interface-feeding; S, soil-feeding); (*b*) number of times encountered using both TS and DQS; and (*c*) average biomass density (mg m^{-2}) across all sites as estimated by QDS. Species found only by casual collecting or only in transects are marked as C or TS respectively. Clade classifications follow Kambhampati & Eggleton (1999). Data are shown across all sites due to the absence of clear differences between sites in this study and can be thought of as indicative of the forest system as a whole (i.e. a mosaic of gaps, edges, logged areas and primary forest).)

species	(*a*)	(*b*)	(*c*)
Kalotermitidae			
Glyptotermes sepilokensis Thapa	W	2	1.44
Glyptotermes paracaudomunitus Thapa	W	4	1.73
Glyptotermes brevicaudatus (Haviland)	W	2	0.73
Glyptotermes sp. A	W	1	0.04
Glyptotermes sp. B	W	1	TS
subtotals		**10**	**3.96**
Rhinotermitidae			
Heterotermes tenuior (Haviland)	W	78	205.71
Coptotermes curvignathus Holmgren	W	2	TS
Coptotermes sepangensis Krishna	W	5	0.38
Coptotermes kalshoveni Kemner	W	1	TS
Parrhinotermes aequalis (Haviland)	W	8	3.00
Schedorhinotermes sarawakensis	W	20	129.09
Schedorhinotermes javanicus Kemner	W	24	10.86
Schedorhinotermes brevialatus (Haviland)	W	8	3.26
subtotals	**146**	**352.25**	
Termitidae			
Macrotermitinae			
Macrotermes malaccensis (Haviland)	WL	26	13.50
Macrotermes gilvus (Hagen)	WL	15	312.45
Odontotermes oblongatus Holmgren	W	18	23.05
Odontotermes sarawakensis Holmgren	W	48	21.28
Odontotermes sp. B	W	1	0.48
Odontotermes sp. C	W	7	47.73
Hypotermes xenotermitis (Wasmann)	W	17	1.98
Hypotermes sp. A	W	8	58.77
subtotals		**140**	**479.24**
Apicotermitinae			
Anoplotermes-group			
Euhamitermes sp 1	S	7	0.41
Euhamitermes sp 2	S	7	TS
subtotals		**14**	**0.41**
Termitinae			
Foraminitermes-group			
Labritermes emersoni Krishna & Adams	S	13	7.33
Labritermes kistneri Krishna & Adams	S	4	0.04
Labritermes buttelreepeni Holmgren	S	1	TS
subtotals		**18**	**7.37**
Amitermes-group			
Protohamitermes globiceps Holmgren	I	1	TS
Protohamitermes sp. 1	I	1	TS
Prohamitermes mirabilis (Haviland)	I	41	140.78
Globitermes globosus (Haviland)	W	66	97.67
Microcerotermes serrula (Desneux)	W	96	400.33
Microcerotermes dubius (Haviland)	W	27	157.42
Microcerotermes distans (Haviland)	W	1	C
subtotals		**233**	**796.20**
Termes-group			
Termes borneensis Thapa	I	5	5.11
Termes propinquus (Holmgren)	I	5	0.10
Mirocapritermes near *connectens*	S	25	8.07
Homallotermes eleanorae Krishna	I	1	22.51
Homallotermes exiguus Krishna	I	15	24.63
Procapritermes setiger (Haviland)	S	1	0.10
Procapritermes minutus (Haviland)	S	10	0.30
Procapritermes near *sandakanensis*	S	27	174.87
Procapritermes sp. A	S	1	0.88
Procapritermes sp. B	S	13	2.21
Procapritermes sp. C	S	8	0.01
Procapritermes sp. D	S	1	24.41
Procapritermes sp. E	S	57	157.75
Pericapritermes semarangi (Holmgren)	S	48	57.22
Pericapritermes near *nitobei*	S	42	41.97
Pericapritermes near *dolichocephalus*	S	14	9.56
Pericapritermes sp. A	S	11	TS
Pericapritermes sp. B	S	11	0.08
Pericapritermes sp. E	S	1	4.01
Pericapritermes sp. F	S	1	0.12
Pericapritermes sp. G	S	1	< 0.01
Malaysiocapritermes prosetiger	S	13	57.02
Malaysiocapritermes sp. A	S	1	1.69
Oriencapritermes sp. A	S	24	53.17
Oriencapritermes sp. B	S	1	C
Oriencapritermes sp. C	S	3	0.48
Syncapritermes sp. A	S	13	TS
Dicuspiditermes santschii (Silvestri)	S	34	23.12
Dicuspiditermes nemorosus (Haviland)	S	39	38.00
Coxocapritermes sp. A	S	11	60.31
Genus et sp. nov.	S	2	TS
subtotals		**439**	**767.68**
Nasutitermitinae			
Nasutitermes group			
Hirtitermes spinocephalus (Oshima)	W	2	0.68
Nasutitermes longinasus (Holmgren)	W	27	37.68
Nasutitermes neoparvus Thapa	W	11	14.77
Nasutitermes matangensiformis (Holm.)	W	1	TS
Nasutiermes rectangularis Thapa	W	1	140.39
Nasutitermes sp. A	W	3	TS
Nasutitermes sp. B	W	3	1.17
Havilanditermes atripennis (Haviland)	W	4	TS
Bulbitermes flavicans (Holmgren)	W	34	437.56
Bulbitermes sp. A	W	69	247.93
Bulbitermes sp. C	W	13	15.59
Bulbitermes sp. E	W	1	0.07
Bulbitermes sp. G	W	3	55.32
Genus et sp. nov.? near *Bulbitermes*	W	1	0.38
Lacessititermes sp. A	W	1	TS
Lacessititermes sp. B	W	1	0.18
Longipeditermes longipes (Haviland)	W	5	3.43
Hospitalitermes hospitalis (Haviland)	E	3	0.06
Hospitalitermes sp. A	E	1	C
Hospitalitermes sp. B	E	1	C
Leucopitermes sp. A	S	1	0.18
Proaciculitermes sp. A	S	31	49.58
Proaciculitermes sp. B	S	13	< 0.01
Proaciculitermes sp. C	S	1	C
Aciculioiditermes sp. A	S	29	28.10
Oriensubulitermes sp. A	S	4	1.42
Oriensubulitermes sp. B	S	1	4.28
Oriensubulitermes sp. C	S	1	1.10
Subulioiditermes sp. A	S	3	0.22
subtotals		**269**	**1040.09**
grand totals		**1269**	**3447.20**

