

Response of termite community and wood decomposition rates to habitat fragmentation in a subtropical dry forest

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Abstract: The effects of habitat fragmentation on termite communities and wood decomposition rates were investigated in subtropical dry forest fragments in the southwestern region of Puerto Rico. The composition of the termite community and the abundance of individual termite species were determined in small (<1 ha), medium (1-10 ha), and large (>10 ha) forest fragments and compared to a relatively undisturbed tract of contiguous dry forest (Guánica Commonwealth Forest). In a subset of these sites, wood bundles were set out for a period of 1 year in order to estimate rates of wood decomposition. The composition and structure of termite communities did not differ significantly between the forest fragments and the contiguous forest site, while rates of wood decomposition for a representative dry forest tree species were significantly lower in the fragments. These results indicate the problems associated with inferring the response of an ecosystem process to habitat fragmentation based solely on the response exhibited by the community of organisms that mediates the process.

Resumen: En la región sudoccidental de Puerto Rico se investigaron los efectos de la fragmentación del habitat sobre las comunidades de termitas y las tasas de descomposición de Madera en fragmentos de bosque seco subtropical. La composición de la comunidad de termitas y la abundancia de especies individuales de termitas fueron determinadas en fragmentos pequeños (< 1 ha), medianos (1-10 ha) y grands (> 10 ha), y comparadas con una porción contigua relativamente inalterada de bosque seco (Guánica Commonwealth Forest). En un subconjunto de estos sitios se colocaron al aire libre haces de Madera por un periodo de un año para estimar las tasas de descomposición de madera. La composición y la estructura de las comunidades de termitas no difirieron significativamente entre los fragmentos de bosque y el sitio de bosque contiuo, mientras que las tasas de descomposición de Madera para una especie arbórea representativa de bosque seco fueron significativamente menores en los fragmentos. Estos resultados señalan los problemas que se surgen al inferir la respuesta de un proceso ecosistémico a la fragmentación del habitat basándose solamente en la respuesta que exhibe la comunidad de organismos que median el proceso.

Resumo: Os efeitos da fragmentação do habitat nas comunidades de térmitas e nas taxas de decomposição de madeira foram investigadas em fragmentos de floresta subtropical seca na região sudoeste de Porto Rico. A composição da comunidade de térmitas e a abundância individual de espécies de térmitas foram determinadas em fragmentos de floresta classificados como pequenos (< 1 ha), médios (1-10 ha) e grandes (> 10 ha) e comparadas com tratos contíguos de floresta seca relativamente intacta (Guanica Commonwealth Forest). Num

subconjunto destas estações, dispuseram-se feixes de madeira para avaliar as taxas de decomposição lenhosa. A composição e a estrutura das comunidades de térmitas não diferiam significativamente entre os diferentes fragmentos florestais e as estações de floresta contígua, enquanto que as taxas de decomposição da madeira para as espécies arbóreas representativas da floresta seca eram significativamente menores nos fragmentos. Estes resultados indicam os problemas associados com a inferência da resposta de um processo de fragmentação do habitat num ecossistema baseada unicamente na resposta exibida ou uma comunidade de organismos que mediam o processo.

Key words: Habitat fragmentation, Isoptera, Puerto Rico, subtropical dry forest, termites, wood decomposition.

Introduction

The fragmentation of terrestrial habitat is believed to be one of the leading threats to biological diversity and ecosystem functioning (Laurance & Bierregaard 1997; Saunders *et al.* 1991; Turner 1996; Wilcox & Murphy 1985). While the majority of studies supporting this tenet demonstrated declines in species richness and densities of individual species within fragments (see Turner 1996), the concomitant demonstration of altered ecosystem processes as a result of these declines has usually been neglected.

Over the past decade there has been a dramatic increase in the number of studies investigating the effects of fragmentation on insects, including native insect pollinators (Aizen & Feinsinger 1994a), termites (Fonseca de Souza & Brown 1994), butterflies (Brown & Hutchings 1997; Daily & Ehrlich 1995), and beetles (Didham *et al.* 1998). However, only a few studies have simultaneously measured the effects of habitat fragmentation on the distribution of a community of organisms and an ecosystem process mediated by these organisms. These studies have examined insect communities and ecosystem processes such as dung decomposition (Klein 1989), pollination (Aizen & Feinsinger 1994b), and litter decomposition (Didham 1998). In order to gain a better understanding of the relationship between biodiversity and ecosystem processes in fragmented habitats, research needs to address the alteration of ecosystem functions in addition to the changes in species abundance and diversity resulting from fragmentation (Didham *et al.* 1996; Robinson *et al.* 1992).

Throughout the tropics, termites (Isoptera) are important mediators of ecosystem processes such

as soil turnover (Lee & Wood 1971; Lobry de Bruyn & Conacher 1990) and nutrient cycling (Peakin & Josens 1978; Wood & Johnson 1986; Wood & Sands 1978). Previous studies of the effects of disturbance and fragmentation on termite communities have yielded similar results; soil-feeding termites appear to be more sensitive to disturbance than wood-feeding species (Collins 1980; Eggleton *et al.* 1995; Wood *et al.* 1982) and more sensitive to fragmentation than either litter-feeders or species intermediate between soil- and wood-feeding (Fonseca de Souza & Brown 1994). However, these investigations looked at the response of termite communities to disturbance events that had happened less than 15 years prior. In order to allow sufficient time for faunal relaxation, the process whereby the number of species inhabiting an area approaches some dynamic equilibrium between rates of colonization and local extinction (Diamond 1972, 1973; Terbourgh 1974), studies are required in areas that have been disturbed or fragmented for multiple decades. Information concerning the long term viability of fragments and the new equilibrium point that they reach will contribute the most to developing conservation strategies (Turner 1996).

