Journal of Tropical Ecology (2003) **19**:509–524. Copyright © 2003 Cambridge University Press
DOI:10.1017/S0266467403003560 Printed in the United Kingdom

Environmental and spatial influences upon species composition of a termite assemblage across neotropical forest islands

Richard G. Davies*†[1], Luis M. Hernández*, Paul Eggleton*, Raphael K. Didham‡, Laura L. Fagan¶ and Neville N. Winchester¶

*Termite Research Group, Department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK
†Department of Biology, University College London, Wolfson House, 4 Stephenson Way, London NW1 2HE, UK
‡Zoology Department, University of Canterbury, Private Bag 4800, Christchurch, New Zealand
¶Department of Biology, University of Victoria, Victoria, British Columbia, Canada
(*Accepted 19th September 2002*)

Abstract: Patterns of species composition in a neotropical termite assemblage were studied in relation to early effects of forest fragmentation as well as other sources of environmental and spatial heterogeneity. Termite diversity surveys were carried out at three mainland forest sites, and 10 islands of varying size, in an area of lowland tropical forest that had been flooded 4 y earlier, during the creation of the Petit Saut hydroelectric project in French Guiana. The 'ghost forest' of dead emergent trees in the flooded zone was also studied for its influence on island termite assemblages. Results suggested that the effects of forest fragmentation upon the total assemblage, and upon soil-feeders in particular, were subordinate to the influence of forest understorey palm density, and the closely associated gradients of soil humus depth and soil pH. Moreover, gradients for these three variables were uncorrelated with forest fragmentation and probably reflected spatial environmental heterogeneity pre-dating inundation events. Nevertheless, factors associated with forest fragmentation appeared to have had a significant effect on changes in termite species composition across the study site, primarily in structuring the wood- and leaf-litter-feeder assemblage. Effects upon the latter were not apparently a result of influx of species from the ghost forest. Purely spatial variation also influenced β-diversity changes in species composition across the site. In conclusion, the effects of forest fragmentation upon termites appear to have been relatively mild compared with other faunal groups, 4 y after flooding. Nevertheless, we predict that the effects of fragmentation on termite assemblages will ultimately be negative. This study also points to the importance of Amazonian understorey palms in structuring a tropical forest termite assemblage.

Key Words: diversity, French Guiana, palms, similarity, spatial autocorrelation, tropical forest fragmentation

INTRODUCTION

Tropical forest fragmentation is one of the major causes of loss of tropical forest biodiversity (Didham *et al*. 1996, Laurance & Bierregaard 1997, Turner 1996). Understanding of this process has expanded from the fragment area and isolation emphasis of island biogeography theory (MacArthur & Wilson 1967) to a greater appreciation of the complex interplay between many factors including edge effects and the influence of the surrounding matrix habitat (Bierregaard *et al*. 1992, Debinski & Holt 2000, Saunders *et al*. 1991).

Much of our present knowledge concerning the effects of tropical forest fragmentation upon biodiversity has come from the Biological Dynamics of Forest Fragments Project (BDFFP) in Brazil, north of Manaus (Cosson *et al*. 1999, Debinski & Holt 2000, Turner 1996). However, the BDFFP findings are by no means universally applicable (Cosson *et al*. 1999). In addition, most tropical forest fragmentation research has focused on vertebrate groups – birds in particular (Turner 1996).

Few tropical fragmentation studies test for environmental correlates of species composition other than the most well known (e.g. area, edge distance and measures of moisture and humidity gradients). In particular, purely spatial turnover in species composition across sites, as well as environmental variables indicative of spatial habitat heterogeneity predating fragmentation events, are frequently neglected. Inclusion of these factors in investigations gives a fuller picture of the relative influence of fragmentation vs. other spatial or environmental gradients, especially in studies of the early effects of fragmentation where a changeover of environmental influences may be underway. Moreover, purely spatial or environmental gradients may be confounded with fragmentation gradients, in which case their effects need to be factored out.

[1] Corresponding author. Email: R.G.Davies@sheffield.ac.uk

https://doi.org/10.1017/S0266467403003560 Published online by Cambridge University Press

This is a study of species-level patterns of termite diversity across real forest islands created by the flooding of an area of Amazonian lowland evergreen rain forest in French Guiana. The relative influence of forest fragmentation, spatial environmental heterogeneity, and purely spatial variation upon species composition of the termite assemblage was investigated 4 y after the original inundation events. The termite assemblage predominating in the flooded matrix habitat surrounding forest islands was also studied in order to determine its likely origins, and its possible influence upon island assemblages.

METHODS

Study site

The St Eugène Fragmentation Project (SEFP) (4°59′N, 53°08′W) is a system of forested islands located in the Petit Saut hydroelectric reservoir in French Guiana. The SEFP is situated in a flooded area that used to be continuous lowland evergreen rain forest either side of the Coursibo river. Islands range from < 1 ha up to *c*. 80 ha (Figure 1). Flooding took place between January 1994 and June 1995, although most islands were isolated by August 1994 (see Cosson *et al*. 1999, de Granville 1996, Granjon *et al*. 1996, Ringuet *et al*. 1998). Since inundation, the forest surrounding the 365-km^2 reservoir has been protected by law.

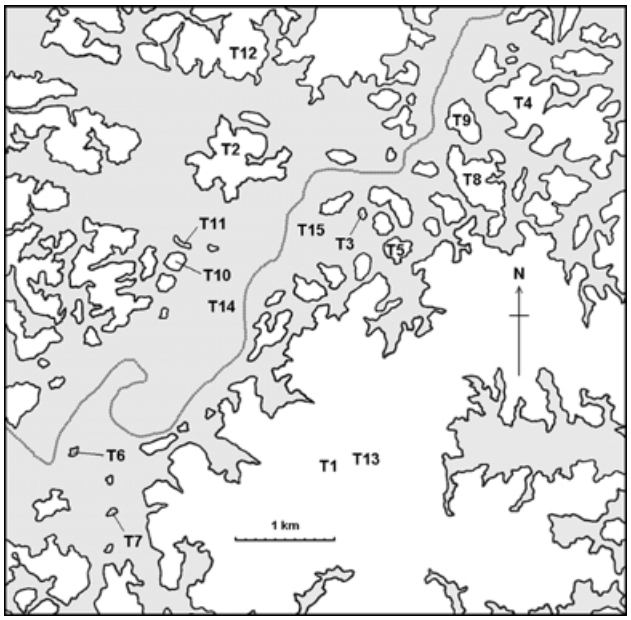

Figure 1. Map of the St Eugène Fragmentation Project (SEFP) research site, Petit Saut hydroelectric reservoir, French Guiana, showing the locations of each of the standardized termite diversity transects: terrestrial, T1–T13; and ghost forest, T14–15. Mainland and islands are shown as white areas while shading represents the inundated zone. The wavy dotted line indicates the original course of the Coursibo river before flooding.

The SEFP site is typical of inundated tropical forest sites where the forest was not cleared prior to inundation. The resulting 'ghost forest' in the inundated zone consists of a tangle of dead branches, tree-trunks, crowns and palm stems, much of which still projects above water level. This forest has numerous bromeliads and other epiphytes, as well as many arboreal termite nests, attached to the dead trees. Smaller plants, fungi and invertebrates (including termites) also live on or within rotting wood in the ghost forest. Species persisting within the ghost forest may influence communities inside forest fragments.

Seasonal fluctuations in the water level of the Petit Saut dam result in the exposure, during low-water periods, of a band of shoreline up to tens of metres wide at the perimeter of each island fragment or mainland site. In addition to standing dead trees, this shoreline contains fallen tree and palm trunks, as well as other woody debris, constituting a seasonally available resource for termites. When not actually submerged, the soils of the littoral zone are unprotected from extremes of climate, including the direct impact of sunshine and rainfall.

