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Successional response of a tropical forest termite assemblage to experimental habitat perturbation

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Summary

1. Research into the successional responses of tropical forest communities following disturbance has potential applications for habitat restoration. Currently little is known of how these responses relate to the recovery of biodiversity and ecosystem processes. Succession of assemblages of decomposer arthropods is essential for the recovery of the soil community and nutrient cycling processes.

2. This study investigated the successional response of a termite assemblage to the experimental perturbation of forest habitat in southern Cameroon, examining the implications for tropical forest restoration. A randomized block design consisting of four experimental perturbations of differing severity was established in an old secondary forest in the Mbalmayo Forest Reserve. Isolated control sites were left in undisturbed forest. Recovery of the termite assemblage was assessed by measuring termite species richness and abundance at regular intervals over the subsequent 12 months.

3. The speed of recovery of the termite assemblage varied with the type and extent of perturbation. In treatments involving severe soil and canopy disturbance, termite species richness and abundance recovered more rapidly when dead wood was left on the ground following perturbation. The availability of dead wood also resulted in recolonization by a subset of the termite assemblage that was distinct compositionally from that sampled from all other treatments. This subset at sites with additional dead wood included not only certain wood-feeding species, but also soil feeders.

4. The positive effects upon the termite assemblage of leaving substantial dead wood on the ground has implications for the restoration of tropical forests following human-induced disturbances such as logging. The accelerated recovery of termite diversity and assemblage composition is a significant component of soil community recovery and the restoration of nutrient cycles. These benefits are expected to influence soil fertility and, ultimately, forest regeneration. The duration and persistence of these effects will depend crucially on the type, scale and intensity

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of the original disturbance. The impact of termites on soil properties, and vice versa, clearly deserves more attention in studies of tropical forest regeneration and recovery.

Key-words: forest disturbance, restoration, succession, termite diversity.

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Introduction

Current levels of anthropogenic disturbance to the world's forest ecosystems, and to tropical forests in particular, are unprecedented (McNeely *et al.* 1995). The consequences of this disturbance, including the compaction and erosion of soils leading to nutrient loss and landscape degradation, mean that tropical forest restoration is a lengthy and difficult process (Jansen 1997). Although numerous studies of the initial loss of species diversity following perturbation have been made, we know little of the successional responses of tropical forest ecosystems to such perturbations, or of the mechanisms governing the recovery of biodiversity (Tilman 1993). Studies that increase our understanding of these forces should enhance habitat restoration efforts (Palmer, Ambrose & Poff 1997).

Theories of forest succession have originated largely from studies on the diversity and structure of temperate zone plant communities (Clements 1916; Odum 1969). Subsequent developments have attempted to incorporate what we know of community patterns in tropical as well as temperate zones, and to recognize features of animal and plant succession. As such, ideas have moved forward from a wholly deterministic stand-point, assuming the importance of competition and the validity of the equilibrium paradigm, to a substantial body of theory that takes greater account of stochastic factors, and which increasingly recognizes the validity of non-equilibrium scenarios (Connell & Slayter 1977; Tilman 1993; Palmer, Ambrose & Poff 1997). In response to these developments, restoration ecologists are recognizing the dynamic complexity of communities, and the role of successional processes as a tool for restoring levels of species diversity and ecosystem function, rather than simply the restoration of particular individual species (Palmer, Ambrose & Poff 1997).

Plant successional recovery following disturbance is known to be closely linked to soil conditions. For example, during plant primary succession, or secondary succession on poor soils, total plant biomass increases with increase in soil nitrogen (Tilman 1986). However, it is not plants themselves that form soil, but soil micro- and macro-organisms (Tilman 1986). There is increasing awareness of the importance of soils for the provision of ecosystem services, as 60–90% of terrestrial primary productivity is decomposed in the soil (Giller 1996). Following habitat disturbance, the restoration of processes such as litter decomposition is essential for ecosystem recovery (Andersen 1997).

Soil communities are among the most species-rich components of terrestrial ecosystems (Anderson 1975; Ghilarov 1977; Stanton 1979; Usher *et al.* 1979). Most terrestrial insect species live in the soil for at least part of their life cycles (Ghilarov 1977; Behan-Pelletier 1993). In tropical forests, arthropods, particularly insects, make up the majority of known biodiversity (Wilson 1992). The proportion of these species that are found in the rain forest soil and leaf litter, rather than canopy, ranges from 70% to 75% (Stork 1988; Stork & Brendell 1990; Hammond, Stork & Brendell 1997). The overall effect of forest clearance upon insect diversity is negative (Watt *et al.* 1997). Clearly, this has much to do with the effects of accompanying soil perturbation on soil communities. However, little is known of the successional responses of soil communities following such perturbation (Giller 1996). A number of studies have reported the relatively rapid establishment of detritivorous arthropods following habitat disturbance, compared with that of higher trophic levels (Hendrix, Brown & Dingle 1988; Williams 1993; Jansen 1997).

Termites are a particularly important part of the soil arthropod community in tropical forests. In some African forests, the abundance and biomass of termites is up to an order of magnitude greater than any other insect group (Eggleton & Bignell 1995). Termites play key roles in decomposition processes, nutrient cycling, nitrogen fixation, carbon flux, soil creation and soil distribution (Collins 1983; Jones 1990; Bond 1993; Lawton *et al.* 1996; Bignell *et al.* 1997). These functions are largely dependent on the species composition of the termite assemblage.

Termite assemblages differ in forests at different successional stages after logging (Eggleton *et al.* 1995, 1996, 1997) and they change further following conversion of land for agriculture (Lee & Wood 1971). Little is known, however, of the progress of termite succession generating contrasting assemblages. Usher (1975) studied termite communities at different stages of recovery following clearance of fallow scrubland in an agricultural area of West Africa. This revealed a variation in the responses and recovery trajectories between species; however, only wood-feeding species were sampled.

In this investigation, we studied the response of termite assemblages in a tropical African forest to experimental habitat perturbation, and successional recovery over the subsequent 12 months. The study involved a comparison between five experimental treatments in which forests were perturbed to differing degrees of severity (including undisturbed controls). The perturbations were analogous to those accompanying plantation forestry and clearance for agriculture. They were intended to result in a variety of starting points in terms both of environment (i.e. microclimate, soil conditions and availability of dead organic material) and the degree of attenuation of the termite assemblage. To this end, perturbations included direct physical destruction of mound- and soil-dwelling components of the assemblage, and more indirect effects via changes in vegetation cover and availability of dead wood. Monitoring the effects of forest treatments involved quantitative sampling of all trophic groups of termites. Additionally, both termite- and fungus-mediated decomposition of wood, and various soil variables, were measured. With regard to tropical forest restoration, the most important considerations concerned the trajectories of recovery of the termite assemblages in each treatment. These were investigated in terms of the speed and extent of recovery of termite species richness, abundance and assemblage composition. In respect to the latter, the study focused on the pathways of termite assemblage succession in each treatment, and the extent to which these varied from the undisturbed controls.

Materials and methods

STUDY SITE

The study was carried out in the Mbalmayo Forest Reserve in southern Cameroon (3°23′ to 3°31′ N, 11°25′ to 11°31′ E), an area of semi-deciduous forest that has been at least partly logged several times in the past century (Lawson *et al.* 1990). The forest is classified as tropical premontane moist forest (Holdridge *et al.* 1971), with annual rainfall averaging 1520 mm and falling predominantly during two wet seasons, March–June and September–November. Average monthly temperatures fluctuate from 22·6 °C in August to 25·5 °C in January. The experimental plots at Mbalmayo were established at the Ebogo site (3°25′ N, 11°29′ E) in July 1995. This is a regenerating forest (approximately 90 years old), with closed canopy, that is representative of the forests of the surrounding area. The mean diameter at breast height of trees (> 20 cm d.b.h.) is around 39 cm, with approximately 185 trees ha^{-1}, and a total basal area averaging 28 m^2 ha^{-1}. Qualitative and quantitative methods, which have for the first time comprehensively sampled termites living in forest soils rather than just mounds and dead wood, have recently been employed at Mbalmayo (Eggleton *et al.* 1995, 1996). As a result of their use, Mbalmayo Forest Reserve now has the highest recorded termite abundance and species richness of any tropical site surveyed (Eggleton *et al.* 1996). These levels of species richness and abundance are almost certainly representative of equatorial West African forests as a whole, and this subregion is known to have the highest generic richness for termites in the world (Eggleton, Williams & Gaston 1994; P. Eggleton unpublished data). Termites may constitute as much as 95% of all soil insect biomass at Mbalmayo (Bignell *et al.* 1997).