Due to favorable climatic conditions and productive soils, the dry forests of Puerto Rico represent an ecosystem that historically has been impacted through human activities (Murphy & Lugo 1986). As a result, the landscape is a mosaic dominated by agriculture and urban developments interspersed with patches of native forest vegetation. Many of these habitat patches have been isolated for decades (at least 60 years), and are thus suitable for investigations into the long-term survival of species in forest fragments. The objectives

of this study were to determine: (1) whether termite communities in subtropical dry forest fragments are distinct from those in a relatively undisturbed tract of contiguous dry forest, (2) how the composition and structure of termite communities vary relative to characteristics of forest fragments and their surrounding landscape, (3) the impact of habitat fragmentation on wood decomposition, and (4) the contribution of termites to the decomposition of wood in a subtropical dry forest ecosystem.

Materials and methods

The study region

This study was conducted in the southwestern coastal region of Puerto Rico (approximately 18° N and 66°35' W to 66°12' W). The southwestern portion of Puerto Rico comprises the majority of the island's subtropical dry forest life zone (*sensu* Holdridge 1967). Although there is considerable year-to-year variation, annual precipitation ranges from 600 mm in the west of the dry forest life zone to about 1,000 mm in the east (Ewel & Whitmore 1973). Mean annual temperature is 25.1°C. The majority of the region is highly disturbed due to industrial, agricultural, and urban land uses, resulting in the fragmentation of natural habitats. However, Guánica Commonwealth forest, situated

within the center of the dry forest life zone, represents one of the best remaining examples of subtropical dry forest in the world (Murphy & Lugo 1990). This area of approximately 4000 ha has been protected since the 1930's and encompasses a variety of edaphically determined plant associations, and thus served as the reference contiguous subtropical dry forest in this study.

Twelve forest fragments (Fig. 1) were randomly selected for study from a total of 40 sites in which the vegetative composition and structure had previously been documented (Ramjohn *et al.* unpublished). Site selection was stratified such that there were four fragments in each of the following size categories: small (<1 ha), medium (1-10 ha), or large (>10 ha) (Table 1). The majority of these selected fragments were deciduous forest with only one (site 16) representing a coastal-scrub forest and another (site 2) with portions classified as coastal-scrub forest.

Guánica forest is comprised of three major intergrading plant associations: coastal scrub forest, deciduous forest, and semi-evergreen forest. Two deciduous-forest sites and one coastal-scrub site were selected in order to characterize termite communities in a contiguous subtropical dry forest. Since semi-evergreen forest is restricted to ravines and sinkholes that are patchily distributed throughout Guánica forest, the sampling regime

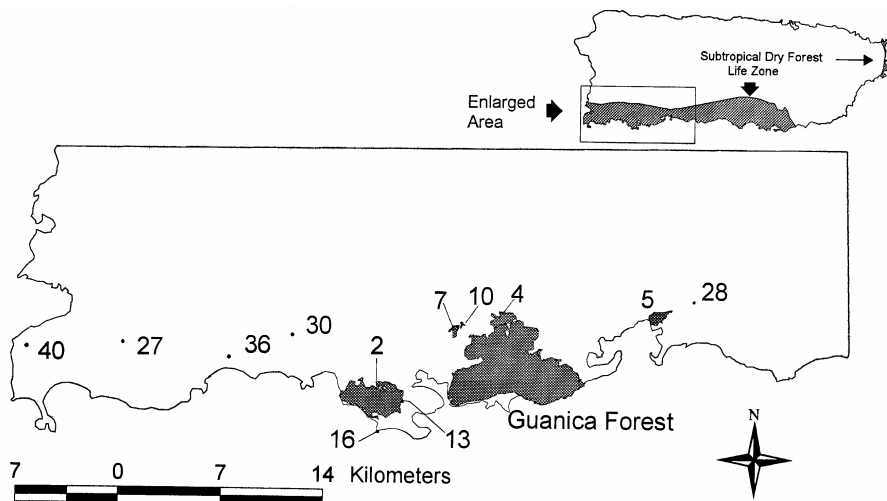


Fig. 1. Map of Puerto Rico illustrating the extent of the subtropical dry forest life zone on the island. Enlarged area showing the relative size and location of the 12 forest fragments (site numbers from Ramjohn *et al.* unpublished) and Guánica forest within the southwest region of the island.

Table 1. Fragment and landscape characteristics of the twelve study sites and Guánica forest.

Site-ID*	Area (ha)	Perimeter (m)	Patch Compactness	Distance to Nearest Forest Fragment (m)	Primary Aspect
Small					
40	0.006	27	0.99	392	S
36	0.06	92	0.90	110	S
30	0.26	226	0.79	364	E
27	0.69	408	0.72	10	W
Medium					
28	2.0	835	0.60	7.5	E
13	3.1	919	0.68	20	Flat
16	3.4	832	0.79	278	E + S
10	6.3	1723	0.52	15	N
Large					
7	33.6	3517	0.59	10	All
5	97.1	5258	0.66	30	All
4	136.8	7562	0.55	10	All
2	854.1	23277	0.45	20	All
Guánica**	3724	47885	0.45		All

* from Ramjohn *et al.* (unpublished)

** area and perimeter measurements are for entire tract of continuous forest in which the eastern portion of Guánica forest lies.

included this forest type by designating a "ravine" category in the stratified sampling design for the deciduous-forest and coastal-scrub sites (see *Termite sampling*). The two deciduous-forest sites differed in their history of human disturbance. One of the deciduous-forest sites is a mosaic of recovering and relatively unimpacted forest stands while the other site is located in an area that has received a minimal amount of human disturbance over the past 60 years.

