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# Feeding group responses of a Neotropical termite assemblage to rain forest fragmentation

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**Abstract** Biomass collapse and its associated microclimatic stresses within recently isolated rain forest fragments may negatively affect species diversity of most resident taxa. However, for some decomposer organisms, increased resource availability via accompanying tree die-off may effect positive responses, at least for a time, with implications for rates of nutrient cycling and greenhouse gas release. This study investigates the early effects of forest fragmentation on a Neotropical termite assemblage. Numbers of encounters (surrogate for relative abundance) and species richness of wood and leaf-litter feeders, soil feeders, and the whole assemblage, were studied across true forest islands and mainland sites at a hydroelectric reservoir in French Guiana. Results showed no overall effect of fragmentation on either total termite encounters or species richness. However, numbers of encounters and species richness of wood and leaf-litter feeders showed positive responses to forest fragmentation. By contrast, soil feeders showed a negative response for numbers of encounters and no significant effect for species richness. Environmental data suggest that increased tree die-off, and other edge effects associated with biomass collapse, were underway at the time of sampling. Resulting increase in resource availability may therefore explain the positive influence on wood and leaf-litter feeders. A possible decrease in predation pressure from ants with decrease in island size was not tested for, but was a likely effect of the flooded matrix habitat. Fragmentation effects on soil feeder encounters may be due to the energetic and microclimatic constraints of feeding lower down the humification gradient of termite food substrates, but were not sufficient to affect species richness. The patterns revealed suggest that rates of wood decomposition following tree die-off, and of soil nutrient cycling, under different rain forest fragmentation scenarios, merit further study.

**Keywords** Biomass collapse · Forest islands · Species richness · Soil feeder · Wood feeder

## Introduction

Changes in community trophic structure accompanying biodiversity loss are a commonly observed outcome of tropical forest fragmentation. These changes are important in influencing trajectories of ecosystem function as well as ecosystem collapse of forest fragments.

A number of factors are thought to drive trophic structural changes in habitat fragments generally. Area and isolation effects may drive differential species loss from higher trophic levels resulting in shortening of food chain lengths in small habitat fragments (Schoener 1989). Models developed by Holt (1996) mirror much empirical observation in predicting that the slope of species-area relations should increase with trophic rank. Biotic and abiotic edge effects of fragmentation can also influence trophic structuring of rain forest communities via the sum of differential species responses to microclimatic and other gradients. The type of matrix habitat surrounding forest fragments may also have a profound influence on trophic structuring. In the case of rain forest fragments surrounded by a terrestrial matrix, influx of disturbed habitat species may be important. However, where the matrix habitat is aquatic, trophic distortions affecting communities of tropical forest islands are known to be more exaggerated (Terborgh et al. 1997). This is thought to be due to the greater restrictions on species dispersion and mobility and their greater negative impact on persistence of species at higher trophic levels.

Studies of changes in trophic structuring resulting from rain forest fragmentation have largely focused on

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**Table 1** Description of St. Eugène Fragmentation Project (*SEFP*) transects sampled for termite diversity and environmental data

| Transect code (this study) | Location: SEFP island number; mainland or ghost forest | Area (ha) | Mean distance to nearest forest edge (m) | Season sampled |
|---|---|---|---|---|
| T1 | Mainland | 1,000 | 740 | Wet |
| T2 | Island 2 | 38.31 | 87 | Wet |
| T3 | Island 22 | 0.72 | 19.5 | Wet |
| T4 | Island 3 | 80 | 111.5 | Wet |
| T5 | Island 16 | 3.89 | 75.5 | Wet |
| T6 | Island 40 | 0.2 | 10.9 | Wet |
| T7 | Island 27 | 0.7 | 14.5 | Wet |
| T8 | Island 103 | 25.5 | 170 | Wet |
| T9 | Island 14 | 7.22 | 70 | Wet |
| T10 | Island 24 | 1.67 | 40 | Dry |
| T11 | Island 23 | 0.35 | 7.5 | Dry |
| T12 | Mainland | 1,000 | 176.5 | Dry |
| T13 | Mainland | 1,000 | 800 | Dry |

above- rather than below-ground food webs, and upon vertebrates rather than invertebrates. Hence, the responses of decomposer communities is poorly known. Yet decomposers of plant-derived organic material are likely to be strongly directly affected by forest fragmentation due to the process of biomass collapse.

An 18-year study of tree community structure and dynamics at the Biological Dynamics of Forest Fragments Project (BDFFP) in Brazil, has shown that hotter, drier microclimatic conditions and greater exposure to wind, with decreasing distance to fragment edges, are responsible for increased tree mortality, and consequent tree recruitment (Laurance et al. 1998). Laurance et al. (1997) have shown that BDFFP forest fragments have undergone a net loss in biomass of around 10% within 2–4 years of isolation, the time interval during which the rate of tree die-off may be maximal. We might expect that the increased availability of dead plant matter would present a resource bonanza for decomposer organisms that are able to tolerate the negative influences of forest fragmentation. Changes in diversity and abundance of decomposers surviving in forest fragments over time should have a direct bearing on rates of breakdown of dead plant biomass and greenhouse gas production. Moreover, we would expect these changes to have an impact on above-ground food webs inside forest fragments.

Termites are a particularly important part of the decomposer arthropod community in tropical forests and play key roles in nutrient cycling, nitrogen fixation, carbon flux, soil creation and soil distribution (Bignell et al. 1997; Bond 1993; Collins 1983; Jones 1990; Lawton et al. 1996). These functions are largely dependent on the species composition of the termite assemblage. This study presents an investigation of the early effects of forest fragmentation on functional group composition of a Neotropical termite assemblage across forest islands in French Guiana. Environmental data are also presented in order to establish the extent to which biotic and abiotic edge effects had become established on islands at the time of sampling. In particular, evidence for tree-die off and consequent changes in canopy cover and availability of dead wood are assessed. The findings are compared with those of a study on the effects of forest fragmentation of termite assemblages at the BDFFP by De Souza and Brown (1994), particularly in the context of the profound differences in matrix habitat surrounding fragments at the two sites. Possible hypotheses to explain the observed patterns are reviewed, and the implications for changes in ecosystem function and carbon flux discussed.