Another feature of the St Eugène study site is that forest island centres are invariably ridge crests or summits. Therefore mainland sites were selected to span, or be close to, ridge crests. This constraint may not apply in other types of fragmentation site. St Eugène is a legally protected area, and so human effects are minimized. At the BDFFP site in Brazil, fragments within areas subject to human-induced fire-disturbance have more open edges compared with fragments in areas not subject to regular burning (Didham & Lawton 1999). In contrast, Cosson *et al*. (1999) reported that islands at St Eugène became girdled by a dense band of undergrowth vegetation by 1997 (*c*. 3 y after inundation) and that this may buffer island interiors from the harsh climate of the adjacent ghost forest. The absence of fire at St Eugène probably explains these sealed edges.

Data collection

Termite diversity was measured at three mainland sites and 10 island sites. Forest islands were selected randomly using satellite imagery (IRD) data and ground-truthing (see Figure 1, Table 1). 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). Both dry- and wet-season sampling covered the full range of fragment sizes.

Termite relative encounter and species richness sampling Termite species richness and numbers of encounters per spe-

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Table 1. Description of St Eugène 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)	Date sampled	Season sampled
T1	Mainland	1000.00	740	April 1998	Wet
T2	Island 2	38.31	87	April 1998	Wet
T3	Island 22	0.72	19.5	April 1998	Wet
T4	Island 3	80.00	111.5	April 1998	Wet
T5	Island 16	3.89	75.5	April 1998	Wet
T6	Island 40	0.20	10.9	April 1998	Wet
T7	Island 27	0.70	14.5	May 1998	Wet
T8	Island 103	25.50	170	May 1998	Wet
T9	Island 14	7.22	70	May 1998	Wet
T10	Island 24	1.67	40	Nov 1998	Dry
T11	Island 23	0.35	7.5	Nov 1998	Dry
T12	Mainland	1000.00	176.5	Dec 1998	Dry
T13	Mainland	1000.00	800	Dec 1998	Dry
T14	Ghost forest	–	–	Dec 1998	Dry
T15	Ghost forest	–	–	Dec 1998	Dry

cies (a surrogate for relative abundance) were sampled using the standardized transect method described in Jones & Eggleton (2000). A single transect of fixed area (200 m^2) was used at each of the 13 sites (T1–T13, Table 1). Forest-island transects were positioned at or near the centre of each island. Mainland transects were randomly positioned within a pre-selected area of several hectares (see above). Each transect measured 100 m × 2 m and was subdivided into 20 contiguous sections each of 2 m × 5 m. One hour of sampling effort was spent in each section, giving a total of 20 h sampling effort for each transect. All microhabitats in which termites occur were searched including: tree trunks up to a height of 2 m; stumps, logs and twigs, termite mounds; and soil beneath logs, fallen branches, surface rocks, and at the base of tree buttresses. Soil microhabitats were sampled by searching, in turn, the contents of 12 small soil pits in each section (each approximately 12 cm × 12 cm wide by 10 cm deep, spaced apart so as to sample all parts of the section).

Minor adjustments to the standardized transect method allowed more accurate approximation of termite relative abundance. Specifically, each encounter with a population of termites was recorded. An encounter refers to all the termites found simultaneously at one point of excavation, either in wood or soil etc., and includes all species collected from that point. All termite encounters were recorded, even if two or more of these in the same section were of the same species. If woody items more than 1 m in length were present within the boundaries of the 5-m × 2-m section, then further positions along the length of the wood (one for each additional 1 m length) were excavated for termites. Again, each encounter (i.e. from each point along the timber) was recorded separately.

In order to assess the influence of the ghost forest assemblage on remnant forest islands, termites were sampled during the dry season along two ghost-forest transects of the same dimensions as terrestrial transects. With the aid of a boat, each transect was marked out with a 100-m length of string secured in a straight line through a randomly selected area. All trunks, branches and epiphytes within 1 m either side of the string, and from water level up to 2 m above, were investigated for termites. All termites found in or on a continuous above-water section of trunk/branch, were considered to be from the same encounter. Relative encounters within ghost forest and terrestrial forests were, therefore, not comparable and were not treated as such in the analyses. There was no time limit to sampling along the ghost forest transects as each took much less time to complete than a terrestrial transect.

Termites were sorted to morphospecies and named, where possible, after comparison with the collections at the Natural History Museum, London, and descriptions in the available literature (Araujo 1961, 1977*a*, *b*; Constantino 1990, 1991*a*, *b*, 1992*a*, 1995; Constantino & De Souza 1997, Emerson 1925, 1935; Emerson & Banks 1957, Fontes 1979, 1981, 1985; Fontes & Bandeira 1979, Krishna 1961, 1968; Krishna & Araujo 1968, Mathews 1977, Mill 1983). Species/morphospecies diagnosis of members of the taxonomically problematic soil-feeding Apicotermitinae was carried out through dissection and inspection of the guts of worker termites, with special attention paid to the enteric valve.

Total encounters for each termite species in each given transect were a surrogate for relative abundance. These estimates were unrelated to, and independent of, the sectional division of transects. Division of transects into 20 sections simply facilitated consistency of sampling effort along the 100-m length of the transect. Effectively, therefore, total transect termite data were the result 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

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including small wood items in proportion to their occurrence along the transect.

Environmental variables The following environmental variables were measured during the dry season only (October to December 1998).

Fragmentation variables. Estimates of island area were obtained from satellite imagery. The distance of each transect to the nearest forest edge bordering flooded shoreline was calculated as the mean of the shortest distance from the edge to both the nearest and furthest part of the transect line. For statistical analyses, these variables were converted to $\log_{10}$ (fragment area + 1) (LGAREA) and $\log_{10}$ (distance to fragment edge) (LGEDGE).

Dead wood volumes. These were estimated by a combination of methods. The dead wood encountered within the boundaries of each transect was divided into three main categories: fallen large wood (m^3 m^{-2} logs with a diameter $\geq$ 10 cm) (V-LARGE); fallen small wood (m^3 m^{-2} twigs and branches with diameters $\geq$ 0.5 cm and < 10 cm) (V-SMALL); and standing dead wood (m^3 m^{-2} standing dead trunks with mean diameter of $\geq$ 10 cm; anything smaller was included with small wood, above) (V-STAND). Wood volume estimates were only made up to the same height as the termite sampling (2 m). Large wood volume was estimated by walking along a transect with a tape-measure and measuring the lengths, and diameters, of fallen logs and trunks (or portions of them) lying within the transect boundaries. These dimensions were used to calculate simple cylindrical volumes. Small wood was too abundant to be estimated by this method. Instead, we used a line-transect method, adapted from that recommended by Van Wagner (1968). Diameters of branches and twigs were measured as traversed by a randomly positioned 2-m-length straight-line transect marked out with string. Ten such transects were run, randomly positioned along the length of each 100-m transect, and perpendicular to its central axis. The diameters of small twigs and branches (diameter 0.5–10 cm) traversed by the line of the string were measured, including all those lying at ground level or suspended up to a height of 2 m. During the sampling of small wood, all large wood items were ignored. The volume of small wood per transect was estimated using the formula

$$V = (\pi^2 \times \Sigma d^2)/8L$$

where V is volume of wood per unit area, d is diameter of each piece encountered, and L is the sum of lengths of all the sampling lines. Standing dead wood volume was estimated by walking down the transect and measuring diameter at breast height (dbh) of each standing dead trunk, or diameter at maximum height for shorter trunks. Height was measured up to a maximum of 2 m above ground level. For each transect, the volume per unit area (m^3 m^{-2}) of wood within each of the three categories was calculated from the data collected, as well as the total volume (m^3 m^{-2}) summed across all categories (V-TOTAL).

Frequency of dead woody items. The frequencies of encounter with individual items of large dead wood (F-LARGE) and standing dead wood (F-STAND) were recorded for each transect. For small dead wood (F-SMALL), only the relative frequency of encounter could be estimated, by summing the numbers of small wood items measured in each transect during estimation of small wood volume.