Fragment and landscape characterization

Photointerpretation of color aerial photographs (1:20,000 scale) taken in February 1998 was used to create land use maps for the areas surrounding the 12 forest fragments and Guánica forest (Fig. 2). Polygons were delineated from the aerial photographs by tracing their outlines onto mylar overlays. Each polygon was assigned to one of nine land use classes using the criteria specified in Lugo *et al.* (1996). Photointerpreted polygons were then digitized into a geographic information system (ARC/INFO version 7.1, ESRI). Once topology was constructed, the digitized data were then

georeferenced and transformed into Universal Transverse Mercator (UTM) Grid Zone 19 coordinates to allow accurate measurements and overlay with other geographic data sets.

To investigate spatial patterns of termite species richness and abundance, three fragment characteristics were calculated: area, perimeter, and compactness (Table 1). Compactness (K_1) is a measure of the shape of a polygon based on perimeter and area estimates [Bosch 1978; Davis 1986; $K_1 = (2\sqrt{\pi \text{area}})/\text{perimeter}$]. As compactness decreases from a theoretical maximum of one (a perfect circle), it indicates an increasing perimeter to area ratio and thus a greater exposure of the fragment core to its edge.

In order to ascertain the degree of isolation and disturbance experienced by the 12 study sites, seven landscape variables were examined. Within 1 km of each forest fragment, the following landscape variables were measured: (1) number of closed canopy forest fragments, (2) percentage of closed canopy forest, (3) percentage of open canopy forest, (4) percentage of total forest, (5) percentage of agriculture, (6) percentage of urban land use, and (7) distance to the nearest closed canopy forest

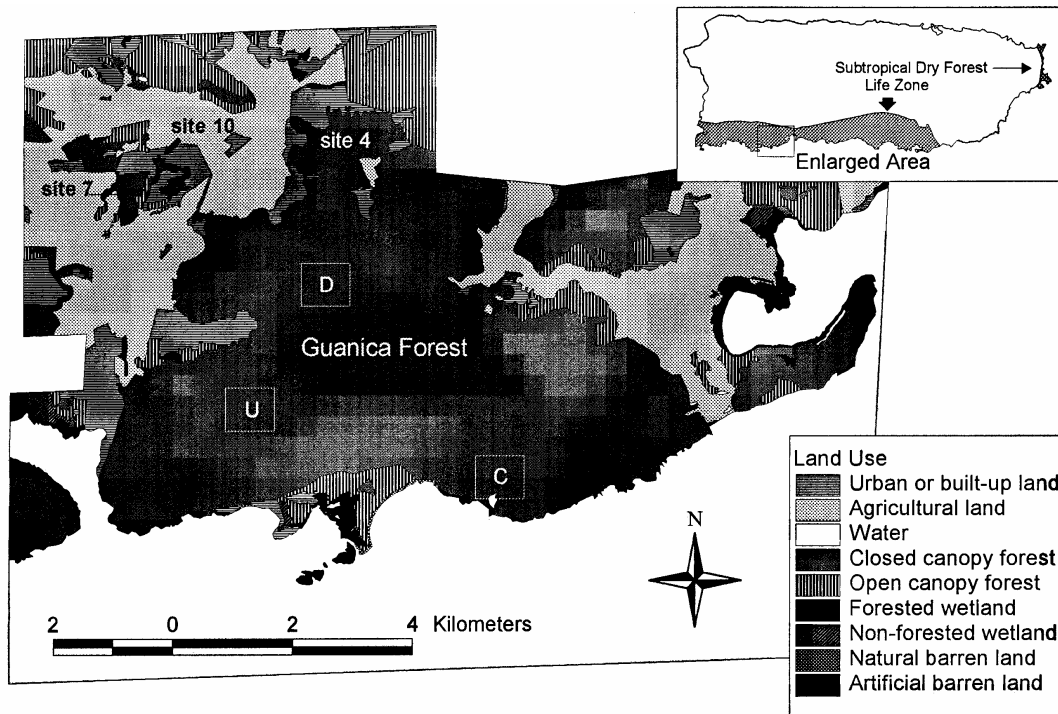


Fig. 2. Land use map of Guánica Commonwealth Forest and its vicinity, including the location of the interior forest study sites (C,U,D) and fragments 4,7 and 10. Inset: Map of Puerto Rico illustrating the extent of the subtropical dry forest life zone on the island.

fragment. The percentage of urban land use in close proximity to the study sites was investigated in order to determine if areas of concentrated light sources (e.g., residential areas, factories, etc.) were acting as barriers to termite dispersal by attracting winged reproductives (alates) exhibiting positive phototactic behavior during nocturnal flights (Nutting 1969).

Termite sampling

A quantitative survey of the termites was conducted during the summer months of 1997 (May, June and July) and 1998 (July and August). Due to the variability in nest sizes among the different termite species, two sampling techniques were necessary to obtain accurate estimates of abundance. Two species, *Nasutitermes costalis* (Holmgren) and *Nasutitermes acajutlae* (Holmgren), build large, conspicuous arboreal nests and were sampled using 100 m x 10 m belt transects. The location for establishing transects was determined by randomly selecting points on a grid overlay of the aerial photos of each site. Large fragments

(>10 ha) and Guánica forest sites were stratified using four aspect categories (N-,S-,E-,W-facing slopes) and one category for ravine areas. The number of transects established in each aspect category was proportional to the total area that each category represented.

The remainder of the species have inconspicuous nesting locations, such as within small pieces of wood or underneath rocks and logs. Nest abundance for these species was determined by exhaustively searching three 2 m x 2 m plots randomly selected from within the first 10 m segment of each belt transect. All dead wood within the plot was sampled for termites, including standing dead wood and attached dead branches up to a height of 2 m. The litter layer was also searched and all rocks were cleared in order to detect foraging termites and subterranean nests.

The vast area of some of the sites precluded thorough sampling with the plot and transect methods. Therefore, qualitative searches of the sites were necessary in order to document species that were not detected within the samples. These searches focused on habitat types that the random-

ized sampling design failed to include and were used only to supplement the species richness data for the site.

