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Effects of habitat fragmentation on Amazonian termite communities

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ABSTRACT. Intuitively, termites would seem to be a very suitable group to illustrate effects of ecosystem fragmentation. Being detritivores, they do not control directly the rate at which their resources are available, nor do they restrict the ability of the resources to regenerate. Consequently, termites do not mask the ecosystem depletion caused by fragmentation. With this in mind, we compared the communities of termites in undisturbed Amazonian forest with those of two isolated fragments nearby, aiming to show that the differences observed may have resulted from habitat fragmentation. Dissimilarities between communities in the undisturbed forest suggest natural patchiness in their distribution, which could lead to misinterpretation of the effects of fragmentation. Continuous forest had higher species richness and fewer rare species than the fragments. Guild structure in the forest was biased towards soil-feeding termites, which are subterranean and soft bodied, and therefore more sensitive to variation in microclimate. In the fragments, litter-feeders and species intermediate between soil-feeding and wood-feeding types were numerically more important. Habitats in the forest were more equally used than in the fragments, suggesting habitat unsuitability increased with fragmentation. It is suggested that the community composition of the fragments is a result of the intrinsic patchiness of the original forest and deterministic and stochastic extinctions caused by fragmentation. The need for manipulative experiments to test such ideas is discussed.

RESUMO: Cupins são intuitivamente bastante adequados para o estudo da fragmentação de ecossistemas. Por serem detritívoros, eles não controlam diretamente a taxa sob a qual seus recursos tornam-se disponíveis, nem prejudicam a capacidade de regeneração de tais recursos. Portanto, cupins não mascaram a depauperação do ecossistema causada pela fragmentação. Mantendo tal consideração em mente, comparámos as comunidades de cupins em floresta Amazônica nã-perturbada com aquelas de duas reservas isoladas vizinhas, objetivando mostrar que as diferenças observadas poderiam ter sido causadas pela fragmentação do habitat. Dissimilaridades entre comunidades dentro da floresta sugerem uma variegação natural do ambiente, a qual poderia causar erros na interpretação dos efeitos da fragmentação. A floresta contínua teve maior riqueza em espécies e menor proporção de espécies raras do que os fragmentos. Cupins geófagos – subterrâneos e de corpo pouco esclerotizado, portmanto mais sensíveis a variações microclimáticas – dominaram a guilda da floresta. Nos fragmentos, os comedores de serrapilheira e os de hábito alimentar intermediário entre geofagia e xilofagia foram numericamente mais importantes. Os habitats na floresta foram usados mais equitativamente que nos fragmentos, o que sugere uma inadequabilidade de habitat crescente com a fragmentação. Sugere-se que a composição das comunidades dos fragments é resultado da variegação intrínseca da floresta e de extinções causadas pela fragmentação. É discutida a necessidade de experimentos manipulativos para se testar tais ideias.

KEY WORDS: Amazonia, Brazil, ecosystem fragmentation, habitat islands, Isoptera, rainforest, termite ecology.

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INTRODUCTION

The consequences of ecosystem fragmentation are controversial, mainly due to unpredictability, which results both from the inherent complexity of ecosystems and the relative scarcity of empirical evidence (but see Gilpin & Soulé 1986, Quinn & Harrison 1988, Simberloff 1986, Wilcox & Murphy 1985). These constraints are particularly apparent in Amazonian ecosystems.

It is agreed that fragmentation increases the chance of local extinction, and that this can be deterministic or stochastic (Gilpin & Soulé 1986). Deterministic extinctions are those resulting from some irreversible change or force, e.g. deforestation or severe erosion. Stochastic extinctions originate from normal, random changes or environmental perturbations, which diminish population fitness, but do not necessarily result in immediate extinction. However, once populations are reduced in size their vulnerability to stochastic perturbations is increased, leading eventually to local extinction (Jaenike 1978, Jennersten 1988, Klein 1989). Communities so affected are normally reduced in species number.