## Materials and methods

### Study site

The study was carried out at the St. Eugène Fragmentation Project (4° 59′N, 53°08′W) at the Petit Saut hydroelectric reservoir in French Guiana. Islands within the study site range from less than a hectare up to ca. 80 ha and were created by the inundation of lowland rain forest between January 1994 and June 1995 [for further site details see Cosson et al. (1999), Davies et al. (in press), de Granville (1996), Granjon et al. (1996), Ringuet et al. (1998)]. Since inundation, the remaining forest surrounding the reservoir has been protected by law. The flooded zone bordering islands and mainland includes an extensive “ghost forest” of dead emergent trees which are home to a limited termite assemblage (Davies et al., in press).

### Data collection

#### *Termite data*

Termite diversity was measured at each of three mainland sites and ten island sites. Forest islands were selected randomly while mainland sites were pre-selected at the maximum feasible distance from the nearest shoreline. Termite sampling was divided into two periods: wet season sampling of one mainland site and eight islands of varying size (April–May 1998); and dry season sampling of a further two mainland and two island sites (October–December 1998). Termite species richness and numbers of encounters per species (a surrogate for relative abundance) were sampled using the transect method described in Davies et al. (in press) adapted from Jones and Eggleton (2000). At each of the 13 sites, a single transect was used (T1–T13, see Table 1). In the case of forest islands, positioning was at or near the centre of each island. Mainland transects were randomly positioned within a pre-selected area of several hectares (see above). Termite data from each transect were the result of 20 h of sampling, within a 100 m×2 m area, of 240 randomly positioned soil samples, of all items of large dead wood and termite mounds, and of other suitable microhabitats including small wood items in proportion to their occurrence along the transect. Additionally, sampling of two 100 m×2 m ghost forest transects was conducted in order to assess species overlap with terrestrial transects. Methods and results of the ghost forest sampling have been dealt with in a species level study (Davies et al., in press) and are only discussed further here with respect to factoring out ghost forest assemblage influence (see analyses).

### *Environmental data*

Environmental data collection is fully presented in Davies et al. (in press) and included measurement of the following variables: $\log_{10}$ (fragment area+1); $\log_{10}$ (distance to fragment edge); volumes of fallen large wood ($m^3\ m^{-2}$ logs with diameter ≥10 cm), fallen small wood ($m^3\ m^{-2}$ twigs and branches with diameters <10 cm), standing dead wood ($m^3\ m^{-2}$ standing dead trunks with mean diameter ≥10 cm), and total wood volume ($m^3\ m^{-2}$) summed across all categories; frequencies of encounter of items of large dead wood, standing dead wood, and small dead wood; frequency of stems of live palms (height ≥2 m) and trees [≥10 cm diameter at breast height (DBH)]; percentage canopy cover; soil moisture (% g $H_2O$ $g^{-1}$ oven dry soil); mean depth of the A-horizon (cm)= upper-most layer of humus-rich soil; total soil organic carbon; total soil nitrogen (% mg $g^{-1}$ dry weight of soil); and soil pH.

### Termite feeding 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 relatively mineralised soil that is poor in organic matter. In the present study, termites were classified into the two broadest feeding group categories: wood and leaf-litter feeders, and soil feeders. In the recent termite feeding group classification proposed by Donovan et al. (2001) wood and leaf-litter feeders correspond to groups I and II, while soil feeders correspond to feeding groups III and IV.

### Analyses

#### *Relationships between environmental variables across sites*

Logistic regression was used to analyse the apportionment of the total numbers of large standing tree trunks (≥10 cm DBH) per transect, between standing dead and live trunks, in relation to $\log_{10}$ (distance to fragment edge) and $\log_{10}$ (area), and to analyse the relationship between percentage canopy cover and the same two fragmentation variables.

In order to control for any possible influence of the ghost forest termite assemblage upon smaller island assemblages, all four ghost forest species that were also found in terrestrial transect samples were excluded from datasets, both of termite relative encounters and species richness across sites.

#### *Relationships between environmental variables and termite relative encounters and species richness*

The relationships between both $\log_{10}$ (encounters) and species richness and the two main fragmentation variables, $\log_{10}$ (edge distance) and $\log_{10}$ (fragment area), were tested using linear regression. Regressions were performed on data for wood and leaf-litter feeders combined, soil feeders, and the whole assemblage. However, season is known to affect termite relative abundances (Dibog et al. 1998), with potential knock-on effects on relative species richness. For this reason, significant seasonal effects were tested for and removed from relative encounter and species richness data before testing for the effects of fragmentation. This was performed by first regressing $\log_{10}$ (encounters) and species richness data against season (wet vs. dry season transects) and, in cases where significance at the 95% level was found, using the residuals of such regressions for subsequent regression against fragmentation variables.

Additionally, forward stepwise multiple regression was used to determine which of the 17 environmental variables measured were significant predictors of $\log_{10}$ (encounters) and species richness for wood and leaf-litter feeders, soil feeders, and for the whole assemblage. Variables were entered into the model when $P<0.05$. This procedure was used to test whether fragmentation variables, or uncorrelated environmental gradients, were having the greatest influence on the distribution of $\log_{10}$ (encounters) and species richness between functional groups, and for the whole assemblage, across sites.

