

Termite assemblage collapse along a land-use intensification gradient in lowland central Sumatra, Indonesia

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Summary

1. Termites are major decomposers in tropical regions and play an important role in soil processes. This study measured the impact of land-use intensification on the termite assemblage of lowland rain forest in Jambi Province, on the Indonesian island of Sumatra. Termite composition was assessed in seven land-use types along a disturbance gradient, from primary forest, through different silvicultural systems, to grassland and cultivated land without trees. A range of environmental variables was also measured.

2. Termite species richness and relative abundance declined as follows: primary forest > selectively logged forest > mature 'jungle rubber' (a diverse agro-forest dominated by rubber trees) > mature rubber plantation > young *Paraserianthes falcataria* plantation (a softwood tree) > *Imperata cylindrica* grassland > cassava garden. Termite richness fell from 34 species in the primary forest to one species in the cassava garden. The relative abundance of soil-feeding termites showed a significantly greater decline along the gradient than did wood-feeding termites.

3. Of the environmental variables, woody plant basal area was most strongly correlated with termite species richness ($r = 0.973$) and relative abundance ($r = 0.980$). This reflects the response of forest-adapted termites to progressive simplification of the physical structure of the habitat, resulting in the reduction of canopy cover and alteration in microclimate, and the loss of feeding and nesting sites.

4. *Synthesis and applications.* Comparisons with other studies show that the decline in termite species richness and relative abundance seen at Jambi is a general trend that occurs elsewhere when forests are converted to other land uses. To help mitigate the loss of termites when forests are disturbed, we recommend the following management practices: the use of reduced-impact logging techniques, maximizing forest patch size and connectivity, minimizing length of forest edges, and leaving dead wood to decay *in situ*.

Key-words: canopy cover, disturbance, Isoptera, rain forest, selective logging, soil communities, species richness.

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Introduction

Invertebrates are an integral part of healthy soils and play a critical role in ecosystem services such as decomposition and nutrient cycling (Giller 1996; Brussaard

et al. 1997; Lavelle *et al.* 1997). Lowland tropical forests are the world's most species-rich terrestrial habitats, and soil communities represent a large component of their biodiversity (Giller 1996; Brussaard *et al.* 1997). Over recent decades many pristine tropical forests have been replaced with agricultural and silvicultural systems (Noble & Dirzo 1997; Tilman *et al.* 2001) while the amount of degraded land has increased rapidly (Dobson, Bradshaw & Baker 1997). The relentless disturbance, conversion and fragmentation of the tropical forest biome is a major cause of global biodiversity loss (Sayer & Whitmore 1991; Pimm *et al.* 1995; Whitmore 1998). There has been much debate over the extent to which declining biodiversity and changes in trophic structure will impact on ecosystem functioning and stability (Johnson *et al.* 1996; Chapin *et al.* 1997; Schwartz *et al.* 2000; Hector *et al.* 2001). Moreover, there is growing concern that land-use intensification and loss of biodiversity threatens soil fertility and the sustainability of agricultural production (Giller *et al.* 1997; Matson *et al.* 1997).

Termites are the dominant macroarthropod detritivores in many tropical soils, and are particularly diverse and abundant in lowland equatorial forests (Wood & Sands 1978; Collins 1983; Eggleton *et al.* 1996, 1999; Eggleton 2000). They are major agents of decomposition, and play an important part in nutrient and carbon fluxes (Lawton *et al.* 1996; Bignell *et al.* 1997; Tayasu *et al.* 1997). Termite activity, such as soil feeding, subterranean tunnelling and mound building, maintains macropore structure, redistributes organic matter and improves soil stability and quality (Lee & Wood 1971; Holt & Lepage 2000; Donovan *et al.* 2001b). Given the central role of the decomposer food web in regulating plant growth (Laakso & Setälä 1999; Wardle 1999), and the particular influence that termites have over soil processes (Lavelle *et al.* 1997; Bignell & Eggleton 2000), it is important to understand how land-use intensification affects termite assemblages. While a few studies have shown that termites are sensitive to habitat disturbance (Bignell & Eggleton 2000; Eggleton *et al.* 2002; Discussion), no studies have correlated termite assemblage parameters along a disturbance gradient with quantitative measures of vegetation structure or habitat modification.

Jambi Province, in central Sumatra, provided the opportunity to examine termite assemblages along a land-use intensification gradient in a localized habitat mosaic, from primary forest through different silvicultural systems, to grassland and agricultural sites without trees. Under Indonesia's intense socio-economic pressures, large areas of Sumatra's forests have been greatly altered by commercial and illegal logging, or converted to large-scale silvicultural systems such as plantations of rubber, oil palm and fast-growing softwood trees (Riswan & Hartanti 1995). Logging roads have allowed farmers to establish permanent or shifting subsistence agriculture in areas that were once inaccessible, and there are now many indigenous agro-forestry

systems that vary from species-rich multi-storey gardens to cash-crop monocultures (Aumeeruddy & Sansonnens 1994). 'Jungle rubber' is one such diverse agro-forestry system frequently operated by small-scale farmers in Jambi. In this system, which has a forest-like structure in its mature phase, a high concentration of rubber trees *Hevea brasiliensis* Müll. Arg. is grown within disturbed forest, providing an income from latex as well as fruits, fuel wood and timber (Gouyon, De Foresta & Levang 1993). After being farmed, exhausted land is often abandoned to the coarse grass *Imperata cylindrica* (L.) Raeusch. known locally as alang-alang. Sumatra now has about 2.2 million ha of *Imperata* grassland (Garrity *et al.* 1997).