EXPERIMENTAL DESIGN

Four experimental treatments were established in a fully randomized block design, and an additional set of isolated controls was established in a similar area of undisturbed forest about 50 m downslope. The treatments are summarized in Table 1 and represented a gradient of disturbance. The randomized block layout contained 30 cells (5 × 5 m each), arranged in six columns by five blocks, with a footpath of at least 2 m width between adjacent treatment cells. Each treatment was replicated five times, once in each block, and positioned randomly with respect to column (Fig. 1), leaving two unused cells in each block. There were also five replicates of the isolated control cells, and these were positioned contiguously with each other in one block.

The rationale for the four treatments, and isolation of controls, was as follows. At Mbalmayo, the

Table 1. Description of forest cell treatments

Treatment name	Treatment description
Mounds removed (MR)	All epigeal termite mounds removed
Under-brushed (UB)	All epigeal termite mounds, litter and saplings (up to 8 cm d.b.h.) removed
Complete clearance (CC)	All epigeal termite mounds, litter and saplings (up to 8 cm d.b.h.) removed; soil dug out to a depth of 10–15 cm and all roots, termites and fungus combs removed from it, then the perturbed soil added back
Logs added (LA)	As for CC (above) but with the addition, following perturbation, of fresh logs to forest floor (average of 12 logs per treatment cell, at a density averaging 860 cm^2 m^{-2})
Control (CN)	Undisturbed forest, 50 m from the four randomized block treatments (above)

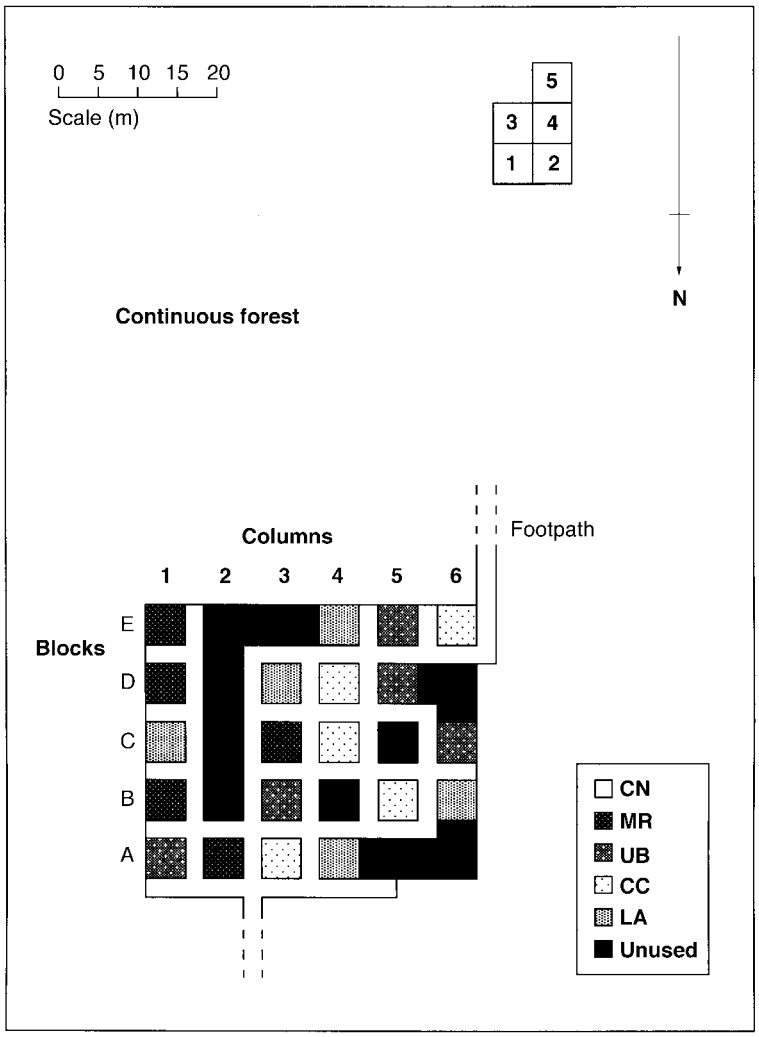

Fig. 1. Plan of the randomized blocks indicating their position relative to the isolated control cells (CN), and showing the layout of the five replicates of each of the four perturbation treatments [mounds removed (MR); under-brushed (UB); logs added (LA); complete clearance (CC)].

termite assemblage is dominated by soil feeders (Eggleton *et al.* 1996) and much of the energy they harness passes through the large-bodied, mound-building species (Eggleton, Davies & Bignell 1998). By eliminating the main mound-building colony centres, as well as inquiline colonies living in mound walls, the mound-removal (MR) treatment was expected to have a profound effect on this part of the termite assemblage. Mound-building soil feeders do not forage far from their nests. Nevertheless, the control cells (CN) were isolated from the randomized blocks as a precaution against any influences upon them from mound removal in adjacent cells, and vice versa. The under-brushing (UB) treatment was expected to cause drying out of top soil, through reduction of canopy density, providing contrasting microhabitat conditions to MR. The most severe treatment, complete clearance (CC), was an extreme perturbation akin to that resulting from logging operations, in which acute soil disturbance leads to severe loss in soil structure. Fungus-growing termites (subfamily Macrotermitinae, see below) make fungus combs in their nests, and the removal of these from the soil was necessary to eliminate all termites. In an elaboration of this treatment, the logs added (LA) treatment, the addition of fresh timber was intended to provide an organic nutrient source, and additional microhabitat structure, that might lead to a contrasting successional response to that of CC. Furthermore, LA was intended as an analogue to severe disturbance associated with forest gap formation, or logging processes, which leave dead wood on the ground.

TERMITE CLADES AND FUNCTIONAL GROUPS

In dietary terms, tropical forest termite assemblages exploit a humification gradient of plant-derived material. The least humified substrates are sound

wood, lichens/bryophytes and fresh leaf litter, followed by increasingly rotten wood and leaf litter, progressing to very humus-rich soil and ending up with humus-poor, mineralized soil at the most humified extreme. Habitat disturbance is already known to change the termite assemblage, reflecting a shift in the proportions of species feeding at different points along this gradient (Eggleton *et al.* 1995, 1996, 1997). Termite species collected in this study all belonged to the higher termites (Termitidae) and were assigned to one of the following putative termite clades reflecting functional groupings (S. Kambhampati & P. Eggleton unpublished data) (see also Appendix 1).

Macrotermitinae

These are wood and leaf litter feeders that, because of their association with *Termitomyces* species of basidiomycete fungi, cultivated inside their nests, are able to consume relatively undecomposed dead plant material. *Sphaerotermes sphaerothorax* (Sjöstedt), although included in the Macrotermitinae, is unusual in not being a fungus-grower, and may yet prove not to be a member of this subfamily.

Termes-group (Termitinae)

This is one of the two soil-feeding clades within the subfamily Termitinae, and includes *Pericapritermes* species, some of which apparently feed at the interface between soil and wood.

Cubitermes-group (Termitinae)

This is the other soil-feeding clade within the subfamily Termitinae, although *Unguitermes trispinosus* Ruelle is a soil–wood interface feeder. *Foraminitermes valens* (Silvestri) probably belongs in a separate clade but has been included in this group because of its ecological similarities.