Insects are very suitable for studies on the effects of fragmentation, due to their short generation time, high densities, wide variety of dispersal abilities and host selection, as well as responses to resource quality and quantity. Moreover, insects can contribute towards the maintenance of a disturbed state (Schowalter 1985). Being detritivores, termites possess features which make them particularly suitable for studying ecosystem fragmentation:

(i) they do not control directly the rate at which their resources are available (as is the case of herbivores). Rather, termites and other detritivores have to rely entirely on the rate at which some other ecological factor releases the resource on which they live. Indeed, ecosystem fragmentation could be such a factor, by promoting plant stress, senescence or even death, or by changing the quality of other resources due to increased light penetration.

(ii) they do not affect the ability of the resources to regenerate (as predators do). So, termites do not mask ecosystem depletion caused by fragmentation.

This paper compares termite communities in Amazonian forest relicts with continuous, undisturbed forest. It aims to demonstrate that differences between the communities may have been promoted by ecosystem fragmentation.

METHODS

Definition of terms

Fragmentation, or ecosystem fragmentation, refers to processes reducing the area of a site. The new smaller sites are called fragments, which are considered synonymous with islands, reserves, remnants, isolates, or relicts. The larger, unfragmented ecosystem which gave rise to such fragments (in our case, undisturbed Amazonian forest) will be referred to as continuous forest, a synonym of MacArthur & Wilson's 'continent'. Terms were chosen for consistency with those used in the Biological Dynamics of Forest Fragments series (see Lovejoy *et al.* 1986 and papers therein).

Community composition refers only to the species of termites present, regardless of their ecological relationships, while guild structure refers to how species are proportionally distributed between groups exploiting resources in a similar way. Species are grouped according to their dietary requirements, as in Bandeira (1983), Gontijo & Domingos (1991), Mathews (1977); or according to our own field observations. Four classes are recognized: litter feeders, soil feeders, wood feeders and intermediate feeders. Soil feeders are those ingesting mineral particles of soil mixed with organic matter, and are distinct from litter feeders, feeding on leaf litter. Intermediate feeders are those with a mixture of wood-feeding and soil-feeding.

Experimental sites

Collections of termites were undertaken as part of the Biological Dynamics of Forest Fragments Project (Lovejoy *et al.* 1986), 80 km north of Manaus, Brazil (2° 25′ S, 59° 50′ W). The area, typically tropical moist forest (Holdridge 1967), has a 20–30 m canopy with open understorey, dominated by stemless palms. The relief is gently sloping with many streamlets, and soils are mainly poor latosols. Annual rainfall is 1900–2300 mm, with a dry season between July and September, and mean daily temperatures fluctuating little, between 26–28°C.

Four sites were demarcated within continuous forest (Sites A–D). Approximately 2.5 km from this, routine forest clearing in 1980 isolated almost perfectly rectangular fragments, one of area 1 ha (Site E) and another of 10 ha (Site F). These are at 100 and 300 m respectively from the continuous forest, which extends more than 350 km north of the study area. Lovejoy *et al.* (1986) give details of these sites, under the codes 1113 and 1301 for continuous forest, and 1104 and 1202 for fragments. To standardize sampling size and restrict sampling effort, comparisons have been made between fragments and continuous forest by randomly selecting two of the four sites in undisturbed forest (Sites C and D). Thus, throughout the paper, comparisons are made between forest and fragments using Sites C and D (forest) and Sites E and F (fragments). When applicable, data from sites A and B were used for additional information.

Sampling procedures

One 110 m × 3 m transect was demarcated within each of the sites. This width was selected since it provided a good range of morphospecies in preliminary studies. The transect was situated in the middle of the fragments.