Whenever possible, soldiers and/or alates were collected from each colony and preserved in 80% ethanol for subsequent identification. One soldierless species (*Anoplotermes* sp.) was identified to genus using characteristics of the workers since alates were rarely found within the nest. Identifications were made using the taxonomic key of Snyder (1956).

Abundance estimates for each species represent nest densities (nests ha⁻¹), not the number of individuals per hectare. Certain assumptions were necessary in order to estimate the nest densities of subterranean species. For instance, termites belonging to the genus *Heterotermes* have foraging territories that likely extend 10 m or more from the nest (R. Scheffrahn pers. comm.). If this species was detected multiple times within the same 10 m x 10 m plot then these termites were considered foragers from the same colony, and only one colony was recorded for the entire plot. Thus, the results reported here represent conservative estimates for *Heterotermes* spp. nest density. The above assumption was not applied to the other subterranean species (*Anoplotermes* sp., *Parvitermes wolcottii* (Snyder), *Caribitermes discolor* (Banks)) because nothing is known of the foraging territory for these species. The nest density estimates for these species may, therefore, be positively biased.

Wood decomposition

At the end of the dry season (August 1997) wood was harvested from two sites within the subtropical dry forest life zone. Only fresh-cut wood from the common secondary growth tree, *Leucaena leucocephala* (Lam.) de Wit (Fabaceae: Mimosoideae), was collected. This species was used as an indicator of wood decomposition rates for this subtropical dry forest ecosystem because it has an intermediate density (specific gravity = 0.7), is very abundant throughout the dry forests of Puerto Rico, and is one of only a few tree species present in all of the study sites. The wood was cut into 50 cm lengths and wrapped in wire mesh. Subsamples were periodically collected, immediately weighed, and later oven-dried in the laboratory at 68°C until a constant weight was attained in order to estimate the dry weight of the wood.

Each bundle consisted of one "log" (diameter between 4-6 cm), two "branches" (2-4 cm), and two "twigs" (1-2 cm). This criterion for bundle assembly was an attempt to minimize the initial variability among the bundles. The initial wet weight of the wood within the bundles ranged from 936 to 2285 g (mean \pm SE, 1545 \pm 42 g), while the estimates of initial dry weight ranged from 639 to 1637 g (mean \pm SE, 1108 \pm 32 g).

Two types of bundles were assembled: experimental and control. The wood in the control bundle was wrapped in a fine aluminum mesh (1 mm) in an attempt to exclude termites and other macroinvertebrate decomposers. Experimental bundles were constructed with a wider mesh (5 mm) that would allow invertebrates access to the wood inside. The two mesh treatments were used in order to ascertain the relative role of termites and other invertebrates in the decomposition of wood.

Bundles were placed in pairs (control and experimental) around the large nests of the common arboreal termite, *N. acajutlae*, at one site in each of the three size categories (<1 ha, 1-10 ha, >10 ha) and at two locations within Guánica forest. Three replicates (3 pairs) were placed within 2 m of the base of the tree that supported the nest and were equidistant from each other. In addition, three replicates were placed approximately 20 m from the nest, making sure that they were not near other *Nasutitermes* spp. colonies. This stratification of the sampling units was an attempt to differentiate the contribution made by the patchily distributed and numerically dominant *N. acajutlae* from the contribution made by other invertebrates to the decomposition of wood in this ecosystem. A total of 58 bundles were assembled, with 12 at each of three fragments and 22 at Guánica forest (one bundle array had 10 instead of 12 wood bundles).

Bundles were retrieved approximately one year after they had been placed at the study sites. The wood was carefully removed from the mesh and termite mud (or carton) was removed prior to weighing. Once again, subsamples were taken for dry weight estimation. Upon collection of the bundles, the discovery was made that the mesh size of the control bundles failed to exclude invertebrates, including termites. Therefore, a list of invertebrates was compiled for each bundle in order to determine if bundles attacked by termites lost more weight than those that were attacked by

other invertebrate decomposers (e.g., beetles) or those that were not attacked by any invertebrates (natural controls). Immature insects were identified to the lowest taxonomic unit using the keys and descriptions of Stehr (1987, 1991), while adults were identified using the taxonomic keys of Bland & Jacques (1978). In addition, evidence of decomposer activity was classified as either termite or beetle based on the size and shape of the remnant tunnels within the wood.

Statistical analyses

In order to determine whether termite communities in forest fragments were distinct from those in Guánica forest, a one-way analysis of variance (ANOVA) was performed. Since it could not be determined if the samples came from a population with a normal distribution both parametric and nonparametric (Kruskal-Wallis) ANOVAs were used to analyze the data. These ANOVAs were applied to test for differences in species richness and individual species' abundances among the three fragment size classes and contiguous forest sites. In all cases with significant ANOVAs, multiple comparisons were performed with Dunnett's test.

Pearson correlation analysis was used to examine the associations between the termite diversity and abundance measures and the characteristics of fragments and their surrounding landscape. Fragment area was log transformed and percentage data were arcsine transformed in order to satisfy the assumptions of correlation (Zar 1984).

The effect of fragmentation on wood decomposition was analyzed using a one-way ANOVA to test for differences in biomass loss from the bundles among the sites (<1 ha, 1-10 ha, >10 ha, Guánica forest). Once again, in the case of a significant ANOVA, Dunnett's test was used for multiple comparisons. In order to determine whether control and experimental bundles could be grouped in the analysis, a paired-sample t test was performed. Similarly, a two-sample t test was used to test for differences in biomass loss between bundles that were near and bundles that were away from *N. acajutlae* nests.