Amitermes-group (Termitinae)

This is a predominantly wood-feeding clade of the Termitinae, represented in this study by a single species, *Microcerotermes parvus* (Haviland).

Nasutitermitinae

This can be subdivided further into the *Nasutitermes*-group, comprising wood-feeding species, and the *Subulitermes*-group, comprising soil-feeding species. However, only three Nasutitermitinae species were found in this study (see Appendix 1), all of which were excluded from the ordination analyses of assemblage composition because each occurred in one sample only.

Apicotermitinae

This can be further subdivided into two clades, the *Anoplotermes*-group and the *Apicotermes*-group. Both clades consist of soil-feeding species, with the exception of *Amalotermes phaeocephalus* Sands, a member of the former group that feeds at the soil–wood interface.

DATA COLLECTION

Termites were collected on five sampling occasions over a 12-month period (August and November 1995; February, March and July 1996), from four randomly located soil pits dug in each of the 25 cells of the experimental plots (including the isolated control cells; Fig. 1). On the same sampling occasions (excluding February 1996), decomposition processes were assessed from the breakdown of wooden stakes planted in each treatment cell (see below). In March 1996, soil variables were also measured; some were from the same soil pits as described below for termite sampling, but others were measured separately from additional soil samples.

Termite data from soil pits

Each of the four soil pits dug in each treatment cell measured 20 × 20 cm by 10 cm deep. The four measurements of each variable from each plot were pooled for each cell to avoid pseudoreplication. Soil from pits was hand-sorted (Eggleton & Bignell 1995), and all termite soldiers and workers were collected and stored in 80% ethanol. These were subsequently counted and sorted to species/morphospecies at the Natural History Museum (NHM), London, UK, using the available taxonomic literature, the NHM main collections and the NERC-TIGER (Natural Environment Research Council–Terrestrial Initiative in Global Environmental Research) reference collections (see Appendix 1). All immature termites (nymphs and larvae) were excluded from counts because of the difficulty of species identification. These stages were relatively rarely encountered and, being much smaller in body size, constituted a minor proportion of total biomass.

Data from wooden stakes

Both fungus- and termite-mediated decomposition of wood were assessed, as fungi are important competitors of termites for dead wood in tropical forests (Amburgey 1979; Swift 1987; Lodge 1993). Decomposition of wooden stakes was assessed following standard methods of trialling timber resistance to termite and fungal attack (European Committee for Standardization; Anonymous 1989). Stakes were of 'Ayous' (*Triplochiton scleroxylon*

Schum, family Sterculiaceae). In July 1995, 10 stakes, each measuring $500 \times 50 \times 25$ mm, were planted in the ground to 250 mm depth. They were arranged in a regular configuration, in each of the 25 treatment plots, including the five isolated control cells (CN). On each subsequent sampling occasion (November 1995, March and July 1996), each stake was extracted from the ground and assessed visually for decomposition state. Damage attributable to fungi or termites was clearly distinguishable: termite-mediated = presence of clearly defined cavities, conversion of wood to carton (woody faecal material), and presence of soil plastered into the wood; fungus-mediated = slow weakening of wood, wood discoloration, presence of fungal hyphae and/or fruiting bodies. The extent of termite- and fungus-mediated decomposition was scored separately for each stake on a semi-quantitative scale from 0 to 4 (Anonymous 1989; Table 2). For consistency, assessment of all stakes was carried out by the same two people (LD and PE).

Soil variables

During March 1996 only, 8 months after the initial disturbance, the following soil variables were measured. Total organic carbon, total nitrogen and soil texture/granulometry were assessed using the same soil excavated from the four replicated soil pits in each cell (described above). Following extraction of all termites and roots, each replicate soil sample was then homogenized. A subsample weighing between 1 and 2 g from each of these replicates was assessed for total organic carbon and total nitrogen (percentage mg g^{-1} dry weight of soil) using a Nitrogen Carbon Sulphur Analyser (NA 1500; Carlo Erba Instruments, Austin, TX). Additionally, a 20–30-g subsample was removed from each replicate and used for granulometric analyses to determine the percentage of coarse sand, fine sand, silt and clay (percentage mg soil fraction g^{-1} mineral soil). After organic matter destruction (using H_2O_2) and complete soil dispersion, the soil texture/granulometric distribution was determined, by separating off the sand fraction by sieving (0·05–2·00-mm diameter particles). This was then sieved further in order to determine weights of coarse sand (0·50–2·00-mm diameter) and fine sand (0·05–0·50-mm diameter). The known total weight of sand was subtracted from the sample total to give the total weight of finer fractions, which were analysed using a laser granulometer that measures particle sizes optically (Mastersize E; Malvern Instruments, Malvern, UK) (0–0·05-mm diameter particles). A computer program was used to convert these optical data to particle weight data for clay (less than 0·002-mm diameter) and silt (0·05–0·002-mm diameter) fractions. Percentage by weight of each fraction was then calculated.

The remaining variables were measured from additional fresh soil samples taken from each treatment cell. Soil water content (percentage g H_2O g^{-1} soil) was measured from three soil samples per treatment cell. For each sample, a soil core was extracted from the surface down to 60 cm depth using an auger (5-cm diameter), and subsequently divided into six subsamples corresponding to six consecutive 10-cm depth intervals. Water content at each depth was determined by oven-drying soil subsamples and calculating the percentage weight of water per wet weight of soil. Pore volume of soil (cm^3 pore space g^{-1} soil) was measured from each of two soil horizons (0–7-cm and 7–14-cm depth). One sample was taken from each horizon in each treatment cell. The specific volumes of the samples were deduced from hydrostatic pressure in water (each sample was

Table 2. Method for scoring termite- and fungus-mediated decomposition of wooden stakes on a scale from 0 to 4, following the European Committee for Standardization (Anonymous 1989)

Attack score	Termite attack	Fungal attack
0 (sound wood)	No perceptible termite attack	No perceptible fungal attack or softening
1 (perceptible but very limited changes)	Very superficial deterioration to 1–2 mm in depth at some points or over several cm^2	Discoloration and very superficial degradation or softening up to 1 mm in depth
2 (clear changes to a moderate extent)	Damage from 2 to 5 mm in depth over several cm^2, or with scattered points down to a depth exceeding 5 mm, or by different combinations of the two types	Softening to a depth of 2–3 mm deep over all or part of the stake
3 (severe changes)	Extended and deep destruction from 5 to 10 mm in depth, or tunnels reaching the centre of the stake, or by different combinations of the two	Marked decay in wood to a depth of 3–5 mm over a wide surface area or by softening to a greater depth (10–15 mm) over a small area
4 (breakage of the stake while up-rooting prior to inspection)	Breakage due to extent of termite tunnelling	Breakage due to fungal attack and softening

sealed in a plastic bag under vacuum and submerged in water). The pore volume was calculated by subtracting the specific volume of the solid phase (volume of 1 g of soil excluding pore space) from the specific volume of the total soil (volume of 1 g of soil including water and air filling the pore space). Microbial biomass (μg C g^{-1} soil) was also measured using the fumigation extraction method (Amato & Ladd 1988), from two soil samples of 3–10-g from each treatment cell.

ANALYSES

Analyses of individual variables for effects of treatment

Each variable, including termite soil pit, wooden stake and soil data, was tested separately for significant effects of treatment (excluding CN cells) using a randomized complete block two-way ANOVA, with the interaction term pooled with the error MS (Sokal & Rohlf 1995). Where a significant overall effect of treatment was found, post-hoc comparisons between all four treatments within the randomized block design were performed using the Tukey HSD test (Sokal & Rohlf 1995). Additionally, planned comparisons were performed to test for significant differences between the CN cells and the four other treatments (significant if $P < 0{\cdot}0125$ using a Bonferroni correction). This was necessary because of the absence of comparable blocks in the CN treatment. Termite abundance data were normalized using a $\log_{10}(x + 0{\cdot}5)$ transformation.

