The Diversity, Abundance and Biomass of Termites under Differing Levels of Disturbance in the Mbalmayo Forest Reserve, Southern Cameroon

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SUMMARY

This paper presents data on the abundance, biomass and species richness of termites in the Mbalmayo Forest Reserve, southern Cameroon. Five plots of differing disturbance level (near primary forest, old secondary forest, young plantation, weeded *Chromolaena* fallow, and completely cleared forest) were sampled for termites in two successive years (July 1992 and July 1993, giving a total of ten sampling areas, plus one in the completely cleared plot in November 1992). A stratified sampling regime of soil pits, wood samples, mound samples and soil scrape samples was used. Estimated abundance and biomass were extremely high in the near primary and old secondary plot (maximum estimated abundance, old secondary sampling area 1, 10488 m^{-2}, maximum biomass density, near primary sampling area 1, 123.2 g m^{-2}). In all cases termite abundance was highly clumped. Disturbance had apparently little effect on termite abundances and biomass in forested plots, but there were clear reductions in abundance and biomass in the cleared plots. In the completely cleared plot, abundance and biomass fell sharply from year 1 to year 2, presumably because colonies left after clearance had dried out and died. There were large differences in the taxonomic-, nesting- and feeding-group composition of the plots, with soil feeding termites being especially strongly affected by disturbance. The sources of error associated with this sampling programme are discussed.

It is argued that the near primary forest plot may have higher microhabitat and concomitant termite assemblage heterogeneity than the more disturbed plots. In most cases over 90% of the overall abundance

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in a sampling area was due to a few species; however, the same species were not dominant in all sampling areas. This may be due to the unpredictable dynamics of colony foundation and extinction, and will make estimations of the effect of termites on overall ecosystem processes (from abundance and biomass data alone) problematical. There is no evidence of immigration of savanna termites into the forest reserve, and thus cleared areas have depauperate forest assemblages. It is concluded that this is the most accurate estimation of termite assemblage parameters yet attempted.

1. INTRODUCTION

Termites are dominant invertebrates in tropical soils (Wood & Sands 1978) and are important, perhaps vital, as direct mediators of decomposition (Peakin & Josens 1978; Wood & Johnson 1986). They are also important as mediators of humification, soil conditioning, the fragmentation of organic detritus, nitrogen-fixation, aggregate binding, and the formation of clay-mineral complexes (Lee & Wood 1971; Wood 1981; Collins 1983; De Bruyn & Connacher 1992; Martius 1994; Tayasu *et al.* 1994; Brussard 1995). Some species are highly destructive agricultural and silvicultural pests (Wood 1978; Wood & Pearce 1991). The role of termites as keystone species and in the production of trace gases is discussed in Jones (1990), Kresleman & Bouwman (1994), and Lawton *et al.* (1995).

The importance of termites as decomposers of organic matter has been confirmed in some savanna systems by quantitative studies (Wood & Sands 1978; Collins 1981; Holt 1987, 1990; Jones 1990), fewer data are available for tropical forests. However, as termite species richness appears to be highest in forests (De Souza & Brown 1994; Eggleton *et al.* 1995) and biomass density also appears to be high (Wood & Johnson 1986; Martius 1994; Eggleton & Bignell 1995), there is a need to define their role in forest systems with more accuracy. Pioneering work by Matsumoto & Abe (see, for example, 1979) and Collins (1983) in Malaysian tropical forest suggests that 14–33% of annual litter production is consumed by termites. Undersampling of some forms, especially soil-feeding and arboreal forms, contributes to inaccuracies (Eggleton & Bignell 1995), so that the contribution of termites to humification and their physical roles in the soil may be underestimated in tropical forests.

Few data are available to show the effects of forest disturbance on insect faunas (Sutton & Collins 1991; Holloway *et al.* 1992). Severe disturbance, such as replacement of forest with agriculture generally leads to a decrease in diversity (Holloway 1987), but lighter perturbations, such as foraging, hunting, selective logging, or even conversion to plantation, may have no measurable effect or may even increase diversity (Janzen 1987; Raguso & Llorente-Bosquets 1990). Where logging and conversion to arable reduce termite diversity, there is a disproportionate loss of some functional groups (chiefly soil-feeders) and an increase in the relative prominence of savanna species where they are available for colonization (Collins 1980; Wood *et al.* 1982). Although concern for forest conservation often centres on the effect of logging, progressive conversion to subsistence agriculture is a more serious issue in the remaining forest blocks of West and Central Africa.

In this paper we present termite assemblage data from across a gradient of forest disturbance in a semi-deciduous forest in the Mbalmayo Forest Reserve (MFR), southern Cameroon. An earlier qualitative study (Eggleton *et al.* 1995) showed a clear effect of extreme disturbance (forest clearance) on species richness, but revealed similar species richnesses between forest-like (near primary, secondary and plantation forest) plots. However, there were some differences in functional groups and taxonomic composition between forest-like plots. Here we examine quantitative differences in abundance and biomass between the same five plots.

Although termites are sometimes thought of as an indicator taxon (Brown 1991) we have concentrated on the direct (and indirect, regulatory) contribution of termites to ecosystem processes and how this changes with anthropogenic disturbance. Here we present data describing assemblage structure. We will discuss the ecosystem processes associated with these assemblages, especially carbon fluxes, in a later paper.

2. METHODS

(*a*) *Characteristics of the plots*

All plots were within the Mbalmayo Forest Reserve, Southern Cameroon (11° 25′ to 11° 31′ E, 3° 23′ to 3° 31′ N), an area of lightly to highly disturbed semi-deciduous forest which has been at least partly logged several times in the past century (Lawson *et al.* 1990). The forest is classified as moist pre-montane tropical forest (Holdridge *et al.* 1971), with annual rainfall averaging 1520 mm and falling during two wet seasons, March to June, and September to November. Average monthly temperatures fluctuate by only 3 ° C, from 22.6 °C in August to 25.5 °C in January. The study plots are on a gently undulating plateau about 650 m above sea level, in the midstream catchment area of the Nyong River, which forms the western boundary of the reserve.

The MFR was established in 1949 and is administered by the Ministry of Environments and Forests, representing the Government of Cameroon. The Reserve covers about 9000 ha and now includes surviving areas of primary or near-primary forest, extensive secondary forest, forestry plantations of various kinds, and experimental farmland established after forest clearance. Hunting, foraging and subsistence agriculture (slash and burn) are practised by local villagers, often illegally, but without vigorous policing. Legal agriculture has shortening fallow periods. Vegetation cover, patterns of land use and the problems of encroachment are typical of the Forest Zone of southern Cameroon.

Inventories of tree species are available through the Ministry of Environments and Forestry for many parts of the MFR. The International Institute of Tropical Agriculture (IITA) maintains continuous weather records from instruments located in the Reserve.

Development projects being undertaken in the Reserve include clonal forestry (Office National de Developpment d'Eaux et Forets, ONADEF and the Overseas Development Administration, ODA) and the management of short fallow agricultural regimes (IITA). These projects have imposed a range of disturbance treatments under controlled conditions on 1 ha plots; we chose five of these to represent a spectrum of disturbance. From most to least disturbed are listed as follows.

1. Complete clearance (CC). An area of forest cleared by bulldozer and chain saw in February 1992, resulting in the top soil being removed. The larger trees were milled on site, but all other dead wood was bulldozed into windrows (two per ha). The cleared area was planted with lines of *Terminalia ivorensis*, a fast-growing indigenous species of moderate timber value, at a spacing of 5 × 5 m, and weeded to promote early sapling growth.
2. Weeded *Chromolaena* fallow (WCF). A part of the IITA experimental farm site cleared manually from secondary forest in 1990 (i.e. cleared by machete and chain saw but without the use of heavy machinery). The plot was left fallow, but weeded to prevent tree regeneration. Most of the original felled timber was removed or burned on site, but a proportion was sawn up, spread and left to rot naturally to provide a crude nutrient input to the soil. The plot developed a dense growth of the alien composite, *Chromolaena* sp.
3. Young plantation (YP). A plantation of *Terminalia ivorensis* established in 1987 by the 'manual récrû' technique. This technique involves the cutting of all vegetation under 20 cm diameter by machete, except identified valuable timbers which were left *in situ* or salvage felled and milled on site as planks. Remaining undesirable trees were felled or poisoned *in situ* to leave a final canopy cover of about 30%. Planting lines were cleared by chain saw at a separation of 5 m and planted with saplings at a separation of about 5 m along the lines. The lines were weeded to promote early growth of the saplings, and thinned after three years.
4. Old secondary forest (OS). This plot was clear felled 30 years ago and has been left to regenerate. There is still a large amount of dead wood and woody litter lying on the ground (appreciably more than in the near primary plot). A bulldozed dirt track was run through the centre of the plot between the two main sampling periods, disturbing it.
5. Near primary forest (NP). This plot was subject to selective logging approximately 70 years ago, but retains a few large mature trees. There is relatively little litter and dead wood on the plot (in comparison to the plantation and secondary plots), except in gaps caused by natural tree falls. Disturbance is very light, confined to local villagers gathering fruits and firewood.