Frequency of live stems. The number of live palms (PALMS) > 2 m tall (including leaf petioles) and the number of live trees (TREES) > 10 cm dbh were recorded within the 100-m × 2-m area of each transect.

Canopy cover. Percentage canopy cover (CANOPY) was assessed using a concave spherical densiometer (Model-C made by Robert E. Lemmon, Forest Densiometers, 5733 SE Cornell Drive, Bartlesville, OK 74006, USA). An estimate of canopy cover was made for each section of each transect. This was achieved by taking the average of four readings from the centre of the section concerned, as if from four points of an imagined compass, assuming that two of these directions were along the axis of the transect line and the other two were perpendicular to it. A mean percentage canopy cover value was then computed for each site from the 20 estimates taken along the corresponding transect.

Soil variables. Soil moisture (percentage g H_2O g^{-1} oven dry soil) was measured using a portable Lincoln (porous plate) soil moisture meter (supplied by Lincoln Irrigation Inc., P. O. Box 67274, 2324 S. 74th St., Unit #4, Lincoln NE 68506, USA) calibrated against a soil moisture content varying across a range between fully saturated and oven dried. Due to the limitations inherent in one field-worker attempting to take soil moisture readings that are directly comparable between sites, three series of 60 readings were taken on three separate occasions, and the average used to estimate soil moisture percentage (MOISTURE). Each series of 60 readings was taken sequentially along the central axis of each 100-m × 2-m transect, three readings per 2-m × 5-m section. The mean depth of the A-horizon (HUMUS) (cm), or upper-most layer of humus-rich soil (Foth 1990), was estimated for each transect using a soil sampling tube (1-inch diameter) to sample soil cores from the centre of each of the 20 transect sections. Once extracted, each soil core was inspected to assess the maximum depth of the A-horizon. This was made obvious by the sudden change in soil

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colour (from dark brown to lighter orange-red over a few mm of soil depth) at the boundary between A- and B-horizons. The mean thickness of the A-horizon across all 20 samples was calculated for each transect. After measuring A-horizon depth, the top 8-cm depth of each soil core (including A-horizon) extracted from each section, was collected in an open polythene bag prior to air-drying in a sheltered storage area at the field station. Air-dried samples were subsequently homogenized and tested for total organic carbon (C) and total nitrogen (N) (% mg g^{-1} dry weight of soil) in a local soil laboratory (IRD, Cayenne). Additionally, soil pH (PH) was measured from four small soil samples, taken from random positions along each transect (using a Piccolo Plus pH meter supplied by Hanna Instruments Inc., 584 Park East Drive, Woonsocket, RI 02895, USA).

Analyses

Similarity Similarities in species composition between the 13 terrestrial transects were estimated for all pair-wise comparisons using the Morisita–Horn index (Horn 1966) as recommended for log-transformed data by Wolda (1981). Termite relative encounters were $\log_{10}$ (x + 1)-transformed before calculating similarity indices. For each transect, the mean similarity for all comparisons with other transects was calculated.

Ordinations of species and environmental data Ordination analyses were performed using the Canoco (version 4) program (ter Braak & Šmilauer 1998). Firstly, principal components analysis (PCA) was used to investigate species-composition relationships between sites, without including environmental data. Redundancy analysis (RDA) was then used to investigate species–environment relationships (Verdonschot & ter Braak 1994). In both types of analysis, the seasonal effects upon species composition were partialled out by entering season as a nominal covariable with two categories (wet and dry), hence partial PCA and partial RDA. Again, termite relative encounter data were $\log_{10}$ (x + 1)-transformed prior to analyses.

For the partial RDA, forward selection was used to rank environmental variables in order of their importance in determining assemblage composition. Marginal eigenvalues were computed for each environmental variable, and significance at each stage (i.e. for each variable selected) was tested using a Monte Carlo permutation test with 999 random permutations.

Feeding-group analyses of the same dataset (Davies 2002) indicated different effects of forest fragmentation upon wood- and leaf-litter-feeding termites compared with soil-feeders. These two groups of species were therefore additionally analysed in separate RDAs. For all RDAs, the influence of ghost-forest species upon forward selection results was estimated by excluding those species from the analyses.

Ordinations to assess spatial autocorrelation

The spatial component of variation in species relative encounter data across sites was assessed following Borcard *et al*. (1992). This method included the use of the environmental data matrix, as well as a matrix of positional coordinates (x, y) and all additional terms for a cubic trend surface regression (x^2, xy, y^2, x^3, x^2y, xy^2, y^3) (see Legendre 1990) for each of the 13 sites, in a series of RDA analyses performed in order to estimate the decomposition of total variation into four components: non-spatial environmental variation; spatially structured environmental variation; spatial species variation not shared by the environmental variables; and unexplained variation and stochastic fluctuations (see Appendix 1 for a detailed description of methods as applied to the present dataset). As part of the series of RDA analyses, an RDA of species and spatial matrices was performed in order to determine which spatial terms showed marginal significance.

RESULTS

Termite assemblage compositional differences between sites

Standardized transect sampling across 13 terrestrial and two ghost-forest transects yielded a total of 100 termite species/morphospecies (see Appendix 2). Previously recorded total termite species richness in single neotropical rain-forest locations has ranged between 25 and 78 (Bandeira & Macambira 1988, Bandeira & Torres 1985, Constantino 1992*b*, De Souza & Brown 1994, Emerson 1925, Mill 1982*a*, *b*). The larger total recorded in the present study is likely to be due to the greater sampling effort inherent in the standardized transect method used, its demand for random sampling of forest soil, and the greater resolution (through worker gut dissection) of morphospecies separations for the Apicotermitinae. Of these 100 species, 27 were wood- (and leaf-litter-) feeders, while the remaining 73 were soil-feeders. Alternatively, using the feeding-group classification key in Donovan *et al*. (2001), which places termite species along a humification gradient reflecting the level of decomposition of their food substrates, there were nine group I wood-feeders (least humified substrate), 18 group II wood- and/or leaf-litter-feeders, 60 group III soil-feeders, and 13 group IV soil-feeders (most humified substrate). Ninety-nine of the total 100 species were found in terrestrial transect samples, while only six species occurred in the ghost-forest transects. Species richness of terrestrial transects ranged between 38 and 51, while the two ghost-forest

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transects yielded four species each. Five species from the ghost-forest transects were wood-feeders (two from group I and three from group II), while *Inquilinitermes* sp. A nr. *inquilinus* (a group III soil-feeder) was probably feeding on highly decomposed wood/humus within the dead trunks. None of these species were abundant in terrestrial samples (*c.* 1.0% of total transect encounters). Nevertheless, the single ghost-forest transect species not found on any terrestrial transects, *Nasutitermes costalis* Holmgren, was collected in a casual sample from high in the canopy of mainland forest. The ghost forest, therefore, yielded a subset of the species in mainland and island terrestrial forest sites, albeit a subset that was not abundant at ground or understorey levels.

Similarity

When transects were grouped into four categories (mainland, large islands, medium islands and small islands) average Morisita–Horn similarity indices for pair-wise transect-sample comparisons, both within and between categories, showed clear patterns (Figure 2). Most notably, mean similarity for small-island/small-island comparisons, as well as comparisons between small islands and all other transect samples, were markedly lower than corresponding within- and between-category comparisons for the three larger fragment-size categories. Mainland and medium-sized islands shared the maximum mean similarities, in both cases for within-category comparisons.

Ordinations of species and environmental variable data

For the partial RDA of all species data constrained by the environmental variables (see Appendix 3 for raw values), greatest marginal significance was shown by density followed by soil pH, soil humus depth, $\log_{10}$ (distance to forest edge), frequency of small wood, $\log_{10}$ (fragment area), and frequency of large wood (Table 2). Forward selection results showed that after fitting palm density, $\log_{10}$ (distance to forest edge), followed by frequency of small wood, explained significant remaining variation in the data. A second partial RDA, which included only significant marginal environmental variables, showed that eigenvalues for the first two axes (0.14, 0.13) were not markedly lower than for the partial PCA (0.18, 0.13), and that both species–environment correlations were high (0.973, 0.993). The measured environmental variables, therefore, explained the major variation in species composition across sites.