Examination of the invertebrate lists from the bundles revealed two major decomposer groups: termites and beetles. The relative contribution of these groups was assessed by categorizing the bundles based on the presence and amount or evi-

dence of each group. The categories used to classify the bundles were as follows: (1) no major decomposer activity (less than 10 wood-consuming individuals present), (2) termite-dominated activity (termites present with less than 10 wood-consuming beetles), (3) beetle-dominated activity (wood-consuming beetles present with no termites), and (4) combination of termite and beetle activity (termites present with more than 10 wood-consuming beetles). One-way ANOVA (both parametric and nonparametric) was used to test for differences in biomass loss among the above decomposer categories. Multiple comparisons were made using Tukey's Honestly Significant Difference (HSD).

Results

Termite communities in fragments vs. contiguous forest

A total of 9 species from 8 genera and 3 families were encountered during this study (Table 2). Only one species, *Neotermes mona*, was not detected within Guánica forest and two species, *Caribitermes discolor* and *Incisitermes bequaerti*, were not represented in the fragments. Of the seven species present in the fragments, all were represented in each of the size categories (Table 2). Species richness was not significantly different between the <1 ha, 1-10 ha, >10 ha, and Guánica forest sites ($F = 2.147$, $df = 3$, $P = 0.152$, ANOVA; $H = 4.984$, $df = 3$, $P = 0.173$, Kruskal-Wallis). In addition, none of the species had densities that were significantly different among the four size categories (all $P > 0.05$, ANOVA and Kruskal-Wallis).

Fragment and landscape characteristics

The majority (92%) of correlations between termite and fragment variables were not statistically significant (Table 3). Species richness was the only termite variable to be significantly correlated with the fragment characteristics (area and compactness). However, fragment area and compactness are strongly correlated ($r = -0.886$, $P < 0.001$), and forcing both variables into multiple regression models (Type I Sum of Squares), manipulating their order of inclusion, resulted in only the first variable being significant. Thus, it is difficult to conclude which variable has an influence

Table 2. The occurrence of termite species within the 12 forest fragments (listed by site codes) and Guánica forest. X = present, detected from plot and transect sampling methods. P = present, detected during qualitative site search.

Species	<1 ha			1-10 ha				>10 ha			Guánica Forest*					
	40	36	30	27	28	13	16	10	7	5	4	2	C	U	D	T
Family: Kalotermitidae																
<i>Incisitermes bequaerti</i> (Snyder)															X	X
<i>Neotermes mona</i> (Banks)				X	X				X		P					
<i>Procryptotermes corniceps</i> (Snyder)	X	X	X	X	X	X	X	P	X	X	X	X	X	X	X	X
Family: Rhinotermitidae																
<i>Heterotermes</i> spp**	X		P		P	X	P	X	X	P	P	X	X	X	X	X
Family: Termitidae																
<i>Anoplotermes</i> sp.			X		P				X	X	P	X			P	P
<i>Caribitermes discolor</i>														X		X
<i>Nasutitermes costalis</i>				X			X	X	X		X	X		P		P
<i>Nasutitermes acajutlae</i>	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X
<i>Parvitermes wolcottii</i>			X	X	P			P	X	X	P			X	X	X
Site species richness	1	2	5	5	6	3	4	4	7	5	7	5	3	6	6	8

* C = Coastal scrub site; U = upland deciduous forest that has remained relatively unimpacted; D = upland deciduous forest that has undergone human disturbance; T = total of all three Guánica forest sites.

** The taxonomy of this genus in the West Indies is currently unresolved (see Shreffrahn *et al.* 1994).

on termite communities in the forest fragments. Only three (5%) of the 56 correlations between termite diversity and abundance variables and landscape characteristics were statistically significant (Table 4). The percentage of open forest and total forest in the surrounding landscape was positively correlated with *N. acajutlae* and *Procryptotermes corniceps* (Snyder) abundance, respectively. None of the landscape variables were significantly correlated with termite species richness.

Wood decomposition

Even though invertebrates penetrated the mesh enclosing the control bundles, the smaller mesh size significantly reduced the amount of biomass loss compared to the experimental bundles ($t = 2.771$, $df = 28$, $P = 0.010$). There was no significant difference in biomass loss between the bundles that were near and the bundles that were away from *N. acajutlae* nests ($t = -0.391$, $df = 56$, $P = 0.698$). Therefore, one-way ANOVAs to test for differences in biomass loss among the sites were performed separately for the control and experimental bundles, but data from near and away bundles were pooled within each site. Biomass loss in both the control and experimental bundles

varied significantly among sites ($P < 0.05$, ANOVA). Experimental wood bundles lost significantly more biomass in Guánica forest than they did in any of the fragment size categories (all $P < 0.05$, Dunnett's test; Fig. 3A). In addition, control bundles in the 1-10 ha site exhibited significantly reduced levels of wood decomposition compared to Guánica forest ($P = 0.007$, Dunnett's test; Fig. 3B).

Table 3. Pearson correlation coefficients (r) among termite diversity and abundance (nests ha^{-1}) measures and fragment characteristics. * $P < 0.05$

Termite Variables	Fragment Characteristics		
	Area	Perimeter	Compactness
<i>Anoplotermes</i> sp.	-0.141	-0.100	0.127
<i>Heterotermes</i> spp	-0.422	-0.060	0.365
<i>Nasutitermes acajutlae</i>	-0.179	-0.029	0.261
<i>Nasutitermes costalis</i>	0.086	-0.046	-0.001
<i>Neotermes mona</i>	-0.070	-0.219	-0.151
<i>Parvitermes wolcottii</i>	-0.113	-0.201	0.088
<i>Procryptotermes corniceps</i>	-0.238	-0.262	0.291
Species richness	0.710*	-0.305	-0.728*

Table 4. Pearson correlation coefficients (r) among termite diversity and abundance (nests ha^{-1}) measures and landscape characteristics. * $P < 0.05$