The WCF and NP plots were within large, similar areas and they (and the remaining plots) were surrounded by secondary forest. In the text the first two plots (CC and WCF) are referred to as the 'cleared' plots, whereas the other three plots are referred to as the 'forest-like' plots.

(*b*) *Plot parameters*

(*i*) *Soil samples*

Soils within the MFR are hydromorphic, of a mull type with variable organic content and stable mineralizing conditions (Holland *et al*. 1992). We took nine soil samples for analysis from 5 cm deep scrape samples (see below) from each sampling area in 1993. In each sampling area, three of the scrapes consisted of the top 5 cm of a 50 cm pit. In addition we took soil from each pit under these three scrapes. Soil analyses were undertaken at the IITA laboratories in Nkolbisson, Cameroon.

(*ii*) *Lying dead wood samples*

We estimated lying dead wood using a modification of the line intersection method of Van Wagner (1968). At each plot, items greater than 10 cm diameter (big logs) were assessed with a randomly positioned, randomly orientated line of 20 m length, replicated 10 times in each 20 × 30 m sampling area (see below). Items less than 10 cm diameter (small wood) were assessed with a randomly positioned, randomly orientated line of 1 m length, replicated 10 times per 20 × 30 m sampling area. Preliminary analysis of the data showed that items > 10 cm diameter were consistently underestimated by 1 m transects, compared with 20 m transects.

Volume calculations (cm^3 m^{-2}) were made for each size class, then transformed as log vol + 0.05 (big logs) and as log vol + 0.0025 (small wood). The small quantities added before log transformation were to allow samples without wood (zeroes) to be included; the quantities added are an arbitrary 1% of the smallest volumes that could be estimated by each method. Because of high initial variance, a third 20 × 30 m plot was sampled for big logs at the NP plot. The windrows in the CC plot were not sampled for dead wood or termites.

(*c*) *Sampling methods*

We sampled from mid-July to mid-August (the 'short dry' season) in 1992 and 1993. The first year was unusually dry (35.9 mm in July/August), whereas the second year was unusually wet (282.9 mm in July/August). In addition, there were obvious differences between the two years in the CC and YP plots (due to ecological succession) and in the OS plot (due to human disturbance). For these reasons we have not treated the samples in the two years as replicates but as independent samples.

All the collected material (wood, litter, soil, termite mounds) was hand sorted in a field laboratory by the authors (except W.A.S.) and a team of trained Cameroonian field assistants. Termites differ markedly in their density in different substrates, and the substrates themselves differ in the ease and speed with which they can be sorted. It was therefore not possible to use a single 'quadrat' of fixed size. We therefore proceeded as follows.

The sampling programme differed slightly between the first and second years. In 1992 we marked a sampling area of 30 × 20 m within each hectare plot and where necessary cleared along the perimeter lines by machete to permit access. This size of sampling area was the largest that could be accommodated in the NP plot in each of the two successive years without unacceptable disturbance to the plot. Plots are thus defined in this paper as hectare-sized areas within which one 20 × 30 m sampling area was chosen in each of two years. Within each sampling area, we marked ten 2 × 2 m quadrats using random coordinates. When pits could not be dug because large trees occurred within a quadrat, new random coordinates were chosen and the quadrat repositioned. We took all dead wood within each quadrat to the laboratory and removed all termites. In the centre of the quadrat we dug a 20 × 20 × 50 (depth) cm pit dug and again the sample was taken back to the laboratory and hand-sorted. All removed termites were preserved in 70% alcohol. We undertook qualitative sampling from a belt transect of 100 × 2 m three months later (Eggleton *et al.* 1995). At the same time we repeated the quantitative sampling on the CC plot, to assess short term temporal changes due to forest clearance.

Using the qualitative transects as a species richness baseline, it was clear that the 1992 quantitative samples had underestimated species richness, due to undersampling of termites (especially soil-feeding species) that live at the wood/soil interface and in microsites such as soil between the buttress roots of trees. Therefore, during the second quantitative sampling (1993) we followed the same quantitative regime, in contiguous or near contiguous plots within the same hectare treatments, but additionally removed the top 5 cm of soil from the pit and sorted it separately (a 'soil scrape'). We also took another nine randomly located 20 × 20 × 5 cm scrapes from within each quadrat. This gave us strictly comparable pit samples as well as additional scrape samples.

After wood and soil sampling had been completed in 1993, we removed all surface termite mounds and nests in all the 20 × 30 m sampling areas (i.e. 11 in total) for the extraction and enumeration of termites within them. In the case of very large mounds a combined homogenization and subsampling procedure was employed to estimate total numbers.

The soil and wood samples do not include immature termites, because they were generally not encountered. Mounds did include immatures. We quote mound data as a total per m^2 without standard errors as all mounds were taken off each single (20 × 30 m) sampling area.

Mounds were not sampled from the plots in the first year because of fears that such drastic disturbance would affect the second year's sampling. Foraging ranges of termites are poorly known, especially for wood feeders, and it is conceivable that some individual colonies may forage over the whole hectare. Thus our estimates of overall abundance in the second year are composite year 1 (wood and soil) and year 2 (wood, soil and mound) estimates. The possible errors associated with this procedure are discussed below.

Biomass calculations are for the worker caste only, as this is by far the predominant caste in natural systems (soldiers represent from 0–50% of the total individuals within species, but most species found here have < 5% soldiers). Individual live mass measurements were taken for the 24 most abundant species. We estimated the masses of remaining species from head widths using regression lines.

(*d*) *Methods of analysis*

(*i*) *Identification*

Identification of species was undertaken by W.A.S. and P.E. at the Natural History Museum. Many of the names are tentative, as a great deal of taxonomic work is needed within certain critical genera (i.e. *Microcerotermes*, *Cubitermes*, *Pericapritermes*). In *Odontotermes* species names are even less certain, and we have only referred to them by numbers. In *Microtermes* we have simply referred to all specimens as *Microtermes* spp. Among the soldierless Apicotermitinae we have sampled a number of genera and species new to science, and these have all been given numbers. We will describe these new species at a later date.

(*ii*) *Biological characteristics of species*

Accurate information on the natural history of termites is scarce, especially for soil-feeders. For this reason it is not possible to assign termites unambiguously to functional groups. Instead, we have examined three interconnected elements of termite biology across the plots: trophic groups, taxonomic groups, and nesting groups (Eggleton & Bignell 1995).

Trophic groups Termites were split into four putative trophic groups, which we assigned by site of discovery, colour of abdomen and known dietary requirements of the workers (gut content analysis was not possible for all species due to small sample sizes, F. Sleaford, D. E. Bignell & P. Eggleton, unpublished data).

1. Soil feeders. Termites distributed in the soil profile, surface litter (leaves and twigs), and/or epigeal mounds (including purse nests on above ground vegetation), apparently feeding on mineral soil. Some of them may be root feeders, but strong evidence is lacking.

2. Soil-wood feeders. Termites collected only or predominantly within soil under logs, within soil plastered onto the surface of rotting logs or within highly decayed (friable) wood. This group includes termites whose gut contents are predominantly mineral in nature. In Eggleton *et al.* (1995), all *Pericapritermes* species were included in this group. However, recent sampling suggests that only *P. magnificus* is a true soil-wood feeder, and the other *Pericapritermes* species are

reassigned as soil feeders. In contrast, *Termes* is reclassified here as a soil-wood feeder (F. Sleaford, D. E. Bignell & P. Eggleton, unpublished data). This group is synonymous with 'intermediate feeders' *sensu* De Souza & Brown (1994), but we feel that the term 'soil-wood feeders' is more clearly descriptive.

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 nests in which fungus gardens are cultivated (Macrotermitinae).

4. Litter foragers. Termites that forage for leaf litter and small woody litter. It includes some subterranean and other mound building Macrotermitinae with fungal associates (Johnson *et al.* 1982). *Pseudacanthotermes* and *Acanthotermes* are both litter foragers and wood feeders, and are counted as 0.5 for each relevant functional group in the analyses.

No grass- or lichen-feeding species are found in the MFR.

Taxonomic groups Soil feeding termites show clear morphological and anatomical differences between three taxonomic components (Apicotermitinae, Termitinae, and Nasutitermitinae), the functional significance of which are as yet unknown (see also Bignell & Eggleton 1995; Eggleton *et al.* 1995). We have therefore examined the effects of forest disturbance on the taxonomic composition of the termite assemblages, treating taxonomic position as a possible pointer to ecological function. In these analyses, the Macrotermitinae are, with the exception of *Sphaerotermes*, all fungus-growers.

Nesting group 1. Wood nesting. Termites whose colony centres are normally within dead logs or standing trees. Sometimes the dead wood is slowly replaced with carton material, in others the wood is tunnelled through without being significantly altered.

2. Hypogeal nesting. Termites whose colony centres are below the ground. Centres are often poorly defined and amorphous (especially in the soldierless Apicotermitinae), with little obvious internal structure, although some have complex underground nests (e.g. some Macrotermitinae and Apicotermitinae). This group includes many species that are facultative secondary inhabitants of epigeal mounds.