The termite study was part of a larger multi-disciplinary research programme co-ordinated by the Center for International Forestry Research (CIFOR) at Bogor, Indonesia. The programme aimed to examine the impact of different land-use regimes on a range of plants, animals (other insects, birds and mammals) and environmental variables. In this study we asked two questions. (i) How does land-use intensification affect termite assemblage structure? (ii) What factors are correlated with the observed changes in the termite assemblage?

In order to address these questions, data on termites and habitat variables were collected from seven sites using standardized sampling methods. The termite sampling protocol has been shown to produce samples that represent accurately the taxonomic and functional composition of the local termite assemblage (Jones & Eggleton 2000).

Methods

STUDY SITES

Seven sites near Pasir Mayang, in Jambi Province, were sampled during November 1997, each representing a distinct land-use type. All sites were at altitudes of between 30 and 80 m a.s.l. One vegetation survey plot (40 × 5 m) was established at each site and used as a reference point for the multi-taxa assessment. One termite transect (100 × 2 m) was run across relatively flat terrain at each site. The area has an annual rainfall of nearly 3000 mm (Ketterings *et al.* 1999), with a wetter season of 6 months (wettest months December and January) and a drier season of 6 months (driest months July and August). Sites 1–5 were all within a 5-km radius. Sites 6 and 7 were about 40 km to the south-east of the other sites. The six disturbed sites were originally mixed dipterocarp forest.

Site 1 (PF; primary forest) was a patch of undisturbed mixed dipterocarp forest (1°5'S, 102°6'E) consisting of about 5 ha along the sides of a shallow stream gully. Although the canopy was closed and dense, PF was surrounded by an extensive but selectively logged area. Those trees making up the greater part of the canopy ranged in height from about 20 m to emergents at about 40 m. **Site 2** (LF; logged forest) (1°5'S, 102°6'E) comprised forest selectively logged in 1984 (about

13 years before sampling) and was contiguous with PF. The transect ran through remnants of disturbed and regenerating forest with a closed canopy and heavy growth of liana and creepers, and across open skid rows with no canopy. **Site 3** (JR; jungle rubber) ($1^{\circ}10'S$, $102^{\circ}7'E$) was selectively logged about 30 years before sampling. Rubber seedlings were planted among the remaining forest trees, probably after the ground was cleared by burning. At the time of sampling, the site consisted of a high density of mature rubber trees growing among regenerating forest. The rubber trees were estimated to be about 25–30 years old and nearing the end of their productive cycle. The closed, dense canopy was about 14–18 m in height. **Site 4** ($1^{\circ}5'S$, $102^{\circ}7'E$) comprised a line-planted monospecific rubber plantation (RP) in current production for latex. The trees were 8 years old at the time of sampling, with a thin but more or less closed canopy of between 8 m and 12 m height. Some decaying tree stumps and dead wood remained from previous forest clearance. **Site 5** (PP; *Paraserianthes* plantation) was a plantation of *Paraserianthes falcataria* (L.) I.C. Nielson, a fast-growing indigenous softwood. The site ($1^{\circ}5'S$, $102^{\circ}7'E$) was completely cleared in 1994 and planted with lines of saplings. At the time of sampling (about 3.5 years after establishment) the trees were between 3 m and 6 m in height with a thin, open canopy, and many large items of dead wood remained on the ground. **Site 6** (IG; *Imperata* grassland) ($1^{\circ}36'S$, $102^{\circ}21'E$) was devoid of trees and consisted of a dense, near-uniform stand of *I. cylindrica* grass about 1 m in height. There was very little dead wood, and the soil surface between the grass swards was bare and hard. This site was previously a cassava *Manihot esculenta* Crantz garden but had been abandoned about 4 years before sampling. The grassland was burnt at least once a year. **Site 7** ($1^{\circ}36'S$, $102^{\circ}21'E$) comprised a line-planted cassava garden (CG) about 1 ha in size that adjoined IG. The garden was regularly weeded to prevent the growth of other vegetation, and the garden was about 2 years old at the time of sampling. The soil surface between the cassava plants was bare and very disturbed, with very little dead wood.

Sites 1–5 are referred to as forested habitats because trees form the dominant structural vegetation. Sites 6 and 7 had no trees and are referred to as non-forested. The sites could also be categorized as mixed forest and monoculture systems, while three of the forested sites were silvicultural systems. Using these divisions, the seven sites were arranged into an ordinal ranking along a putative land-use gradient, based on increasing habitat modification (Fig. 1). This was a qualitative assessment reflecting the degree of alteration from the original mixed dipterocarp forest. The ranking did not imply that altered sites had been through the previous 'less modified' land-use regimes. The ordinal ranking of sites was not used in the statistical analyses but provided a convenient sequence for data presentation. The cassava garden was considered to be 'more modified' than the *Imperata* grassland because the former was

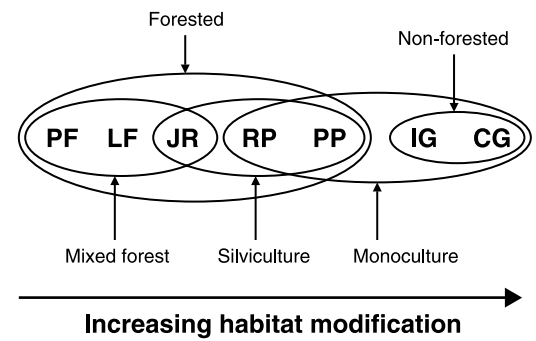


Fig. 1. Schematic diagram showing the seven sampling sites in Jambi Province, Sumatra, arranged in an ordinal ranking based on increasing habitat modification. The ranking represents a putative land-use intensification gradient. The land-use types are: primary forest (PF), logged forest (LF), jungle rubber (JR), rubber plantation (RP), *Paraserianthes* plantation (PP), *Imperata* grassland (IG) and cassava garden (CG).

more intensively managed. Although the ranking of these two non-forested sites was somewhat arbitrary, their positions relative to each other were of minor importance within the context of the modifications over the entire gradient.