Table 2. *Assemblage characteristics of the three DVCA sites* ($\pm$ *s.d.*)

($n = 3$ for QDS, $n = 2$ for TS.)

	primary forest	old secondary forest	young secondary forest
biomass (QDS) (g m^{-2})	3.49 ± 1.02	4.71 ± 2.14	2.70 ± 1.31
abundance (QDS) (m^{-2})	1511 ± 566	1761 ± 573	886 ± 383
species richness (QDS)	29 ± 2.0	28 ± 2.8	26 ± 7.5
species richness (TS)	33 ± 2.8	31 ± 2.8	28.5 ± 0.7

Table 3. *Results of the partial canonical correspondence analysis for the extended assemblage data set* (*TS and QDS results*)

	axis 1	axis 2	axis 3	axis 4
eigenvalues[a]	0.659	0.467	0.358	0.289
species-environment correlations[b]	0.998	0.998	0.991	0.996
total inertia = 3.765 (after fitting covariable)[c]				
variable (site is:)	conditional eigenvalues[d]	cumulative % fit	p-value	gradient lengths[e]
montane versus lowland (axis 1)	0.64	31	<0.001	4.30
in Peninsular Malaysia versus Sumatra–Borneo (axis 2)	0.46	53	0.025	2.38
in Central Sumatra versus Borneo (axis 3)	0.37	70	0.022	0.90
lower montane versus heath forest (axis 4)	0.29	84	<0.001	1.52
young secondary versus old secondary–primary forest (axis 5)	0.18	93	0.002	0.40
old secondary versus primary forest (axis 5)	0.15	100	0.004	0.41

[a] Eigenvalues for the axes show the length of the gradient observed (on a scale of 0–1). Note, however, that the higher the axis number the lower the eigenvalue and thus the lower proportion of the overall variation it explains.

[b] Species-environment correlations indicate how good the fit is between the environmental variables and species-within-site data given these extracted axes. Here, all are very high.

[c] Total inertia is an eigenvalue measure of the total variation in the data set. Here, therefore, the first four axes explain 47% of the total inertia.