3. Epigeal mounds. Termites whose colony centres are above ground (excluding arboreal mounds), often associated with the buttresses of trees, but may be free-standing. These mounds are all well defined and highly complex structures. Included in this group are the large termites closely related to *Cubitermes* (*Apilitermes longiceps* and *Crenetermes albotarsalis*) that appear as secondary occupants in mounds, but seem to use them in a similar way to the original occupants. Also included are apparently obligate secondaries that occupy the mounds at the same time as the original builders (i.e. *Euchilotermes*, *Ophiotermes*, *Tuberculitermes*; P. Eggleton & D. E. Bignell, unpublished data).

4. Arboreal mounds. Nests found attached to trees at various heights. Termites collected from this group have been excluded from the nesting group analysis as they could only be reached in an unsystematic way.

(*iii*) *Statistical treatments*

Termite abundances in wood and soil throughout this study fit a negative binomial distribution with $k < 1$ for all sampling areas; k gives a measure of the degree of dispersion of the samples (Elliott 1971; Krebs 1989), with a low k indicating a clumped distribution. This means that we had to transform the data to produce an approximately normal distribution. As k is less than 2 for all the samples, the $\log(x+k/2)$ transformation recommended by Krebs (1989), cannot be employed (because for abundances close to zero this produces negative transformed values). Instead we have used a more general $\log(x+1)$ transformation. For the soil and wood samples, this transformation normalizes the distribution (except in some of the CC sampling areas), generally removes the correlation between the variance and the mean, and produces homogenous variances from group to group. However, there was a large proportion of zero values in the scrape samples, and neither a log nor a loglog transformation normalized the data, which were therefore analysed non-parametrically (see below).

Here we quote means for untransformed data and backtransformed (i.e. geometric) means and confidence limits for $\log(x+1)$ transformed data, and use the transformed data for comparative purposes. Wood and soil samples were treated separately in these analyses, due to the statistical difficulties of combining them at the same spatial scales. We have, however, given an overall arithmetic mean number per m^2 for each sampling area, quoted without confidence limits. Other termite studies have used arithmetic means (Wood & Sands 1978; Eggleton & Bignell 1995), and these means are probably the best rough guide to overall abundance (Lyons 1964), especially when estimating the ecological impact of termite populations.

We used Parametric statistics (ANOVAS) to assess significant differences between sampling areas for the wood and soil samples, with plot disturbance treated as a categorical variable, and with each year's samples analysed separately. We undertook a one-way ANOVA on the log $(x+1)$ transformed data with a null hypothesis of no significant effect of disturbance. Pairwise tests of significance between individual sampling areas were performed *post hoc* using the Tukey-HSD test. This test protects against declaring pairs of means different when they could differ by chance alone among a relatively large number of tests.

We used non-parametric one-way ANOVAS (Kruskal-Wallis) to assess significant differences between the scrape samples. A series of pairwise *post hoc* Wilcoxon signed ranks test were then performed between samples, with significant results being accepted at the $p = 0.005$ level (i.e. 0.05 divided by the number of individual comparisons) to protect against declaring pairs of means different when they could differ by chance alone among a relatively large number of tests.

We measured the similarity in species composition and abundance between the 11 sampling areas using the Morisita coefficient (Krebs 1989). Given the very high abundances of the few most common species (often five orders of magnitude difference between most common and rarest), we (log + 1) transformed the abundance data, before clustering the data using the UPGMA algorithm (Krebs 1989).

3. RESULTS

(*a*) *Plot characteristics*

(*i*) *Living trees*

The MFR has a high tree species-richness. This is reflected in the species lists available for the three forested plots (YP, OS and NP), although direct comparisons between them are not possible because of differences in the method and thoroughness of survey. The figure of 149 species recorded for YP is derived from a catalogue of seven adjacent 1 ha plots (including the manual récrû hectare actually sampled for termites in this study) made in 1987 and probably comes close to representing the Reserve as a whole. Fewer species occurred on the hectare chosen for sampling due to the felling and poisoning employed in the preparation of the plot for the *Terminalia* planting. Conversely, the 37 species recorded from the NP plot (1993 survey) were identified in an area of just 1200 m^2 making it very likely that the entire plot would contain more. Tree density in the NP plot (533 ha^{-1}) was more than twice that of the other two forest-like plots, but few large trees were present. Consequently, total basal area was greatest in the OS plot, where some trees exceeded 75 cm basal diameter. We are uncertain whether the difference in tree density between the OS and NP plots reflects the inherent nature of forest successions or the absence of recent disturbance in the NP plot.

(*ii*) *Lying dead wood*

Quantities of dead wood are consistent with the known histories of site treatment, where substantial proportions of the pre-existing forest biomass were lost by burning, milling or windrow formation. The two size-classes of wood are positively correlated (see figure 1) ($p < 0.01$). The forest plots have more dead wood than the cleared plots (CC and WCF), although there was considerable, apparently random, variation between sampling areas within two forest-like plots (OS and NP).

(*iii*) *Soil*

Bulk pH of the soil decreased along the gradient of disturbance from CC to NP, excepting WCF where the highest values (up to 5.85) were recorded (see table 1). The WCF treatment reflects indigenous agricultural practices and includes the burning of felled wood *in situ*. This released cations, principally Ca^{2+}, Mg^{2+} and K^+ (up to 5 milliequivalent %; cation assays not tabulated), which raise the pH on a temporary basis. Acidic $Al^{(3+,1+)}$ varied inversely with pH, reaching 7.6 milliequivalents % in the deeper level of the NP plot. Soil pH was correspondingly lowest in the NP plot.

Organic carbon in the surface 5 cm increased along the disturbance gradient from CC to NP. Similar, though less marked increases occurred at the lower level. The large variance associated with the organic carbon determinations, especially in the forest-like plots, indicates an uneven distribution of soil organic matter. Total nitrogen content of soil was marginally greater in forest-like than cleared plots. As a consequence C:N ratios broadly rise along the disturbance gradient from CC to NP, more markedly so in the surface 5 cm. The C:N ratio in the NP plot (38:1), together with the low pH, suggests a net immobilization of nitrogen.

(*b*) *Termites*

(*i*) *Species richness*

We collected a total of 114 species from the MFR by casual sampling, qualitative transects, and quantitative sampling (Eggleton *et al.* 1995; P. Eggleton, D. E. Bignell, W. A. Sands, N. A. Mawdsley, J. H. Lawton, T. G. Wood & N. C. Bignell, unpublished data). We encountered 65% of these species during the quantitative sampling (74 species in 47 genera; see table 3).

Table 4 shows the overall species richness for the 11 plots. The UPGMA tree for the 11 sampling areas is figure 2.

(*ii*) *Abundances in dead wood*

Termite abundances in the dead wood samples are summarised in figure 3. In both years there were significant treatment effects (ANOVA, $P < 0.001$ in both cases) on abundance. The Tukey-HSD pairwise comparisons between plots are shown in table 5.

The highest abundances from wood were recorded in the YP plots, which also had the highest density of available wood (see table 2). However, there was no significant correlation between 'small wood' volume and termite abundance within the wood samples ($r^2 = 0.001, p > 0.1$), although estimates of 'big logs' volume and termite abundance within wood samples were positively correlated ($r^2 = 0.58$, $p < 0.01$).

(*iii*) *Abundances in soil pits*

Transformed means and confidence limits for termite abundances in the soil pits are shown in figure 4. In both years there was a significant treatment effect (ANOVA, $p = 0.035$ in year 1, and $p < 0.001$ in year 2) on abundance. The Tukey-HSD pairwise comparisons for both years are in table 5*c*, *d*.

(*iv*) *Mound samples*

Note that termite abundance in mounds is a small fraction (< 8%) of the overall mean abundance estimated in table 4.

(*v*) *Abundances in soil scrape samples*

The Kruskal-Wallis ANOVA showed a significant treatment effect ($p < 0.001$) on abundance. The *post hoc* Wilcoxon signed test pairwise comparisons are in table 7.

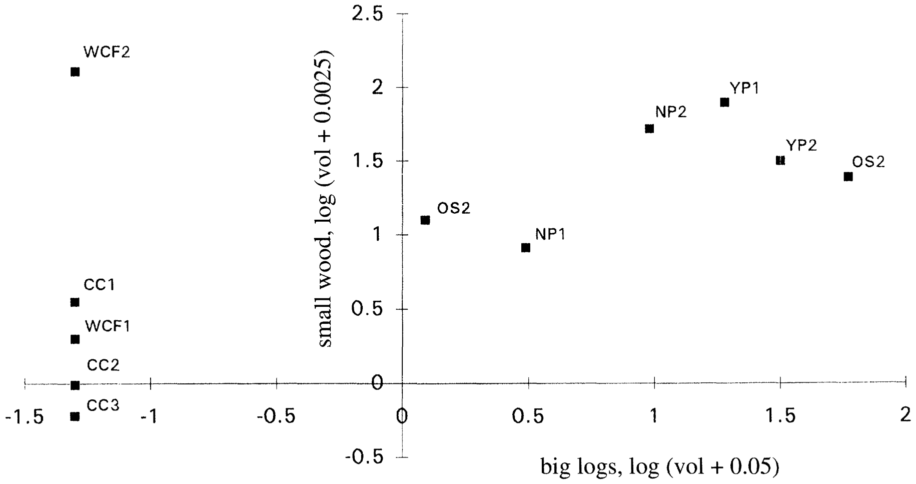

Figure 1. Plot of estimated volume of big logs (> 10 cm diameter) and small wood (< 10 cm diameter) on each 20 × 30 m plot (regression line (not shown) is $y = 0.53x + 0.86$, $r^2 = 0.801$). WCF1 was removed from the regression as an outlier.