THE TRANSECT PROTOCOL

One transect (100×2 m) was run in each site, following the sampling protocol described by Jones & Eggleton (2000). In order to standardize sampling effort, each transect was divided into 20 contiguous sections of 5×2 m, and each section was sampled by two experienced collectors for 30 min (i.e. 1 h of sampling per section). In each section the collectors searched the following microhabitats, which are common sites for termites: 12 samples of surface soil (each about 12×12 cm to 10 cm depth); accumulations of litter and humus at the base of trees and between buttress roots; the inside of tree stumps, dead logs, branches and twigs; the soil within and beneath very rotten logs; subterranean nests, mounds, carton sheeting and runways on vegetation, and arboreal nests up to a height of 2 m above ground level. Specimens from every termite population encountered were sampled and preserved in 80% ethanol. Mounds were sampled destructively to allow sampling of inquiline species (Eggleton & Bignell 1997).

The *Imperata* grassland and the cassava garden transects had no epigeal termite mounds, trees or tree stumps and virtually no dead wood to sample. In these two transects, the collectors did not use all the sampling time available but stopped after all the soil microhabitats had been examined.

The transect protocol provided a measure of the relative abundance of termites based on the number of encounters with each species in a transect (Jones 2000). An encounter was defined as the recorded presence of a species in one section. The number of encounters per transect could then be used to compare the relative abundance of termites between transects. It gave no measure of the absolute abundance per unit area.

IDENTIFICATION OF SPECIMENS

Most specimens were identified to named species at the Natural History Museum, London, UK. Remaining taxa were identified to genus and assigned to morpho-species applied consistently across regional voucher collections (Eggleton *et al.* 1997, 1999; Jones & Brendell 1998; Gathorne-Hardy, Jones & Mawdsley 2000; Jones 2000; Gathorne-Hardy, Syaukani & Eggleton 2001; Jones & Prasetyo 2002).

Termites were assigned to one of four feeding groups following the classification given in Donovan, Eggleton & Bignell (2001a). The groupings reflected feeding preferences along a humification gradient of the dietary substrate, and correlated with the variations in the amount of plant tissue fragments and silica in the gut (Donovan, Eggleton & Bignell 2001a). The groups were as follows. Group I: all lower termites. In this study this group included only species of Kalotermitidae and Rhinotermitidae, all of which feed on wood. Group II: some Termitidae species. These have a range of feeding habits, including wood-feeding, litter-feeding and micro-epiphyte-feeding. Group III: species of Termitidae that feed on highly decayed wood that has lost its structure and become friable and soil-like, and those that feed on soil with a high organic content. These termites can be considered organic-rich soil-feeders. Group IV: species of Termitidae that feed on soil with a lower organic content. These termites can be considered true soil-feeders.

For analytical purposes, groups I and II were combined to give a single wood-feeding group. Many species of group II wood-feeders also consume small items of woody trash and leaf litter. However, termites that feed predominantly on leaf litter (e.g. *Longipeditermes longipes*) and which are known to occur in Sumatra were not found in this study. Only one species in group IV was recorded, so this was combined with group III to give a single soil-feeding group.

ENVIRONMENTAL VARIABLES

Vascular plant species richness and mean canopy height (m) were recorded in one survey plot (40 × 5 m) at each site, following Gillison (2000). Basal area of all woody plants (m² ha⁻¹) was estimated using the Bitterlich infinite radius measurement method (Gillison 2000). All tree diameter estimates above 5 cm in the forest plots were converted into above-ground carbon (kg m⁻²) with an allometric equation modified from Brown (1997) on the basis of additional data collected in the Jambi area (Q.M. Ketterings, unpublished data): $Y(\text{kg tree}^{-1}) = 0.092 \text{ Diam}^{2.60}$, where tree diameter (Diam) is measured in centimetres. Understorey and herbaceous vegetation was measured in eight 0.25-m² quadrat samples (or four 1-m² samples for non-forest plots); total fresh weight was measured, and subsamples were collected for determining dry matter content. Canopy cover was measured using a spherical densiometer. Diameter and length of dead wood (> 5 cm diameter)

were measured within each 40 × 5 m plot and converted to volume on the basis of a cylindrical form; three apparent density classes were used and ring samples were taken to assess the dry weight bulk density (g cm⁻³) of the partly decayed wood. Surface litter (including wood < 5 cm diameter) was collected down to the surface of the mineral soil in eight 0.25-m² samples. To remove mineral soil particles, the litter samples were washed and sun-dried; subsamples were taken for dry matter content.

Soil bulk density was measured for the 0–5 cm top soil layer (eight samples per plot) by carefully inserting a 165-cm³ ring from the mineral soil surface, just below the litter layer. Another eight soil samples (0–30 cm depth) were collected per plot, passed through a 2-mm sieve and air-dried for analysis of pH (H₂O), organic carbon (Walkley & Black method) and total nitrogen (Kjeldahl method) as described by Anderson & Ingram (1993). Further details of the soils are available in Van Noordwijk *et al.* (1997).

ANALYSES

Forward stepwise multiple regression was used to determine which environmental variables were significant predictors of the species richness and relative abundance of (i) all termites; (ii) wood-feeding species; and (iii) soil-feeding species in the transect samples. Variables were entered into the model when $P < 0.05$.

