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DIVERSITY AND ABUNDANCE OF TERMITES (ISOPTERA)
IN A FRAGMENTED SUBTROPICAL DRY FOREST
LANDSCAPE

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# THE DIVERSITY AND ABUNDANCE OF TERMITES (ISOPTERA) IN A FRAGMENTED SUBTROPICAL DRY FOREST LANDSCAPE

By

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# ABSTRACT

# THE DIVERSITY AND ABUNDANCE OF TERMITES (ISOPTERA) IN A FRAGMENTED SUBTROPICAL DRY FOREST LANDSCAPE

By

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The fragmentation of natural habitats currently represents one of the most serious threats to biodiversity. However, it is becoming apparent that not all components of an ecosystem respond similarly to fragmentation. The effects of forest fragment size on termite community composition and wood decomposition was determined in the subtropical dry forests of southwestern Puerto Rico. These components were measured in small (<1 ha), medium (1-10 ha), and large (>10 ha) forest fragments and compared to those in Guánica Commonwealth Forest, a relatively undisturbed, contiguous tract of dry forest. Since very little autecological information exists for most of the termite species included in this study, data were collected concerning termite population densities, diet, and habitat preferences. The composition and structure of termite communities did not differ significantly between the forest fragments and Guánica Forest, while rates of wood decomposition decreased significantly within the fragments as compared to the contiguous forest. These results indicate the problems associated with inferring the response of an ecosystem process to forest fragmentation based solely on the response exhibited by the community of organisms which controls the process.

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# INTRODUCTION

Rates of deforestation in the tropics and subtropics have continued to increase over the past several decades (FAO 1993, Whitmore 1997). Concomitantly, the majority of remaining forests throughout these regions are represented by small patches set in a matrix of non-forested vegetation. Due to their high degree of biodiversity and the rapid rate at which they are currently being deforested, the conversion of wet tropical forests has received much attention in the past few decades (e.g., Lovejoy & Bierregaard 1990, Whitmore & Sayer 1992, see also Turner 1996). However, as a result of their productive soils and reasonably comfortable climate, it has been the dry forests that have historically undergone the greatest alterations (Tosy & Voertman 1964, Murphy & Lugo 1986, Janzen 1988a).

Dry forests constitute approximately 42 % of the world's tropical and subtropical forests (Brown & Lugo 1982), yet they have been disturbed to such a great extent that they could be considered endangered ecosystems (Janzen 1988a, 1988b, Murphy & Lugo 1990, 1995). Only within the past few years have studies emerged concerning the impacts of fragmentation in dry forest life zones (Aizen & Feinsinger 1994a, 1994b, Kramer 1997). While there are a few exceptions (e.g., Corlett & Turner 1997), the majority of fragments created by the deforestation of tropical wet forests have only existed for a relatively short period of time (less than a decade) (Turner 1996, Turner & Corlett 1996). Therefore, questions concerning the long-term survival of species within fragments may be better answered through studies of dry forest fragments, the majority of which have been isolated for many decades.

In Central America and the Caribbean there exists only a few intact representatives of dry forest (Janzen 1988a, 1988b, Murphy & Lugo 1995). Clearly, the conservation of these ecosystems will depend on the protection and management of forest remnants as well as the restoration of areas following disturbance (Janzen 1988a, 1988b). The culmination of such processes would be the coalescence of habitat fragments back into a contiguous forest with the fragments providing the 'seeds' for the re-establishment of native flora and fauna in the recovering landscape (Janzen 1988b, Turner & Corlett 1996). While it is unlikely that this will produce tracts of forest of the same extent and ecological integrity as the original forest, it will nonetheless result in a significant contribution to the maintenance of ecosystem function and preservation of biodiversity. The success of such initiatives, however, relies on the knowledge of how species have responded to habitat fragmentation and the factors that control these responses.

Habitat fragmentation is currently one of the most serious threats to biological diversity (Wilcox & Murphy 1985, Turner 1996, Laurance & Bierregaard 1997). The primary mechanism of this decline in diversity is the decrease in local species richness associated with the division of a continuous habitat into isolated remnants of vegetation set in a matrix of alternate land uses. There are a multitude of ways, however, that fragmentation can lead to local extinctions of native populations, including: (1) reduction in population sizes; (2) reduction in immigration rates; (3) increased human disturbance during and after fragmentation; (4) deleterious edge effects; (5) changes in community interactions; and (6) immigration of exotic species (Saunder *et al.* 1991, Turner 1996). In addition, biogeographic factors such as remnant size and shape, degree of isolation, and time since excision from the continuous habitat can affect the intensity of the above mentioned circumstances (Saunder *et al.* 1991, Turner 1996).