Table 1. *General characteristics of the five plots in the MFR from which termites were sampled*

				soil characteristics (mean ± 1 s.d.)				
site	no. tree species > 20 cm dbh[a]	tree density (per ha[a])	total basal area (m^2 ha^{-1a})	bulk pH (H_2O)[b]	bulk pH ($BaCl_2$)[b]	organic C %[b]	total N %[b]	C:N ratio[b]
CC	0	0	0	4.47 ± 0.15	4.14 ± 0.11	1.12 ± 0.21	0.10 ± 0.01	11.2
				4.47 ± 0.37	4.25 ± 0.38	0.98 ± 0.03	0.09 ± 0.03	10.8
WF	0	0	0	5.85 ± 0.13	5.53 ± 0.18	2.53 ± 0.94	0.19 ± 0.03	13.3
				4.92 ± 0.03	4.26 ± 0.04	0.90 ± 0.26	0.07 ± 0.01	12.9
YP	149[c]	120 (51 poisoned)	21.3	4.43 ± 0.30	4.24 ± 0.29	2.91 ± 1.02	0.20 ± 0.04	14.6
				4.33 ± 0.10	3.96 ± 0.10	1.39 ± 0.72	0.12 ± 0.04	11.6
OS	66	133	2196	3.96 ± 0.17	3.69 ± 0.13	4.49 ± 1.57	0.21 ± 0.01	21.4
				4.21 ± 0.12	3.79 ± 0.07	1.42 ± 0.44	0.11 ± 0.03	12.9
NP	37[d]	533[d]	728[d]	3.72 ± 0.29	3.51 ± 0.33	10.30 ± 6.67	0.27 ± 0.03	38.1
				3.84 ± 0.22	3.50 ± 0.21	3.54 ± 1.31	0.20 ± 0.12	17.7

[a] Data supplied by ONADEF staff and Institute of Terrestrial Ecology, Penicuik.
[b] Upper figure is for the top 5 cm ($n = 9$), lower figure is 5–50 cm depth ($n = 3$).
[c] Based on 7 one-hectare plots.
[d] No. of species determined only within the two 30 × 20 m sampling areas on this site.

Table 2. *Estimates of lying dead wood on the five plots in the MFR sampled for termites*

(Two areas of 30 × 20 m were sampled: three in complete clearance and near primary sites. Small wood < 10 cm diameter, big logs > 10 cm diameter.)

	small wood			big logs		
site	mean volume (cm^3 m^{-2})	mean log (vol + 0.0025)	95 % confidence interval	mean volume (cm^3 m^{-2})	mean log (vol + 0.05)	95 % confidence interval
CC1	26.49	0.60	0.26	0	—	—
CC2	66.79	−0.01	0.34	0	—	—
CC3	10.27	−0.22	0.35	0	—	—
WF1	53.52	0.55	0.34	0	—	—
WF2	296.8	2.11	0.14	0	—	—
YP1	67.27	1.39	0.14	95.67	1.77	0.31
YP2	131.32	1.50	0.20	72.78	1.50	0.65
OS1	721.92	1.90	0.21	55.33	1.28	0.64
OS2	61.37	1.10	0.18	35.34	0.09	0.97
NP1	26.99	0.91	0.14	41.51	0.49	0.84
NP2	312.33	1.72	0.17	18.87	0.98	0.54
NP3	—	—	—	62.81	1.19	0.69

Table 3. *Full list of termite species collected, with mean abundances in each sampling area* (m^{-2})

(Taxonomic and functional groups abbreviated as follows. Taxonomic groups: R = Rhinotermitidae; M = Macrotermitinae; A = Apicotermitinae; T = Termitinae; N = Nasutitermitinae. Feeding groups: W = wood feeding; WL = wood and litter feeding; W/S = wood/soil feeding; S = soil feeding; (F) = fungus growing. Nesting groups: H = hypogeal; E = epigeal; L = log nesting; A = arboreal.)

	mean abundances at each site											
Termite species	CC1	CC2	CC3	WCF1	WCF2	YP1	YP2	OS1	OS2	NP1	NP2	groupings
Coptotermes sjoestedti									258.8			R, W, H
Acanthotermes acanthothorax							20	1		162	25.09	M, WL(F), H
Microtermes spp.	322	36.5	35.18	1352	218	399.5	673.3	592	81.28	96	92.77	M, W(F), H
Odontotermes sp. 1			27.5		3.03		10	30			181.9	M, W(F), H
Odontotermes sp. 2							12				27.58	M, W(F), H
Protermes prorepens						62.5	57.5		0.33	5		
Pseudacanthotermes militaris	83			65	3.5	76	2.5	1.41	5.5	13	1.8	M, WL(F), H
Sphaerotermes sphaerothorax				7.5		1	9.42	14		40		M, W, H
Synacanthotermes heterodon				38	3.9						9.3	M, W(F), H
Coxotermes bukokensis										70	2.04	A, S, H
Duplidentitermes furcatidens								5			0.01	A, S, H
Eburnitermes sp. n. 1		185				10				13	52.27	A, S, H
Eburnitermes sp. n. 2									347.5			A, S, H
Jugositermes tuberculatus											158.35	A, S, H
Labidotermes sp. n. 1										4598		A, S, H
Phoxotermes cereberus						70	92.5	3	5			A, S, H
Adaiphrotermes sp. n. 1						15	11.37	5	12.5	95		A, S, H
Aderitotermes cavator								35				A, S, H
?*Aganotermes*					2.5							A, S, H
Alyscotermes sp. n. 1									0.5			A, S, H
Amicotermes sp. n. 1						75		3				A, S, H
Amicotermes sp. n. 2	650							1	22.5			A, S, H
Amicotermes sp. n. 3								3				A, S, H
Anenteotermes ?ateuchestes											0.05	A, S, H
Anenteotermes sp. n. 1							2.5	5	74.4			A, S, H
Anenteotermes sp. n. 2						13						A, S, H
Anenteotermes sp. n. 3										4		A, S, H
Astalotermes quietus						6.3	10.04	594.3	13.46	35	635.46	A, S, HE
Astalotermes sp. n. 14					30		2.5					A, S, H
Astalotermes sp. n. 12						25		10				A, S, H
Astalotermes sp. n. 6								2	2.4		2	A, S, H
Astalotermes sp. n. 4	5	10				40				2.5		A, S, H
Astalotermes sp. n. 5									0.53		1.98	A, S, H

Astalotermes sp. n. 7				10.1					178.8	A, S, H
Astalotermes sp. n. 2				5	36.1				5.49	A, S, H
Astalotermes sp. n. 8						1				A, S, H
Astralotermes nr. *apochetus*				10	5	5				A, S, H
TC1Astratotermes sp. n. 1				500						A, S, H
Ateuchotermes sp. n. 1					5.47	4		2.3	2.93	A, S, H
Amalotermes phaecocephalus				44.2		464	36.95		6.48	A, W/S, H
Apilitermes longiceps				7	52.5	80.6	2437.2	233	1.14	T, S, E
nr. *Basidentitermes* sp. n. 1						4				T, S, H
Basidentitermes aurivilli							1.53			T, S, H
Cephalotermes rectangularis						241	43.37		0.04	T, W, E
Crenetermes albotarsalis						3373	98.08		17.2	T, S, E
Cubitermes heghi				37		3223	8.72	163	15.45	T, S, E
Cubitermes fungifaber				90.6	17.5	66	1.86	693		T, S, E
Fasitigitermes jucundus					99.5			127	4.84	T, S, H
Foraminitermes valens				570		20				T, S, H
Microcerotermes edentatus							4.3			T, W, A
Microcerotermes fuscotibialis						12.3				T, W, A
Microcerotermes parvus	20	1	327.4	2979	2962.69	1303	669.48	108.3	992.83	T, W, L
Noditermes indoensis							4.21			T, S, H
Ophiotermes grandilabius									4.06	T, S, H?
Orthotermes depressifrons						38	135		0.4	T, S, H
Pericapritermes chiasognathous	1818			10	1.05		0.54	15		T, S, H
Pericapritermes ampliganthous	1			50	10	1		34	292.27	T, S, H
Pericapritermes nigerianus				208			2.53	23	0.36	T, S, H
Pericapritermes sp. n. 1				3	23.5	13		338	150.03	T, S, H
Procubitermes arboricola				33.4	6.47	58	26.82	17	26.57	T, S, H
Pseudomicrotermes sp. n. 1			2.5							T, W, H
Termes hospes					229.5		3.05			T, W/S, E(A)
Thoracotermes macrothorax				1532	174					T, S, E
Tuberculitermes bycanistes						0.001		12	2.72	T, S, H?
Unguitermes trispinosus					2.6	170	0.03		0.06	T, S, H
Nasutitermes arborum					1.17				0.53	N, W, A
Nasutitermes diabolus									3.18	N, W, A
Nasutitermes fulleri	50			320	137.8	1	0.03	42	11.42	N, W, A
Nasutitermes latifrons			189.2		1.2			16		N, W, L
Nasutitermes lujae							15.3		0.03	N, W, A
Leptomyxotermes doriae						65			15.91	N, W/S, H
Postsubulitermes parviconstrictus								0.2	8.06	N, S, H
Verrucositermes tuberosa								0.1	2.27	N, S, H

Table 4. *Live-biomass* ($g\ m^{-2}$), *Arithmetic mean abundance* (m^{-2}) *and species richness* (*total species encountered in quantitative samples*) *for all sampling areas*

(In Nov 1992, samples were only taken on the CC plot. Abundance and species richness data are shown with (*s*) and without the effect of scrape samples for year 2. No biomass estimates were made 'with scrapes' for the second year.)