Results

THE TERMITE ASSEMBLAGE

A total of 54 species was collected from the seven Jambi sites (see the Appendix in Supplementary material). Two families of lower termites (Kalotermitidae and Rhinotermitidae) and three subfamilies of higher termites (Termitidae: Macrotermitinae, Termitinae and Nasutitermitinae) were represented. The primary forest transect was the richest with 34 species, while the two non-forested sites were the most depauperate (Fig. 2a). Two species were found in the *Imperata* grassland transect (6% of the total number of species found in the primary forest transect) while only one species was found in the cassava garden transect (3% of the primary forest transect). The Termitinae was the most species-rich taxonomic group in every transect except the *Paraserianthes* plantation and the cassava garden. There was a very strong positive correlation between termite species richness and relative abundance in the transects ($r = 0.981$, $P < 0.001$). Therefore, relative abundance in the taxonomic groups showed a very similar pattern to that displayed in Fig. 2a.

Relative abundance was highest in the primary forest transect (110 encounters) and lowest in the two non-forested transects (Fig. 2b). The *Imperata* grassland transect had nine encounters (8% of the total number of encounters in the primary forest transect) while the

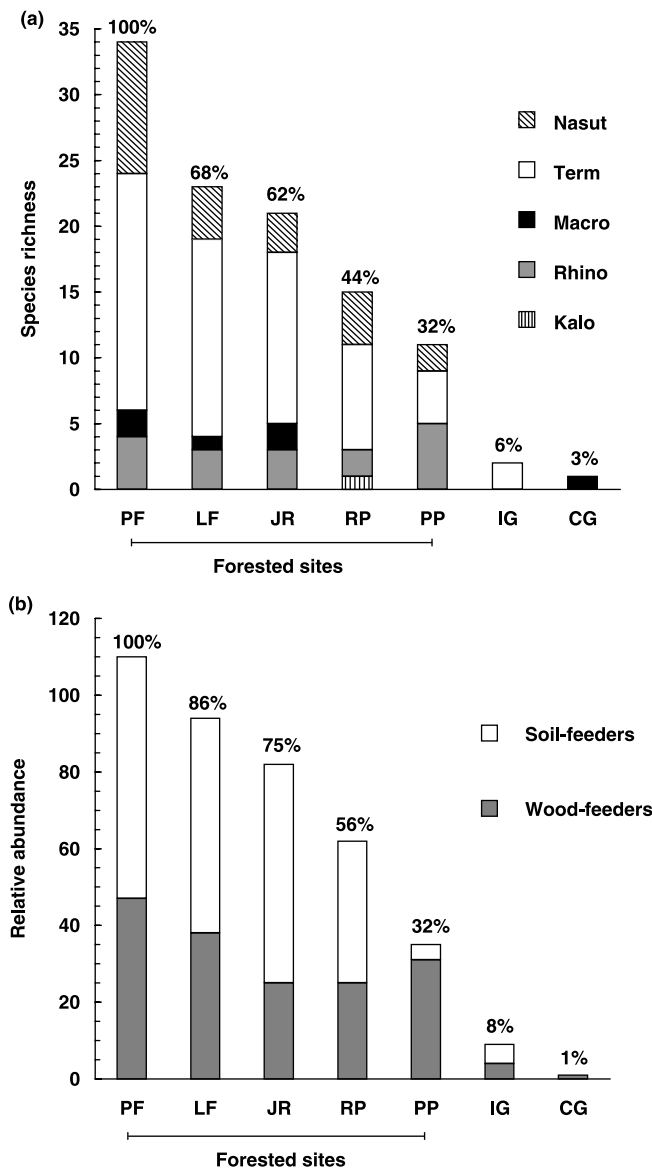


Fig. 2. Termites sampled using standardized transects run in seven sites in a land-use intensification gradient in Jambi Province, Sumatra. The bars in (a) show the species richness in each transect assigned to taxonomic groupings: Kalotermitidae (Kalo), Rhinotermitidae (Rhino), Macrotermitinae (Macro), Termitinae (Term), Nasutitermitinae (Nasut). The bars in (b) show the relative abundance (number of encounters) of wood-feeding termites and soil-feeding termites in each transect. The land-use types are: primary forest (PF), logged forest (LF), jungle rubber (JR), rubber plantation (RP), *Paraserianthes* plantation (PP), *Imperata* grassland (IG) and cassava garden (CG). The percentage in each transect is relative to the number in the primary forest transect.

cassava garden transect had only one encounter. In the forested sites soil-feeding termites were more abundant than wood-feeders, except in the *Paraserianthes* plantation where the ratio of wood-feeder to soil-feeder encounters was 31: 4 (Fig. 2b). The wood-feeders *Coptotermes* and *Schedorhinotermes* had their highest relative abundance in the *Paraserianthes* plantation (22 encounters; see the Appendix in Supplementary material), where they were often found in the dead stumps and boles left from the original forest clearance.

be explained by the environmental variables (Table 1 and Fig. 3). Woody plant basal area accounted for 94% of the variation in termite species richness ($F = 90.4$, d.f. = 1,5, $P < 0.001$, Adj $R^2 = 0.937$) and 95% of the variation in relative abundance ($F = 120$, d.f. = 1,5, $P < 0.001$, Adj $R^2 = 0.952$) among the seven sites. The only other significant variable to enter the model was percentage organic carbon, but this only accounted for 3.9% of the variation in species richness. Similarly, for soil-feeding termites, woody plant basal area accounted for 88% of the variation in species richness ($F = 46.1$, d.f. = 1,5, $P < 0.002$, Adj $R^2 = 0.883$), and 90% of the variation in relative abundance ($F = 56.2$, d.f. = 1,5, $P < 0.001$, Adj $R^2 = 0.902$). The only other significant variables to enter the model for soil-feeders