Given the variety of possible outcomes, it is problematic to formulate generalizations about the responses of species to habitat fragmentation without knowledge of their basic biology (Margules *et al.* 1994). The response of individual species is dictated by their autecologies (McCoy & Mushinsky 1994) and the effects of fragmentation on other species in the community with which they interact. Once this information is obtained it then becomes possible to identify the particular traits that make a species sensitive to habitat fragmentation, thus allowing one to generalize about the responses of species that share these traits. For instance, it has been previously demonstrated that specialists, rare species, patchily distributed species, and wide ranging species are particularly susceptible to fragmentation (Turner 1996). Unfortunately, the necessary biological information for many species is sparse or lacking completely.

In an attempt to gain insight into the processes responsible for the observed impacts of fragmentation, a compilation of the sparse amount of existing information and the descriptive data collected during this study was put together for termites, the organisms at the focus of this investigation. Hence, the first chapter of this thesis deals with the descriptive information collected for each species, with some species getting more attention than others due to their abundance in the study region. The second chapter continues by looking at the relationships between habitat variables and the diversity of the termite community as well as the abundance of individual species. Once this information is reviewed, an analysis of the impacts of habitat fragmentation is undertaken in chapter 3. This last chapter investigates the effects of fragmentation on the composition of the termite community and decomposition of wood by comparing these phenomena in habitat fragments and relatively undisturbed contiguous dry forest.

The main objectives of this study are as follows:

(1) supplement the sparse amount of existing biological data for termites of the subtropical dry forests of Puerto Rico by determining the population densities, diet preferences, colony size, and nesting locations of selected species.

(2) identify characteristics of the habitat that influence the composition and structure of termite communities in a subtropical dry forest. It was hypothesized that structural characteristics which provide cover from direct exposure to sunlight would increase termite diversity and abundance.

(3) determine the composition and structure of the termite community in a relatively undisturbed, contiguous tract of subtropical dry forest (Guánica Forest) and compare this reference community to termite communities found within forest fragments of various sizes. It was hypothesized that individual forest fragments would only support a subset of the termite community found within the reference forest, but when forest fragments were viewed collectively, the diversity and abundance of termites would be comparable to that of the reference forest.

(4) determine the minimum fragment area required to support subsets (50 and 75%) of the termite community found in the reference site.

(5) identify fragment and landscape characteristics that influence the composition and structure of termite communities in forest fragments. Utilizing the principles of island biogeography, it was hypothesized that as fragments became smaller and more isolated, the diversity and abundance of termites would decrease.

(6) compare rates of wood decomposition in a contiguous subtropical dry forest to those in forest fragments of various sizes. It was hypothesized that wood decomposition would proceed at a significantly slower rate in forest fragments as compared to the reference forest. The basis for this hypothesis was the investigation by Klein (1989) which demonstrated declines in the rate of dung decomposition within Amazonian forest remnants.

(7) determine the relative contribution of termites to wood decomposition in a subtropical dry forest ecosystem. It was hypothesized that termites are important contributors to the decomposition of wood within subtropical dry forests. This hypothesis was suggested based on the seasonality of precipitation in subtropical dry forest ecosystems, which would seem to confine the activity of microbial decomposers to the rainy season.

(8) provide recommendations for the conservation and management of southwestern Puerto Rico's fragmented subtropical dry forest landscape.

### *Study Region*

The southwestern portion of Puerto Rico has been categorized as subtropical dry forest (*sensu* Holdridge 1967) by Ewel & Whitmore (1973) (Figure 1). This life zone is characterized by an annual precipitation that ranges from 250 to 2000 mm, an average annual biotemperature greater than 17 °C, a ratio of potential evapotranspiration to precipitation that is greater than one and less than two, and absence of frost throughout the year (Holdridge 1967).