BIOMASS				abundance				species richness			
site	Aug-92	Nov-92	Aug-93	Aug-92	Nov-92	Aug-93	Aug-93 (s)	Aug-92	Nov-92	Aug-93	Aug-93 (s)
CC	19.89	0.43	0.11	2959	244	63	119	8	5	4	7
WCF	1.74		2.09	1542		778	1313	6		10	13
YP	35.13		10.98	6703		5170	5345	28		32	43
OS	114.16		39.11	10488		4319	2328	36		36	51
NP	123.2 g		8.31	6957		2934	2282	30		42	56

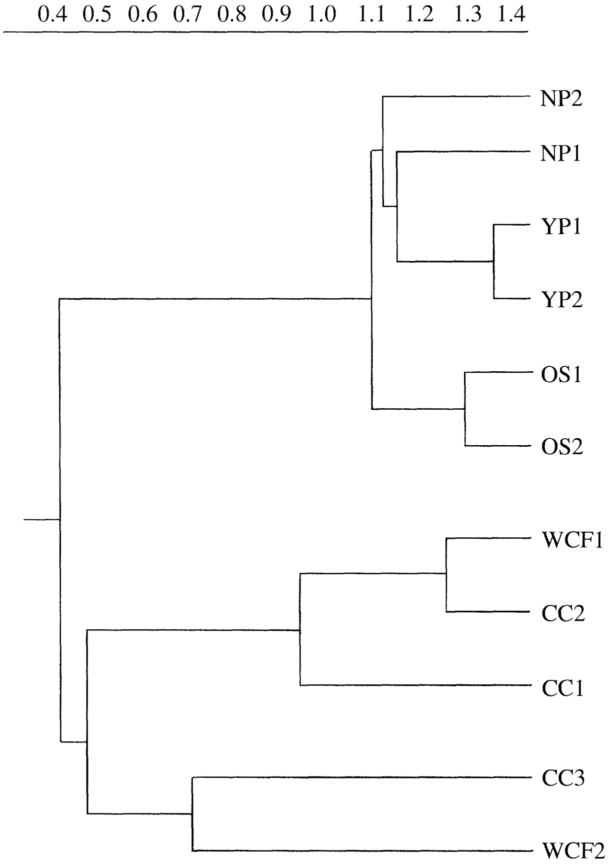

Figure 2. UPGMA tree of similarities between termite assemblages from sampling areas based on Morisita's coefficent using $\log(x+1)$ abundance data (summed arithmetic means for all species, see table 3).

Table 5. *Pairwise* post hoc *significance tests* (*Tukey-HSD*) *for comparisons between sampling areas*

(n.s. = not significant; *$p = 0.05$–0.1; **$p = 0.05$; ***$p < 0.001$.)

	CC	WCF	YP	OS
wood, year 1				
WCF	n.s			
YP	***	***		
OS	***	***	n.s	
NP	*	n.s	***	*
wood, year 2				
WCF	*			
YP	***	*		
OS	**	n.s	n.s	
NP	***	n.s	n.s	*
soil, year 1				
WCF	n.s			
YP	*	n.s		
OS	n.s	n.s	n.s	
NP	**	n.s	n.s	n.s
soil, year 2				
WCF	***			
YP	***	n.s		
OS	***	n.s	n.s	
NP	***	*	n.s	n.s

Arithmetic mean abundances for individual sampling areas (i.e. $n = 5$) are highly significantly correlated with mean N ($r^2 = 0.928$, $p < 0.005$), less so with mean C ($r^2 = 0.810$, $p < 0.05$), and C:N ($r^2 = 0.784$, $p = 0.05$), and not at all with pH ($r^2 = 0.339$, $p > 0.1$).

(*vi*) *Overall abundance from all sampling*

Abundances and biomass across sampling areas, without scrapes, are in table 4. Abundances and biomasses were consistently lower in year 2, most strikingly in the NP plot, where year 2 had 4% of the year 1 biomass; 88% of the biomass at NP in year 1 was due to *Labidotermes* sp. n. (a species not present in year 2). Numbers and biomass declined steadily on the CC plot during the year.

Biomass was concentrated in a small number of species (see table 8*a*, without scrapes estimates). These species were generally not the same between sampling areas within plots (see table 8*b*).

Overall estimated abundance (for second year sampling areas only), including scrapes, are also shown in table 4. Abundances are roughly similar to that estimated without scrapes, except for the OS plots where abundances are roughly half that estimated without scrapes (see discussion section). Species richness estimates are much greater with scrape samples included (see table 4).

(*vii*) *Functional groups*

Data are summarized in figure 5. Soil feeders dominate in the OS and NP plots and wood feeders dominate in the other sampling areas, excepting CC1 where soil feeders are again dominant (see figure 5).

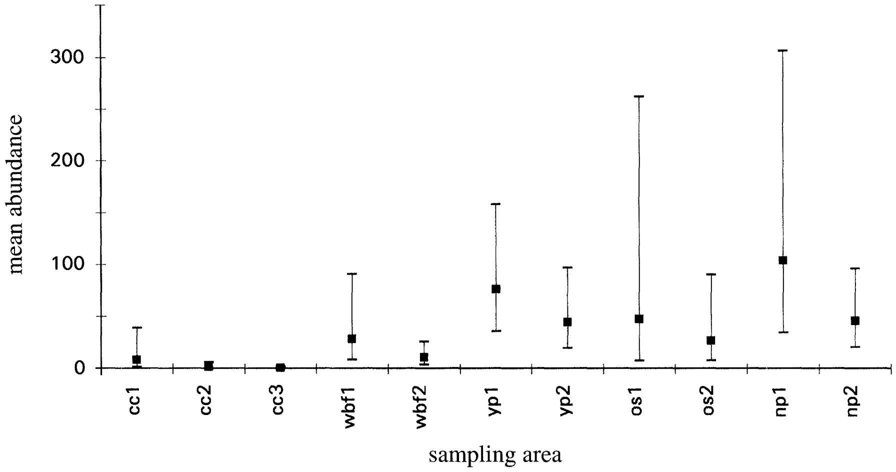

Figure 3. Mean abundances of termites in dead wood in 2 × 2 m quadrat samples, with 95 % confidence limits. Means are back-transformed.

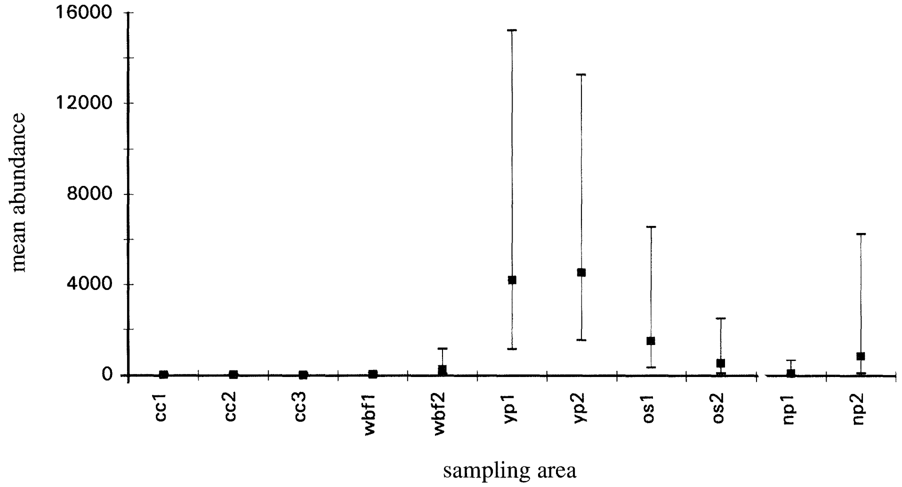

Figure 4. Mean abundances of termites in soil pits from within 2 × 2 m quadrat samples, with 95 % confidence limits. Means are back-transformed.

Litter feeders and soil/wood interface feeders are relatively scarce in all plots.

(*viii*) *Taxonomic groups*

Data are summarized in figures 6–7. The Termitinae are most abundant in the intermediate disturbance sampling areas, whereas the Apicotermitinae are proportionally most species rich in the most disturbed habitats.

(*ix*) *Nesting habit groups*

Data are summarized in figure 8. Hypogeal termites are relatively most abundant in the NP plot, wood nesters in the YP plot (this is almost entirely *Microcerotermes parvus*) and epigeal termites in the OS plot.