ENVIRONMENTAL VARIABLES

Much of the variation in termite species richness and relative abundance along the land-use gradient could

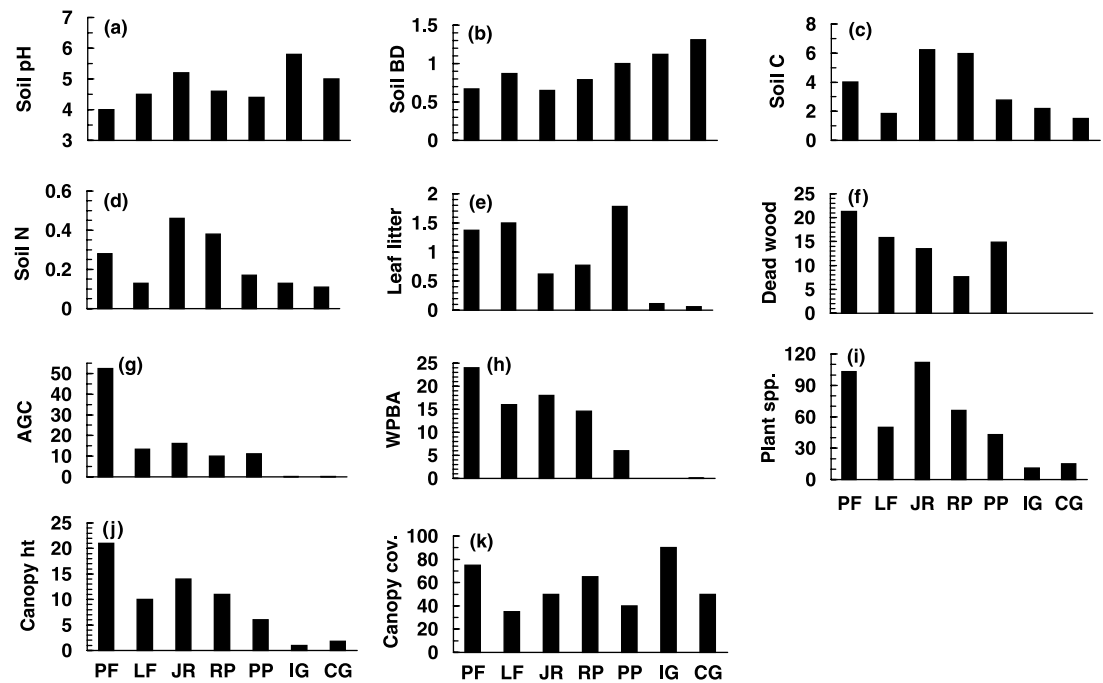


Fig. 3. Bar charts showing the 11 environmental variables recorded in seven sites along a land-use intensification gradient in Jambi Province, Sumatra. The variables are: (a) soil pH (H_2O); (b) soil bulk density (BD) ($g\ cm^{-3}$); (c) soil organic carbon percentage; (d) soil total nitrogen percentage; (e) leaf litter ($kg\ m^{-2}$); (f) dead wood ($kg\ m^{-2}$); (g) above-ground carbon (AGC) ($kg\ m^{-2}$); (h) woody plant basal area (WPBA) ($m^2\ ha^{-1}$); (i) plant species richness per plot ($200\ m^2$); (j) mean canopy height (m); (k) percentage canopy cover. The land-use types are: primary forest (PF), logged forest (LF), jungle rubber (JR), rubber plantation (RP), *Paraserianthes* plantation (PP), *Imperata* grassland (IG) and cassava garden (CG).

Table 1. Correlation coefficient (r) between the species richness (Spp.) and relative abundance (RA) of termites and the 11 environmental variables measured at seven sites along a land-use intensification gradient in Jambi Province, Sumatra. The environmental variables were correlated with all termites (feeding groups I–IV), wood-feeders (groups I + II) and soil-feeders (groups III + IV). After Bonferroni correction * $P \leq 0.05$; ** $P \leq 0.01$

	All termites		Wood-feeders		Soil-feeders	
	Spp.	RA	Spp.	RA	Spp.	RA
Soil pH	-0.694	-0.628	-0.828	-0.826	-0.564	-0.451
Soil bulk density	-0.873	-0.905*	-0.849	-0.785	-0.847	-0.893*
Soil carbon	0.438	0.479	0.479	0.309	0.386	0.537
Soil nitrogen	0.480	0.520	0.482	0.317	0.451	0.594
Leaf-litter	0.633	0.608	0.751	0.874	0.516	0.392
Dead wood	0.915*	0.878	0.930*	0.974**	0.850	0.740
Above-ground carbon	0.890*	0.789	0.883*	0.807	0.843	0.705
Woody plant basal area	0.973**	0.980**	0.924*	0.865	0.950**	0.958**
Plant species richness	0.852	0.845	0.807	0.705	0.833	0.851
Canopy height	0.963**	0.929*	0.935*	0.843	0.925*	0.895*
Canopy cover	-0.100	-0.161	-0.113	-0.257	-0.086	-0.089

were percentage organic carbon and soil pH, which accounted for 5.7% and 3.9%, respectively, of the variation in species richness. In the case of wood-feeding termites, mean canopy height accounted for 85% of the variation in species richness ($F = 34.5$, d.f. = 1,5, $P < 0.003$, Adj $R^2 = 0.848$) while dead wood accounted for 94% of the variation in relative abundance ($F = 90.5$, d.f. = 1,5, $P < 0.001$, Adj $R^2 = 0.937$). In addition, leaf-litter and dead wood accounted for 12.6% and 2.1%, respectively, of the variation in wood-feeder species richness.