[d] Conditional eigenvalues are those due to individual environmental variables, the total fit being the percentage of the overall eigenvalue due to the environmental variables. The analysis begins by testing the most influential environmental variable (montane versus lowland, above). This variable is then treated ('partialed out') as a covariable and the next most influential variable tested, so that each eigenvalue is conditional on the set already removed. The p-values refer to statistical tests of the significance of the eigenvalues in Monte Carlo permutation tests with 999 random draws.

[e] Gradient lengths are in standard deviation (s.d.) units, using Hill's scaling (Ter Braak 1987) along axis 1. S.d.s >4 indicate almost complete species turnover across the length of the gradient. Gradient length is therefore a measure of β-diversity between sites.

proportion of the biomass density of the whole assemblage, with the exception of *Heterotermes tenuior* (nesting in small twigs) and *Schedorhinotermes sarawakensis* (a below-ground nester), both of which are moderately abundant.

Three small clades represent the remaining termites at DVCA, the *Formanitermes*-group, the *Anoplotermes*-group and the Kalotermitidae. Between them they account for only 0.3% of the total biomass density and therefore cannot be considered as functionally significant parts of the assemblage in gas-flux terms at the time of sampling. The Kalotermitidae often nest in tree canopies, however, and so may have been underrepresented in this study.

Epigeal-mound-building termites are also relatively rare at DVCA and make up only 16% of the total biomass density. This drops to <10% if termites collected only in mounds (rather than those collected in soil but assumed to be mound-builders) are included (R. Homathevi, unpublished data).

The DVCA fauna is typical of that recorded from the Sunda region as a whole, with data from Sumatra (D. T. Jones, unpublished data; Gathorne-Hardy, unpublished data) and Peninsular Malaysia (Jones & Brendell 1998) showing a large degree of overlap between faunas (see

also §3(b) below). To the north-west (through Indochina) and south-east (east of Wallace's line), however, there is a clear reduction in species richness (Eggleton 1999). The Sunda region represents a local species richness 'hot spot' for termites.

(b) *Site comparisons*

Species richness (as estimated by both TS and QDS), abundance and biomass did not differ significantly between sites (table 2; Eggleton *et al.* 1997; R. Homathevi, unpublished data). Species composition, however, did seem to vary between sites, with the clearest signal coming from the transect data. In that data set, YSF samples were more similar in composition to PF than OSF, probably due to the existence in YSF of primary forest species remaining, perhaps precariously, in recently disturbed areas (see Eggleton *et al.* 1996, 1997). In addition, there was some indication that soil-feeding termites (*sensu lato*) were being selectively affected by the logging, although this effect was rather subtle (Eggleton *et al.* 1997).