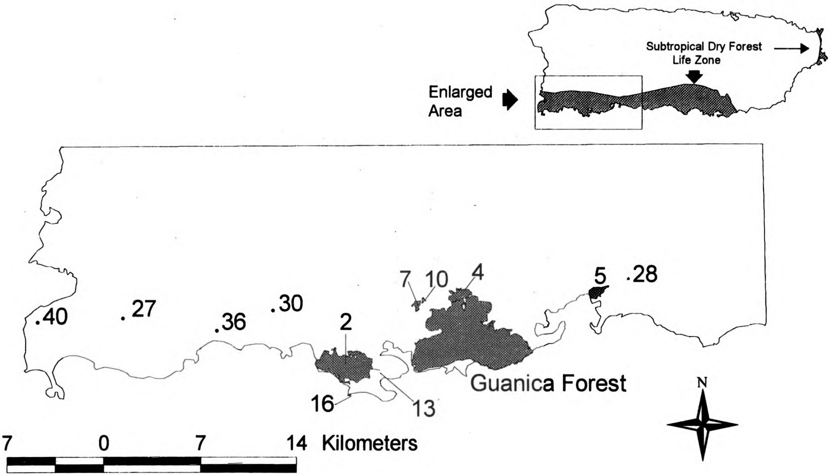

Figure 1. Map of Puerto Rico illustrating the extent of the subtropical dry forest life zone on the island. Enlarged area showing the relative size and location of the 12 forest fragments and the reference site (Guanica Forest) within the southwest region of the island.

Puerto Rico's dry southwestern region is due to a rain shadow effect resulting from the northeasterly trade winds passing over the island's central mountain system. This region extends east along the south coast approximately 120 km from the southwest corner of the island and reaches between 3 and 20 km inland, depending on local topography (Ewel & Whitmore 1973). Although this southwest region contains the majority of Puerto Rico's dry forests, it still only represents roughly 4 % (5000 ha) of the island's original dry forests (Murphy & Lugo 1990, Murphy *et al.* 1995).

Annual precipitation in this region ranges from 600 mm in the west of the dry forest life zone to about 1,000 mm in the east. The majority of the precipitation occurs during two wet seasons, one long period that extends from August to November and a shorter one during the month of May. Variation of year-to-year rainfall is significant and is attributed to the unpredictable passage of large storms and hurricanes over or near the region (Murphy *et al.* 1995). For instance, the southwestern region recently (September 1998) experienced a major storm as Hurricane Georges traversed the entire length of the island and soaked the dry forest life zone with heavy downpours for several hours (Van Bloem *pers. comm.*). The impacts of such severe storms have not been previously determined for subtropical dry forests.

The dry forests of southwestern Puerto Rico represent an ecosystem that has been heavily impacted through human activities. This general trend extends to the rest of the island as well. During pre-colonial times the island was 95% forested, however, this amount was reduced to a mere 5% by 1948 with most of the remaining forests restricted to isolated mountainous areas (Birdsey & Weaver 1982). During the last 60 years a reverse in this trend occurred due to a dramatic shift in the Puerto Rican economy from an agricultural system to a more urbanized industry with an emphasis on manufactured products (Morales-Carrion 1983, Dietz 1986). This significantly reduced the pressure on the remainder of the island's forests and even led to a recovery of previously deforested areas, resulting in forest cover increasing to 34% by 1985 (Birdsey & Weaver 1987). An example from the dry forest life zone can be found in the vicinity of Guánica Forest (see below), where closed canopy forest increased from 3181 to 5502 ha between the years 1936 and 1989 (Lugo *et al.* 1996). This was accompanied by a decrease in agricultural land from 3517 to 1799 ha during the same time period.

The current state of Puerto Rico's southwestern dry forest life zone can best be described as a series of forest fragments sparsely distributed over a highly impacted landscape. A recent characterization of the landscape (Ramjohn *et al. unpublished*) yielded a total of 308 closed and 312 open canopy forest fragments that together only accounted for 23% (16960 ha) of the total land area of the region. The majority of these fragments were less than 5 ha in area and there was only 14 fragments that represented substantial tracts (>100 ha) of closed canopy forest. While the mean fragment size was 42.6 ha, the median fragment size for closed canopy forests was less than 5 ha.

### *Guánica Forest*

Although considered a forest fragment by most measures, Guánica Commonwealth Forest represents one of the best remaining examples of subtropical dry forest in the world (Murphy & Lugo 1990). Situated in the center of Puerto Rico's dry forest life zone (Figure 1), this relatively large (~4000 ha) reserve has been protected at various magnitudes since the 1930's, culminating with its designation as a Biosphere Reserve by the UNESCO Man and the Biosphere Program in 1982. Before Guánica Forest officially received protected status it supported a myriad of services, including tree plantations (*Swietenia mahagoni* and *Haematoxylum campechianium*), fencepost production, charcoal production, cultivated crops (maize, tobacco, sugar cane), cattle pastures, and even human settlements (Murphy *et al.* 1995). Only fencepost production persisted past the 1940s, continuing into the mid-1970s (Canals Mora *pers. comm.*). This complex disturbance history has resulted in a mosaic of forest stands of widely varying structure and composition (Murphy & Lugo 1990).