When the relative abundance of wood-feeding and soil-feeding termites was plotted against the woody plant basal area (Fig. 4) there was a significant difference in the slopes of the regression lines ($F = 5.58$, d.f. = 1,10, $P = 0.039$). Therefore, the reduction in woody plant basal area along the land-use gradient was associated with greater change in the relative abundance of soil-feeding termites than wood-feeding termites. When the number of wood-feeding species and the number of soil-feeding species were plotted against woody plant basal area (graph not shown), the

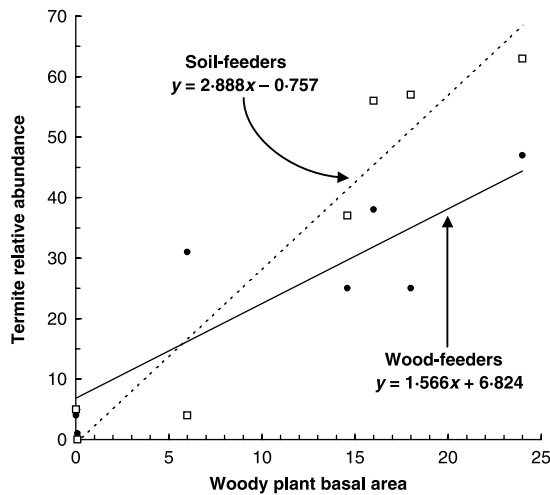


Fig. 4. Relationship between woody plant basal area ($\text{m}^2 \text{ha}^{-1}$) and the relative abundance of termites (number of encounters) in standardized transects run in seven sites along a land-use intensification gradient in Jambi Province, Sumatra. The open squares (dashed line) represent soil-feeding termites, while the closed circles (solid line) represent wood-feeding termites.

soil-feeders showed a steeper decline, although there was no significant difference in the slopes of the two regression lines ($F = 3.35$, d.f. = 1,10, $P = 0.097$).

Wood-feeding termites correlated very strongly with dead wood and litter (Table 1). The large amounts of dead wood and litter in the *Paraserianthes* plantation (Fig. 3e,f) contributed to the high proportion of wood-feeding termites in this transect (Fig. 2b). In contrast, although soil-feeding termites feed on soil organic-matter, the percentage organic carbon in the soil did not correlate significantly with either species richness or relative abundance of soil-feeders (Table 1). Moreover, soil-feeding termites were more strongly correlated with dead wood than with percentage organic carbon. This is probably because many group III species feed on the highly decayed wood found inside and below rotting logs. Therefore, the food resources of group III termites will be related to the availability of decaying wood.

Soil bulk density tended to increase along the land-use gradient (Fig. 3b). The relative abundance of all termites and soil-feeding termites was significantly negatively correlated with soil bulk density (Table 1). This suggests that increasing land-use intensification is associated with soil compaction and a reduction in the abundance of soil-dwelling termites. The lowest correlation coefficients between termite parameters and the environmental variables were with canopy cover.

Discussion

THE JAMBI GRADIENT

The species richness of termites in the Jambi primary forest transect is within the range (28–34 species) for six other transects run using the same protocol in primary

mixed dipterocarp forest up to 300 m a.s.l. in the Sunda region (Jones & Eggleton 2000; Gathorne-Hardy, Syaokani & Eggleton 2001). Termite species richness is lower in isolated fragments compared with continuous forest (De Souza & Brown 1994). Although the Jambi primary forest site was only 5 ha, it was surrounded by an extensive area of selectively logged forest, which appears to have greatly mitigated any effect of its small size. Furthermore, analyses of 24 transects from numerous land-use types in the Sunda region showed that the Jambi primary forest transect was very similar in overall taxonomic and functional composition to the other lowland forest transects run in sites that had remained as rainforest throughout the Quaternary period (Gathorne-Hardy *et al.* 2002). Therefore, the Jambi primary forest termite assemblage represented a typical lowland mixed dipterocarp forest assemblage, and is thus a suitable 'baseline' against which to compare the other Jambi sites.

This study shows that increasing land-use intensification in lowland Sumatra is associated with a progressive and drastic collapse in the termite assemblage. Species richness and relative abundance declined steadily across the forested sites and were considerably lower in the non-forested sites (Fig. 2). As the original forest assemblage was progressively reduced along the land-use gradient, additional species were collected in the modified sites (see the Appendix in Supplementary material). However, all those additional species have been recorded in primary lowland forests elsewhere in the Sunda region (Jones & Brendell 1998; Eggleton *et al.* 1999; Gathorne-Hardy, Jones & Mawdsley 2000; Gathorne-Hardy, Syaokani & Eggleton 2001). Therefore, increasing land-use intensification appears to have caused the incremental loss of forest-dependent termites without their replacement with non-forest species. Sumatra has only a rain forest-adapted termite fauna and so there are no savanna-dependent species available to colonize lowland areas when the forest is opened-up or cleared. The *Imperata* grassland is not exploited by termites because there are no grass-harvesters in the Sunda fauna.

With increasing land-use intensification, sites along the land-use gradient generally had lower woody plant basal area, shorter vegetation, fewer trees and a reduced plant species richness, which together caused the considerable drop in above-ground carbon (Fig. 3). These trends combined to produce increasing simplification of the physical structure of each habitat, which in turn affected the termite assemblage in several distinct ways.