The broad-scale partial CCA (table 3, figure 1) shows a clear effect of altitude (lower montane versus lowland,
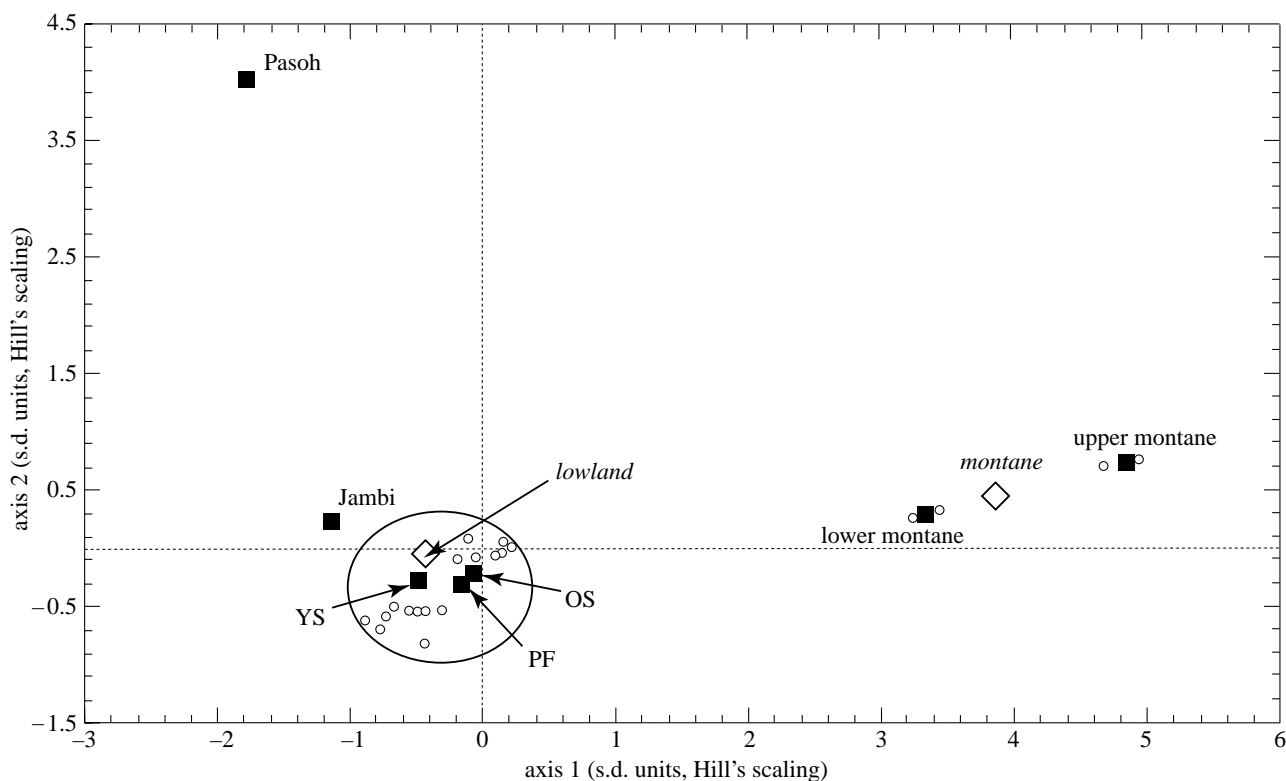
Figure 1. CCA biplot diagram for the enhanced data set. The plot is in Hill's scaling (Ter Braak 1987) so that axes are in standard deviation (s.d.) turnover units (see table 3). Large open diamonds are centroids of nominal variable (montane versus lowland), filled squares are centroids of region–forest-type nominal variable, small open circles indicate position of sites (not labelled), ellipse includes all Danum sampling plots. Note that species points and centroids for regional nominal environmental variables are not shown in order to retain plot clarity.

axis 1) and geographical position (axis 2 and 3), with forest type within the DVCA having relatively little influence (table 3). Considered against the general level of variation within the data set, the effects of forest disturbance on species composition at DVCA are small (only 16% of the total variation in species composition due to the measured environmental variables, and covering less than 0.5 standard deviation units of turnover; table 3). We interpret this as a shift in overall abundances of species across the habitats rather than a replacement of one species complement by another. Therefore, we see no clear evidence of the replacement of a primary fauna with one associated with logged forests. In fact, we cannot exclude the possibility that the differences observed might be due to the geographical separation of the three sites.

It is striking that the Pasoh and Jambi sites are more similar in species composition to the DVCA forest sites as a whole than to the Maliau sites. This suggests that lowland primary forest faunas within the Sunda region are fairly homogenous (e.g. see Appendix B of Tho (1992)). Recently collected additional data from Peninsular Malaysia, and Central and Northern Sumatra also support this assertion (Jones & Brendell 1998; D. T. Jones, unpublished data; F. Gathorne-Hardy, unpublished data).

(c) *Physiological data*

Metabolic rate was found to vary inversely with body weight in a suite of soil-, wood–soil- and wood-feeding species, giving a slope (in a log–log plot) of -0.63. However, a number of large species (actively foraging forms such as *Macrotermes malaccensis*, *M. gilvus*, *Havilanditermes atripennis* and *Hospitalitermes hospitalis*, but also the wood-feeding *Schedorhinotermes sarawakensis*) showed an O_2 consumption greater than expected for their body weight (Jeeva *et al.* 1999) (table 4). The inverse relationship between metabolic rate (and also, broadly, CO_2 production) and body size is to be expected from general physiological principles, and was also seen in the Cameroon assemblage, but the slope coefficients differ (cf. Bignell *et al.* 1997). Rates of CH_4 emission for DVCA termites were above $0.10 \, \mu mol \, g^{-1} \, h^{-1}$ in 17 species, with very high fluxes in two wood–soil-feeders, *Termes borniensis* ($0.55 \pm 0.16 \, \mu mol \, g^{-1} \, h^{-1}$) and *Prohamitermes mirabilis* ($0.30 \pm 0.12 \, \mu mol \, g^{-1} \, h^{-1}$). Out of the remaining 15 species, seven were soil-feeders, five were wood-feeders, two were wood–litter-feeders and a single species fed on micro-epiphytes (table 4). Low or negligible CH_4 emissions ($<0.10 \, \mu mol \, g^{-1} \, h^{-1}$) were observed in five other species, all wood-feeders or wood–litter-feeders. Although there was a broad trend towards higher CH_4 emissions in soil-feeders, the trend is not as marked as in a number of African assemblages and there are therefore implications for regional and global methane budgets, as well as further evidence of metabolic and trophic diversification in higher termites.