Guánica Forest is divided into two portions separated by Guánica Bay, with the more extensive and less disturbed tract of the reserve located on the eastern side on the bay (Figure 1). This area forms a continuous habitat from the shoreline of the Caribbean Sea up to elevations exceeding 200 m, supporting six floristically and structurally distinguishable plant associations (Lugo *et al.* 1978). The three major intergrading plant associations of Guánica Forest are scrub forest located predominantly on limestone outcroppings, deciduous forest located on upland slopes and valleys, and semievergreen forest that is confined to narrow ravines. While there are no permanent water courses within the forest, narrow canyons formed by collapsed cave systems (Farnsworth 1993) run in a north-south orientation throughout the reserve and often flood during large storm events (Murphy *et al.* 1995).

Regardless of its past disturbance history and present conditions, Guánica Forest serves as the best reference system in the region for which comparisons with forest fragments can be made. Although most of its vegetation has been disturbed in the relatively recent past, the forest is reaching a state of maturity that is rivaled nowhere else within Puerto Rico's dry forest life zone (Murphy & Lugo 1990, 1995, Murphy *et al.* 1995).

### *Study Sites*

Twelve forest fragments were selected for study from a set of 40 fragments that had previously been described by Ramjohn *et al.* (*unpublished*) in terms of their vegetative composition and structure (Appendix A, Figure 1). These fragments vary greatly in size, shape, topographic location, vegetative composition and structure, amount of past and present disturbance, as well as the type of substrate (Table 1). For instance, a few of the fragments are in close proximity to the coast and are situated on limestone outcroppings with an almost complete lack of soil. Other fragments are located on abandoned pastures

Table 1. Characteristics of forest fragments and reference site selected for study.

| Site-ID[†] | Area (ha) | Perimeter (m) | Primary Aspect | Elevational Range (m) | Plant Sp. Richness[†] | Tree Sp. Richness[†] |
|---|---|---|---|---|---|---|
| 40 | 0.006 | 27 | S | ~30 | 21 | 7 |
| 36 | 0.06 | 92 | S | 30-35 | 70 | 32 |
| 30 | 0.26 | 226 | E | 30-40 | 76 | 36 |
| 27 | 0.69 | 408 | W | 170-200 | 71 | 27 |
| 28 | 2.0 | 835 | E | 40-100 | 68 | 31 |
| 13 | 3.1 | 919 | Flat | 15-26 | 69 | 31 |
| 16 | 3.4 | 832 | E + S | 0-26 | 69 | 34 |
| 10 | 6.3 | 1723 | N | 50-100 | 101 | 42 |
| 7 | 33.6 | 3517 | All | 25-108 | 149 | 61 |
| 5 | 97.1 | 5258 | All | 10-100 | 152 | 79 |
| 4 | 136.8 | 7562 | All | 40-190 | 153 | 73 |
| 2 | 854.1 | 23277 | All | 0-130 | 128 | 67 |
| Guánica[•] | 3724 | 47885 | All | 0-228 | | |

[†] 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.

and have well developed soils. In addition, some sites have been under extreme pressure from human activities for prolonged periods of time while others have remained virtually untouched following their isolation from adjacent forests. Most of the fragments are located in relatively inaccessible areas such as ravines, steep slopes, and hilltops that were not necessarily suitable for agricultural practices or urban development.

Sites within the reference system, Guánica Forest, were chosen on the basis of having areas that reflected the variability of characteristics displayed by the fragments. For instance, since a few of the sites were in close proximity to the sea and consisted primarily of vegetation characteristic of the scrub forest, a site was selected within Guánica Forest that was located near the sea within the scrub forest. Overall, three sites were selected within Guánica Forest which represented coastal scrub forest, upland deciduous forest with a predominantly south-facing aspect, and upland deciduous forest with a predominantly north-facing aspect.

# CHAPTER ONE

## The Termites of Puerto Rico's Southwestern Dry Forests

A recent survey of the termites (Isoptera) of Puerto Rico (Jones & Scheffrahn *unpublished*) increased the number of recorded species on the island from 16 to 22, with 10 of these occurring within the island's subtropical dry forest life zone (*sensu* Holdridge 1967). Three termite families (Kalotermitidae, Rhinotermitidae, Termitidae) are represented throughout Puerto Rico as well as within the subtropical dry forests.