## Results

### Environmental variables

Linear regressions against the two fragmentation variables produced significant results for only three environmental variables in the case of $\log_{10}$ (distance to fragment edge), with only two of these showing significance with $\log_{10}$ (area) (Table 2). As $\log_{10}$ (distance to fragment edge) showed consistently stronger correlations with the environmental variables than $\log_{10}$ (area), it is the relationships with the former that are presented graphically (Fig. 1). The most significant correlation was with frequency of small wood which showed a strongly negative, and approximately linear, relationship (Fig. 1A). Regressions against volume of standing dead wood and soil moisture showed weaker, albeit significant, linear correlations, but plots of each of these variables suggest non-linear relationships (Fig. 1B, C, respectively). It is notable that two small-island transects, close to forest edges, showed much greater volumes of standing dead wood than any other sites. In addition to a positive relationship with $\log_{10}$ (distance to fragment edge), soil

**Table 2** Significant results of linear regressions of $\log_{10}$ (distance to fragment edge) and $\log_{10}$ (area) against 15 environmental variables, across 13 standardised transects (see also Fig. 1)

| Dependent variable | Independent variable | *F* | *df* | *P* | $r^2$ | Slope |
|---|---|---|---|---|---|---|
| Frequency of small wood | $\mathrm{Log}_{10}$ (distance to fragment edge) | 13.42 | 1, 11 | 0.004 | 0.550 | –ve |
| Frequency of small wood | $\mathrm{Log}_{10}$ (fragment area) | 6.70 | 1, 11 | 0.025 | 0.378 | –ve |
| Volume of standing dead wood | $\mathrm{Log}_{10}$ (distance to fragment edge) | 5.06 | 1, 11 | 0.046 | 0.315 | –ve |
| Soil moisture | $\mathrm{Log}_{10}$ (distance to fragment edge) | 9.21 | 1, 11 | 0.011 | 0.456 | +ve |
| Soil moisture | $\mathrm{Log}_{10}$ (fragment area) | 5.85 | 1, 11 | 0.034 | 0.347 | +ve |

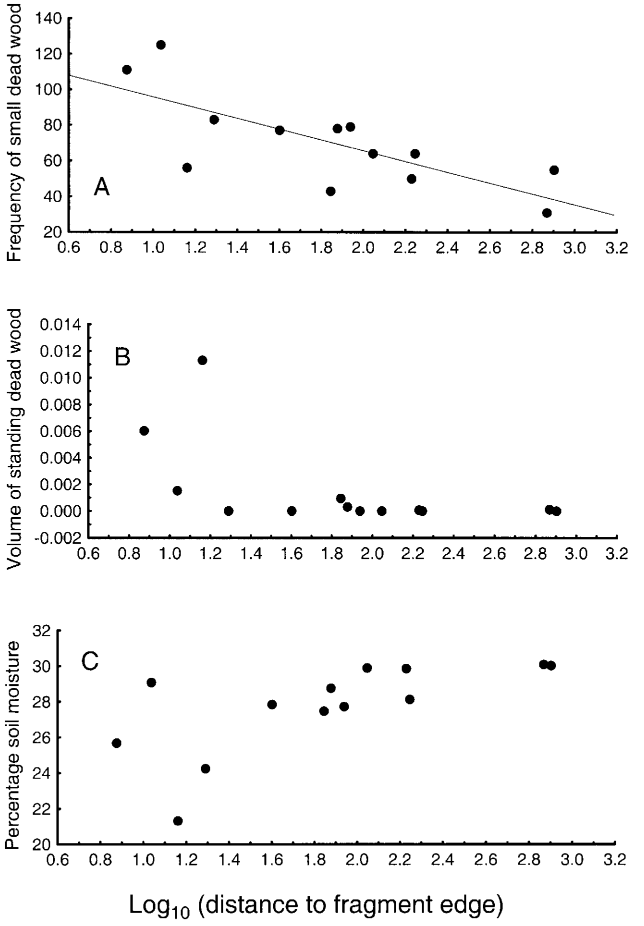

**Fig. 1** Plots of environmental variables showing significant relationships ($P$<0.05) between log$_{10}$ (distance to fragment edge) (see Table 2) and: **A** frequency of small wood (a relative measure of numbers of small wood items encountered along transect); **B** volume of standing dead wood (m$^3$ m$^{-2}$ from ground-level up to a height of 2 m); and **C** soil moisture (% g $H_2O$ g$^{-1}$ oven dry soil). A regression line was fitted for **A** only, as relationships for **B** and **C** appear to be non-linear

moisture showed greater variation among small islands, compared with larger sized islands and mainland sites.

There were significant non-linear decreases in the proportion across all standing woody stems of those that were standing dead, both with increasing log$_{10}$ (distance to fragment edge) (logistic regression: $\chi^2$=8.85, $df$=1, $P$=0.003) and with increasing log$_{10}$ (area) (logistic regression: $\chi^2$=6.08, $df$=1, $P$=0.014). Logistic regression also showed that there was a significant increase in percentage canopy cover with increase in log$_{10}$ (distance to fragment edge) ($\chi^2$=8.77, $df$=1, $P$=0.003), but not with increase in log$_{10}$ (area) ($\chi^2$=2.69, $df$=1, $P$=0.01).

### The termite assemblage: relative encounters and species richness relationships with environmental variables

Standardised transect sampling across 13 terrestrial and two ghost forest transects yielded a total of 100 termite species/morphospecies (see Appendix 1). Of these, 27 were wood and/or leaf-litter feeders and 73 were soil feeders. Ninety-nine of the species were found in terrestrial transect samples. Only six species occurred in the ghost forest transects, all but one being wood feeders – one of which was not found in any of the terrestrial transects. None of the ghost forest species were abundant in terrestrial samples, averaging only 1.0% of total transect encounters of termites (Davies et al. in press). Species richness of terrestrial transects ranged between 38 and 51.