Ordination analyses of termite assemblage composition

Assemblage data were ordinated using canonical correspondence analysis (CCA) in the CANOCO (version 4) program (ter Braak & Šmilauer 1998). As our interest was in treatment effects, we assessed intersample distances using Hill's scaling. Hill's scaling allows samples to be plotted in CCA triplots showing turnover distances (ter Braak & Verdonschot 1995).

Contribution of treatments to variation in species assemblage data for each sampling period.

A partial CCA was performed on termite log(abundance) data across all treatment cells and all five sampling periods (for a total of 125 samples). The five perturbation treatments, each sampled on five occasions, were entered in the analysis as 25 nominal variables (ter Braak & Šmilauer 1998). Block effects were partialled out by treating blocks as five covariables. The CN treatment cells were assigned to a separate arbitrary block in order to allow them to be included in the analysis (ter Braak & Šmilauer 1998). Marginal eigenvalues were computed for each nominal treatment variable, and significance at each stage (i.e. for each variable selected) was tested by a Monte Carlo permutation test with 999 random permutations. This test was conditioned on the covariable blocks.

Contribution of treatments and environmental variables to variation in species assemblage data in March 1996.

For the March 1996 data, a further partial CCA was performed. This included: all nominal treatment variables; termite-mediated decomposition; fungus-mediated decomposition; total organic carbon; total nitrogen; water content (0–10-cm depth); percentage of clay, silt, fine sand and coarse sand; and pore volume (0–7-cm and 7–14-cm depth). Microbial biomass was excluded because of missing data for the MR and UB treatments. To have included all six soil depths at which water content was measured would have been cumbersome and, in any case, the first 10-cm depth corresponded to the layer from which termites were sampled. Marginal eigenvalues were computed for each nominal treatment variable and environmental variable. Additionally, forward selection was used to rank variables in order of their importance in determining species composition. This procedure selects the variable with the highest marginal eigenvalue followed, stepwise, by those with the highest conditional eigenvalues (additional fit) (ter Braak & Verdonschot 1995). Significance of eigenvalues was again determined using Monte Carlo permutation tests.

Termite species occurring in only one treatment cell, on only one sampling occasion, were excluded from all the ordination analyses because they had no significant effect on ordering of environmental variables. Otherwise, there was no down-weighting of rare species.

General comments on the analyses

Due to the inherent difficulties of tropical field research undertaken by a large multidisciplinary team, there were a few missing data points for some of the environmental variables measured. Prior to analysing the data, these missing values were estimated by taking the mean of the other replicate measurements for the treatment cell in question.

The method of sampling termites from soil pits was the most efficient way to assess diversity and abundance of the termite assemblage in the time available. Due to the inherently patchy distribution of termite colonies in the soil, however, there was an increased chance of type II statistical errors occurring in the subsequent statistical analyses, for example where a statistically significant treatment effect was masked by the large error term.

Results

EFFECTS OF TREATMENTS

Termite data from soil pits

Termite abundance. Significant overall effects of treatment on $\log_{10}$ (termite abundance) were found in August 1995 and March 1996 (Table 3). For August 1995, immediately following imposition of treatments, there was a markedly significant difference (Tukey HSD tests $P < 0{\cdot}01$) between both CC and LA treatments compared with MR, UB and CN (Fig. 2a). With a Bonferroni correction (i.e. significant if $P < 0{\cdot}0125$), the difference between CC and CN cells in November 1995 was not formally significant ($F_{1,20} = 6{\cdot}99$, $P = 0{\cdot}0156$). In February 1996, no significant differences were found either between CC and CN cells ($F_{1,20} = 4{\cdot}04$, $P < 0{\cdot}06$), or between LA and CN cells ($F_{1,20} = 3{\cdot}87$, $P < 0{\cdot}07$). In March 1996, CC again showed a significantly lower $\log_{10}$ (termite abundance) compared with all other randomized block treatments (Tukey HSD tests $P < 0{\cdot}01$) as well as CN cells ($F_{1,20} = 16{\cdot}42$, $P < 0{\cdot}001$). Seasonal fluctuations in termite abundance (Dibog, Eggleton & Forzi 1998) tended to mask the actual progress of recovery of the most disturbed treatments, relative to least disturbed, so the results have been illustrated with the four treatments presented as proportions of the CN mean for each sampling period (Fig. 2a). By March 1996, LA $\log_{10}$ (termite abundance) was not significantly different from MR, UB and CN. In contrast, it was not until July 1996 that $\log_{10}$ (termite abundance) of CC cells had recovered to levels that were insignificantly different from CN cells ($F_{1,20} = 3{\cdot}59$, $P < 0{\cdot}08$).

Termite species richness. Individual ANOVAs for species richness in each sampling period confirmed significant treatment effects on all five occasions (Table 3). Means for the four treatments have been illustrated as proportions of the CN mean per sampling period (Fig. 2b). Again LA and CC cells showed a gradual recovery over time relative to the CN cells. For August 1995, CC and LA treatments had significantly fewer species than the UB, MR (Tukey HSD tests $P < 0{\cdot}01$) and CN cells ($F_{1,20} > 52$, $P < 0{\cdot}001$). By March 1996, LA had recovered species richness sufficiently to show no significant difference with UB, MR and CN. However, in July 1996, CC still showed a significant difference with UB (Tukey HSD tests $P < 0{\cdot}05$) while the difference with CN was insignificant ($F_{1,20} = 3{\cdot}02$, $P < 0{\cdot}1$).

Data from wooden stakes

Termite- and fungus-mediated decomposition. There were no significant overall treatment effects for termite-mediated decomposition (Table 3 and Fig. 3a), but there was a significant effect for fungus-mediated decomposition (Table 3 and Fig. 3b). In March 1996, CC showed significantly lower fungus-mediated decomposition scores than UB (Tukey HSD tests $P < 0{\cdot}05$). With a Bonferonni correction, the greater fungus-mediated decomposition score in CN compared with CC cells was not formally significant ($F_{1,20} = 6{\cdot}45$, $P = 0{\cdot}019$).

Soil variables

For the randomized block treatments, significant overall effects of treatment in March 1996 were found for total organic carbon, total nitrogen, percentage of clay in the soil and soil water content (0–10 cm depth) (Table 4). Additional soil variables, only showing significant differences between CN cells and one or more of the four other treatments (i.e. through planned comparisons), included percentage of silt in soil, soil pore volume and soil microbial biomass. Results for all of these variables are illustrated graphically in Fig. 4, with lettering codes indicating significant outcomes of Tukey HSD tests ($P < 0{\cdot}05$) and planned comparisons ($P < 0{\cdot}0125$). No other variables showed significant overall effects of treatment (within randomized blocks) or significant differences between CN cells and any other treatments (planned comparisons).