Sampling aimed to collect the maximum number of termite species, and was undertaken in rotting logs, living trees (DBH >10 cm), bases of stemless palms and epigeous (soil-surface) termitaria, which in addition to the primary builders also contain inquilines. Samples from living trees were taken at the base of the tree, galleries on the surface of the trunk and arboreal nests, up to approximately 2 m from ground level. Epigeous termitaria were those on the soil surface, without contact with any of the above habitats. The transects were divided into subplots, 3 m (width of transect) × 5 m. Therefore, each 110 m transect was composed of 22 contiguous subplots. Sampling was performed within one subplot at a time, until either the entire subplot had been searched or one hour had elapsed. Colonies/galleries overlapping two subplots were recorded only once. Sampling was performed between 0800–1400 h and at least 1 h after heavy rain, to standardize for termite activity.

Sampling took place between April and June 1986 and specimens were preserved in 80% alcohol and labelled. They were subsequently identified to genus and then to species or morphospecies as practical. Identifications were confirmed using the collections of the Museu Paraense Emílio Goeldi and Museu de Zoologia da Universidade de São Paulo, Brazil. Voucher specimens were deposited in the Entomological Museum of the Universidade Federal de Viçosa and in the Entomological Museum of the National Institute for Amazonia Research (INPA), Brazil.

RESULTS

Termite communities

Termites belonged to two families, 32 genera and 64 species (or morphospecies). Of these, 10 species were restricted to fragments, 36 to continuous forest, and 18 were common to both (Tables 1, 2 and 3). Continuous forest had a higher species richness (54) than the fragments (28). The fragments themselves were different: the larger fragment having a higher species richness (21) than the smaller one (13). *Neocapritermes* spp were restricted to the fragments, and all but two species of *Nasutitermes* spp and *Velocitermes* spp were typical of continuous forest. Most of the species confined to fragments were found on only one occasion. The species more commonly encountered were two litter feeders (*Nasutitermes* sp c and *Velocitermes* sp c) and two intermediate feeders (*Neocapritermes* sp a and *Neocapritermes* sp c). Of the species restricted to continuous forest, 19 of the 36 were only single records (52.8%), proportionally less than the rare species confined to fragments (six species, 60%). The remaining 17 species, represented by two or more records, were mostly soil feeders (Table 1). Of the 10 species confined to fragments, two (20%) were soil feeders, four (40%) intermediates, one (10%) a wood feeder, and three (30%) were litter feeders (Table 2). Among the 36 species confined to continuous forest, 19 (52.8%) were soil feeders, five (13.9%) were intermediates, seven (19.4%) wood feeders and five (13.9%) litter feeders (Table 1). Thus, the guild structure between fragments and continuous forest was significantly different ($X^2 = 90.71$; 3 df; $P < 0.001$). Species common to both forest and fragments were mainly wood feeders (13 spp, 72.2%). The remainder were either soil (three species, 16.7%) or intermediate feeders (two species, 11.1%) (Table 3).

The species composition of the fragments and the four continuous forest sites was compared by the Sörensen's coefficient of similarity (Figure 1). The highest

Table 1. Number of records (number of species) of termite species which were found only in continuous forest sites in Central Amazonia, Brazil.