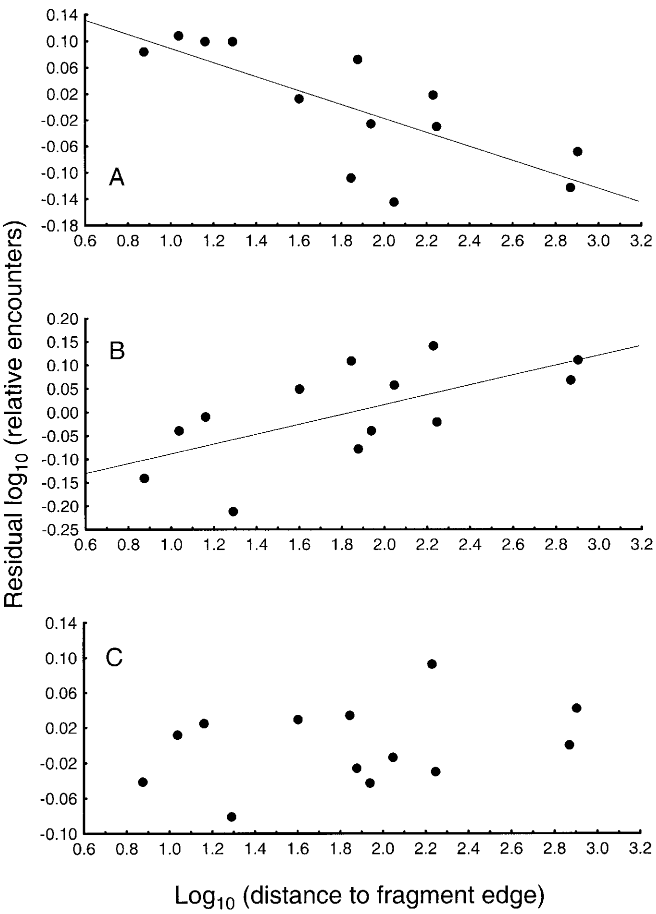

**Fig. 2** Plots of residual log$_{10}$ (termite relative encounters), with season partialled out, against log$_{10}$ (distance to fragment edge) across the 13 terrestrial sites for: **A** wood and leaf-litter feeders; **B** soil feeders; and **C** the whole assemblage. Regression lines fitted only where $P$<0.05

#### *Relative encounters*

Relative encounter data summed within feeding group showed some seasonal trends, with generally higher termite relative encounters in the dry season compared with the wet season. One-way ANOVAs showed that season was significant for log$_{10}$ (relative encounters) of wood and leaf-litter feeders ($F_{1,11}$=7.82, $P$<0.02), and for log$_{10}$ (total encounters) ($F_{1,11}$=14.29, $P$<0.003). All re-

**Table 3** Linear regressions of $\log_{10}$ (relative encounters) of wood and leaf-litter feeders, soil feeders, and the whole assemblage, against $\log_{10}$ (distance to fragment edge) and $\log_{10}$ (area), across 13 standardised termite diversity transects (see also Fig. 2)

| Dependent variable: feeding group(s) | Independent variable | *F* | *df* | *P* | $r^2$ | Slope |
|---|---|---|---|---|---|---|
| Wood/leaf-litter feeders | $\text{Log}_{10}$ (distance to fragment edge) | 14.58 | 1, 11 | 0.003 | 0.570 | –ve |
| Wood/leaf-litter feeders | $\text{Log}_{10}$ (fragment area) | 13.96 | 1, 11 | 0.003 | 0.559 | –ve |
| Soil feeders | $\text{Log}_{10}$ (distance to fragment edge) | 8.05 | 1, 11 | 0.016 | 0.422 | +ve |
| Soil feeders | $\text{Log}_{10}$ (fragment area) | 3.87 | 1, 11 | 0.075 | 0.260 | +ve |
| Whole assemblage | $\text{Log}_{10}$ (distance to fragment edge) | 1.25 | 1, 11 | 0.288 | 0.102 | +ve |
| Whole assemblage | $\text{Log}_{10}$ (fragment area) | 0.20 | 1, 11 | 0.667 | 0.017 | +ve |

**Table 4** Forward stepwise multiple regression of 17 environmental variables as predictors of $\log_{10}$ (termite encounters) (with season held constant) within two feeding groups (wood and leaf-litter feeders, and soil feeders) and the whole assemblage, across 13 standardised transects

| Dependent variable: feeding group(s) | Independent variable | Step | *F* | *df* | *P* | $r^{2a}$ | Slope |
|---|---|---|---|---|---|---|---|
| Wood/leaf-litter feeders | $\text{Log}_{10}$ (distance to fragment edge) | 1 | 14.58 | 1, 11 | 0.003 | 0.57 | –ve |
| Soil feeders | Frequency of small wood | 1 | 8.53 | 1, 11 | 0.014 | 0.437 | –ve |
| | Soil moisture | 2 | 5.45 | 1, 10 | 0.042 | 0.797 | +ve |
| Whole assemblage | – | – | – | – | – | – | – |

[a] Values of $r^2$ are for the whole model for each step presented

**Table 5** Linear regressions of species richness of wood and leaf-litter feeders, soil feeders, and the whole assemblage, against $\log_{10}$ (distance to fragment edge) and $\log_{10}$ (area), across 13 standardised termite diversity transects (see also Fig. 3)

| Dependent variable: feeding group(s) | Independent variable | *F* | *df* | *P* | $r^2$ | Slope |
|---|---|---|---|---|---|---|
| Wood/leaf-litter feeders | $\text{Log}_{10}$ (distance to fragment edge) | 5.53 | 1, 11 | 0.038 | 0.335 | –ve |
| Wood/leaf-litter feeders | $\text{Log}_{10}$ (fragment area) | 2.78 | 1, 11 | 0.124 | 0.202 | –ve |
| Soil feeders | $\text{Log}_{10}$ (distance to fragment edge) | 0.18 | 1, 11 | 0.680 | 0.016 | +ve |
| Soil feeders | $\text{Log}_{10}$ (fragment area) | 0.04 | 1, 11 | 0.839 | 0.004 | +ve |
| Whole assemblage | $\text{Log}_{10}$ (distance to fragment edge) | 0.68 | 1, 11 | 0.426 | 0.059 | –ve |
| Whole assemblage | $\text{Log}_{10}$ (fragment area) | 0.53 | 1, 11 | 0.480 | 0.046 | –ve |

gression analyses for $\log_{10}$ (encounters) were, therefore, performed with season held constant.