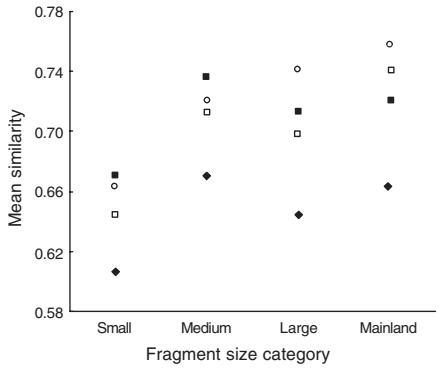

Figure 2. Plot of mean Morisita–Horn similarity for pair-wise transect comparisons within and between fragment categories: ◆, small islands (< 1 ha); ■, medium islands (1–10 ha); □, large islands (10–100 ha); ○, mainland sites (1000 ha).

The environmental arrows in the ordination space for axes 1 and 2 of the partial RDA (Figure 3) account for 46.5% of the variance in the weighted averages of termite species with respect to the marginally significant environmental variables. The intraset correlation coefficients for marginally significant environmental variables (Table 3) showed that the first axis represented variation in positively intercorrelated palm density and soil humus depth. Soil pH was also most closely associated with the first axis and was strongly negatively correlated with palm density. The second axis represented change in $\log_{10}$ (distance to forest edge) which was negatively correlated with frequency of small wood. Frequency of small wood was, however, somewhat weakly correlated with axis 2, being also negatively correlated with soil humus depth.

Greater density of palms and soil humus depth were associated with the species compositions of one mainland transect (T12), two large-island transects (T8 and T2) and two medium sized-island transects (T9 and T5), whereas low palm density and soil humus depth were associated with the species composition of two mainland transects (T1 and T13), one large-island transect (T4), and one small-island transect (T6). Log_{10} (distance to forest edge), as represented by the second axis, was still shown to have a significant effect on species composition, with the result that the two mainland transects furthest from the forest edge (T1 and T13) showed greatest compositional differences with the four smallest islands (T3, T7, T6 and T11).

The partial RDA for soil-feeders was almost identical to that for the complete assemblage, because the latter was numerically dominated by soil-feeding species. Hence, only the resulting RDA bi-plot is presented (Figure 4) but not the accompanying statistical details. There was a noticeable taxonomic trend in the axis 1 scores for species arrows, namely that the 34 Apicotermitinae species (see also Appendix 2) showed a pattern of higher axis 1 scores compared with the 38 remaining soil-feeder species not belonging to this subfamily. This taxonomic difference was statistically significant (ANOVA: $n = 72$, $F = 7.61$, $df = 1$, $P < 0.01$) whereas there was no significant difference for a similar test of axis 2 scores (ANOVA: $n = 72$, $F = 0.42$, $df = 1$, $P = 0.52$). Although strictly a *post hoc* comparison, this result suggests a difference in the ecolo-

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Table 2. Results of partial RDA forward selection procedure, showing environmental variables explaining significant variance in termite species composition across 13 transect sites. All species were included except those also found in the ghost forest. 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. Abbreviations for environmental variables are explained in Appendix 3.

Marginal effects			Conditional effects			
Variable	λ_1	P	Variable	λ_2	P	$\Sigma\lambda_2$
PALMS	0.13	0.006	PALMS	0.13	0.006	0.13
PH	0.13	0.010	LGEDGE	0.12	0.005	0.25
HUMUS	0.12	0.009	F-SMALL	0.11	0.035	0.36
LGEDGE	0.12	0.014				
F-SMALL	0.12	0.035				
F-LARGE	0.12	0.045				

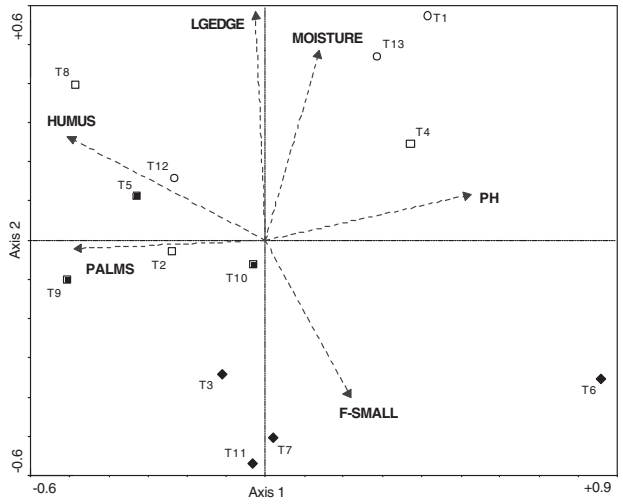

Figure 3. Ordination bi-plot for partial RDA of complete species data and environmental variables, with season (wet and dry) entered as nominal categorical covariables. Centroids (weighted averages) for transects are coded as: ◆, small islands (< 1 ha); ■, medium islands (1–10 ha); □, large islands (10–100 ha); and ○, mainland (1000 ha). Abbreviations for environmental variables (thick dashed arrows) are as follows: LGEDGE, $\log_{10}$ (distance to fragment edge); MOISTURE, mean percentage soil moisture; PALMS, number of live palms of 2 m height or more; F-SMALL, number of items of small fallen wood (relative count from samples); HUMUS, mean depth of the soil A-horizon; and PH, soil pH (see also Appendix 3 for environmental raw data). The two axes represent linear combinations of environmental variables. Each environmental arrow (vector) points in the direction of increase in magnitude for the given variable. Any pair of environmental variables are positively correlated in their relationship with species-assemblage data across sites if their arrows point in the same direction, negatively correlated if they point in opposite directions, and uncorrelated if they are at 90° to each other.

Table 3. Termite species composition data for Figure 3: intraset correlation coefficients of marginally significant environmental variables with the first four axes of the partial RDA. Abbreviations for environmental variables are explained in Appendix 3.

	Axis 1	Axis 2	Axis 3	Axis 4
LGEDGE	–0.039	0.955	0.106	–0.085
F-SMALL	0.332	–0.666	–0.574	–0.087
PALMS	–0.886	–0.043	–0.284	–0.136
MOISTURE	0.208	0.790	–0.483	–0.044
HUMUS	–0.762	0.435	–0.099	0.290
PH	0.793	0.193	0.427	–0.157

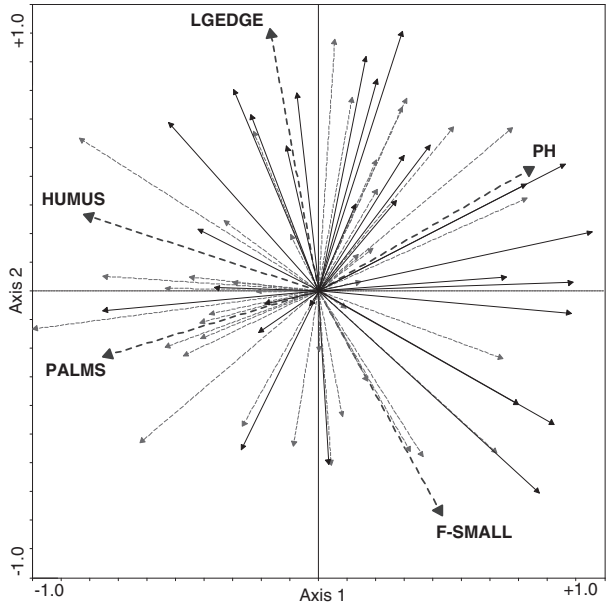

Figure 4. Ordination bi-plot for partial RDA of soil-feeder-species data and environmental variables, with season (wet and dry) entered as nominal categorical covariables. For clarity, centroids for transects have been omitted. Taxonomic affiliation of species arrows is coded as follows: solid arrows = Apicotermitinae species; dashed arrows = non-Apicotermitinae species (i.e. Termitinae, Nasutitermitinae, see Appendix 2). Abbreviations for environmental variables (thick dashed arrows) are as for Figure 3.

gical responses of Apicotermitinae and non-Apicotermitinae sub-assemblages. The positions of environmental arrows in the ordination space of axes 1 and 2 indicates that the Apicotermitinae were generally more strongly associated with sites having relatively low palm densities and soil A-horizon depth, and relatively higher soil pH, while non-Apicotermitinae were associated with

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Table 4. Results of partial RDA forward selection procedure, showing environmental variables explaining significant variation in species composition of wood- and leaf-litter-feeding termites across 13 transect sites. 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. Abbreviations for environmental variables are explained in Appendix 3.