Termite Variables	Landscape Attributes [°]						
	1	2	3	4	5	6	7
<i>Anoplotermes</i> sp.	0.484	-0.454	-0.213	-0.252	-0.372	-0.546	0.566
<i>Heterotermes</i> spp.	0.410	0.101	0.147	-0.232	-0.036	-0.106	0.301
<i>Nasutitermes acajutlae</i>	-0.090	-0.014	-0.412	0.585*	0.027	0.225	-0.110
<i>Nasutitermes costalis</i>	-0.026	0.053	-0.369	0.028	-0.273	-0.267	-0.100
<i>Neotermes mona</i>	-0.372	0.492	-0.035	0.510	0.265	-0.148	0.080
<i>Parvitermes wolcottii</i>	0.275	-0.348	-0.337	-0.057	-0.358	-0.573	0.646*
<i>Procryptotermes corniceps</i>	-0.213	-0.127	0.259	0.399	0.603*	-0.033	-0.457
Species richness	-0.516	0.244	-0.045	-0.009	0.112	0.118	0.093

[°]1 = distance to nearest closed canopy forest fragment, 2 = number of closed canopy fragments, 3 = percentage of closed canopy forest, 4 = percentage of open canopy, 5 = percentage of total forest, 6 = percentage of urban land use, 7 = percentage of agriculture (2,3,4,5,6 and 7 represent values within 1 km of fragment).

Role of termites in wood decomposition

Identification of the invertebrates collected from the wood bundles revealed an invertebrate community composed of 5 classes and at least 13 distinct orders, including Coleoptera, Embioptera, Hymenoptera, Isoptera, Isopoda, and Thysanura. Coleoptera was the most diverse group with 10 identified families (e.g., Cerambycidae, Botrichidae, Buprestidae, Scolytidae, Tenebrionidae) and 12 immature specimens that could not be assigned to families. Of the list of invertebrates, only beetles and termites emerged as potentially significant consumers of wood due to their frequency of occurrence and abundance in the wood bundles.

The categorization of the wood bundles based on invertebrate decomposer activity resulted in 4 bundles being classified as having no major activity, 15 as termite-dominated activity, 16 as beetle-dominated activity, and 23 as a combination of both termite and beetle activity. The amount of biomass loss varied significantly among the four decomposer categories ($P < 0.001$, ANOVA; $P < 0.001$, Kruskal-Wallis). Bundles dominated by termite activity lost significantly more biomass than those classified as having no major decomposer activity, beetle-dominated activity, or termite and beetle activity (all $P < 0.05$, Tukey's HSD; Fig. 4). In addition, bundles which were classified as having a combination of beetle and termite activity lost more biomass than those classified as having beetle-dominated activity ($P < 0.05$, Tukey's HSD).

Discussion

Termite communities in fragments vs. contiguous forest

The composition and structure of termite communities did not differ between dry forest fragments and contiguous forest. Forest fragments and contiguous forest were not significantly different in terms of termite species richness or abundance of individual species. There are a multitude of reasons why termites are able to persist within forest fragments. First, termites may be able to establish colonies within non-forested land use types, eliminating the need for long dispersal flights between forested areas. Four of the seven species found within the forest fragments have been reported to occur in structural lumber (Schefrahn *et al.* 1990), and a fifth species, *P. corniceps*, was commonly observed in natural wood occurring within residential areas (pers. obs.). If termites are able to become established within the surrounding matrix, then populations within forest fragments may be maintained by relatively high colonization rates.

Second, even if termites are not able to maintain populations within non-forested area, perhaps these alternate land uses do not serve as barriers to dispersal. While the majority of termite dispersal studies have focused on the environmental variables that initiate alate swarming, very little information exists on the factors that affect the

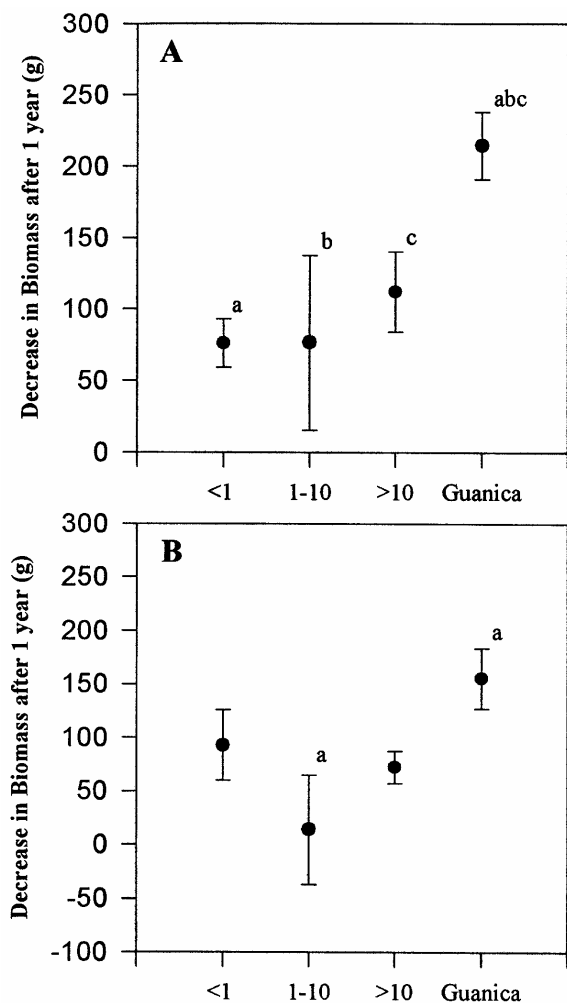


Fig. 3. Mean (\pm SE) loss of biomass from (A) experimental and (B) control bundles at the <1 ha, 1-10 ha, >10 ha, and Guánica forest study sites. Points within a graph with at least one of the same superscripts are significantly different ($P < 0.05$, Dunnett's test).