(*c*) ***Possible sources of error in results***

1. *Sample size*. Ten pits and ten wood quadrats give largely overlapping confidence limits for abundances in the forest-like and cleared plots (figure 3–4). However, much larger numbers of scrape samples appear to show significant effects of forest disturbance, at least between the forest-like and cleared plots. We cannot, therefore, discount the possibility that the wood quadrat and soil pit samples lacked the statistical power to reveal real differences between the forest-like plots. However, the logistical effort required to sample quantitatively at or above the scale attempted here may be prohibitive (Eggleton & Bignell 1995).

2. *Hand sorting*. The error associated with this method of extracting termites was estimated by Wood *et al*. (1982) at 12 % for a dry riverine forest in Nigeria. We have no way of knowing how close this is to a true estimate for our system and our labour force. Alternative methods (e.g. Berlese funnel, winkler bags, flotation) are either not practicable or ineffective for quantitative work on termites (Eggleton & Bignell 1995).

3. *We did not sample below 50 cm*. Wood *et al*. (1982) show (for the same Nigerian site as above) that an average of 18 % (in the dry season) and 15 % (in the wet season) of individual termites were below 50 cm (maximum depth 150 cm). Some of our differences between the two sampling years may therefore be due

Table 6. *Overall abundance of termites in mounds* (m^{-2}) *and for scrape samples* (*year 2 only*, m^{-2}, *back-transformed means*) *across the sampling areas*

	termite abundance		
	Mounds		
site	Year 1	Year 2	Scrapes
CC	*[a]	0	3.2
WCF	0	0	12.14
YP	531	429	18.21
OS	524	215	22.9
NP	401	67	30.95

[a] A small number of moribund mound-building colonies survived on dead tree stumps on the CC plot in the year 1, but were not sampled.

Table 7. *Pairwise* post hoc *significance tests* (*Wilcoxon signed rank*) *for comparisons between sampling areas for scrape samples*

(n.s. = not significant; *p = 0.005–0.01; **p = 0.005; ***$p < 0.0001$.)

	CC	WCF	YP	OS
wood, year 1				
WCF	n.s			
YP	***	***		
OS	***	***	n.s	
NP	*	n.s	***	*
wood, year 2				
WCF	*			
YP	***	*		
OS	**	n.s	n.s	
NP	***	n.s	n.s	*
soil, year 1				
WCF	n.s			
YP	*	n.s		
OS	n.s	n.s	n.s	
NP	**	n.s	n.s	n.s
soil, year 2				
WCF	***[d]			
YP	***	n.s[a]		
OS	***	n.s	n.s	
NP	***	*[b]	n.s	n.s

Table 8. *Proportion of biomass in the 10% of species contributing most to overall biomass, and identity of the top 10% of species*

site	August 1992	November 1992	August 1993
	proportion of biomass in top 10% of species		
CC	87%	79%[a]	49%[a]
WCF	63%	—	57%
YP	84%	—	73%
OS	95%	—	96%
NP	94%	—	69%
	identity of top 10% species		
CC	*Pericapritermes chiasognathus*	*Eburnitermes* sp n 1	*Microtermes congoensis*
WCF	*Microtermes congoensis*	—	*Microcerotermes parvus*
YP	*Microcerotermes parvus* *Thoracotermes macrothorax* *Foraminitermes valens*	—	*Microcerotermes parvus* *Microtermes congoensis* *Astratotermes* sp n 1
OS	*Crenetermes albotarsalis* *Cubitermes heghi* *Microcerotermes parvus* *Astalotermes quietus*	—	*Apilitermes longiceps* *Microcerotermes parvus* *Eburnitermes* sp n 2 *Coptotermes sjoestedti*
NP	*Labidotermes* sp n 1 *Cubitermes fungifaber* *Pericapritermes* sp n 1	—	*Microcerotermes parvus* *Astalotermes quietus* *Pericapritermes amplignathus* *Odontotermes* sp 1

[a] Biomass in top 20%, where there were less than ten species sampled.

to individuals moving below 50 cm in the wet season. Assuming that 2 and 3 are cumulative in effect (i.e. that if we dug to 150 cm we would still have a hand-sorting error of 12%) gives us an overall underestimate of ca. 30% in the soil pit samples.

Evidence that some hypogeal termites migrate or move colony centres downwards in the soil profile (below 50 cm) during dry seasons is provided (for *Microtermes*) by T. G. Wood & H. Black (unpublished data). *Microtermes* forms a component of the 'remnant' termite fauna in cleared plots in the MFR and one that persists to the second year of sampling. We have no idea whether *Microtermes* colonies are abundant below 50 cm on the cleared plots. However, the possibility that downwards migration of *Microtermes* might be a permanent response to forest clearance must be considered.

4. *Arboreal mounds that we were unable to reach.* We were able roughly to survey arboreal nests in the sampling areas when we could see them. The figures for the plots were: YP (year 1, 1; year 2, 1), OS (0,1), NP (2,5). Rough estimates of sizes of these nests were made and calibrated against accessible *Nasutitermes* and *Microcerotermes* mounds of known nest and colony size, assuming that population size is proportional to nest volume (see, for example, Abe & Matsumoto 1978). The rough estimates of arboreal termite abundance m^{-2} in each plot were: YP (20, 300), OS (0, 20), NP (1000, 2000), implying that arboreal nests and their wood-feeding occupants may contribute significantly to abundance in near primary forest. The problem deserves more attention.

5. *Termites within dead* (*and living*) *standing trees*. The error associated with this microhabitat is impossible to estimate, although we know that the number of standing dead trees per sampling area is typically not more than 1 (there were, however, many more in the YP plot where many old trees have been poisoned). If we assume 100000 individual termites per dead standing tree, this might indicate a minor but significant contribution (i.e. about 100 m^{-2}).

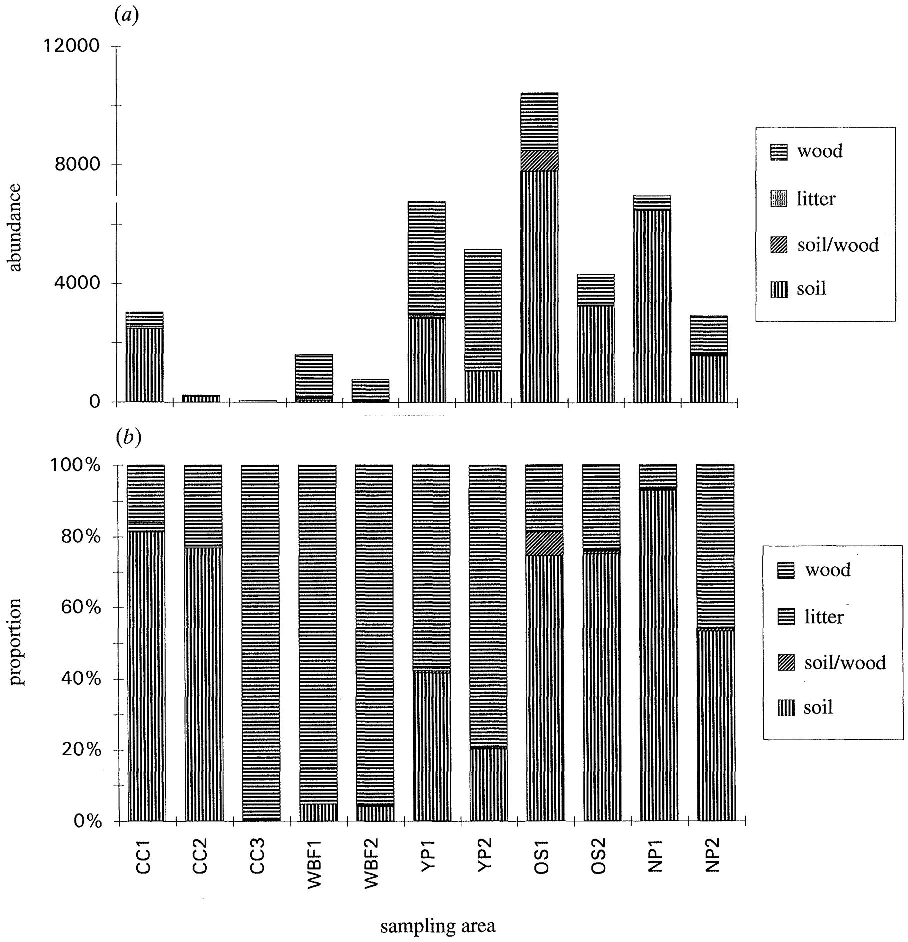

Figure 5. (*a*) Abundances (m^{-2}) and (*b*) proportions of different functional (trophic) groups of termites (see text) across the sampling areas.

6. *Right-skewed distribution of population sizes.* This will tend to underestimate the arithmetic mean, for a given sample size, as means of skewed distributions move in the direction of the skew with increased sample size (Sokal & Rohlf 1981).

7. *Problem of taking scrapes from within a quadrat.* Scrapes and pits take a long time to dig, and some termites may be sensitive to disturbances while sampling and so leave the sampling area.