Marginal effects			Conditional effects			
Variable	λ_1	P	Variable	λ_2	P	$\Sigma\lambda_2$
V-STAND	0.16	0.013	V-STAND	0.16	0.013	0.16
MOISTURE	0.14	0.005	PH	0.11	0.028	0.27
PH	0.12	0.024				

the opposite conditions. The lack of significance of axis-2 scores suggests that this taxonomic difference did not extend to the forest-fragmentation gradient (LGEDGE).

In contrast, the partial RDA for wood- and leaf-litter-feeders showed that environmental variables associated with fragmentation had the greatest influence on species composition. Specifically, forward selection showed that volume of standing dead wood had greatest marginal significance in explaining variation in species composition, followed by soil moisture and soil pH (Table 4). Again, the eigenvalues for the partial RDA (0.16, 0.12) were not markedly lower than those for the partial PCA (0.18, 0.15), and both species–environment correlations were high (0.978, 0.972). A notable feature of the resulting bi-plot (Figure 5) (with only significant marginal variables included), was that the four smallest islands showed the greatest differences in species composition – their centroids are widely spaced across the ordination space for axes 1 and 2 (T3, T6, T7 and T11). In particular, the centroid for T6 from the smallest island, was most closely associated with those for mainland and large-island transects (T1, T13 and T4). In addition, there was a strong association between the centroids for transects (T11 and T7) from the second- and third-smallest islands, respectively, and species of *Cornitermes*. This genus is known to inhabit hard epigeal soil mounds which are likely to protect resident colonies from microclimatic harshness.

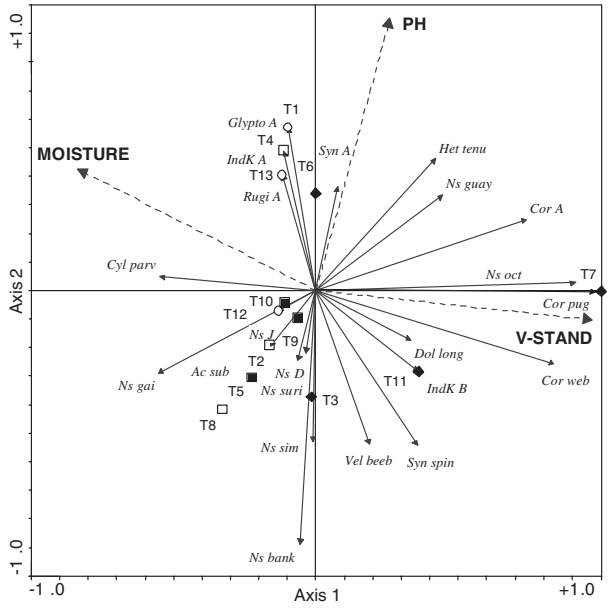

Figure 5. Ordination bi-plot for partial RDA of wood- and leaf-litter-feeder species data and environmental variables, with season (wet and dry) entered as nominal categorical covariables. Centroids for transects are coded as for Figure 3. Abbreviated species names are as follows: *Ac sub*, *Acorhinotermes subfusciceps*; *Cor A*, *Cornitermes* sp. A nr. *cumulans*; *Cor pug*, *Cornitermes pugnax*; *Cor web*, *Cornitermes weberi*; *Cyl parv*, *Cylindrotermes parvignathus*; *Dol long*, *Dolichorhinotermes longilabius*; *Glypto A*, *Glyptotermes* sp. A. nr. *guianensis*; *Het tenu*, *Heterotermes tenuis*; *IndK A*, Indeterminate Kalotermitidae sp. A; *IndK B*, Indeterminate Kalotermitidae sp. B; *Ns bank*, *Nasutitermes banksi*; *Ns gai*, *Nasutitermes gaigei*; *Ns guay*, *Nasutitermes guayanae*; *Ns oct*, *Nasutitermes octopilus*; *Ns sim*, *Nasutitermes similis*; *Ns suri*, *Nasutitermes surinamensis*; *Ns D*, *Nasutitermes* sp. D; *Ns J*, *Nasutitermes* sp. J; *Rugi A*, *Rugitermes* sp. A; *Syn spin*, *Syntermes spinosus*; *Syn A*, *Syntermes* sp. A nr. *longiceps*; *Vel beeb*, *Velocitermes beebei*. Abbreviations for environmental variables (thick dashed arrows) are: V-STAND, standing dead wood; and the remainder are as for Figure 3.

Ordinations to assess spatial autocorrelation

The forward selection procedure for the partial RDA of the complete species dataset across all 13 terrestrial sites, and the nine-term spatial matrix, indicated that three terms (x, y and xy) showed significant marginal effects upon variation in species composition (Table 5) indicating significant spatial autocorrelation in the species-composition data. With these spatial terms entered as covariables, together with season, a further partial RDA of the complete species data and measured environmental variables revealed that only soil moisture showed marginal significance in explaining the variance in species composition. Nevertheless, soil moisture is significantly positively correlated with distance to the forest edge and forest area (Davies 2002).

Partitioning of the variation in species composition revealed that 33.2% of the total variance in species composition was spatially structured, of which over a third (12.1% of total variance) was spatially structured environmental variation, the remainder (21.1% of total) being purely spatial variation. A further 51% of total variation was due to non-spatial environmental variation, leaving 15.8% as unexplained variation. Again, as soil-feeders make up the majority of species, the results of an analysis for soil-feeders were very similar to those for the overall

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Table 5. Results of partial RDA forward selection procedure, showing spatial positioning terms explaining significant variance in termite species composition across 13 transect sites. 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	$\Sigma\lambda_2$
y	0.12	0.011	y	0.12	0.011	0.12
xy	0.12	0.020				
x	0.12	0.030				

assemblage and are hence not quoted. Analysis of wood- and leaf-litter-feeders revealed that there were no spatial terms showing marginal significance. Hence, 35.2% of total variation was explained by marginally significant environmental variables (volume of standing dead wood, soil moisture and soil pH) while 64.8% remained unexplained. However, ignoring significance levels, if spatial terms x and y are included in the analyses, the decomposition of total variance becomes: 34.9% non-spatial environmental variation; 4.6% spatially structured environmental variation; 16.6% purely spatial variation; and a reduced (but still considerable) 43.9% unexplained variation.

DISCUSSION

Overview of main environmental and spatial effects upon assemblage composition

Four years after the original inundation events, the influence of forest fragmentation upon the total termite assemblage, and upon soil-feeders in particular, appeared to be subordinate to that of forest understorey palm density and closely associated gradients of soil A-horizon depth and pH. Moreover, species compositional variation associated with these three habitat variables was uncorrelated with any fragmentation gradient, and showed a significant spatial component indicating the role of spatial environmental heterogeneity as well as purely spatial species turnover. Forest fragmentation influences on species composition also appeared to be somewhat spatially confounded. However, soil moisture, which is strongly correlated with $\log_{10}$ (distance to fragment edge), explained significant variation even after controlling for spatial positioning of sites. Moreover, species composition of soil-feeders accounted for a significant component of spatial variation whereas the wood- and leaf-litter-feeder sub-assemblage appeared not to be significantly spatially structured, suggesting a real effect of fragmentation. These findings complement a feeding-group-level analysis of the same dataset showing a negative effect of fragmentation on total encounters of soil-feeders, but not species richness, and a positive effect on encounters and species richness of wood- and leaf-litter-feeders (Davies 2002).