Estimates for xCO_2 and xO_2 (corrected for CH_4 emission, but not H_2) were used to calculate an apparent respiratory quotient (RQ_{app}) for 21 species. Mean RQ_{app}

Table 4. *Gas exchanges (for worker castes) of 26 species of lower and higher termites from the DVCA, grouped by feeding habit and (within each feeding group) by the ratio xCH_4/xCO_2*

(xO_2 and xCO_2 were determined by Warburg manometry, with correction for methane production. xCH_4 was determined by incubation in closed containers, with analysis of headspace gases by gas chromatography. Details of methods are given in Nunes *et al.* (1997). For gas fluxes, means of 3–16 determinations $\pm$ s.d. are given, except where stated. Major and minor are the separate worker castes of *Macrotermes malaccensis* and *M. gilvus*. Wood–litter feeders are all foraging species. F indicates mutualism with fungal associates. n.d., not detectable.)

termite	worker wt (mg)	xCO_2 (μmol g^{-1} h^{-1})	xO_2 (μmol g^{-1} h^{-1})	xCH_4 (μmol g^{-1} h^{-1})	xCH_4/xCO_2 (molar ratio, %)
soil-feeders					
Dicuspiditermes santschii	2.6	1.43 ± 1.107	2.18 ($n=2$)	0.22 ± 0.02	15.4
Dicuspiditermes nemorosus	3.5	4.13 ± 0.02	4.84 ($n=2$)	0.22 ± 0.03	5.4
Pericapritermes semarangi	1.3	5.16 ± 0.86	5.96 ($n=2$)	0.27 ($n=2$)	5.2
Procapritermes nr. *sandakanensis*	5.9	4.82 ($n=2$)	3.54 ($n=1$)	0.19 ± 0.07	3.9
Homallotermes eleanorae	2.2	6.25 ± 1.14	6.17 ± 1.01	0.27 ± 0.05	3.6
Proaciculitermes sp. A	1.1	6.24 ($n=2$)	7.47 ($n=2$)	0.17 ($n=2$)	2.7
Pericapritermes nitobei	1.2	9.04 ($n=1$)	8.84 ($n=1$)	0.27 ($n=2$)	1.0
Procapritermes sp. E	2.7	3.24 ($n=2$)	5.29 ($n=1$)	n.d.	—
Syncapritermes sp. A	6.7	4.24 ± 1.70	4.41 ± 1.65	n.d.	—
Aciculioiditermes sp.	1.8	7.46 ± 0.58	10.1 ($n=1$)	n.d.	—
Labritermes kistneri	0.7	36.37 ($n=2$)	24.17 ($n=2$)	n.d.	—
soil–wood-feeders					
Termes boreensis	3.0	6.40 ± 0.17	6.58 ($n=2$)	0.55 ± −0.16	8.5
Prohamitermes mirabilis	3.5	4.69 ± 0.40	5.21 ± 0.99	0.30 ± 0.12	6.5
wood-feeders					
Bulbitermes sp. C	2.8	7.13 ± 0.11	7.53 ($n=2$)	0.26 ± 0.06	3.7
Nasutitermes longinasus	2.6	5.57 ± 2.27	5.25 ($n=2$)	0.20 ($n=2$)	3.5
Hypotermes xenotermitis	2.6	10.25 ± 2.09	10.38 ± 2.22	0.18 ($n=2$)	1.8
Heterotermes tenuior	1.4	12.85 ± 1.07	12.37 ($n=2$)	0.20 ($n=2$)	1.5
Schedorhinotermes javanicus	2.7	10.28 ± 0.74	9.96 ($n=2$)	0.09 ± 0.02	0.9
Globitermes globosus	1.9	6.85 ± 1.69	6.76 ± 1.96	0.05 ± 0.04	0.8
Schedorhinotermes sarawakensis	8.3	17.26 ± 7.82	21.20 ± 7.82	0.12 ($n=2$)	0.7
Microcerotermes dubius	2.2	13.45 ± 5.38	12.01 ± 1.12	0.07 ± 0.01	0.4
Microcerotermes serrula	1.9	8.11 ($n=2$)	11.48 ($n=2$)	n.d.	—
wood–litter-feeders					
Macrotermes malaccensis MAJORS	11.6	11.32 ($n=2$)	11.38 ($n=1$)	0.20 ($n=2$)	1.7
Macrotermes malaccensis MINORS	9.0	6.32 ($n=1$)	6.66 ($n=1$)	0.10 ($n=2$)	1.6
Macrotermes gilvus MAJORS	7.0	7.44 ($n=2$)	7.35 ($n=1$)	0.11 ($n=2$)	1.4
Macrotermes gilvus MINORS	3.4	5.58 ($n=1$)	6.53 ($n=1$)	0.08 ($n=2$)	1.4
Havilanditermes atripennis	8.0	9.97 ($n=2$)	9.20 ($n=2$)	n.d.	—
Hospitalitermes hospitalis	7.7	6.66 ± 0.70	6.81 ($n=2$)	0.12 ± 0.02	1.8