Species belonging to the primitive family Kalotermitidae are commonly known as drywood termites because their diet and therefore nests are almost exclusively restricted to dry, dead wood. Colonies are established and remain completely contained within their food source with the end result of foraging and nest expansion being one and the same. Nests are constructed primarily within fallen dead branches and standing dead wood, although, the colony does not require contact with the soil for moisture. Instead, the termites are able to obtain water as a metabolic by-product of cellular metabolism as well as from external water and living plant tissue. The typical mature colony consists of a pair of primary reproductives (king and queen) or replacement reproductives, nymphs, worker-like pseudergates, soldiers, larvae, and eggs. In addition, winged imagos (alates) may be present within the nest at certain times of the year before they disperse to establish new colonies. Mature colonies generally do not exceed a few thousand individuals (Nutting 1969, Lenz 1994).

Most members of the family Rhinotermitidae have subterranean nests constructed directly in the soil. However, some species build their nests within buried, rotting wood or in logs above ground. All species consume wood, and many are economically important pests, including *Reticulitermes flavipes* (Kollar) in the eastern United States and *Heterotermes* spp. in the West Indies (Gillot 1995).

Three-quarters of all termite species belong to the diverse family Termitidae. It is within this family that the greatest range of social development and specialization exists (Gillot 1995). Members of this family from the West Indies belong to three subfamilies: (1) Termitinae, (2) Apicotermitinae, and (3) Nasutitermitinae. The Nasutitermitinae are characterized by the evolutionary development in soldiers of a rostrum (nasus) from which defensive secretions of the frontal gland can be exuded or forcefully ejected onto nest invaders.

Little information exists concerning the basic biology of the majority of termite species native to Puerto Rico beyond the few comments and observations within their original descriptions and a recent paper by Jones *et al.* (1995). In fact, it still is unclear exactly how many species there are in Puerto Rico. As recently as 1994 there was a new species described from the island (Scheffrahn 1994), and the taxonomic status of others remains unresolved. Therefore, the objective of this chapter is to augment the sparse information that currently exists for termites native to Puerto Rico's southwestern dry forests.

## MATERIALS & METHODS

### *The Study Region*

The southwestern portion of Puerto Rico includes the majority of the island's subtropical dry forest life zone. This region extends east along the south coast approximately 120 km from the southwest corner of the island (Ewel & Whitmore 1973) and reaches between 3 and 20 km inland, depending on local topography. 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. 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 (Figure 1), 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 associations.

Twelve forest fragments of various sizes were randomly selected for study from a total of 40 sites in which the vegetative composition and structure had previously been documented by Ramjohn *et al.* (*unpublished*) (Appendix A, Figure 1). In addition, three sites within Guánica Forest were selected in order to obtain baseline data for termite communities in a subtropical dry forest. These sites within Guánica Forest were located within a coastal scrub forest and upland deciduous forests on north- and south-facing slopes. A more complete description of the study sites, Guánica Forest, as well as the dry forest life zone of Puerto Rico can be found in the main Introduction of this thesis.

### *Nest Density*

A quantitative survey of the termites of the southwestern dry forests of Puerto Rico 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 regimes were necessary in order to obtain accurate estimates of abundance. Two species (*Nasutitermes costalis* (Holmgren) and *Nasuititermes acajutlae* (Holmgren)) build large, conspicuous arboreal nests and were sampled using 100 m x 10 m belt transects. The location for establishing the transects was determined by randomly selecting points on a grid overlay of the aerial photos of each site. Large fragments (>10 ha) and Guánica sites were stratified using four aspect categories (N-, S-,E-, W-facing slopes) and one category for ravine areas. The number of samples selected from each category was largely determined by the proportion of the total area that each category represented.

The remainder of the termites have less conspicuous nesting locations such as within small pieces of wood or underneath rocks and logs. Nest abundance for these species was determined by exhaustively searching 2 m x 2 m plots randomly selected from within the first 10 m segment of the belt transect. However, transects were not established at all of the selected sampling points. Instead, a single 10 m x 10 m plot was demarcated from which the 2 m x 2 m plots were randomly selected (see Table 2 for summary of sampling design at all sites). All dead wood within the plot, including standing dead wood (SDW) and dead branches up to a height of 2 m, was searched. The host plant was identified whenever possible using the taxonomic keys and descriptions in Little & Wadsworth (1964) and Little *et al.* (1974). The litter layer was then searched,

Table 2. Summary of sampling design at forest fragments and reference site (Guánica Commonwealth Forest).