Forest palms and the composition of termite assemblages from soil to understorey

The distribution of palms in a neotropical rain-forest community has been shown to be strongly influenced by microhabitat heterogeneity at spatial scales less than 10^3 m (Svenning 1999). In the present study, the observed spatial heterogeneity in forest palm density probably predated the inundation events that created forest islands. Indirect support for this comes from the findings of Scariot (1999) in the BDFFP site in Brazil showing that, between 10 and 15 y following habitat fragmentation, species richness of adult and juvenile palms (but not seedlings) was unaffected by fragmentation, with no evidence of differential adult mortality. Soil drainage, topography and forest architecture are all considered to be important in influencing palm distributions in Amazonian *terre firme* forests (Kahn & de Granville 1992). Although the relationship between palm density and soil pH has not been reported previously, a Costa Rican study showed that lowest palm species richness occurred on the soil type (alluvium) with highest fertility and pH (Clark *et al.* 1995).

Palms dominate the understorey plant communities of Amazonian *terre firme* forests (Kahn & de Granville 1992). The understorey of upper slopes and ridge crests at St Eugène, where termites were sampled, are dominated by the palms *Bactris oligocarpa* Barbosa Rodrigues, *Astrocaryum paramaca* Martius and *A. sciophilum* (Miquel) Pulle (de Granville 1996). The last two species accumulate canopy leaf-litter (de Granville 1977). The funnel-like form of these and many other understorey palms with large leaves, concentrates the fall of canopy leaf-litter and small woody debris in towards their stems (Kahn & de Granville 1992) and can result in conspicuous raised accumulations of litter at the base of such palms. Some canopy litter may remain suspended in the crowns of understorey palms or attached to stems, especially in species with strongly armed stems and petioles. These observations help to explain the positive correlation between palm density and soil humus depth indicated at St Eugène.

This study is not the first to suggest that presence of understorey palms may influence macroinvertebrate com-

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munities in neotropical forests. Vasconcelos (1990) reported greater litter depth, and biomass of litter per square metre of ground, in close proximity to acaulescent palm species compared to areas outside of the projection zone of the palm crown. Moreover, palm-associated litter samples showed significantly higher macroinvertebrate abundance and a greater number of macroinvertebrate groups present. With its much narrower invertebrate taxonomic focus and much greater taxonomic resolution, the present study lends further support for the likely importance of understorey palms in structuring neotropical forest macroinvertebrate communities.

The apparently greater influence of palm density, and accompanying environmental gradients, upon soil- rather than wood-feeding termites may relate to the rich humus accumulations associated with many palms (see above). The observed shift in higher taxonomic affiliation of soil-feeders with change in palm density also suggests underlying changes in levels of soil humification. The majority (10 of 13 species) of termites found to be group IV soil-feeders upon the most humified substrates were Apicotermitinae. As the other three non-Apicotermitine group IV soil-feeders were rarer and were not associated with high palm density, the patterns for Apicotermitinae suggest a possible increase in the level of humification of soil with decrease in proximity to understorey palms. Furthermore, the fact that termites actively increase their gut pH to facilitate digestion (Bignell & Eggleton 1995) points to the possible significance of the lower soil pH associated with high palm densities observed in the present study. However, this latter relationship is in need of verification through more detailed botanical studies.

Forest fragmentation effects and the influence of the ghost forest assemblage

Species composition of wood- and leaf-litter-feeders appeared to be more strongly influenced by fragmentation-associated environmental gradients than by others, even after removing any influence of ghost-forest species. However, the possible influence of populations within the seasonally exposed littoral zone surrounding forest fragments upon forest assemblages was not adequately assessed although casual sampling indicated that this zone was dominated by ghost-forest species and lacked any soil-feeders in its structureless seasonally flooded soils.

In most studies that show an increase in invertebrate abundance and diversity close to forest edges or in smaller fragments, increase in relative abundance of gap- or disturbance-adapted species and/or influx from surrounding matrix habitat have been variously invoked as explanations (Didham 1997). There was no savanna or other open, flood-free habitat within a 50-km radius of St Eugène and the ghost-forest matrix was dominated by a limited number of species that were either absent or rare at ground and understorey levels in terrestrial forest sites. The distinctiveness and low diversity of the ghost-forest termite fauna in comparison with terrestrial forest strongly echoes the contrast between naturally flooded Amazonian forest, or 'várzea', and adjacent *terra firma* forest (Constantino 1992*b*, Martius 1997, Mill 1982*a*) with the exception of the apparent lack of flood-tolerant *Anoplotermes*-group species in the present study. Nevertheless, the ghost-forest fauna is almost certainly a surviving remnant of the original living-forest canopy fauna.

Invertebrate studies from elsewhere have shown that communities encountered near ground level at forest edges showed more in common with those of forest canopies than of forest interiors (Malcolm 1997, Toda 1992). In spite of the contrary evidence posed by the distinct ghost-forest fauna, an increase in encounters of certain other terrestrial species in response to fragmentation may indicate a similar effect. One such example is *Anoplotermes parvus* Snyder, which was the only soil-feeder also found during casual sampling of epiphyte-associated humus at *c*. 25-m height in the canopy (R. G. Davies, unpubl. data).

The results of species compositional similarity comparisons resembled those of a study on beetle responses to tropical forest fragmentation at the BDFFP (Didham *et al*. 1998) where highly disturbed sites did not share a common beetle fauna. Moreover, in the present study, mean similarity among small-island transects was not only lower than that among mainland-forest transects, but was also lower than mean similarity between small-island and mainland transects. This result suggests that small islands have not been colonized by generalist disturbance-adapted species from more open habitats elsewhere.

Overall, it seems likely that forest fragmentation and isolation have resulted in a shift in species composition towards the appearance of more canopy-, treefall-, gap- and forest-edge-adapted species at ground and understorey levels on smaller islands. The fact that small islands are even less similar in species composition to each other than to larger islands and mainland sites suggests different trajectories of divergence over time and possibly different starting points with respect to the composition of the original forest. Another factor is also likely to be the greater environmental and microclimatic heterogeneity observed across smaller island sites (Davies 2002), a phenomenon that is also well documented from the BDFFP in Brazil (Camargo & Kapos 1995).

Overall conclusions

This study reveals termite diversity patterns suggesting two main conclusions: first, that the effects of forest fragmentation on species composition of termite assemblages at St Eugène are rather subtle 4 y after forest inundation; second, that understorey palms may be an important com-

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ponent of habitat heterogeneity influencing species composition of neotropical termite assemblages.

Numerous studies across the tropics have shown that termite assemblages are very sensitive to habitat disturbance in the medium- to long-term (more than *c*. 5–10 y after perturbation) (Eggleton *et al*. 1995, 1996, 1997) but that colonies of vulnerable species may persist in the short-term (under 5 y) at disturbed sites (Eggleton *et al*. 1997). A study of the effects of forest fragmentation upon termite assemblages at the BDFFP site in Brazil showed a decline in species richness of both wood- and soil-feeding termites 6 y after fragment isolation (De Souza & Brown 1994). The profound differences in matrix habitat between St Eugène and the BDFFP make comparison between the two studies difficult. Nevertheless, we predict that the longer-term outcome of forest fragmentation at St Eugène will include more marked changes in species composition and a decline in species diversity.