Linear regressions of relative encounters against the two main fragmentation variables, with season held constant, showed that both $\log_{10}$ (distance to fragment edge) and $\log_{10}$ (area) were highly significantly negatively correlated with $\log_{10}$ (encounters) for wood and leaf-litter feeders, whereas $\log_{10}$ (distance to the forest edge) alone was significantly positively correlated with $\log_{10}$ (encounters) for soil feeders (Table 3). Neither $\log_{10}$ (distance to the forest edge) nor $\log_{10}$ (area) were significantly correlated with relative encounters of the whole assemblage across sites. Again, as $\log_{10}$ (distance to the forest edge) showed stronger correlations with termite-encounter data than $\log_{10}$ (area), it is relationships with the former that are illustrated graphically (Fig. 2).

Forward stepwise multiple regression, holding season constant, showed that $\log_{10}$ (distance to the forest edge) remained the strongest predictor of $\log_{10}$ (encounters) for wood and leaf-litter feeders (Table 4). Frequency of small dead wood correlated most strongly with $\log_{10}$ (encounters) for soil feeders, showing a negative relationship, while soil moisture accounted for significant remaining variance in the data.

### Species richness

There were no significant effects of season upon species richness of wood and leaf-litter feeders, soil feeders, or the whole assemblage. Hence, there was no reason to partial out season in any of the regression analyses.

Linear regression of species richness of wood and leaf-litter feeders against the two fragmentation variables showed that only $\log_{10}$ (distance to the forest edge) was significantly correlated (Table 5). Neither fragmentation variables showed significant linear relationships with species richness of either soil feeders or the whole assemblage. The relationships between $\log_{10}$ (distance to the forest edge) and species richness are presented graphically (Fig. 3).

Forward stepwise multiple regression showed that volume of small dead wood was the best predictor of species richness of wood and leaf-litter feeders, with

**Table 6** Forward stepwise multiple regression of 17 environmental variables as predictors of termite species richness within two feeding groups (wood and leaf-litter feeders; and soil feeders), and the whole assemblage, across 13 standardised transects

| Dependent variable: feeding group(s) | Independent variable | Step | *F* | *df* | *P* | $r^{2a}$ | Slope |
|---|---|---|---|---|---|---|---|
| Wood/leaf-litter feeders | Volume of small wood | 1 | 12.96 | 1, 11 | 0.004 | 0.541 | +ve |
| | Soil moisture | 2 | 8.90 | 1, 10 | 0.014 | 0.757 | –ve |
| Soil feeders | Soil pH | 1 | 5.92 | 1, 11 | 0.033 | 0.350 | +ve |
| | Frequency of live trees | 2 | 6.40 | 1, 10 | 0.030 | 0.604 | +ve |
| Whole assemblage | Volume of small wood | 1 | 6.29 | 1, 11 | 0.029 | 0.364 | +ve |

[a] Values of $r^2$ are for the whole model for each step presented

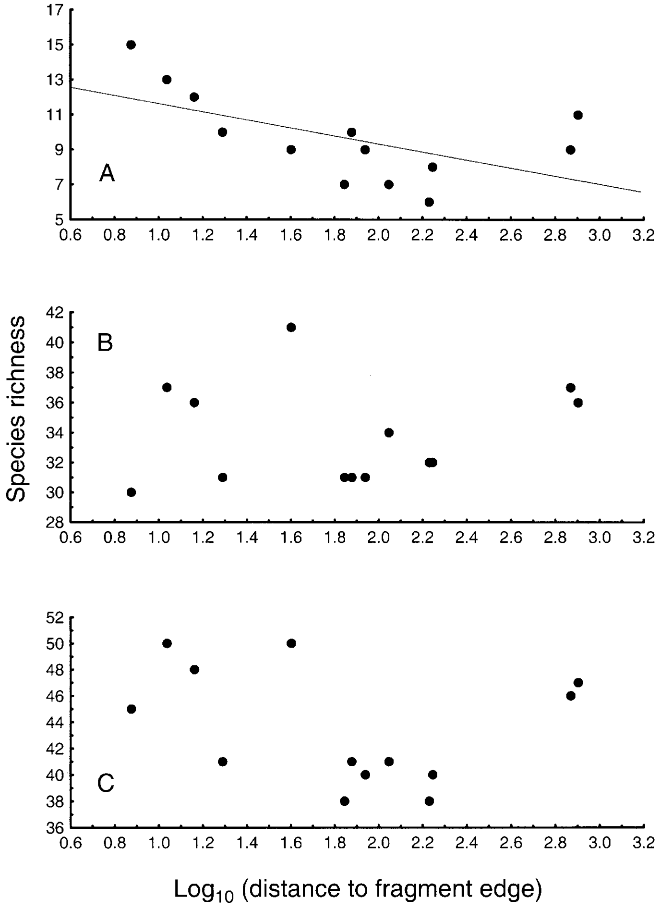

**Fig. 3** Plots of termite species richness against $\log_{10}$ (distance to fragment edge) across the 13 terrestrial sites for: **A** wood and leaf-litter feeders; **B** soil feeders; and **C** the whole assemblage. Regression lines fitted only where $P<0.05$

soil moisture explaining significant remaining variance (Table 6). In contrast, soil pH was the best predictor of species richness for soil feeders with tree density explaining significant remaining variance. These results indicate that environmental variables associated with forest fragmentation were having the greatest influence on species richness of wood and leaf-litter feeders, but that a soil variable (pH), uncorrelated with fragmentation variables, was having the greatest influence upon species richness of soil feeders, at the time of sampling.