| Site ID # | Area (ha) | Total Area of Belt Transects ($m^2$) (No. of transects) | No. of Plots | | Percentage of Site Searched | | Site Walk?[**] |
|---|---|---|---|---|---|---|---|
| | | | 10 x 10[*] | 2 x 2 | Belt Transect | 2 x 2 Plots | |
| 40 | 0.006 | 0.006[†] | - | 4 | 100 | 33 | No |
| 36 | 0.06 | 0.06[†] | - | 4 | 100 | 3.2 | No |
| 30 | 0.26 | 0.26[†] | - | 5 | 100 | 0.8 | Yes |
| 27 | 0.69 | 2000 (3)[††] | 4 | 12 | 29 | 0.7 | No |
| 28 | 2.0 | 2000 (3)[††] | 4 | 12 | 10 | 0.2 | Yes |
| 13 | 3.1 | 2000 (2) | 4 | 12 | 6.4 | 0.2 | No |
| 16 | 3.4 | 2000 (2) | 4 | 12 | 5.9 | 0.1 | Yes |
| 10 | 6.3 | 2000 (2) | 4 | 12 | 3.2 | 0.1 | Yes |
| 7 | 33.6 | 6000 (6) | 8 | 24 | 1.8 | 0.03 | No |
| 5 | 97.1 | 8000 (8) | 12 | 36 | 0.8 | 0.02 | Yes |
| 4 | 136.8 | 8000 (8) | 12 | 36 | 0.6 | 0.01 | Yes |
| 2 | 854.1 | 8000 (8) | 12 | 36 | 0.1 | 0.002 | Yes |
| reference site[‡]: | | | | | | | |
| C | 3724 | 6000 (6) | 8 | 24 | - | - | - |
| S | 3724 | 6000 (6) | 8 | 24 | - | - | - |
| N | 3724 | 6000 (6) | 8 | 24 | - | - | - |
| Total | 3724 | 18000 (18) | 24 | 72 | 0.05 | 0.001 | Yes |

[*] Includes first 10 m segments of belt transects and individually established plots.

[**] Presence/absence data only.

[†] Entire site was searched.

[††] Sites were not large enough to establish two complete 100 m belt transects.

[‡] Reference forest sites: C = Coastal scrub, S = Upland deciduous on predominantly south-facing slope, N = Upland deciduous on predominantly north-facing slope.

and all rocks were cleared in order to locate subterranean nests.

Whenever possible, soldiers and winged reproductives (alates) were collected from each colony and field preserved in 80% ethanol for later 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 original descriptions of Snyder (1923, 1924, 1929) and taxonomic key (Snyder 1956). Two questionable determinations were verified by R. H. Scheffrahn (University of Florida) and included comparisons with reference specimens.

### *Sample Size*

The total number of samples taken from each site was largely a function of area; the number of samples increased as the area of the site increased (Table 2). However, due to the amount of time required for each sample (between 1 and 2 hours on average to search a plot) it was impossible to achieve a constant proportion of area sampled across all sites (Table 2). Ultimately, the determination of the number of samples taken from each site was based on maximizing the number of sites that could be sampled with the given time constraints while maintaining some degree of consistency for the proportion of area sampled. In order to evaluate the effectiveness of this sampling design, performance curves were constructed for each site using data from the 2m x 2m plots. The mean nest density for one of the most common species in the region, *Procryptotermes corniceps* (Snyder), was used to create the performance curves.

### *Colony Composition*

Entire colonies of *Procryptotermes corniceps* were collected during directed searches for their nests. Collecting these colonies proved to be too time consuming to conduct during the 2 m x 2 m plot sampling. Dead branches and SDW were searched until a colony was discovered, whereupon every attempt was made to collect the entire colony into 80% ethanol. Each colony was later examined and enumerated using a dissecting microscope. All termites were placed in one of the following categories: 1) primary reproductives, 2) alates, 3) soldiers, 4) pseudergates and nymphs with short wing pads (tip of mesothoracic wing pad not extending beyond thoracic segments), 5) nymphs with long wing pads, and 6) larvae (first three instars). Lightly pigmented replacement (neotenic) reproductives were unable to be differentiated. The total number of termites within each category was recorded for each colony. In addition, the number of eggs collected was noted, but it is unlikely that these figures accurately represent the amount of eggs within each colony.