ACKNOWLEDGEMENTS

We thank staff of Muséum National d'Histoire Naturelle, especially Gerard Dubost, Pierre-Michel Forget, Jean-Marc Pons, Jean-Christophe de Massary, Jean-François Villiers and Jean-Claude Baloup for their administrative and/or practical support with regard to fieldwork in French Guiana. We are grateful to Renaud Boistel and Erwan Vappreau for additional field assistance. We also thank Philippe Cerdan and staff of Laboratoire d'Environnement de Petit Saut for scientific and logistic support, and Patrick Langbour of CIRAD and Alain Plenecassagne (IRD) for scientific support with wood and soil-chemistry analyses, respectively, in French Guiana. The Natural History Museum, The Royal Society and the British Ecological Society funded fieldtrips to French Guiana. Electricité de France (EDF) and Muséum National d'Histoire Naturelle, Paris, funded running costs of the St Eugène Fragmentation Project in French Guiana (Convention Muséum/EDF GP 7531).

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Appendix 1. Description of the method followed by Borcard *et al*. (1992) for partioning the variation in species abundance data into independent components.

In the RDA output of the Canoco program, the total variation in species abundance data equals 1. The fractions of total variation needed to calculate the partitioning of variation were taken as the following sums of canonical eigenvalues outputs:

A. For the partial RDA of the species data constrained by marginally significant environmental variables (with season entered as two categorical environmental covariables, wet and dry).
B. For the partial RDA of the species data constrained by the matrix of marginally significant spatial terms (for a cubic trend surface regression, see Legendre 1990) (with season entered as categorical covariables, wet and dry).
C. For the partial RDA of species data: like A, but with marginally significant spatial terms entered as covariables (with season also entered as two categorical covariables, wet and dry).
D. For the partial RDA of species data: like B, but with the marginally significant environmental variables (from A above) entered as covariables (with season also entered as two categorical covariables, wet and dry).
E. For the RDA of species data constrained by season entered as two categorical variables (wet and dry). (This RDA was performed so that the variation due to season could be subtracted from the total variation, as we were not interested in the seasonal effects.)

The total variation we were interested in partitioning was that excluding variation due to season, hence: total variation = 1 − E. The four components of variation in species data that we wanted to partition were: a = non-spatial environmental variation; b = spatially structured environmental variation; c = spatial species variation not shared by the environmental variables; and d = unexplained variation. Calculation of each of these components is as follows:

$$a = C/(1 - E);\ b = (A - C)/(1 - E);\ c = D/(1 - E);\ d = (1 - (a + b + c + E))/(1 - E)$$

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Appendix 2. List of 100 termite species/morphospecies found in 13 diversity transects across three mainland (T1, T12, T13), 10 island and two ghost-forest (T14, T15) sites at St Eugène Fragmentation Project, French Guiana. Feeding group (FG) codes: W = wood-feeder; L = leaf-litter-feeder; and S = soil-feeder. Alternative feeding group (FG2) codes according to level of humification of food substrate (Donovan *et al*. 2001): I = group I (least humified); II = group II; III = group III; and IV = group IV (most humified). Numbers refer to relative encounters per species per transect (see methods). N.B. Relative encounters from ghost-forest transects are not comparable with those from terrestrial forest.

Taxon	FG	FG2	Terrestrial forest													Ghost forest	
			T1	T2	T3	T4	T5	T6	T7	T8	T9	T10	T11	T12	T13	T14	T15
KALOTERMITIDAE																	
Glyptotermes sp. A nr. *guianensis*	W	I	2														
Rugitermes sp. A	W	I													1		
Indet. Kalotermitidae sp. A	W	I				1											
Indet. Kalotermitidae sp. B	W	I											2				
RHINOTERMITIDAE																	
Acorhinotermes subfusciceps (Emerson)	W	I		3													
Coptotermes testaceus (L.)	W	I	2			1					1		1	3	7		3
Dolichorhinotermes longilabius (Emerson)	W	I	2	6	7	3	1		7	2		2	1	2	2		
Heterotermes tenuis (Hagen)	W	I	7	10	6	21	9	32	24		15	27	10	23	8		
Rhinotermes marginalis (Linnaeus)	W	I						1			1						1
TERMITIDAE																	
Termitinae																	
Amitermes-group																	
Cylindrotermes parvignathus Emerson	W	II	28	31	31	20	35	37	14	22	17	37	32	41	44		
Microcerotermes sp. A	W	II				2							4		1	1	
Orthognathotermes-group																	
Dentispicotermes brevicarinatus (Emerson)	S	IV	2					1									
Orthognathotermes sp. A	S	IV	1						8								
Termes-group																	
Cavitermes tuberosus Emerson	S	III			1		1		1	1	1	3					
Cornicapritermes mucronatus Emerson	S	III	6			3	1		5					1			
Crepititermes verruculosus Emerson	S	III	2	6	3		3	2		1	12	4	3	4	8		
Dihoplotermes sp. A nr. *inusitatus* Araujo	S	III	3			6	5	4	3						19		
Inquilinitermes sp. A nr. *inquilinus*	S	III						3					3			1	3
Neocapritermes angusticeps (Emerson)	S	III	2	4		3		1				1		1	2		
Neocapritermes araguaia Krishna & Araujo	S	III		8	3	5	3	1		9	4	10	11	4			
Neocapritermes longinotus (Snyder)	S	III		1					1		1	2			1		
Neocapritermes pumilis Constantino	S	III	1				3				5	1	1	1	1		
Neocapritermes talpa (Holmgren)	S	III	2			3	2					1	1				
Neocapritermes taracua Krishna & Araujo	S	III						1	5		1	2					
Neocapritermes sp. A	S	III	2	1	2	1	4	3	1	1	1	1	2	3			
Planicapritermes planiceps Emerson	S	III			1	7	1		4	1	10	2		1	3		
Spinitermes trispinosus (Hagen & Bates)	S	III		1			2							3			
Termes fatalis Linneaus	S	III		2	2		2	2		1		3	6	9	8		
Termes-grp. sp. nov. A	S	III			4						8	9		2	2		
Apicotermitinae																	
Anoplotermes-group																	
Anoplotermes banksi Emerson	S	III	4	3		4					1			1	3		
Anoplotermes parvus Snyder	S	III			1		3		3	2		1	9				
Anoplotermes-grp. sp. A	S	IV										1					
Anoplotermes-grp. sp. B	S	III	8	3	7	8	7	9	2	13	15	6	2	7	14		
Anoplotermes-grp. sp. C	S	III	7	10	2	10	4	3	16	19	5	6	4	23	17		
Anoplotermes-grp. sp. D	S	III		2						3	2						
Anoplotermes-grp. sp. E	S	III	4				4	1	2	5		2		3	3		
Anoplotermes-grp. sp. G	S	III		1		3		12	1			2			8		
Anoplotermes-grp. sp. H	S	III						3	1				1				
Anoplotermes-grp. sp. I	S	III	1		2	1		2	1	3		5		3	5		
Anoplotermes-grp. sp. J	S	IV	5	2	1	5			8	7	2	7	2	4	3		
Anoplotermes-grp. sp. K	S	III	2	5	2	11	5	8	3	8	3	18	8	5	17		
Anoplotermes-grp. sp. N	S	IV				2											
Anoplotermes-grp. sp. O	S	IV	1					1							1		