## Discussion

### Environmental effects of fragmentation

The findings of greater frequency and volumes of standing dead trunks close to forest edges, and lower percentage canopy cover, on smaller islands, suggests similar patterns of tree die-off to those reported for the BDFFP, where large numbers of standing dead trees were observed near newly formed fragment edges (Ferreira and Laurance 1997; Lovejoy et al. 1986). Laurance et al. (1998) speculate that these may have been killed by sudden changes in soil and air temperature and humidity. Hence, increased tree mortality near edges may result in increased frequency and volume of standing rather than fallen dead trunks. Such a scenario matches well the findings of the present study.

The very significant negative correlation between frequency of small fallen woody items and $\log_{10}$ (distance to fragment edge) may also be a direct consequence of greater wind exposure across smaller islands and to accompanying increases in tree die-off. It is possible that drier microclimate leading to lower rates of fungus-mediated decomposition of small woody items on islands might also be contributing, although there are no data to support this.

Overall, the greater heterogeneity observed in canopy cover and volumes of dead wood, across small islands compared with mainland forest sites, mirrors the increased heterogeneity in vegetation structure 4 years after fragmentation reported for the BDFFP by Camargo and Kapos (1995). The likelihood that this heterogeneity has resulted in a similar increase in the complexity of microclimatic gradients to that reported in the same study, is also suggested by the relatively greater variability in soil moisture across small island transects compared with larger islands and mainland sites (Fig. 1C).

### Effects of fragmentation on the termite assemblage

The regression analyses showed the importance of forest fragmentation effects upon functional structure of the termite assemblage in terms of relative encounters. What was remarkable about these results was the diametrically opposite responses of the two major functional sub-divisions of the termite assemblage (Fig. 2). The positive response of wood- and leaf litter-feeding termites on the one hand, to forest fragmentation, and the negative response of soil feeders on the other, suggests very different ecological constraints affecting these two sub-divisions of a single taxonomically closely related group of organisms. The positive response of wood- and leaf litter-feeding species richness to forest fragmentation is also remarkable, given that it appears not to have been due to any positive influence of the ghost forest assemblage upon species richness of smaller islands. A further potential influence upon wood- and leaf litter-feeder relative encounters, which was not assessed, was the seasonal exposure above water level of dead tree debris in the littoral zone girdling fragments. However, casual sampling revealed that this zone was dominated in abundance terms by ghost forest termite species.

Overall, these results contrasted with the findings of a similar termite study at the BDFFP in Brazil, 6 years after forest fragmentation, in which both wood/leaf-litter and soil feeders showed negative responses to fragmentation in terms of numbers of encounters (abundance) and species richness (De Souza and Brown 1994). Nevertheless, the BDFFP study also revealed a stronger negative influence of fragmentation upon soil feeders than wood and leaf-litter feeders in terms of termite encounters. Before attempting to explain termite patterns observed in the present study, and their differences with those from the BDFFP, some discussion of the environmental data is required.

## The role of edge distance and island area

In this study, $\log_{10}$ (distance to fragment edge) and $\log_{10}$ (area) measurements were strongly correlated, and hence differences in the relative influences of these variables upon other biotic or abiotic variables could not be conclusively resolved (Didham 1997). Nevertheless, the regression analyses consistently showed stronger and more significant relationships between $\log_{10}$ (distance to fragment edge) and termite or environmental variables than $\log_{10}$ (area). This suggests that edge effects were having a more direct influence upon these other variables than area effects. In fact $\log_{10}$ (distance to fragment edge) in this study can be considered a composite fragmentation variable which was primarily a measure of edge distance but also an indirect gauge of island/fragment area.

## Soil feeders

Differences in microclimatic tolerances of wood and leaf-litter feeders compared with soil feeders were proposed as possible explanations for patterns observed in the BDFFP study (De Souza and Brown 1994). Putting this in a broader theoretical framework, the attenuation of termite assemblage penetration down the humification gradient of organic matter decomposition in response to forest fragmentation is analogous to the shortening in length of more classical food chains (i.e. herbivore-predator) studied by Holt (1996) and Schoener (1989). However, closer scrutiny of the likely constraints affecting the most vulnerable levels of each of these two energy pathways suggests some limitations to such an analogy. What makes predators more vulnerable than their prey is lower absolute population sizes (Holt 1996), higher population variability (Kruess and Tscharntke 1994), dependence on prey species (Holt 1996; Schoener 1989), and the constraints of foraging area (Terborgh 1992). For soil-feeding termites feeding on more humified substrates, the constraints imposed by resource availability upon population sizes are negligible given that soil is a much more abundant and evenly distributed resource. The energetic knife-edge of feeding on more humified substrates (Eggleton et al. 1998) is likely to be the main constraint which makes soil-feeding termites more vulnerable than wood and leaf-litter feeders to forest fragmentation and other habitat disturbances.

Soil-feeding termites are less dispersive than wood and leaf-litter feeders (Gathorne-Hardy et al. 2000) which should lead to lower overall soil-feeder relative abundance resulting from stochastic extinctions of soil-feeder colonies on small islands. However, in the present study there was no significant decline in soil-feeder species richness within fragments, 4 years after inundation (Fig. 3B). Given the relatively recent isolation of forest islands, and that termites are known to show at least some short-term species compositional resilience in response to disturbance (Eggleton et al. 1996, 1997), it appears that stochastic extinctions had not had time to make a noticeable impact at St. Eugène at the time of the study. It seems, therefore, that edge effects upon microhabitat conditions are likely to be the primary force driving soil-feeder population declines in forest fragments ahead of area and isolation effects.