Species	Site C	Site D	Total
SOIL FEEDERS:[1]	(10)	(14)	(19)
Angularitermes sp a	1	-	1
Anoplotermes sp a	-	1	1
Anoplotermes sp e	1	-	1
Anoplotermes sp h	1	2	3
Anoplotermes sp i	1	-	1
Anoplotermes sp k	-	1	1
Anoplotermes sp l	-	1	1
Atlantitermes osborni (Emerson)	-	2	2
Atlantitermes snyderi (Emerson)	1	1	2
Cavitermes tuberosus (Emerson)	1	1	2
Coendutermes tucum Fontes	-	1	1
Crepititermes verruculosus (Emerson)	-	4	4
Curvitermes sp a	1	-	1
Cyrilliotermes sp a	-	3	3
Embiratermes sp a	1	1	2
Embiratermes sp c	-	1	1
Labiotermes sp b	-	1	1
Spinitermes sp a	1	-	1
Subulitermes sp a	1	1	2
INTERMEDIATE FEEDERS:	(3)	(4)	(5)
Araujotermes sp a	2	1	3
Araujotermes sp b	-	1	1
Coatitermes sp a	1	1	2
Planicapritermes planiceps (Emerson)	-	3	3
Termes sp b	1	-	1
WOOD FEEDERS:	(2)	(7)	(7)
Heterotermes sp a	-	2	2
Microcerotermes sp a	1	2	3
Nasutitermes octopilis Banks	-	2	2
Nasutitermes sp f	-	1	1
Nasutitermes sp i	1	3	4
Nasutitermes sp j	-	3	3
Rhinotermes sp b	-	1	1
LITTER FEEDERS:	(2)	(3)	(5)
Cornitermes sp b	-	1	1
Rhynchotermes sp a	-	1	1
Syntermes molestus (Burmeister)[2]	-	2	2
Velocitermes sp b	1	-	1
Velocitermes sp d	1	-	1
Totals:	(17)	(28)	(36)

[1] Diet classes are based on Bandeira (1983), Gontijo & Domingos (1991) and Mathews (1977), as well as personal observations.

[2] *Syntermes* are also reported to feed on living grasses.

similarity occurred between the forest sites C and D (46.4%), which were more similar than sites A and B (40%). The larger fragment (Site F) was marginally more similar to sites A and B than to sites C and D. However, the smaller fragment (Site E) had a low similarity to all the other sites (29.1%). Thus, the larger fragment (Site F) was more similar to the continuous forest than the smaller fragment (Site E).

Table 2. Number of records (number of species) of termite species which were found only in forest fragments in Central Amazonia, Brazil. Site E = 1 ha; Site F = 10 ha.

Species	Site E	Site F	Total
SOIL FEEDERS:[1]	(1)	(1)	(2)
Amitermes sp a	-	1	1
Unidentified	1	-	1
INTERMEDIATE FEEDERS:	(1)	(3)	(4)
Convexitermes sp a	-	1	1
Neocapritermes sp a	3	-	3
Neocapritermes sp c	-	5	5
Neocapritermes sp d	-	1	1
WOOD FEEDER:	(0)	(1)	(1)
Heterotermes sp b	-	1	1
LITTER FEEDERS:	(2)	(2)	(3)
Nasutitermes sp c	2	2	4
Nasutitermes sp o	-	1	1
Velocitermes sp c	2	-	2
Totals:	(4)	(7)	(10)

[1] Diet classes are based on Bandeira (1983), Gontijo & Domingos (1991) and Mathews (1977), as well as personal observations.

Table 3. Number of records (number of species) of termite species which were found in both continuous forest and fragments in Central Amazonia, Brazil. Site E = 1 ha; Site F = 10 ha.

Species	Forest			Fragments		
	Site C	Site D	Total	Site E	Site F	Total
SOIL FEEDERS:[1]	(2)	(3)	(3)	(2)	(1)	(3)
Anoplotermes sp d	1	2	3	-	1	1
Anoplotermes sp f	3	4	7	1	-	1
Rupititermes sp a	-	1	1	1	-	1
INTERMEDIATE FEEDERS:	(0)	(2)	(2)	(1)	(1)	(2)
Termes sp a	-	1	1	1	-	1
Termes sp d	-	1	1	-	2	2
WOOD FEEDERS:	(9)	(10)	(13)	(6)	(12)	(13)
Coptotermes[2] *sp a*	1	-	1	-	2	2
Cornitermes sp a	1	-	1	-	2	2
Cornitermes pugnax Emerson	-	1	1	-	3	3
Cylindrotermes sp a	-	16	16	4	2	6
Cylindrotermes sp b	-	2	2	1	1	2
Dolichorhinotermes sp a	-	2	2	-	1	1
Heterotermes tenuis (Hagen)	3	-	3	-	4	4
Nasutitermes sp a	5	12	17	1	5	6
Nasutitermes sp b	2	5	7	-	2	2
Nasutitermes sp e	3	6	9	4	1	5
Nasutitermes sp g	4	1	5	2	2	4
Nasutitermes sp l	1	3	4	-	1	1
Nasutitermes sp m	2	2	2	4	-	4
Totals: (common to both = 18 spp)	(11)	(15)		(9)	(14)	