was at or above 1.0 in 12 species and at or above 0.95 in a further six species, these two sets of species representing all trophic groups, including epiphyte-feeders (Jeeva *et al.* 1999). As in African termites (Bignell *et al.* 1997; Nunes *et al.* 1997), this is argued to be consistent with carbohydrate as the principal substrate supporting the overall respiration of the termite and its mutualistic intestinal community in all trophic groups, contrary to some previous assertions. However, the result does not preclude the possibility that some other substrates, notably lignin or lignin-derived polyaromatic compounds, are used to a minor extent or chemically and physically modified during gut passage.

(d) *Methane fluxes*

Gross CH_4 and CO_2 fluxes can be calculated from biomass density and physiological data from individual species summed over particular areas (see table 5). As with biomass density there is no obvious difference between sites in either carbon flux or methane production.

In all cases the soils were methane sinks (table 5), and the contribution of termites to methane fluxes was therefore negligible. In only one case (the primary forest), were measured fluxes significantly positively correlated with below-ground termite biomass, suggesting that generally termites were not significantly affecting methane fluxes within the soil. Termites within epigeal mounds (above the ground, so therefore theoretically less likely to produce methane that is subsequently oxidized) were also not significant sources of methane (table 5).

We observed the largest oxidation rate in the primary forest and the smallest was observed in the most recently disturbed forest plot; however, these differences were not significant. The most disturbed site was significantly associated with a high soil bulk and low organic carbon content (table 5). However, the differences in oxidation rate between undisturbed and disturbed sites were not particularly pronounced probably because logging methods were selective and/or due to intrinsic soil properties. The young secondary forest was on a

Table 5. *Methane and soil parameter results for Danum forest types* ($\pm s.d.$, *where calculable*)

	primary forest	old secondary forest	young secondary forest
gross CO_2 flux ($ng^{-1} m^{-2} s^{-1}$)	370 ± 90	403 ± 167	205 ± 101
gross CH_4 flux ($ng^{-1} m^{-2} s^{-1}$)	7.3 ± 0.4	8.2 ± 2.8	5.6 ± 3.3
measured CH_4 flux ($ng^{-1} m^{-2} s^{-1}$)	-15.4 ± 6.4	-13.9 ± 8.4	-10.8 ± 9.5
total CH_4 emission from mounds ($ng^{-1} m^{-2} s^{-1}$)	0.3	0.6	0.0
net CH_4 flux ($ng^{-1} m^{-2} s^{-1}$)	-15.1	-13.3	-10.8
soil water content (% dry weight)	34.4 ± 5.1	35.4 ± 4.9	31.7 ± 7.0
soil temperature (°C)	24.8	25.1	25.5
bulk density (top 5 cm, $g\,cm^{-2}$)	0.75 ± 0.06	0.76 ± 0.07	1.0 ± 0.14
pH (in H_2O)	3.3	3.1	3.5
organic carbon (%)	3.6 ± 0.8	3.3 ± 1.3	3.0 ± 2.0
total N (%)	0.33	0.25	0.22

slope and had a slightly lower average soil water content than the other two sites, which could have increased oxidation rates thereby masking any disturbance effect. A significant correlation between soil water content and CH_4 oxidation rates from each chamber was observed ($p < 0.05$) at the young secondary forest. The logging resulted in a very heterogeneous environment as described previously. Descriptions of each chamber site were noted and scored according to level of disturbance, and showed that small rates of CH_4 oxidation were associated with the skid trails and other highly disturbed areas, compared with the undisturbed areas where rates of CH_4 oxidation were comparable with those found in the primary forest. Throughout, oxidation rates were comparable with other studies in the tropics (e.g. Keller *et al.* 1990; Tathy *et al.* 1992; Keller & Reiners 1994).