Changes in canopy structure

Forest canopies buffer the forest interior from extreme variations in microclimate (Gehlhausen, Schwartz & Augspurger 2000; Szarzynski & Anhof 2001). Temperature, relative humidity, wind speed and solar radiation at ground level are all highly sensitive to changes in

canopy depth and structure (Chen *et al.* 1999), and the buffering capacity along the Jambi gradient will be reduced as the canopy becomes more open. This must have exposed an increasing number of forest-dependent termite species to microclimatic conditions outside their tolerance range, causing a decline in the survival and reproductive success of their colonies and eventual local extinction. Studies in West Africa suggest that a closed or very dense forest canopy is one of the key factors favouring high termite species richness and abundance (Eggleton *et al.* 1996; Dibog *et al.* 1999; Eggleton *et al.* 2002).

The canopy cover readings at Jambi (Fig. 3k) appear to contradict this idea. However, spherical densiometer measurements of canopy cover only record the proportion of ground area shaded by overhead vegetation. As a result, the dense swards of *Imperata* grass and the large leaves of the cassava plants gave these two sites canopy cover readings that were similar to those of the forested sites. Thus, densiometer readings give no direct indication of the depth or multi-layered structure of the canopy, and therefore are not a useful surrogate for microclimate buffering capacity.

Increased extremes in microclimate may have a greater impact on soil-feeding termites due to the energetic limitations imposed by their feeding habit when compared with wood-feeders. Soil-feeders ingest a mixture of mineral soil and humified organic matter, and this has a much lower concentration of cellulosic material per unit volume than the relatively high-energy resources consumed by wood-feeders (Eggleton, Davies & Bignell 1998). This poor-quality resource may leave many soil-feeding species with insufficient energy reserves to overcome the metabolic costs of any additional stress (Bignell 1994). Exposure to increasing fluctuations in microclimate will be associated with rising physiological costs. Significantly more colonies of soil-feeders may therefore have become energetically unviable compared with wood-feeders, thus resulting in the disproportionate elimination of soil-feeders along the Jambi gradient (Fig. 4).

Loss of microhabitats

The reduction in physical complexity along the Jambi gradient has caused a decline in the variety and abundance of suitable nesting and feeding sites. Many termite species occupy microhabitats such as rotting tree stumps, dead logs, humus around the base of big trees, and the mounds of other termite species (Sands 1965; Eggleton & Bignell 1997). Increasing land-use intensification will reduce the chances of termite alates finding unoccupied nesting sites and establishing new colonies. A study at 1000 m a.s.l. in Borneo (Jones 2000) suggested that the greater structural complexity and denser canopy of lower montane forest, compared with adjacent upper montane forest, provided more microhabitats and a more buffered microclimate, thus allowing greater termite species richness. Clearing or

cultivation in savanna woodland is also known to reduce termite nesting and feeding sites (Wood, Johnson & Ohiagu 1977).

Increasing bulk density

Subterranean termites in tropical forests usually occur in the organic layer of the soil (Collins 1989), and a Malaysian forest study reported that termites were found mainly in the top 15 cm (Abe & Matsumoto 1979). With the exception of the primary forest and jungle rubber sites, heavy machinery was used at some point in all the other Jambi sites. This will have caused compaction of the surface soil and an increase in soil bulk density. Soil compaction is known to reduce the abundance of soil macrofauna (Radford *et al.* 2001) and may have had a negative impact on soil-dwelling termites.

HOW GENERAL IS THE TREND OBSERVED AT JAMBI?

From a conservation and ecosystem function perspective, it is important to know if the collapse in the termite assemblage at Jambi could be expected elsewhere when forests are severely modified. While some studies have looked at part of the termite assemblage (e.g. mound-building species; Sands 1965), we have identified eight studies where all or much of the assemblage was examined along a local disturbance gradient (Table 2). Overall, these studies show a similar general trend of declining species richness and abundance with increasing land-use intensification. The trend is most apparent when examining a long, steep gradient (e.g. from primary forest to sites with no trees). It is more difficult to detect significant changes when only a short gradient is sampled. For example, at Danum Valley there was no obvious decline between primary forest and two selectively logged forest sites (Table 2; Eggleton *et al.* 1997). This differs from the Jambi findings, where a decline between primary and logged forest was evident (Fig. 2). However, this was probably because the Jambi logged forest site had been used as a log ramp and was therefore more disturbed than the Danum logged sites.

Eggleton *et al.* (2002; not included in Table 2) produced a synthesis of the effects of disturbance on termites by combining the results of several studies from West African countries. They found that species richness showed a strong negative correlation with disturbance, and that the number of soil-feeding species declined more steeply along the disturbance gradient than the number of wood-feeders. Other studies have also suggested that soil-feeders are more vulnerable to disturbance than wood-feeders (De Souza & Brown 1994; Eggleton *et al.* 1997; Bandeira & Vasconcelos 2002).

In savannas, populations of certain termites may increase significantly with agricultural intensification, a trend that is less evident in rain forest areas. In

Table 2. Tropical studies of termite assemblages along disturbance gradients caused by increasing land-use intensification. The methods used to sample termite species richness (spp.) and relative abundance (RA) or density (m^{-2}) are given for each study. Termites were sampled in the natural primary habitat and in disturbed habitats and agricultural systems in the local area derived from the natural habitat