PARTIAL CCA RESULTS FOR TERMITE ASSEMBLAGE COMPOSITION ACROSS TREATMENTS

Association between experimental treatments and the termite assemblage over time

None of the treatments explained significant variance in assemblage composition for August 1995,

Table 3. $F_{3,12}$ values for treatment effects from the two-way ANOVAs for each variable at each sampling period. Significant treatment effects are coded as: $*P < 0{\cdot}05$; $**P < 0{\cdot}01$; $***P < 0{\cdot}001$

Variable	August 1995	November 1995	February 1996	March 1996	July 1996
Termite species richness (soil)	36·85***	4·37*	6·06**	4·97*	4·66*
Log_{10} (termite abundance)(soil)	61·89***	2·17	2·10	8·19**	3·14
Termite-mediated decomposition (stakes)		1·65	–	1·73	1·83
Fungus-mediated decomposition (stakes)		0·29	–	4·55*	3·33

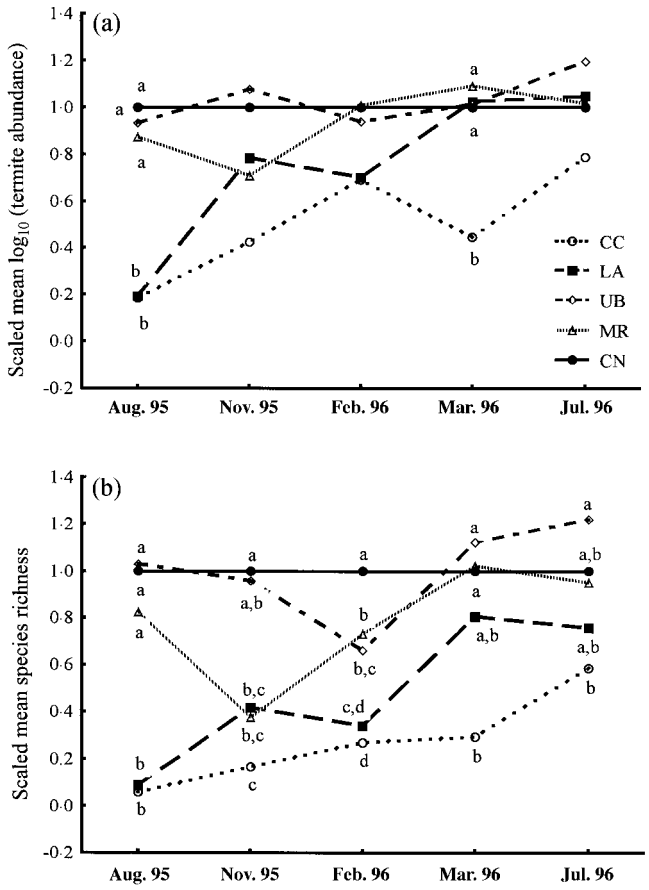

Fig. 2. Relative mean measurements per treatment, of termite variables (i.e. scaled to CN = 1) over time, from soil pits: (a) $\log_{10}$ (termite abundance); (b) termite species richness. For each variable, on sampling occasions for which there was a significant overall treatment effect, Tukey HSD post-hoc comparison outcomes are coded in letters (a is significantly different from b, etc.).

February 1996 or July 1996 (Table 5 and Fig. 5). However, in November 1995 and March 1996, the LA treatment explained significant variance (Monte Carlo permutation test $P < 0{\cdot}05$). In November 1995, the centroid for LA cells was associated with one species of Macrotermitinae, two soil-feeding Apicotermitinae and a wood-feeding Termitinae. By March 1996, LA was associated with one Macrotermitinae and six soil-feeding Apicotermitinae. The species–environment correlation coefficients for the first three axes of the partial CCA were high (Table 6), suggesting that the CCA found significant sources of variation. Overall, the successional sequence of LA recovery was character-

Table 4. $F_{3,12}$ values for treatment effects from the two-way ANOVAs for each soil variable measured in March 1996. Significant treatment effects are coded as: $*P < 0{\cdot}05$; $**P < 0{\cdot}01$; $***P < 0{\cdot}001$

Soil variable						
Total organic carbon	5·51*					
Total organic nitrogen	8·17**					
Soil fraction (fraction)	(clay)	(silt)	(fine sand)	(coarse sand)		
	3·85*	1·47	0·33	2·13		
H_2O content (cm depth)	(0–10)	(10–20)	(20–30)	(30–40)	(40–50)	(50–60)
	5·69*	0·78	1·12	0·09	1·07	0·65
Pore volume (cm depth)	(0–7)	(7–14)				
	3·39	1·00				
Microbial biomass	0·14					

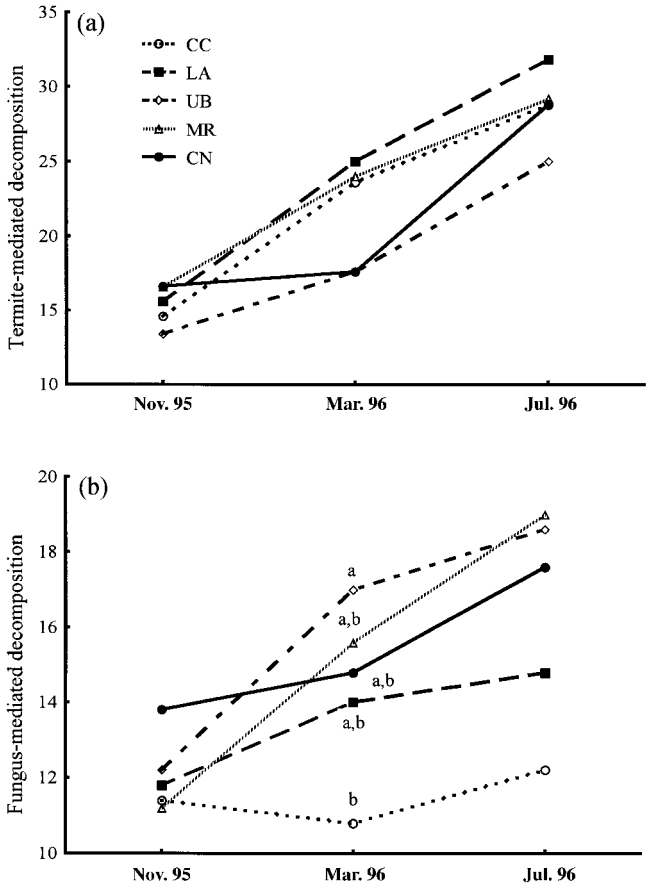

Fig. 3. Mean measurements per treatment, of decomposition variables over time [visual assessment scores (0–4) summed across 10 wooden stakes in each treatment cell]: (a) termite-mediated decomposition; (b) fungus-mediated decomposition. On sampling occasions, for each variable for which there was a significant overall treatment effect, Tukey HSD post-hoc comparison outcomes are coded in letters (a is significantly different from b, etc.).

ized by the presence of a group of Apicotermitinae and Macrotermitinae that were not similarly associated with recovery in other treatments.

Treatment and termite assemblage associations with soil and decomposition variables

In the partial CCA analysis for the March 1996 data, the LA treatment, total soil organic carbon, total soil nitrogen, percentage of silt in soil, and fungus-mediated decomposition, all explained significant variance in termite assemblage composition and abundance (Table 7 and Fig. 6). The partial CCA was then repeated with only these variables included. The species–environment correlations for the partial CCA were high for all four axes (Table 8), showing that our measured environmental variables explained meaningful variation in the data. The interpretation of the axes was unambiguous (Table 9): the first axis was defined by the LA treatment and fungus-mediated decomposition, the second axis was defined by soil variables. The LA treatment centroid was associated with low fungus-mediated decomposition, soil silt, organic carbon and nitrogen. As with the partial CCA for all sampling periods combined, LA was again mainly associated with wood/litter-feeding Macrotermitinae and soil-feeding Apicotermitinae.