8. *Mounds were all sampled in the second year* (for reasons outlined above). If differences in the weather between the first and second years contribute to proportionately more (or fewer) termites occupying mounds in the second year, an additional error will enter our calculation. We have no idea what its magnitude might be.

9. *Seasonality.* Two 'snap shots' do not allow real population fluctuations and turnover to be estimated. We hope to start small scale continuous sampling in the MFR soon, that will allow us to take account of seasonal changes in termite numbers.

4. DISCUSSION

(*a*) *General differences between termite assemblages*

There are relatively few clear differences in abundance and biomass between the plots, although the cleared plots differ in overall assemblage composition from the forested plots (see figure 3). The most disturbed (bulldozed) sampling areas are highly depauperate and have very low abundances.

The overall similarity in abundance levels of the forest-like plots is surprising but in agreement with qualitative data from the same plots (Eggleton *et al.* 1995). Termites are decomposer organisms that require dead plant material (and its subsequent decay products) as a food source. These and other (e.g. Eggleton *et al.* 1994) data suggest that termites are not critically limited by tree species number or type. Rather, given a suitable microclimate, adequate food, and a more or less closed canopy, that termites are resilient to quite extreme environmental perturbations. However, it is clear that this resilience is not simply due to the maintenance of the original forest assemblage but is accompanied by large changes in the relative abundances of trophic groups (see figure 5). Soil feeders are particularly strongly affected by disturbance. Data from the CC plot show that immediately after clearance, some soil feeding termites survived. However, over the next year of sampling, abundance and biomass declined to almost nothing.

Overall abundance of wood feeders is significantly correlated with available large logs; occupancy levels in small pieces of wood were clearly lower and there was no significant correlation between abundance of

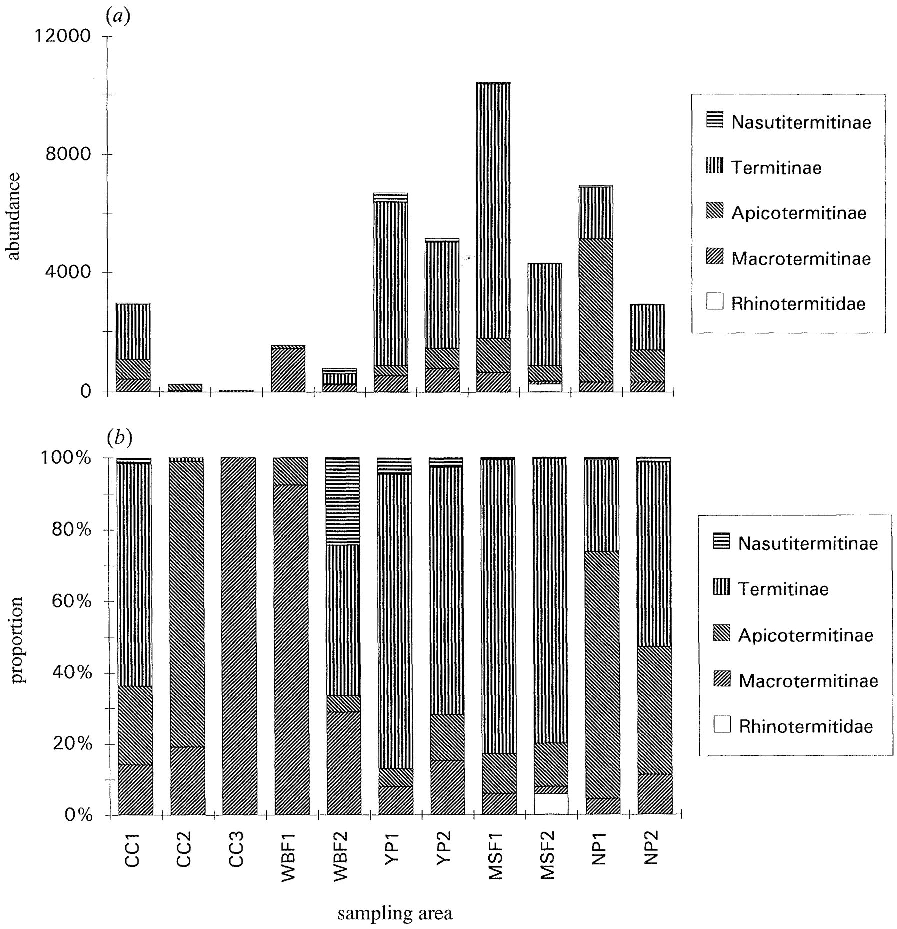

Figure 6. (*a*) Abundances (m^{-2}) and (*b*) proportions of different taxonomic groups of termites (see text) across the sampling areas.

wood-feeding termites and small wood volume. Individual tree falls (rather than a steady enrichment with woody litter) may have the greatest impact on termite diversity. The abundances of soil-inhabiting termites in this system were most highly correlated with available N, but further, larger scale, studies are required to confirm this. Studies on the N-fixing ability of soil-feeding termites would be especially interesting in this context (Tayasu *et al.* 1994).

(*b*) *Functional groups and habitat heterogeneity*

It is not clear exactly what different functional groupings of termites feed on, but it is predominantly woody organic matter at different stages of the humification process, with different species specialising at different stages of the decay process. For example, qualitative sampling in the MFR suggested that soil-feeding Apicotermitinae are proportionately better represented in the more disturbed plots and that soil-feeding Termitinae are proportionately better represented in the less disturbed plots (Eggleton *et al.* 1995). The data here show no clear pattern but do not obviously contradict that finding. In Eggleton *et al.* (1995) these differences may be due to the different nutritional requirements of the different subfamilies; with the Apicotermitinae feeding on organic matter at an earlier stage of humification than the Termitinae.

In primary forest the spatial and temporal patterns of tree falls will lead to a highly complex mosaic of decaying organic matter at different stages of humification. Major inputs (fall of trees and large limbs) will be detectable for several years or decades. Superimposed on these large scale, long-lasting, events will be inputs (the fall of twigs and leaves) that occur on smaller spatial scales, with the result that primary forest might be expected to have a high heterogeneity of termite species and functional groups across most spatial scales. Other types of plots may have a more homogenous forest floor: both spatially and in terms of the age and state of decomposition of the wood. The YP plot is a good example, dominated by wood feeders utilizing the major inputs of dead wood created by the manual récrû.

There is some evidence for greater small scale heterogeneity in soil characteristics for the NP plot over the other forest-like plots. The variance in total % carbon in the soil is much higher for NP2 (10.30 ± 6.67, coefficient of variation (CV) = 0.64) than for the other forest-like plots (YP2 [2.91 ± 1.02, CV = 0.35] and OS2 [4.49 ± 1.57, CV = 0.35]). The dead wood samples, in contrast, are not so easily characterized and do not appear to show differences in heterogeneity between the NP and other forest-like plots. More work is required to explore relations between termite species' spatial distribution and richness and the spatial and

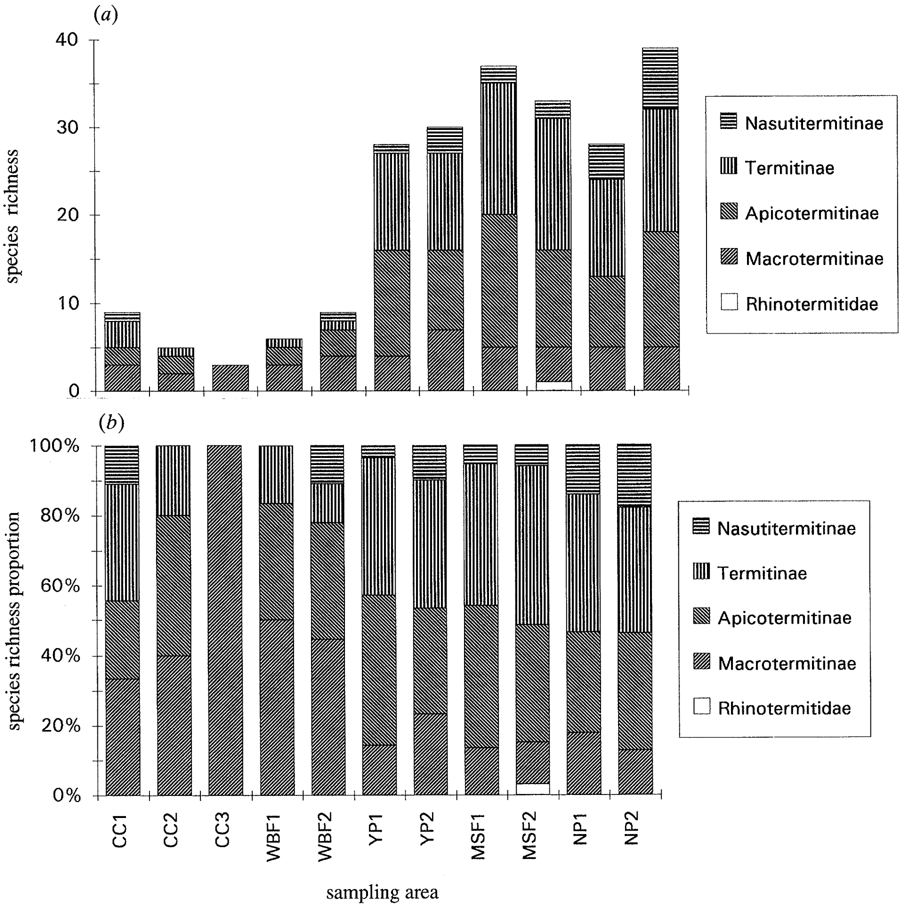

Figure 7. (*a*) Species richness and (*b*) species richness proportions of different taxonomic groups of termites (see text) across the sampling areas.

temporal heterogeneity of the wood and litter on the forest floor.