## Wood and leaf-litter feeders

The influx of super-abundant generalist species from matrix habitat surrounding forest fragments is thought to be the most common explanation for observed positive effects of fragmentation on insect relative abundance and species richness (Didham 1997). However, elimination of the influence of ghost forest species from analyses of terrestrial transects in the present study indicated that this was not the case.

Relative encounters of termites occurring in dead wood were biased towards encounters in small wood items due to the greater overall sampling effort (per unit volume of wood) directed at small wood using the standardised transect method. It was not surprising, therefore, that the very strong negative correlation between $\log_{10}$ (distance to fragment edge) and frequency of small wood was matched by an equally strong correlation between $\log_{10}$ (distance to fragment edge) and $\log_{10}$ (relative encounters) of wood and leaf-litter feeders. However, the result for wood- and leaf litter-feeder encounters was not necessarily an artefact of sampling bias. As discussed above, the increased volume and frequency of standing dead wood accompanying increased frequency of small wood items close to forest edges on small islands are likely to represent real evidence of biomass collapse in forest fragments.

Nevertheless, if tree die-off and wind exposure were the only reasons for the positive response of wood- and leaf litter-feeder termite encounters and species richness, a similar response would have been expected at the BDFFP rather than the negative one observed. The profound difference in matrix habitat surrounding islands at St. Eugène and forest fragments at BDFFP may partly explain the different patterns observed at these sites. Land-bridge islands, such as at St. Eugène, and at Lago Guri in Venezuela, are found to undergo gross ecological distortions, soon after island formation, that may be more accentuated than those which occur in forest fragments embedded in a mainland habitat matrix (Terborgh et al. 1997). Specifically, studies focused mainly on vertebrates indicate that predators are differentially prone to extinction on land-bridge islands compared with herbivores, leading to dramatic increases in herbivore abundance. The possibility of similar higher order interactions affecting insect herbivores or decomposers at fragmentation sites has remained largely unstudied. Some indirect support is indicated by the findings of studies on leaf-cutter ants from sites with contrasting matrix habitats (Terborgh et al. 1997; Vasconcelos 1988).

Numerous species of tropical vertebrates and invertebrates are known to include termites in their diet, however, by far the most important predators of termites are ants (Hölldobler and Wilson 1990). Evidence for a negative effect of tropical forest fragmentation upon species richness and abundance of the ant assemblage has been reported from the BDFFP (Carvalho and Vasconcelos 1999; Gascon et al. 1999). Moreover, at the same site, army ants have been observed to suffer stochastic extinctions from smaller (1 and 10 ha) fragments (Harper 1989; Lovejoy et al. 1986). By contrast, both major species of army ant found at Lago Guri were absent from small- and medium-sized forest islands 7 years after inundation (Terborgh et al. 1997), and we might expect species loss of predatory ants in general to be more rapid on land-bridge islands than at BDFFP forest fragments.

Overall, the positive effects of forest fragmentation on wood- and leaf litter-feeder encounters and species richness are in stark contrast to the rapid decline of vertebrate diversity observed at St. Eugène over the same time period (Cosson et al. 1999). This contrast immediately suggests a trophic distortion of sorts, namely the relative increase in abundance and diversity of the most important tropical decomposer arthropod group. The implications for changes in ecosystem functions and carbon cycling within tropical forest fragments are noteworthy.

## Implications for ecosystem function, biomass collapse, and carbon cycling

Biomass collapse as a result of tree die-off in forest fragments constitutes a significant additional carbon loss to the atmosphere that was not previously accounted for in studies of the contribution of tropical forest clearance to greenhouse gas production (Pimm 1998). Differences in the rates of tree die-off and subsequent wood decomposition between fragments embedded in a mainland matrix habitat and land-bridge islands surrounded by water, have yet to be measured. In fact, no studies have yet been carried out on differences in rates of decomposition of large woody litter for tropical forests subject to contrasting land uses (Chambers et al. 2000). Such studies are needed, given the importance of ecosystem responses to land use in determining net fluxes of carbon to the atmosphere (Houghton 1994; Kaufmann et al. 1995; Trumbore et al. 1995).

Termites are likely to be key mediators of carbon cycling within tropical forest fragments. An increased rate of tree die-off immediately following forest fragmentation is likely to result in a pulse of nutrients being passed down the decomposer humification gradient. On land-bridge islands at least, this appears to result in an accompanying ripple of increased wood- and leaf litter-feeder abundance, which may be of relatively short duration. Ultimately, once the pulse of dead plant biomass has been broken down or if effects of area, isolation, or microclimatic edge become dominant, we would expect biomass and species richness of termites and other decomposers to decline.

Clarification of the functional significance of the observed patterns will be assisted by further studies on termite- and fungus-mediated decomposition processes in relation to forest fragmentation. The negative influence of forest fragmentation on soil-feeding termites in particular, is likely to have consequences for the soil fertility of remnant fragments, and hence for the maintenance of nutrient cycling links to above-ground food webs.