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Appendix 2. *Continued.*

Taxon	FG	FG2	Terrestrial forest													Ghost forest	
			T1	T2	T3	T4	T5	T6	T7	T8	T9	T10	T11	T12	T13	T14	T15
Anoplotermes-grp. sp. P	S	IV						5	4								
Anoplotermes-grp. sp. R	S	III	4	2		2	11	4	14	14		18	7	3	19		
Anoplotermes-grp. sp. S	S	IV	13		1	7	6	2	7	13	1	3	3	1	9		
Anoplotermes-grp. sp. T	S	III	28	5	5	3	11		6	10	11		5	4	8		
Anoplotermes-grp. sp. V	S	III	10	2	1	9	3	8	2	4		6	10	6	8		
Anoplotermes-grp. sp. W	S	IV	7	6	4	4	6	9	1	18	7	7	3	21	1		
Anoplotermes-grp. sp. X	S	III	2					5							2		
Anoplotermes-grp. sp. Y	S	III	1					1	2								
Anoplotermes-grp. sp. Z	S	IV			1	3					3	2					
Anoplotermes-grp. sp. AB	S	III		2			1			1					1		
Anoplotermes-grp. sp. AC	S	IV	10			4		1		5	1	3			7		
Anoplotermes-grp. sp. AD	S	III	2			3	4	1				5	1	1	6		
Anoplotermes-grp. sp. AH	S	III						1									
Anoplotermes-grp. sp. AL	S	III						2									
Anoplotermes-grp. sp. AM	S	IV						3									
Anoplotermes-grp. sp. AN	S	III	1					2	1								
Anoplotermes-grp. sp. AO	S	III											2				
Anoplotermes-grp. sp. AQ	S	III		2													
Ruptitermes sp. A	S	III		1	1	5	2	9			4	4	1				
Ruptitermes sp. B	S	III							1								
NASUTITERMITINAE																	
Armitermes-group																	
Armitermes holmgreni Snyder	S	III		3	4	1			4		9	3	5		3		
Armitermes minutus Emerson	S	III		11	6	1	7		3	6	49	5		14	1		
Armitermes teevani Emerson	S	III											3				
Cyrilliotermes angulariceps Mathews	S	III	8	2		10	5		2	1	2	3			7		
Embiratermes brevinasus (Emerson & Banks)	S	III	1	17	3	7	2	3		1				4	1		
Embiratermes neotenicus (Holmgren)	S	III	2	1	2			1		4		2		1			
Embiratermes robustus Constantino	S	III		3	1			9	4			1					
Embiratermes sp. A	S	III	1														
Embiratermes sp. C nr. *parvirostris*	S	III	5		3		1		1	3	3	13	9	2	3		
Cornitermes-group																	
Cornitermes pugnax Emerson	W	II							14								
Cornitermes weberi Emerson	W	II							2			1	4				
Cornitermes sp. A nr. *cumulans*	W	II						1	1								
Syntermes spinosus (Latrielle)	L	II		1	6		16		7			6	1				
Syntermes sp. A nr. *longiceps*	L	II						7					1		1		
Nasutitermes-group																	
Angularitermes ?nasutissimus (Silvestri)	S	III	1									1					
Araujotermes parvellus (Silvestri)	S	III						2					3	3			
Atlantitermes snyderi (Emerson)	S	III	2	3	11	1		1		14	5	4	8	3	2		
Atlantitermes oculatissimus (Emerson)	S	III		5	2				1	1	1				1		
Atlantitermes sp. B nr. *guarinim*	S	III	8	7	4	13		1	6	9	1	10	3	5	9		
?Atlantitermes sp. C nr. *kirbyi*	S	III					1			4	1	1					
Caetetermes taquarussu Fontes	S	III	2							4							
Coatitermes kartaboensis (Emerson)	S	III	2	6	2	5	5		2	7	9	8	2	13	12		
Convexitermes manni (Emerson)	S	III			1	1					1		2				
Cyranotermes caete Cancello	S	IV							8								
Nasutitermes banksi Emerson	W	II			7		8		2	17	3	9	10	8	1		
Nasutitermes costalis Holmgren	W	II														4	1
Nasutitermes gaigei (Emerson)	W	II	2	8	1	3	8	17	1	29	4	3	5	7	3		
Nasutitermes guayanae (Holmgren)	W	II	9				1		2				4		1		
Nasutitermes nigriceps (Haldeman)	W	II			1							1				1	
Nasutitermes octopilus Banks	W	II	2	2					17		1		1	1			
Nasutitermes similis Emerson	W	II	5	12	38	6	12	6	8	9	17	30	42	23	32		
Nasutitermes surinamensis (Holmgren)	W	II			1					4							
Nasutitermes sp. D	W	II	2	1	1		1	1		3		2	16		3		
Nasutitermes sp. J	W	II												1			
Subulitermes baileyi (Emerson)	S	III			2	4		3	2			2	3	4	2		
Subulitermes constricticeps Constantino	S	III				4	1						1				
Velocitermes beebei Emerson	L	II			1		2						5				

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Appendix 3. Environmental-variable measurements from each standardized terrestrial termite diversity transect (T1–T13) at the St Eugène Fragmentation Project, French Guiana. Codes for environmental variables are as follows: LGEDGE, $\log_{10}$ (distance to fragment edge); LGAREA, $\log_{10}$ (fragment area + 1); PALMS, number of live palms (of 2-m height or more); TREES, number of live tree trunks (≥ 10 cm dbh); CANOPY, mean percentage canopy cover; MOISTURE, mean percentage soil moisture (mean percentage g H_2O g^{-1} oven dry soil); HUMUS, mean depth of soil A-horizon (cm); C, percentage total organic carbon (% mg g^{-1} dry weight of soil); N, percentage total nitrogen (% mg g^{-1} dry weight of soil); PH, soil pH (see text for further details). V-LARGE, volume of fallen large wood (m^3 m^{-2} logs with diameters of 10 cm or more); V-SMALL, volume of fallen small wood (m^3 m^{-2} items with diameters less than 10 cm); V-STAND, standing dead wood (m^3 m^{-2} standing dead trunks with mean diameter of 10 cm or more); V-TOTAL, total volume of dead wood (m^3 m^{-2} up to 2 m above ground level); F-LARGE, actual number of items of fallen large wood; F-STAND, actual number of standing dead trunks; and F-SMALL, relative number of items of small fallen wood (relative count from samples).

Transect	LGEDGE	LGAREA	PALMS	TREES	CANOPY	MOISTURE	HUMUS	C	N	PH
T1	2.87	3.00	6	13	94.8	30.1	1.8	7.13	0.46	4.3
T2	1.94	1.59	16	12	94.5	27.7	1.8	4.70	0.28	3.9
T3	1.29	0.23	11	7	95.2	24.2	1.7	6.02	0.37	3.8
T4	2.05	1.91	7	3	96.6	29.9	0.6	6.31	0.41	4.2
T5	1.88	0.69	15	10	96.4	28.8	1.8	7.87	0.48	3.8
T6	1.04	0.08	5	6	88.5	29.1	0.4	3.42	0.25	4.2
T7	1.16	0.23	8	11	96.3	21.3	1.1	6.31	0.38	4.1
T8	2.23	1.42	15	14	93.7	29.9	2.8	10.40	0.60	3.7
T9	1.85	0.91	20	9	93.9	27.5	2.5	4.46	0.24	3.9
T10	1.60	0.43	17	17	94.0	27.8	1.6	4.52	0.32	3.9
T11	0.88	0.13	19	10	81.4	25.7	1.4	8.27	0.51	3.8
T12	2.25	3.00	20	12	90.1	28.1	2.1	7.80	0.47	3.9
T13	2.90	3.00	15	5	95.1	30.0	2.0	6.94	0.44	4.1

Transect	V-LARGE	V-SMALL	V-STAND	V-TOTAL	F-LARGE	F-STAND	F-SMALL
T1	0.00982	0.00189	0.00011	0.01607	21	1	31
T2	0.00615	0.00172	0.00000	0.01172	12	0	79
T3	0.00091	0.00104	0.00000	0.00226	7	0	83
T4	0.00653	0.00093	0.00000	0.00764	18	0	64
T5	0.00814	0.00111	0.00031	0.00857	8	1	78
T6	0.01162	0.00287	0.00152	0.01491	24	1	125
T7	0.00274	0.00108	0.01131	0.00579	17	1	56
T8	0.00345	0.00084	0.00007	0.00579	10	0	50
T9	0.00661	0.00120	0.00094	0.00877	11	2	43
T10	0.00185	0.00172	0.00000	0.00181	8	0	77
T11	0.00931	0.00284	0.00604	0.01621	24	6	111
T12	0.00827	0.00062	0.00000	0.00958	25	0	64
T13	0.00887	0.00150	0.00000	0.00821	31	0	55

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