Primary habitat	Increasing habitat disturbance and land-use intensification \longrightarrow			
	Disturbed or secondary habitat, or agro-forestry		Agricultural systems	
Danum Valley, Sabah, Malaysia (Eggleton <i>et al.</i> 1997; unpublished data). Two transects per site				
Mixed dipterocarp forest	Selectively logged forest (17 years after logging)	Selectively logged forest (3 years after logging)		
29 and 33 spp.	29 and 33 spp.	29 and 28 spp.		
88 and 83 RA	71 and 96 RA	73 and 65 RA		
Sawai, Sarawak, Malaysia (Collins 1980). One day of intensive casual sampling per site				
Mixed dipterocarp forest	Selectively logged forest		Dry rice (forest cleared and burnt)	
25 spp.	12 spp.		6 spp.	
Brejo dos Cavalos, Pernambuco, Brazil (Bandeira & Vasconcelos 2002). Sampling of soil monoliths, dead wood and mounds				
Highland evergreen forest	Secondary forest (40 years old)		Banana plantation	
14 spp.	8 spp.		5 spp.	
4846 m^{-2}	1798 m^{-2}		446 m^{-2}	
Mbalmayo, southern Cameroon (Eggleton <i>et al.</i> 1995, 1996). One transect, plus sampling of soil pits, dead wood and mounds				
Semi-deciduous forest (near-primary)	Secondary forest (30 years old)	Young plantation	Weeded fallow	Complete clearance
46 spp.	53 spp.	53 spp.	24 spp.	16 spp.
2282–6957 m^{-2}	2328–10488 m^{-2}	5170–6703 m^{-2}	778–1542 m^{-2}	63–2959 m^{-2}
Mabira, southern Uganda (Okwakol 2000). Soil pits, dead wood and mounds sampled at each site				
Semi-deciduous forest	Recently cleared forest		Banana grove (5 years old)	Banana grove (20 years old)
25 spp.	11 spp.		5 spp.	2 spp.
Deciduous miombo savanna woodland, Zimbabwe (Dangerfield 1990). Soil monoliths (mean density $m^{-2} \pm 1$ SE)				
Savanna woodland	Disturbed Woodland	Old fallow (trees but no canopy)	Mature <i>Eucalyptus</i> stand (exotic species)	Maize field (6 years old)
100 \pm 43 m^{-2}	49 \pm 18 m^{-2}	51 \pm 22 m^{-2}	19 \pm 15 m^{-2}	0 m^{-2}
Southern Guinea savanna zone, Nigeria (Wood, Johnson & Ohiagu 1977). Soil cores				
Closed savanna woodland	Secondary woodland (15 years old)	Grazed pasture (cleared secondary woodland)	Maize field (1 year old)	Maize field (25 years old)
28 spp.	22 spp.	20 spp.	8 spp.	4 spp.
3472 m^{-2}	2965 m^{-2}	2010 m^{-2}	1553 m^{-2}	6825 m^{-2}
Southern Guinea savanna zone, Nigeria (Wood <i>et al.</i> 1982). Soil cores				
Riparian forest			Sugar cane cultivation	
23 spp.			8 spp.	
2861 m^{-2}			1151 m^{-2}	

Nigeria, for example, the abundance of *Microtermes* rose substantially as they fed on cultivated maize (Table 2; Wood, Johnson & Ohiagu 1977). Such outbreaks usually occur only if the pest species had been present in the original species pool or had been introduced by humans. Also, some species are more tolerant of greater exposure to direct sunlight, and colony density may increase significantly when savanna woodland is cleared, as with the mound-builder *Trinervitermes geminatus* (Sands 1965).

MANAGEMENT RECOMMENDATIONS

The loss of termites that accompanies severe forest modification may have a negative impact on soil processes (Holt & Lepage 2000; Donovan *et al.* 2001b). While research is needed to quantify the relationship between termites and soil quality, the immediate

challenge is to achieve sustainable agricultural and silvicultural production with management practices that protect soil biodiversity and maintain ecosystem functions. To mitigate the reduction in the termite assemblage, we recommend the following strategies. Because these are aimed at retaining as much canopy cover and habitat complexity as possible, they are likely to benefit other vulnerable groups of forest organisms.

1. Reduced-impact logging (RIL) techniques can reduce the amount of damage caused to forests by about 50% compared with conventional logging practices, and significantly reduce soil compaction and loss of canopy cover (Johns, Barreto & Uhl 1996; Pinard & Putz 1996). Adopting RIL practices will help preserve forest assemblages of termites as well as ants (Vasconcelos, Vilhena & Caliri 2000), dung beetles (Davis *et al.* 2001) and insect herbivores (Basset *et al.* 2001).

2. Policies that increase forest or silvicultural patch size and reduce the length of forest edges are likely to have a positive effect on the survival of forest-dependent species (Laurance *et al.* 2002). De Souza & Brown (1994) showed that termite species richness and number of encounters declined with decreasing fragment size. Both fragment size and edge effect are known to have a strong influence on beetle composition, and the probability of local extirpation is significantly higher following fragmentation (Didham *et al.* 1998).
3. Leaving or establishing forest corridors allows the movement of seeds, pollen and animals among patches of forested land, thereby promoting persistence and recolonization in logged areas (Lindenmayer, Margules & Botkin 2000). Improving connectivity will assist recolonization by termites because their poor dispersal abilities makes it difficult for them to disperse across exposed areas to suitable habitat (Gathorne-Hardy, Jones & Mawdsley 2000; Gathorne-Hardy, Syaokani & Eggleton 2001).
4. Rotting wood provides nesting and foraging sites for a range of invertebrates, and a supply of organic debris and nutrients to the soil. Leaving dead wood on the ground following forest disturbance is known to accelerate the recovery of the termite assemblage by increasing the abundance and species richness of both wood-feeders and soil-feeders (Davies *et al.* 1999).

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Supplementary material

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/JPE/JPE794/JPE794sm.htm>

Appendix Checklist of the 54 species of termites collected using the standardised transect sampling protocol from the seven land-use types in Jambi Province, central Sumatra.

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