Discussion

Although unexpected, the negligible effect of MR and UB perturbation treatments upon the termite

Table 5. Results of partial CCA showing nominal treatment variables/sampling periods contributing to significant variance in termite species composition across treatment cells, by determining marginal effects on termite species. λ_1 = eigenvalue (fit) for each nominal treatment variable on its own; P = significance level of effect, as obtained with a Monte Carlo permutation test under the null model with 999 random permutations conditioned on the covariables

Sample	Variable	λ_1	P
November 1995	LA	0·31	0·04
March 1996	LA	0·31	0·035

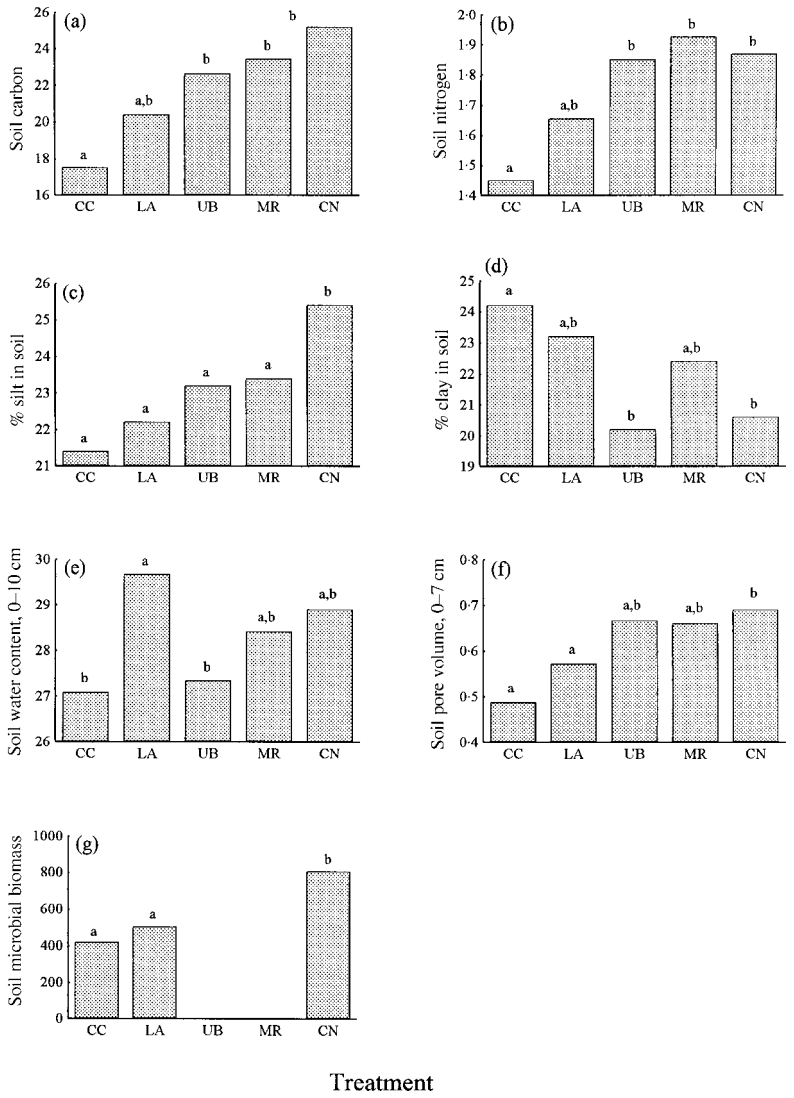

Fig. 4. Mean values for soil variables measured in March 1996 for which there was either a significant overall treatment effect within the randomized blocks, or a significant difference between CN cells and one or more of the randomized block treatments: (a) total organic carbon content (mg g^{-1} dry weight of soil); (b) total nitrogen content (mg g^{-1} dry weight of soil); (c) percentage silt (% μm silt g^{-1} mineral soil); (d) percentage clay (% μm clay g^{-1} mineral soil); (e) water content (0–10 cm depth; % H_2O g^{-1} soil); (f) pore volume (0–7 cm depth; cm^3 g^{-1} soil); (g) microbial biomass (μg C g^{-1} soil) (UB and MR cells were not assessed).

Table 6. Results of partial CCA for termite species composition data for the combined data from all five sampling periods (see also Fig. 5): eigenvalues and intraset species–environment correlation coefficients for the first four axes. Note that axis 4 is not a canonical constrained axis because the number of environmental variables is small (i.e. 2: LA November 1995 and LA March 1996), meaning that only the first three axes are derived as linear combinations of the environmental variables

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0·322	0·296	0·254	0·623
Intraset correlation coefficients	0·851	0·835	0·790	0·000
Sum of all unconstrained eigenvalues (after fitting covariables)				15·730
Sum of all canonical eigenvalues (after fitting covariables)				0·871

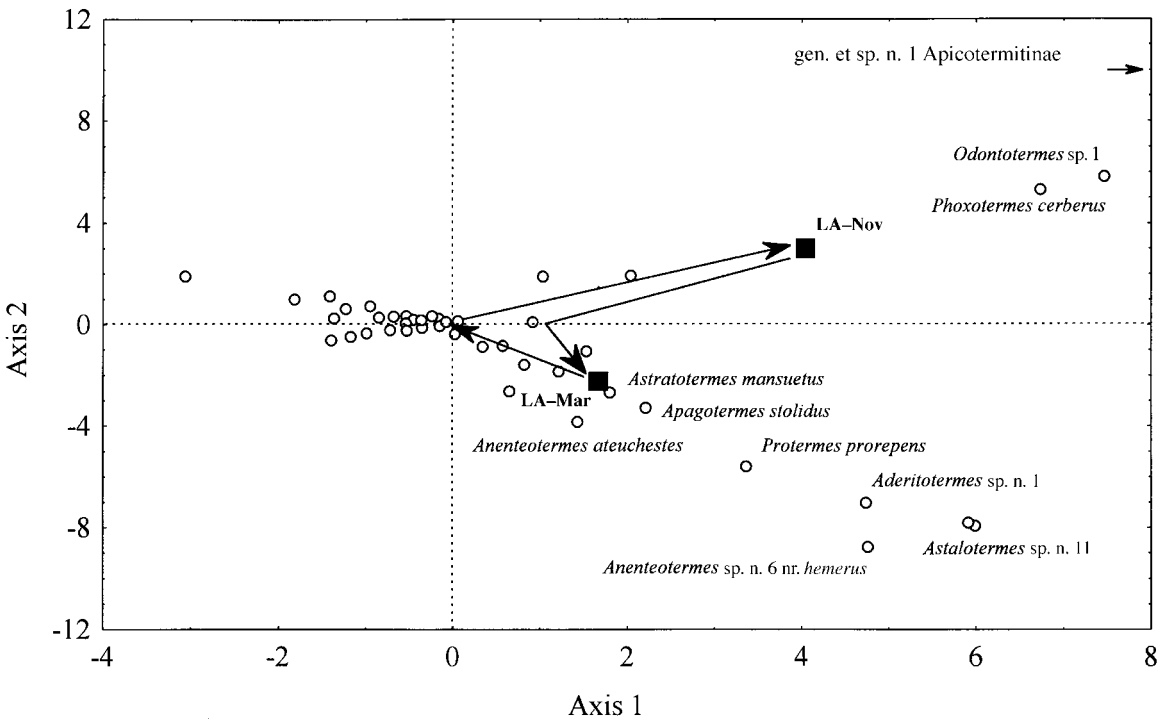

Fig. 5. Ordination bi-plots for partial CCA including nominal treatment variables (but no environmental variables) for the combined data set (all five sampling periods). Centroids for treatments/sampling periods contributing significant variance in termite species composition are marked as filled squares. Only species circles associated with LA November 1995 and LA March 1996 are named.

assemblage, when compared with CN, was almost certainly because the great majority of termite species live in hypogeal nests beneath the soil surface. In the absence of a dramatic loss in canopy cover, which has been shown by Dibog *et al.* (1999) to affect termite assemblages, the only other major disturbance that had a measurably negative effect on termites was severe direct perturbation of the soil. In MR treatment cells, and in the randomized block treatments generally, epigeal termite mounds were probably too rare for their removal to have a significant effect on overall species richness and abundance. The additional canopy thinning and removal of saplings in UB cells would be expected to affect litter-feeding species most strongly. However, there were only two species present that are known to forage in leaf litter [*Pseudacanthotermes militaris* (Hagen) and *Acanthotermes acanthothorax* (Sjöstedt)], and there was no detectable change in their abundances.