duration of flights or the maximum intrinsic distances that termite species disperse in natural habitats (Nutting 1969). The few estimates that exist for the dispersal distance of termites range from a few dozen meters (Wilkinson 1962) up to a few kilometers (Grassé 1949). The greatest distance separating any of the twelve forest fragments of this study from other patches of closed canopy forest was approximately 400 meters. If conditions within the non-forested habitats surrounding forest fragments do not impede termite dispersal, then alates could easily traverse the distances separating the forest fragments surveyed in

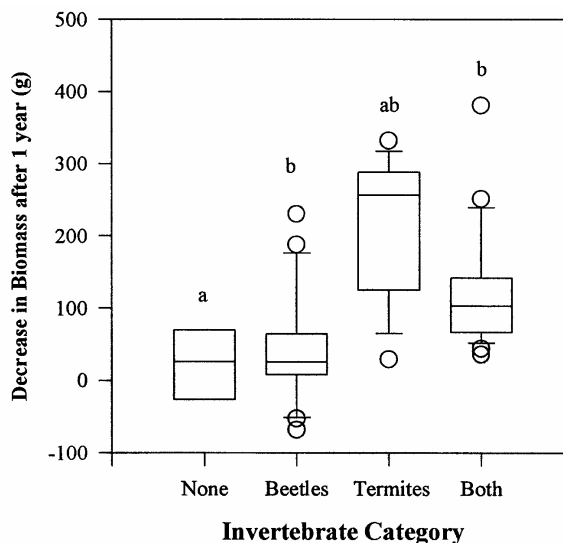


Fig. 4. Boxplots of reductions in wood bundle biomass categorized by the presence/absence and relative amount of the two major wood-feeding invertebrate groups encountered in this analysis. None = no major decomposer activity (group 1). Horizontal lines show the 10th, 25th, 50th, 75th and 90th percentiles increasing up the y axis. Open circles represent all data outside the 10th and 90th percentiles. Boxes within a graph with at least one of the same superscripts are significantly different ($P < 0.05$, Tukey's HSD).

this study. Kalshoven (1960) and Nutting (1969) provide some evidence in support of this idea, both observing the flight of alates within residential areas. However, much more research on the factors affecting termite dispersal in both natural and human-impacted landscapes needs to be conducted before solid conclusions regarding the resilience of alates to conditions within non-forested areas can be drawn.

The two previously discussed explanations are further supported by the lack of observed relationships between termite community attributes and landscape characteristics. For instance, the distance to the nearest fragment was not significantly associated with any of the termite community measures, while the percentage of the various surrounding land uses was only significantly associated with a few of these attributes. Furthermore, none of the species exhibited a positive relationship with the number of closed canopy forest fragments or the amount of closed canopy forest within 1 km. Considering that closed canopy forest sup-

ported the most diverse termite assemblages in the subtropical dry forest life zone (Genet 1999), one would expect that if termites are sensitive to conditions within the matrix, then fragments surrounded by the most preferred habitat type would harbor the most species, or at least higher abundances of some species.

Third, termites may not be affected by the altered microclimatic conditions at the forest edge. In fact, damage to vegetation at the forest edge, either as a direct result of increased wind exposure (Caborn 1957; Grace 1977; Moen 1974), or an indirect consequence of elevated evapotranspiration coupled with reduced humidity and increased desiccation (Lovejoy *et al.* 1986; Tranquillini 1979) may increase available food resources for wood-feeding termites. Since the majority of the termites encountered in this study fed predominantly on wood (Genet 1999), these species might be expected to increase in abundance at the edge or in very small fragments. Although there were no significant correlations, the abundance of six of the seven species occurring within the fragments exhibited a negative relationship with fragment area (Table 3). Eggleton *et al.* (1995) also found that wood-feeding termites in a lowland moist tropical forest were relatively unaffected by deforestation.

Finally, termite communities may appear to be persisting within fragments only because there has been insufficient time since the fragments were isolated to reach a new equilibrium between rates of colonization and extinction. As Pamilo & Crozier (1997) acknowledge, the population dynamics of social insects operate over a much longer time scale in comparison with other insect groups. In extreme cases where species have colonies which may persist for many years with a single queen or by producing supplementary reproductives (e.g., *Nasutitermes* spp.) isolated colonies within fragments may resemble the living dead (*sensu* Janzen 1986). Without immigration into this isolated population, the species will inevitably become locally extinct. However, even considering the slow pace of social insect population dynamics, there has likely been sufficient time to observe the effects of faunal relaxation within the forest fragments of this study, since the majority of these fragments have existed 20 or more years, with some created more than 60 years ago (Lugo *et al.* 1996).

Another important factor that must be addressed by fragmentation studies is the mode of fragment origin. Whether a fragment represents a residual tract of forest that has been reduced in size or an area of forest regrowth after another land use has been abandoned is important in determining the mechanisms for the persistence of termite populations in forest fragments. For instance, it would not be surprising to have most termite species present in relict forest fragments, whereas dispersal might represent an important filter into areas of forest regrowth where all resident populations must have arrived from surrounding sources. Examination of the land use history for the fragments in which this information was readily available reveals an insignificant role of the mode of fragment origin. For example, land use of site 7 has alternated between agriculture and forest while the majority of site 2 has remained forest during the 60 year period for which the land use history could be reconstructed (Vélez Rodríguez 1995a-f), yet species richness was higher in site 7 (see Table 2). This result further supports the above mentioned ideas that termite dispersal is not hindered by alternate land uses and/or termite populations can survive in non-forested habitats.

It is unclear which of these explanations is responsible for the maintenance of termite communities within the subtropical dry forest fragments of southwestern Puerto Rico. In fact, the appropriate explanation may change depending on the species under consideration. For instance, not all of the species in this study feed on wood (e.g., *Anoplotermes* sp.) and may therefore be less resilient to the altered microclimate at the forest edge. Moreover, the persistence of termite populations within forest fragments probably results from a combination of the above explanations rather than one acting in isolation. For example, even if extinction rates for populations of wood-feeding termites were not significantly increased by edge effects, immigration might still be required to prevent stochastic extinctions of populations within the fragments.