This confirms earlier observations that although potential CH_4 fluxes from termites are high (i.e. gross or potential production assessed from laboratory incubations), net emissions from termites in natural settings (in mounds or in the soil) depend on the local oxidation capacity (sink strength) generated by methylotrophic organisms (MacDonald *et al.* 1998, 1999). This is influenced by many factors, for example soil moisture content, texture, pH, organic matter content and porosity, which are in turn affected by disturbance, in some cases severely (MacDonald *et al.* 1998, 1999). The sink strength of tropical soils is poorly documented, but disturbance may be expected to reduce methane oxidation, and where termite populations remain high there is the possibility that fluxes from the soil, and at the landscape level, may become positive (Keller *et al.* 1990; Bignell *et al.* 1997). At the biomass densities of termites present in the DVCA, however, this is unlikely to occur very commonly.

(e) *DVCA termites in context*

The DVCA abundance and biomass density results are comparable to those reported from dipterocarp forests across the Sunda region, where similar assemblage sampling methods have been applied (i.e. Abe & Matsumoto 1979; Collins 1983; Jones 1996). However, these studies did not include measurements of termite physiological processes, and so we need to look farther afield for studies that are directly comparable. In fact, as stated earlier, the DVCA study was intended to complement a slightly more comprehensive termite biodiversity study conducted in the Mbalmayo Forest Reserve (MFR), Southern Cameroon. Essentially the same variables were measured in each case: assemblage structure, termite respiratory exchanges, methane production by individual termites and methane fluxes from soil. In turn, disturbance effects were measured across a gradient, although the range of disturbance was greater in MFR than at DVCA (see Eggleton *et al.* 1995, 1996).

Comparison of the three most lightly disturbed sites in the MFR sequence (near-primary forest, old growth secondary forest and tree plantation) with the three DVCA sites shows broadly comparable trends of species turnover, with relatively small changes in overall termite abundance and biomass density. In MFR, however, a more complete disturbance gradient was available than at DVCA, including two sites completely lacking in canopy cover ('weeded *Chromolaena* fallow' and 'complete clearance'; Eggleton *et al.* 1995, 1996). In these cleared sites, termite assemblages, especially soil-feeding termites, were very negatively affected, as they were in some highly disturbed Sunda sites (e.g. Jambi Province, Sumatra, D. T. Jones, unpublished data).

If the data sets are considered in more detail (table 6) it is clear that the two assemblages differ fundamentally. The overall species richness, population density, biomass density and carbon fluxes are enormously greater in MFR than in DVCA.

Termites are, on average, found in DVCA at a biomass density of 6% of that of Mbalmayo. In addition, the carbon flux through termites in Mbalmayo is 16 times that found in DVCA (table 6).

Of the 13 presently recognized clades (i.e. evolutionary lineages), only six occur at significant population densities at DVCA (see table 1). An additional three groups are present at significant densities in the MFR assemblage (the *Anoplotermes*-group Apicotermitinae, the *Apicotermes*-group Apicotermitinae and the *Cubitermes*-group Termitinae). Strikingly, between them these three groups make up 92% of the biomass density of the forested sites in MFR. Therefore, it is clear that Sabah, indeed the whole Sunda region, although a regional termite diversity hotspot, is, at a global level, depauperate in termites and lacks a number of functionally important clades found in the other main tropical regions (Eggleton 1999).