More predictably, the most severe perturbation treatments (CC and LA) caused the greatest initial

Table 7. Results of partial CCA forward selection procedure, showing environmental variables and nominal treatment variables explaining significant variance in termite species composition across treatment cells, for the March 1996 sampling period. λ_1 = eigenvalue (fit) for each variable on its own; λ_2 = increase in eigenvalue (additional fit); $\Sigma\lambda_2$ = cumulative total of eigenvalues λ_2; P = significance level of effect, as obtained with a Monte Carlo permutation test under the null model with 999 random permutations conditioned on the covariables

Marginal effects			Conditional effects			
Variable	λ_1	P	Variable	λ_2	P	$\Sigma\lambda_2$
LA	0·53	0·005	LA	0·53	0·005	0·53
Carbon	0·47	0·03	Carbon	0·47	0·005	1·00
Nitrogen	0·45	0·03	Nitrogen	0·6	0·035	1·60
Fungus-mediated decomposition	0·45	0·035	Pore volume (0–7 cm)	0·36	0·05	1·96
Silt	0·41	0·04				

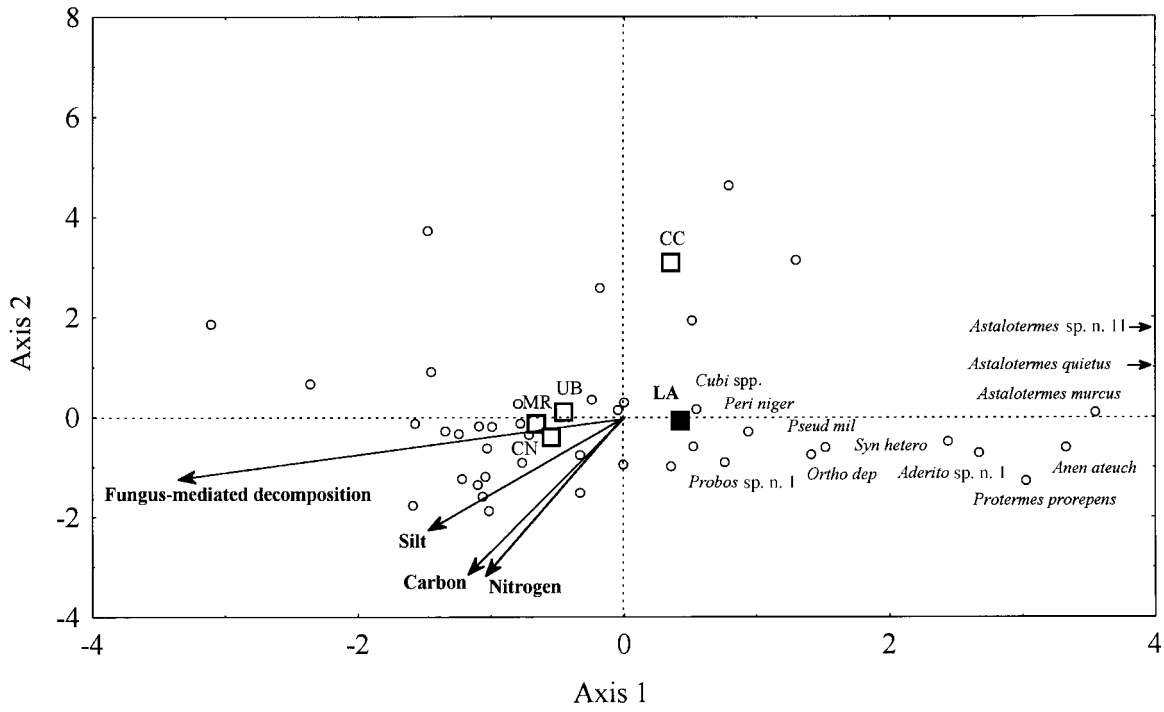

Fig. 6. Species-conditional bi-plot based on the partial CCA for March 1996 species data, environmental variables and nominal treatment variables. Treatment centroids (squares) are coded as follows: open = non-significant; filled = significant. The lengths of arrows (representing quantitative environmental variables) indicate the degree to which each variable explains the variance in community composition. Only species circles associated with LA are named. Abbreviated species names are as follows: *Cubi* spp., *Cubitermes* species complex; *Peri niger*, *Pericapritermes nigerianus*; *Probos* sp. n. 1, *Proboscitermes* sp. n. 1; *Pseud mil Pseudacanthotermes militaris*; *Ortho dep*, *Orthotermes depressifrons*; *Syn hetero*, *Synacanthotermes heterodon*; *Aderito* sp. n. 1, *Aderitotermes* sp. n. 1; *Anen ateuch*, *Anenteotermes ateuchestes*.

decline in termite species richness and abundance. One of the most important outcomes of the perturbation experiments was that termite abundance and, to a lesser extent, species richness, recovered faster in LA cells than in CC cells. The addition of dead wood to LA cells therefore appears to have accelerated recovery of the termite assemblage.

While the recovery observed in different treatments over time was relatively unsurprising, quantitatively, the successional changes in the termite assemblage appeared more complex. In particular, the successional response in LA treatment cells deviated significantly from other treatments. Although the results might also be explained as seasonal effects, rather than succession, this appears unlikely in the light of a study by Dibog, Eggleton & Forzi (1998) that showed that assemblage composition did not change significantly with seasonality in the CN cells when these were monitored monthly across the same 12-month period. Instead, it seems that the addition of a substantial quantity of dead wood encourages re-colonization by a succession of fungus-growing wood-feeding species of Macrotermitinae (as shown for November 1995 and

Table 8. Results of partial CCA for termite species composition data for the March 1996 sampling period (see also Fig. 6): eigenvalues and intraset species–environment correlation coefficients for the first four axes

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0·571	0·510	0·359	0·320
Intraset correlation coefficients	0·960	0·965	0·965	0·933
Sum of all unconstrained eigenvalues (after fitting covariables)				6·139
Sum of all canonical eigenvalues (after fitting covariables)				2·014

Table 9. Termite species composition data from Fig. 6: correlations of marginally significant environmental variables with the first four axes of the partial CCA. LA, although significant, is not included because it is a nominal variable and so its correlation coefficient has no obvious meaning (ter Braak & Šmilauer 1998)

	Axis 1	Axis 2	Axis 3	Axis 4
Carbon	–0·2937	–0·8189	0·3318	–0·2067
Nitrogen	–0·2718	–0·8122	–0·1571	–0·2296
Fungus-mediated decomposition	–0·6836	–0·2436	–0·2492	0·5666
Silt	–0·3752	–0·5776	–0·2727	–0·4971

March 1996). The consequent breakdown of the logs in LA cells appeared to influence soil conditions, as a distinct group of humivorous Apicotermitinae became associated with these cells (March 1996). This may arise either because the added logs result in a more sheltered environment in the soil directly beneath them, or because of an increase in the amount and/or qualitative shift in the type of organic matter reaching this soil.

The results of the partial CCA for March 1996 (including soil variables) reinforced the above findings. The most probable explanation for the low levels of fungus-mediated decomposition in the LA treatment was the very close association between LA and three species of Macrotermitinae. Macrotermitinae live in symbiotic association with *Termitomyces* species of fungi, which they cultivate on faecal combs inside their nests. *Termitomyces* species are completely dependent upon a live termite colony for maintenance of an equitable environment inside the nest, provision of food, as well as protection from competition with other free-living microbes (Darlington 1994). Anti-microbial chemicals are thought to be present in termite saliva used in the construction of termite mounds and underground runways (Darlington 1994). Macrotermitinae plaster soil cemented with saliva into the passageways inside the wood litter upon which they feed. It is likely, therefore, that presence of Macrotermitinae in the wooden stakes at Ebogo would be associated with low fungus-mediated decomposition.

CC treatment cells showed similarly low levels of soil microbial biomass to LA cells (Fig. 4), and even lower levels of fungus-mediated decomposition (Fig. 3b), but were not associated with a distinctive assemblage of termites (Fig. 6). Instead, these conditions were probably a result of the greater exposure of soils and wooden stakes to desiccation. LA cells received identical initial levels of soil and canopy disturbance to CC, but the presence of dead wood on the ground may have protected the soils and wooden stakes from similar physical microclimatic extremes. In conclusion, the CC treatment resulted in an assemblage that was a subset of that which occurred in the original forest.