A qualitative study of termite assemblages in fragments of forest in Amazonia is, however, consistent with these speculations. De Souza & Brown (1994) showed that fragments of forest surrounded by cleared areas have termite assemblages that appear to be dependent on the spatial patchiness of the original forest. Undisturbed forest had high small-scale variability or heterogeneity, and this left forest fragments with an assemblage structure reflecting, at least in part, this heterogeneity.

(*c*) *Nesting group dynamics*

The high abundance of epigeal mound-building termites in the OS plot, and their relative scarcity in the NP plot is not easy to explain. One possibility is a successional process. In a cleared area (or large natural gap caused by a tree fall) many mound-building termites (e.g. *Cubitermes heghi*) will be excluded because there are no suitable large trees to nest against (e.g. the CC, WCF and YP plots in figures 8*a*, *b*). As trees regenerate they will become suitable for colonization by mound-building termites, as on the OS plot which has been regenerating for 30 years. Over time, however, colonies die and the mounds of such colonies will fall into disrepair and/or be occupied by inquilines. Old mounds may therefore act as 'stoppers' on trees that might be used by other mound-builders, resulting in the reduced number of mounds found on the NP plot. Whether this argument also applied to free-standing mound builders is uncertain. Unfortunately, the actual dynamics of soil feeder mound/colony turnover are largely unknown (Maldague 1964) but a proportion of mounds, apparently in fresh condition, are not occupied by the species that built them, or are devoid of termites.

(*d*) *Dominant species*

The top 10% of species make up a disproportionate share of the total biomass on each plot (see table 8*a*). However, the same very abundant species do not consistently dominate assemblages (see table 8*b*), although the wood-feeding *Microcerotermes parvus*, and the large *Cubitermes* mound-builders are abundant in most forest-like sampling areas. A number of species that were dominant in particular sampling areas on one sampling occasion have been collected relatively rarely throughout the study period: *Astratotermes* sp n 1, *Eburnitermes* sp. n. 1, *Labidotermes* sp. n. 1 and *Foraminitermes valens* were all collected on less than five occasions during the two years of intensive sampling. Although some of these dramatic differences in abundance may be due to sampling error, some may be due to the dynamics of colony foundation and decay

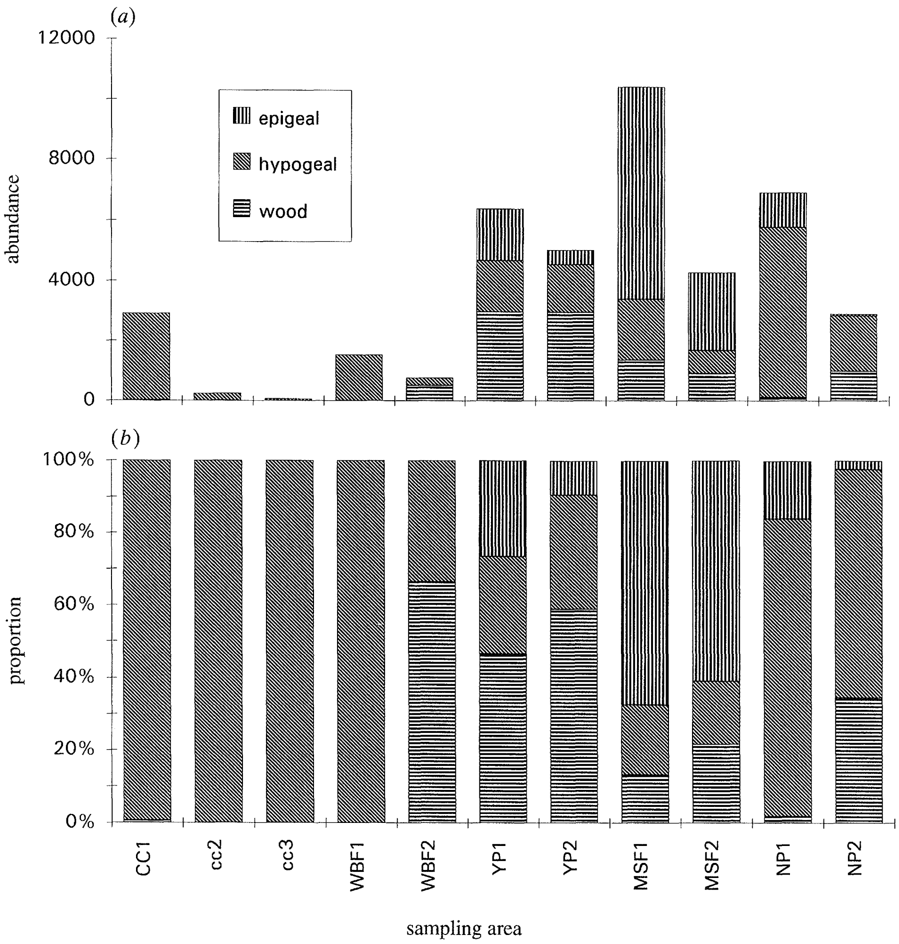

Figure 8. (*a*) Abundances (m^{-2}) and (*b*) proportions of abundances of termites in different nesting groups. Arboreal nests are not included.

in individual species. In the case of *Labidotermes* sp n 1, very large number were present on the NP plot in August and November 1992, but the same areas had no individuals during intensive sampling in August 1993, March 1994 and August 1994. This might be due to a sudden and large scale change in foraging direction from a large central nest, or colony extinction. The ecological effects of this appearance and disappearance of generally rare, but locally temporarily highly abundant, species is difficult to quantify, but it suggests that estimations of the role of termites in ecosystem function (e.g. Lawton *et al.* 1995) may be made difficult by such processes.

(*e*) *Colonization by savanna species*

As suggested in Eggleton *et al.* (1995) for qualitative data, there is no evidence that any species are found in the cleared plots that are not also found in the forest-like plots. Therefore, unlike plots close to savanna areas (Wood *et al.* 1982), there is no influx of savanna species into cleared forest plots in the MFR, and thus cleared plots have depauperated forest assemblages.

The MFR is about 40 km south of the forest-savanna boundary. There is anecdotal evidence of some savanna species (*Macrotermes bellicosus*, *Amitermes evuncifer*) spreading their range southwards with increasing forest clearance and fallow shortening. These might be expected to enter the MFR species pool in the next two or three decades.

(*f*) *Effect of surrounding secondary forest on edge effects*

The plots in this study were all surrounded by a disturbed mix of near primary and old secondary forest. This matrix may reduce the differences between plots, by providing a large OS-like source of termites around each plot. In one ha plots such edge effects may be especially important (Eggleton *et al.* 1995). Edge effects may have been increased on the OS plot, by the dirt track that was bulldozed through it between years 1 and 2. Such disturbance may have reduced overall humidity and temperature stability in the second year, and contributed to a drop in abundance in termites at the OS plot in the second year.

(*g*) *Comparisons with qualitative sampling and other studies*

Only six species were collected in the quantitative samples that were not collected in the qualitative; in the genera *Amicotermes*, *Astratotermes*, *Cephalotermes* and *Foraminitermes*. *Cephalotermes rectangularis* is a fairly common species, but builds nests that are highly clumped in the environment and has not been recorded outside these nests and immediately adjacent dead wood. It is unlikely that a transect would pass through one of these nests. The quantitative sampling, although very intensive and extended to soil scrape samples in the second year, yielded fewer species than the qualitative transect sampling (74 as against 88). This supports the idea that qualitative transects may be the best and quickest way to gather species richness data on termites.

The abundance, biomass and species richness estimates given here (although still underestimates, see above) are the highest recorded for any area examined for termites (see Eggleton & Bignell 1995; Lawton *et al.* 1995). The high assemblage diversity may be due in part to historical factors (Eggleton *et al.* 1994), but may also be due to broad climatic features of Cameroon. The presence of two dry seasons in Cameroon and the overall dryness of the forest may allow termites to compete effectively against fungi that may monopolise a greater share of dead plant biomass in wetter forests (Holt 1987, 1990).

5. CONCLUSIONS

This study represents a considerable advance over earlier quantitative studies of termite assemblages. It is the first that has attempted to deal with the problem of the clumped distribution of termite abundance, and to put confidence limits on abundance estimates (but see Wood *et al.* 1982). Similarly most previous studies, with the probable exception of Wood *et al.* 1982, have underestimated termite abundances in both soil and wood (see Eggleton & Bignell 1995). The additional labour required to improve upon our estimates will be considerable, but it is now clear what might be done to obtain a complete estimate of termite abundance and biomass in tropical forests.

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