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## Appendix 1

Complete list of 100 termite species/morphospecies found in 15 standardised diversity transects across three mainland, ten island, and two ghost forest sites at the St. Eugène study site in French Guiana. W Wood feeder, L leaf-litter feeder, S soil feeder

1. Species found in ghost forest as well as terrestrial transects
2. Species found in ghost forest only

| Taxon | Feeding group |
|---|---|
| **KALOTERMITIDAE** | |
| *Glyptotermes* sp. A nr. *guianensis* | W |
| *Rugitermes* sp. A | W |
| Indet. Kalotermitidae sp. A | W |
| Indet. Kalotermitidae sp. B | W |
| Rhinotermitidae | |
| *Acorhinotermes subfusciceps* (Emerson) | W |
| *Coptotermes testaceus* (L.)[1] | W |
| *Dolichorhinotermes longilabius* (Emerson) | W |
| *Heterotermes tenuis* (Hagen) | W |
| *Rhinotermes marginalis* (L.)[1] | W |
| **TERMITINAE** | |
| **Termitinae** | |
| **Amitermes-group** | |
| *Cylindrotermes parvignathus* Emerson | W |
| *Microcerotermes* sp. A | W |
| **Orthognathotermes-group** | |
| *Dentispicotermes brevicarinatus* (Emerson) | S |
| *Orthognathotermes* sp. A | S |
| **Termes-group** | |
| *Cavitermes tuberosus* Emerson | S |
| *Cornicapritermes mucronatus* Emerson | S |
| *Crepititermes verruculosus* Emerson | S |
| *Dihoplotermes* sp. A nr. *inusitatus* Araujo | S |
| *Inquilinitermes* sp. A nr. *inquilinus*[1] | S |
| *Neocapritermes angusticeps* (Emerson) | S |
| *Neocapritermes araguaia* Krishna & Araujo | S |
| *Neocapritermes longinotus* (Snyder) | S |
| *Neocapritermes pumilis* Constantino | S |
| *Neocapritermes talpa* (Holmgren) | S |
| *Neocapritermes taracua* Krishna & Araujo | S |
| *Neocapritermes* sp. A | S |
| *Planicapritermes planiceps* Emerson | S |
| *Termes fatalis* Linneaus | S |
| *Termes*-grp. sp. nov. A | S |
| *Spinitermes trispinosus* (Hagen & Bates) | S |
| **Apicotermitinae** | |
| **Anoplotermes-group** | |
| *Anoplotermes banksi* Emerson | S |
| *Anoplotermes parvus* Snyder | S |
| *Anoplotermes*-grp. sp. A | S |
| *Anoplotermes*-grp. sp. B | S |
| *Anoplotermes*-grp. sp. C | S |
| *Anoplotermes*-grp. sp. D | S |
| *Anoplotermes*-grp. sp. E | S |
| *Anoplotermes*-grp. sp. G | S |
| *Anoplotermes*-grp. sp. H | S |
| *Anoplotermes*-grp. sp. I | S |
| *Anoplotermes*-grp. sp. J | S |
| *Anoplotermes*-grp. sp. K | S |
| *Anoplotermes*-grp. sp. N | S |
| *Anoplotermes*-grp. sp. O | S |
| *Anoplotermes*-grp. sp. P | S |
| *Anoplotermes*-grp. sp. R | S |
| *Anoplotermes*-grp. sp. S | S |
| *Anoplotermes*-grp. sp. T | S |
| *Anoplotermes*-grp. sp. V | S |
| *Anoplotermes*-grp. sp. W | S |
| *Anoplotermes*-grp. sp. X | S |
| *Anoplotermes*-grp. sp. Y | S |
| *Anoplotermes*-grp. sp. Z | S |
| *Anoplotermes*-grp. sp. AB | S |
| *Anoplotermes*-grp. sp. AC | S |
| *Anoplotermes*-grp. sp. AD | S |
| *Anoplotermes*-grp. sp. AH | S |
| *Anoplotermes*-grp. sp. AL | S |
| *Anoplotermes*-grp. sp. AM | S |
| *Anoplotermes*-grp. sp. AN | S |
| *Anoplotermes*-grp. sp. AO | S |
| *Anoplotermes*-grp. sp. AQ | S |
| *Ruptitermes* sp. A | S |
| *Ruptitermes* sp. B | S |
| **Nasutitermitinae** | |
| **Armitermes-group** | |
| *Armitermes holmgreni* Snyder | S |
| *Armitermes minutus* Emerson | S |
| *Armitermes teevani* Emerson | S |
| *Cyrilliotermes angulariceps* Mathews | S |
| *Embiratermes brevinasus* (Emerson & Banks) | S |
| *Embiratermes neotenicus* (Holmgren) | S |
| *Embiratermes robustus* Constantino | S |
| *Embiratermes* sp. A | S |
| *Embiratermes* sp. C nr. *parvirostris* | S |
| **Cornitermes-group** | |
| *Cornitermes pugnax* Emerson | W |
| *Cornitermes weberi* Emerson | W |
| *Cornitermes* sp. A nr. *cumulans* | W |
| *Syntermes spinosus* (Latrielle) | L |
| *Syntermes* sp. A nr. *longiceps* | L |
| **Nasutitermes-group** | |
| *Angularitermes*?*nasutissimus* (Silvestri) | S |
| *Araujotermes parvellus* (Silvestri) | S |
| *Atlantitermes oculatissimus* (Emerson) | S |
| *Atlantitermes snyderi* (Emerson) | S |
| *Atlantitermes* sp. B nr. *guarinim* | S |
| ?*Atlantitermes* sp. C nr. *kirbyi* | S |
| *Coatitermes kartaboensis* (Emerson) | S |
| *Caetetermes taquarussu* Fontes | S |
| *Convexitermes manni* (Emerson) | S |
| *Cyranotermes caete* Cancello | S |
| *Nasutitermes banksi* Emerson | W |
| *Nasutitermes costalis* Holmgren[2] | W |
| *Nasutitermes gaigei* (Emerson) | W |
| *Nasutitermes guayanae* (Holmgren) | W |
| *Nasutitermes nigriceps* (Haldeman)[1] | W |
| *Nasutitermes octopilus* Banks | W |
| *Nasutitermes similis* Emerson | W |
| *Nasutitermes surinamensis* (Holmgren) | W |
| *Nasutitermes* sp. D | W |
| *Nasutitermes* sp. J | W |
| *Velocitermes beebei* Emerson | L |
| *Subulitermes baileyi* (Emerson) | S |
| *Subulitermes constricticeps* Constantino | S |

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