Why should there be this very large diversity anomaly in the two regions? We cannot attempt a lengthy discussion here, but some evidence is accumulating to suggest major differences in the biogeographical history of the two regions. Eggleton (1999) has recently suggested that the major part of the termite fauna of South-East Asia may be derived from the fauna of the Indian continental mass (originally from the southern palaeocontinent

Table 6. *Comparisons of findings pooled across the three forested site in Cameroon* (*MFR, n = 6*) *and Sabah* (*DVCA, n = 9*) *sites*

	DVCA	MFR
species richness	93	*ca.* 150[a]
clade richness[b]	6	9
true soil-feeders	no?	yes
biomass density[c] (g m^{-2})	3.5	56.9
termite carbon flux[c] (mg C m^{-2} h^{-1})	0.31	4.78
% of NPP[d]	0.2	5.0
effect of logging	significant but small[e]	significant but small[e]
gross methane flux (kg ha^{-1} yr^{-1})[f]	−3.37 to −4.78	−3.05 to −6.15

[a] MFR figure is approximate given equal sampling effort. Overall sampling effort in MFR has been two to three times as great as in DVCA.
[b] Clades as defined in Kambhampati & Eggleton (1999) with the addition of the *Subulitermes*-group Nasutitermitinae. Clades present at less than 5 mg m^{-2} (see table 1) are not included.
[c] Mean values across all forested sites in the two studies.
[d] Approximate value calculated by assuming NPP in MFR as 2.2 kg m^{-2} yr^{-1}, and in DVCA as 3.0 kg m^{-2} yr^{-1} (data from Uchijina & Seino 1987) and that C is fixed as cellulose (i.e. $nC_6H_{12}O_6$).
[e] In both cases changes were observed in species composition but not in species richness, abundance, biomass density or gas fluxes.
[f] These are all methane oxidation rates, implying that the soil is a sink for methane.

Gondwanaland) rather than having evolved autochthonously. If so, then the depauperate nature of the Sunda region may be due to the very harsh conditions that must have been present in the Indian plate as it moved through the Indian ocean to take up its present position as part of Asia (although this implies exceptionally slow rates of evolution).

4. CONCLUSIONS AND RECOMMENDATIONS

The DVCA holds a relatively rich termite assemblage, and one that is broadly representative of the termite fauna of the whole Sunda region. Wood-feeders dominate the assemblage in biomass terms, but the most species-rich group is the *Termes*-group Termitinae. In a worldwide context, however, the assemblage is species, carbon-flux and biomass poor in comparison with tropical forest systems in Africa and South America. Clearly termites are not as important players in Sunda rainforests as they are in these other regions, and it would be interesting to understand the dynamics of the decomposer community as a whole to see what, if anything, is compensating for the relative lack of termites.

The DVCA (like surrounding areas) is a mosaic of forest with different site histories. Especially important is the effect of logging, which has left large areas around the DVCA as secondary forest. Although the sampling here must be considered preliminary (we only examined three sites), our findings suggest no major shift in termite assemblage structure in sites that have been logged, as long as a substantial tree canopy remains. This appears to

be true even if the canopy is patchy, as in our young plantation site. We did not have time to undertake sampling under important agricultural regimes in Sabah (e.g. oil palm plantations) that have low canopy cover and represent higher levels of disturbance. Data are accumulating, however, to suggest that such systems may have highly depauperated termite assemblages (Eggleton *et al.* 1995, 1996; D. T. Jones, unpublished data, from Jambi province, Sumatra). Our tentative conclusions, therefore, are that selective logging followed by a long fallow period may not adversely affect termite populations. However, we still do not know enough about the necessity for sources of primary forest termites or the long-term effects of logging to allow general conclusions to be reached. An important unanswered question is the degree to which the changes in assemblage structure that we have observed (described above and discussed in greater detail in Eggleton *et al.* (1997)) affect ecosystem processes.

The DVCA termites represent a significant gross source of methane. However, as with other systems that have been studied (e.g. Khalil *et al.* 1990), none of this methane is escaping into the atmosphere. Although there are circumstances where Sunda forest systems may be net sources of methane (e.g. in flooded forests), we do not believe that even in such habitats termites will be net sources themselves.

There are clearly a number of areas of termite research that still need to be addressed to allow a wider perspective than we have obtained here. These include:

1. Similar TS and QDS studies in the neotropical region to complement the DVCA and MFR studies, allied with greater statistical replication in resampled sites.
2. Studies to understand the biogeography of termites from one side of the Wallace Line to the other.
3. Studies to investigate the impact of levels of disturbance greater than logging (i.e. agricultural systems).
4. Consequences of changes in termite assemblage structure on soil fertility and soil processes.
5. Modern taxonomic revisions of the *Termes* group, the soil-inhabiting Nasutitermitinae, surface-foraging Nasutitermitinae (especially *Hospitalitermes* and *Lacessititermes*) and *Bulbitermes*.

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