### *Nest Characteristics of Nasutitermes spp.*

For each *N. acajutlae* and *N. costalis* nest encountered along the belt transects, a series of measurements was taken in order to reveal any patterns in their choice of nesting locations and to determine if there are any differences between the two species with respect to nesting location and nest size. These measurements included: 1) tree species in which the nest was situated, 2) height of nest (from ground to base of nest), 3) diameter of all supporting stems (measured at point of entry into nest), 4) general shape of the nest, and 5) nest diameters. Most nests had an ellipsoid shape and therefore required the measurement of three diameters: length, width, and depth. These diameters were used to obtain three radii values for each nest. Depending on the general shape of the nest, volume was calculated using one of three formulas: 1) $V=4/3\pi r^3$ (sphere), 2) $V=4/3\pi r_1 r_2 r_3$ (ellipsoid), and 3) $V=1/3\pi r^2 h$ (cone). The volume of all satellite nests was also determined and combined with that of the main nest in order to obtain a value for total nest volume. Basal area ($A=\pi r^2$) of all supporting stems was calculated for each nest.

## RESULTS & DISCUSSION

The survey of termites from the southwestern region of Puerto Rico revealed 10 species from 8 genera and 3 families (Table 3). One species, *Caribitermes discolor* (Banks), had not been previously documented from this region, while another species (*Incisitermes snyderi* (Light)) listed for this region was not present in any of the samples and could not be located during systematic searches of the sites (Jones & Scheffrahn *unpublished*).

### *Sampling Effectiveness*

Examination of the performance curves revealed that even though a large proportion of the small (< 1 ha) sites was sampled (Table 2), the estimates of *P. corniceps* abundance may not be as accurate as those obtained from larger sites (Appendix B). For instance, the mean nest density at site 36 was still fluctuating widely from sample to sample at the end of the curve. In general, increasing the number of samples as the area of a site increased resulted in more reliable estimates of *P. corniceps* abundance. However,

Table 3. Mean termite nest densities within a relatively undisturbed dry forest (Guánica Forest). + = present but not quantified.

| Species | Nest Density (/ha) |
|---|---|
| Kalotermitidae | |
| *Incisitermes bequaerti* (Snyder) | 35 |
| *Neotermes mona* (Banks) | -- |
| *Procryptotermes corniceps* (Snyder) | 2222 |
| Rhinotermitidae | |
| *Heterotermes* spp. | 13 |
| *H. tenuis* (Hagen) | |
| *H. convexinotatus* (Snyder) | |
| Termitidae | |
| Apicotermitinae | |
| *Anoplotermes* sp. (*meridianus*) Emerson | + |
| Nasutitermitinae | |
| *Caribitermes discolor* (Banks) | 69 |
| *Nasutitermes acajutlae* (Holmgren) | 6.5 |
| *Nasutitermes costalis* (Holmgren) | + |
| *Parvitermes wolcotti* (Snyder) | 243 |

the tremendous number of samples required to obtain relatively accurate density estimates becomes evident when examining the performance curve for all reference sites combined (Appendix B). Approximately 50 samples (200 $m^2$ area sampled) were required before the cumulative mean density of *P. corniceps* became insensitive to fluctuations in the data.

The abundance estimates for the remainder of the termite species in this study was not as reliable as the abundance estimates obtained for *P. corniceps*. Due to their low frequency of occurrence, performance curves for the other termite species never reached a point where the cumulative mean was insensitive to fluctuations in the data. For example, even with all the reference sites combined (96 samples total), the cumulative mean nest density for *Incisitermes bequaerti* (Snyder) would double with the addition of 1 nest in a subsequent sample (Figure 2).