The results of this study have important implications for the restoration of tropical forests following logging activities, agroforestry and slash-and-burn agriculture. The aims of tropical forest restoration efforts usually include the recovery of biodiversity, biomass and habitat structure, as well as ecosystem processes and services. The relationship between these objectives is still a subject of much debate (Palmer, Ambrose & Poff 1997). Nevertheless, leaving substantial unburned woody debris on the ground following a period of forest disturbance may result in an enhanced rate of recovery both of termite diversity and soil fertility. Moreover, this appears to be an example of where manipulation might be used to induce what is either an alternative successional pathway or a leap forward to a later successional stage. Accelerated recovery of termite diversity is unlikely to be seen as a restoration end in itself. Of greater significance is the associated recovery of decomposition processes as well as other processes mediated by soil communities. This is expected to be an important early stage influencing subsequent recovery of forest vegetation structure and biodiversity.

As the Ebogo forest is an old secondary forest, albeit logged 90 years ago, it cannot be assumed that the results observed here would be the same for a primary tropical forest. However, while certain rarer primary forest species of termite may be absent from regenerating forests, the differences between these assemblages, in terms of their contributions to ecosystem functions, are likely to be negligible (Eggleton *et al.* 1999). Notice, also, that despite the small size of the experimental plots, and the fact that the canopy over them remained intact, CC cells had only just recovered 12 months after perturbation. We might expect impacts of more severe large-scale disturbance (logging for instance) on soil termite assemblages to be detectable many years later (Eggleton *et al.* 1995, 1996, 1997). The successful use of woody debris as a means of kick-starting restoration efforts would clearly depend on the type, scale and intensity of the original disturbance events. The persistence of the initial benefits would need to be of sufficient duration to influence further succession, such as seed germination and seedling recruitment.

As termite assemblages recover from disturbance, they will start to have effects on soil properties. In this study we were unable to disentangle change in soil brought about by the experimental treatments from later changes driven by the recolonization of the termites themselves. The impact of termites on soil properties, and vice versa, clearly deserves more attention in studies of tropical forest regeneration and recovery.

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Appendix 1

Complete list of 110 termite species/morphospecies found in the five Ebogo treatments. Feeding group codes: W/F = fungus-growing wood feeder (Macrotermitinae only); W = wood feeder; WS = wood/soil interface feeder; S = soil feeder.

Taxon	Feeding group
Macrotermitinae	
Acanthotermes acanthothorax (Sjöstedt)	W/F
Synacanthotermes heterodon (Sjöstedt)	W/F
Microtermes species complex	W/F
Pseudacanthotermes militaris (Hagen)	W/F
Sphaerotermes sphaerothorax (Sjöstedt)	W/F
Odontotermes sp. 1	W/F
Odontotermes sp. 3	W/F
Protermes prorepens (Sjöstedt)	W/F
Termitinae	
***Termes*-group**	
Pericapritermes amplignathus Harris	S
Pericapritermes nigerianus Silvestri	S
Pericapritermes chiasognathus Sjöstedt	S
Pericapritermes magnificus Silvestri	WS
Pericapritermes sp. n. 1	S
Pericapritermes sp. n. 2	S
Pericapritermes sp. n. 3	S
Pericapritermes sp. n. 4	S
Pericapritermes sp. n. 5	S
***Cubitermes*-group**	
Apilitermes longiceps (Sjöstedt)	S
Cubitermes species complex	S
Procubitermes arboricola (Sjöstedt)	S
Thoracotermes macrothorax (Sjöstedt)	S
Proboscitermes sp. n. 1	S
Fastigitermes jucundus (Sjöstedt)	S
Profastigitermes putnami Emerson	S
Ophiotermes grandilabius Emerson	S
Orthotermes depressifrons Silvestri	S
Unguitermes trispinosus Ruelle	S
Unguitermes magnus Ruelle	S
Mucrotermes sp. n. 1	S
Mucrotermes sp. n. 2	S
Basidentitermes diversifrons Silvestri	S
Crenetermes albotarsalis (Silvestri)	S
Foraminitermes valens (Silvestri)	S
***Amitermes*-group**	
Microcerotermes parvus (Haviland)	W
Nasutitermitinae	
Postsubulitermes parviconstrictus Emerson	S
Nasutitermes latifrons (Sjöstedt)	W
Nasutitermes fulleri Emerson	W
Apicotermitinae	
***Anoplotermes*-group**	
Acholotermes sp. n. 1	S
Acholotermes sp. n. 2 nr. *tithasus*	S
Acholotermes sp. n. 3 nr. *chirotus*	S
Acholotermes sp. n. 4 nr. *imbellis*	S
Adaiphrotermes sp. n. 1	S
Adaiphrotermes sp. n. 2	S
Aderitotermes fossor Sands	S
Aderitotermes sp. n. 1	S
Aderitotermes sp. n. 2	S
Aderitotermes sp. n. 3 nr. *fossor*	S
Aderitotermes sp. n. 4 nr. *fossor*	S
Alyscotermes kilimandjaricus Sands	S
Alyscotermes sp. n. 1	S
Alyscotermes sp. n. 2	S
Amalotermes phaeocephalus Sands	WS
Amicotermes sp. n. 1	S
Amicotermes sp. n. 2	S
Amicotermes sp. n. 3 nr. *galenus*	S
Anenteotermes nanus Sands	S
Anenteotermes ateuchestes Sands	S
Anenteotermes polyscolus Sands	S
Anenteotermes cnaphorus Sands	S
Anenteotermes sp. n. 1	S
Anenteotermes sp. n. 2	S
Anenteotermes sp. n. 3	S
Anenteotermes sp. n. 4	S
Anenteotermes sp. n. 5 nr. *ateuchestes*	S
Anenteotermes sp. n. 6 nr. *hemerus*	S
Anenteotermes sp. n. 7 nr. *amachetus*	S
Anenteotermes sp. n. 8	S
Apagotermes stolidus Sands	S
Astalotermes quietus (Silvestri)	S
Astalotermes murcus Sands	S
Astalotermes concilians Sands	S
Astalotermes sp. n. 2	S
Astalotermes sp. n. 3	S
Astalotermes sp. n. 4	S
Astalotermes sp. n. 5	S
Astalotermes sp. n. 6	S
Astalotermes sp. n. 7	S
Astalotermes sp. n. 9	S
Astalotermes sp. n. 10	S
Astalotermes sp. n. 11	S
Astalotermes sp. n. 12	S
Astalotermes sp. n. 13	S
Astalotermes sp. n. 14	S
Astalotermes sp. n. 15	S
Astalotermes sp. n. 16 nr. *amicus*	S
Astratotermes mansuetus Sands	S
Astratotermes sp. n. 1	S
Astratotermes sp. n. 2	S
Astratotermes sp. n. 3	S
Astratotermes sp. n. 4	S
Astratotermes sp. n. 6	S
Astratotermes sp. n. 7	S
Astratotermes sp. n. 8 nr. *pacatus*	S
Astratotermes sp. n. 9 nr. *prosenus*	S
Astratotermes sp. n. 10 nr. *apocnetus*	S
Ateuchotermes ctenopher Sands	S
Ateuchotermes sentosus Sands	S
Ateuchotermes sp. n. 1	S
Ateuchotermes sp. n. 2 nr. *sentosus*	S
***Apicotermes*-group**	
Duplidentitermes furcatidens Emerson	S
Eburnitermes sp. n. 1	S
Eburnitermes sp. n. 3	S
Coxotermes boukokoensis Grassé & Noirot	S
Phoxotermes cerberus Collins	S
Labidotermes sp. n. 2	S
gen. et sp. n. 1 Apicotermitinae	S
gen. et sp. n. 3 Apicotermitinae	S
gen. et sp. n. 5 nr. *Eburnitermes*	S
gen. et sp. n. 8 Apicotermitinae	S
gen. et sp. n. 9 nr. *Labidotermes*	S