The two species not represented in the fragments were rare even in Guánica forest. *Caribitermes discolor* and *I. bequarti* were detected in less than 2% of the samples. A possible reason for the absence of *C. discolor* from the fragments is that it may be sensitive to the altered conditions within forest fragments. This species is common

in the moist and wet life zones of Puerto Rico and was previously not reported to even occur within the dry forest life zone (Jones & Scheffrahn unpublished). Therefore, perhaps only relatively undisturbed tracts of dry forest with suitable canopy and litter conditions allow this species to exist in the dry forest life zone. In fact, *C. discolor* was only collected from an area of Guánica forest that was selected as a study site because it had received a minimal amount of disturbance during the past 60 years (Vélez Rodríguez 1995a-f).

Previous studies of the effects of forest fragmentation on termite communities have yielded results different than those of the present study. Fonseca de Souza & Brown (1994) discovered that central Amazonia forest fragments supported considerably fewer termite species than contiguous forest. However, the loss of species within the fragments was largely attributable to the decrease of soil-feeding termites, while other feeding guilds were less affected. The present study encountered only one soil-feeding species (*Anoplotermes* sp.), while the rest primarily consumed wood. Therefore, the contrasting results of these two studies could possibly be ascribed to the distinct composition of the termite communities each examined. Another study conducted in the wheat belt region of western Australia also demonstrated significant declines in termite species richness as a result of habitat disturbance and fragmentation (Abensperg-Traun *et al.* 1996). However, habitat disturbance in the form of grazing and invasion by weedy species was determined to be the major factor contributing to the observed decline in species richness. Another potential explanation for the apparent resilience of termites in this study is the type of species found in the Caribbean in general. Given the high frequency of catastrophic natural disturbances (e.g., hurricanes) in these islands, species may be better colonizers and more resilient to disturbance than their counterparts in other regions.

Effects of fragmentation on wood decomposition

In contrast to the termite community, decomposition rates of the indicator species, *L. leucocephala*, appear to be markedly affected by the consequences of forest fragmentation. It is difficult to determine whether these results can be attributed to fragment area or the influence of edge

effects. Due to the small size of the <1 ha and 1-10 ha sites, the array of bundles at these sites was within 20 m of the forest edge. In the >10 ha and Guánica forest sites, bundles were more than 100 m from the edge of the site, but were not greater than 50 m from internal fragmenting factors (e.g., roads, right-of-ways, etc.). Since no studies have investigated the extent of edge penetration into subtropical dry forest fragments, it cannot be assumed that bundles at the >10 ha and Guánica forest sites were beyond the area of altered microclimatic conditions associated with the forest edge.

Examining the invertebrate decomposer data reveals that 80% of the bundles classified as termite-dominated activity were from the Guánica forest site. Conversely, 88% of the bundles classified as beetle-dominated activity were from the fragments. Considering the relative contributions made by beetles and termites (Fig. 4), the differences in decomposition rates probably reflect the differences in the decomposer community at the sites. These results are difficult to reconcile with those of the community comparisons among the sites and the associations between species abundances and fragment area. However, a closer examination of the four sites included in the decomposition investigation (site 2, 16, 30 and U) reveals highly disparate termite communities among these sites. In addition, only three termite species contributed to the breakdown of wood within the bundles. All three of these species had relatively high abundances in the Guánica forest site, whereas the fragments only supported one or two of these species (Table 5). In fact, the species that was found in the most bundles, *Heterotermes* spp., was not even present in the two sites that exhibited the

Table 5. The mean density (nests ha⁻¹) of the three termite species contributing to the decomposition of wood within bundles at four study sites.

Site	Area (ha)	<i>Parvi- termes wol-</i> <i>cotti</i>	<i>Hetero- termes spp.</i>	<i>Nasuti- termes acajutlae</i>
30	0.26	500	0	3.9
16	3.41	0	0	4.6
2	854.11	0	33.3	4.8
U	3724.75	312.5	12.5	9.7
No. of bundles attacked		3	23	17

lowest decomposition rates. An experimental design that encompasses more study sites is needed to resolve the conflicting responses to fragmentation exhibited by the termite community and rates of wood decomposition.

Regardless of the mechanisms responsible, alterations of wood decomposition rates within small (<10 ha) fragments have important implications for maintaining ecosystem functions. Declines in the breakdown rate of wood can lead to accumulation of woody debris on the forest floor, increased retention time of nutrients in the litter, decreased nutrient availability to plants, and consequent reductions in primary productivity. Ultimately, the synergistic relationship of these processes may set small fragments on a trajectory of gradual deterioration. However, long-term investigations into this matter will be required before the fate of small fragments can accurately be predicted.

Conclusions

This study demonstrated that related components of an ecosystem can respond in different ways to habitat fragmentation. Although the composition and structure of termite communities were unaffected by fragmentation, a process largely mediated by wood-feeding termites appeared to be altered. These results indicate the problems with inferring mechanistic responses to fragmentation based on changes in community composition. In addition, the differing contributions of species to important ecosystem function necessitate the inclusion of population estimates into fragmentation studies if the factors responsible for altering these processes are to be elucidated.

This study emphasizes the importance of forest fragments for maintaining native populations within human-altered landscapes. The protection and management of forest fragments will supplement the genetic diversity maintained by termite populations in Guánica forest, the only contiguous tract of subtropical dry forest left in southwestern Puerto Rico. Additional studies of this nature will greatly contribute to the management and conservation of biodiversity in a landscape that is inevitably dominated by anthropogenic influences.

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