[1] Diet classes are based on the findings of Bandeira (1983), Gontijo & Domingos (1991) and Mathews (1977), as well as personal observations.

[2] *Coptotermes* spp are also reported to feed on living trees.

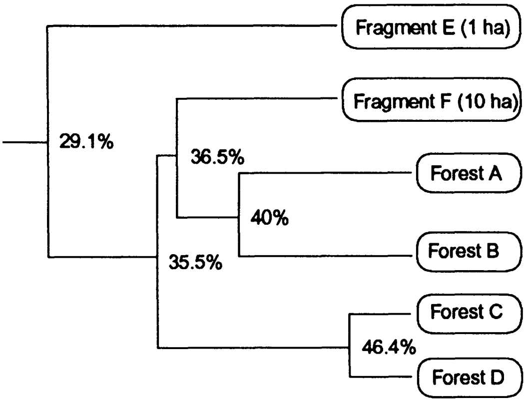

Figure 1. Dendrogram of similarity (Sörensen) for the communities of termites in sites of continuous forest (A, B, C, D) and isolated fragments (E = 1 ha; F = 10 ha) of Amazonian forest.

Habitat associations of the termites

Even though the same size transect was sampled at each site, the total number of samples differed from site to site (Table 4). As all potential nesting and foraging places were searched within each transect, the differences in number of samples can be due to (i) more logs, living trees, etc., in the transect, and/or (ii) the existing nesting/foraging places having more colonies. The percentage of termite samples associated with four different habitat types in the forest and in the fragments is shown in Table 4. In both forest and fragment sites, termites were found associated with rotting logs more than with any other habitat type. However, there was considerable variation in the extent to which other resources were exploited, with the more equal use of habitats being seen in the forest sites, particularly in site D, where most termite samples were found.

Edge effects were analysed by ranking three of the sites according to a gradient of edge/core proportion: site E (1 ha), site F (10 ha) and site D (forest). The numbers of samples and species collected increased as edge/core ratio decreased: site E, 27 samples/13 species; site F, 42/22; site D, 107/42. These differences were significant ($X^2 = 17.17$ and $X^2 = 61.65$; $P < 0.001$ respectively).

Table 4. Percentages of termite samples (total of samples) associated with four different habitat types in continuous forest (C & D) and fragment (E & F) sites in Central Amazonia, Brazil.

	Forest		Fragments	
Habitat	Site C	Site D	Site E (1 ha)	Site F (10 ha)
Rotting logs	55.3	43.0	74.1	66.7
Living trees	36.2	28.0	7.4	23.8
Stemless palms	6.4	19.6	14.8	9.5
Epigeous termitaria	2.1	9.3	3.7	0.0
Total of samples	(47)	(107)	(27)	(42)

DISCUSSION

The dendrogram of similarities (Figure 1) depicts a pattern consistent with theoretical expectations. Since the smaller fragment is likely to be under the highest ecological pressure (smallest area, strongest edge effect), it is not surprising that it has the most distinct termite community. For the same reason, the larger fragment would have more affinities with the forest than with the smaller fragment. However, the forest sites did not show a high degree of similarity (highest level was 46.4% between sites C and D). This suggests that the termite community in undisturbed forest is either very variable or heterogeneously distributed. Thus, at least some of our results comparing fragments with continuous forest could have been due to the intrinsic patchiness in termite distribution. Therefore, in the following discussion, fragmentation is considered as one of the forces – and not the only force – that could have led to the differences observed.

The communities of termites showed certain differences between fragments and continuous forest. The high proportion of rare species in the fragments agrees with observations that population size is lower on islands than on continents. Low species richness in the fragments agrees with other studies where there were fewer species on an island than on an area of continent of equal size (Williamson 1981: p. 37). Two processes could have promoted these trends. Firstly, species could have been excluded by chance. That is, the fragments studied had few species simply because they originated from a patch in the continuous forest which was naturally poorer in species than the surroundings. It follows that highly patchy environments are particularly sensitive to fragmentation, since resource quality could easily decline due to the elimination of whole areas of a given type of habitat. Species with close habitat association would therefore disappear.

Secondly, in the event that fragmentation preserves a whole sub-set of the original environment, the isolated small populations may experience extinction due to loss of fitness promoted by inbreeding (Jaenike 1978, Jennersten 1988, Klein 1989). Alternatively, there could be an increase in niche overlap, because the populations would have to improve their resource utilization in response to the new (and lower) amount available. In highly competitive communities, where extreme levels of niche overlap are not tolerated, the species would have to reduce its niche breadth instead (Morse 1980: p. 262). The more extreme the species packing, the more susceptible to environmental fluctuations the community will be (MacArthur 1970). As a consequence, the populations could be lowered even further, to the point that the individuals are so few that it is impossible to re-establish a viable population even after a small environmental fluctuation; the so-called 'extinction vortex' (Gilpin & Soulé 1986, Thomas 1990). In summary, fragmentation promotes the disappearance of species, either by excluding populations from the area concerned or by demoting species from the status of 'abundant' to 'rare', and from 'rare' to 'extinct'.

Changes in community composition may be brought about by alterations in the habitat affecting species differentially. Evidence of this is the bias towards litter and intermediate feeders in the fragments, whereas in the forest the soil feeders were numerically more important (Tables 1, 2 and 3). In general, soil feeders are small, soft-bodied species living and foraging in the soil matrix (Fontes 1982, Mathews 1977). Litter and intermediate feeders are normally larger, with highly sclerotized bodies, and feed frequently in the open. Thus it seems plausible to assume that soil feeders would be more affected by constraints, such as fluctuations in microclimate. Changes in microclimate, according to the edge/core ratio of the fragment, have been demonstrated by Kapos (1989), working in the same region. She found that the microclimate within 100 ha reserves was substantially more equable than that in the 1 ha reserves. In particular, air temperature was elevated, humidity was reduced and soil moisture was depleted in the outer 20–40 m of fragments. Microclimate can also be altered by gap creation promoted by treefalls (Brokaw 1985), a common consequence of fragmentation on small reserves due to increased exposure of trees to wind. As the fragments used in our study were small (1 and 10 ha), we can expect such changes in habitat quality. These would tend to eliminate the soil feeders. The quantity of resources is also changed by treefalls: fallen trees and the surrounding plants killed or damaged by the falls increase the potential resource for wood and litter feeders.

Additional evidence that termites are sensitive to alterations in the environment is the uneven use of the habitats in the fragments (Table 4). In all sites, termites were associated, in descending rank order, with logs, trees, palms and epigeous termitaria. However, in the forest the difference between habitats was not so strong as in the fragments, suggesting that there the habitats were almost evenly suitable for nesting and/or foraging. Putting it another way, the environment in the forest presented fewer constraints to termites than that in the fragments.

The number of species and the number of occurrences in three sites decreased significantly with an increase in edge/core ratio. However, as habitat heterogeneity increases along this gradient, we cannot distinguish between the two in this study. It would be desirable to set up a manipulative experiment, which compared sites with the same habitat heterogeneity but varying the edge/core ratio. However, such sites would not be easy to find. The opposite approach, i.e. varying habitat heterogeneity and keeping edge/core proportions constant, seems more feasible.

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