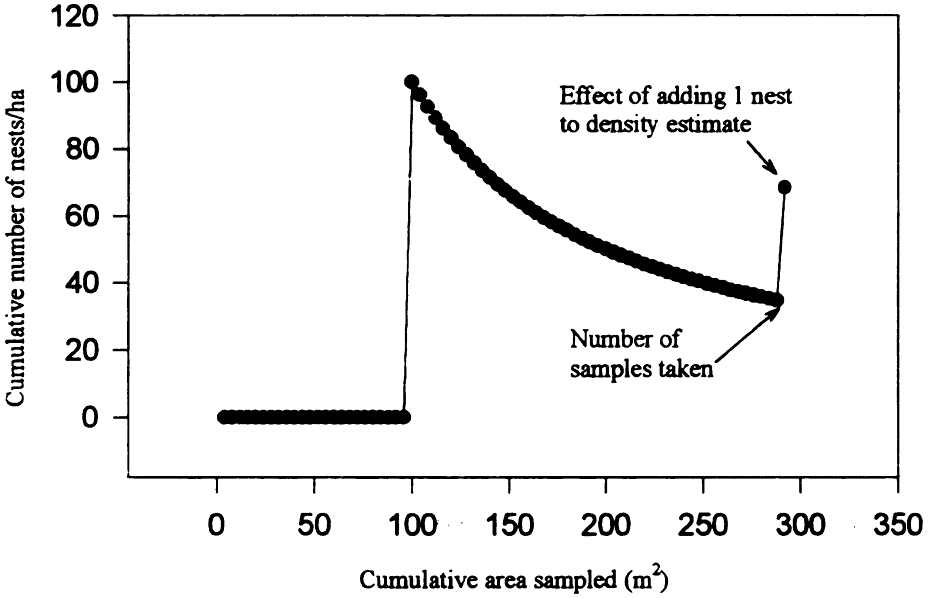

Figure 2. Performance curve for the mean nest density (no. nest/ha) of *Incisitermes bequaerti* at the reference site (all three sites combined).

Eggleton and Bignell (1995) discuss the numerous problems associated with sampling termite populations in terms of the number of individuals. They suggest that the aggregated distribution of termites within colonies and the variety of microhabitats that different species occupy make ecological studies of termites difficult to undertake. It appears that these same problems can be extended to studies which utilize the termite colony rather than individuals as the sampling unit. For example, the majority of the termite species encountered in this study had a patchy distribution of colonies, and there was a wide variety of microhabitat types in which termite colonies were located. In addition, the extremely rare occurrence of some termite species in the southwestern dry forests of Puerto Rico and their inconspicuous nest locations exacerbated the above mentioned difficulties.

### *Kalotermitidae*

*Procryptotermes corniceps* was the most widespread and common termite species in the dry forests of southwestern Puerto Rico. Likewise, it has also been reported as the most common kalotermitid in natural vegetation on Providenciales and Grand Turk Islands (Turks & Caicos Islands) (Scheffrahn *et al.* 1990) and as the most common termite species on Mona Island (Jones *et al.* 1995). It occurred in 14 of the 15 sites sampled (not collected from site 40; Figure 1) and had densities that ranged from 500-4375 nests/ha. The nest density at the three sites within Guánica Forest ranged from 1042-3438/ha (mean = 2222) (Table 3). *P. corniceps* colonies were found in wood spanning a wide range of densities (Table 4). Moreover, Wolcott (1950) rates *B. simaruba* and *C. rosea* as "very

Table 4. List of plant species colonized by *Procryptotermes corniceps* and the frequency each species was colonized (when identification was possible). Type of host species also included: t = tree, s = shrub, v = vine.

| Species | Type | Frequency | Specific Gravity[†] |
|---|---|---|---|
| *Acacia retusa* | v | 2 | |
| *Amyris elemifera* | t | 1 | 1.0-1.1 |
| *Bursera simaruba* | t | 2 | 0.29 |
| *Canella winterana* | t | 2 | 0.9-1.0 |
| *Clusea rosea* | t | 1 | 0.67 |
| *Coccoloba diversifolia* | t | 1 | 0.8 |
| *Coccoloba krugii* | t | 2 | |
| *Coccoloba microstachya* | t | 2 | |
| *Cordia bullata humilis* | s | 1 | |
| *Croton asteroites* | s | 2 | |
| *Eugenia rhombea* | t | 1 | |
| *Gymnanthes lucida* | t | 6 | 1.1 |
| *Krugiodendron ferreum* | t | 1 | 1.3-1.4 |
| *Lantana involucrata* | s | 2 | |
| *Leucaena leucocephala* | t | 17 | 0.7 |
| *Pithecellobium unguis-cati* | t | 4 | |
| *Tabebuia heterophylla* | t | 1 | 0.58 |
| unidentifiable dead branches | - | 88 | |
| unidentifiable SDW | - | 33 | |
| unidentifiable dead vines | v | 8 | |

[†] from Little & Wadsworth (1964)

susceptible", *K. ferreum* as "very resistant", and *A. elemifera* as "repellent" to the closely related drywood termite, *Cryptotermes brevis*. These findings corroborate previous evidence (Jones et al. 1995, Jones & Scheffrahn *unpublished*) that *P. corniceps* is a generalist in subtropical dry forests, where it attacks tree species that span a broad range of wood densities and degrees of relative susceptibility.

The colony size of *P. corniceps* ranged from 4 to 2,394 individuals (not including eggs) (Table 5). Eggs were found in colonies of all sizes, including the largest and smallest colonies collected. Alates were only found in colonies that had 92 or more individuals, although not consistently. For instance, alates were not found in two of the larger colonies, one with n = 203 termites and the other with n = 488 termites. When present, alate percentages ranged from 0.9% to 4.2% of the colony, while soldier percentages ranged from 1.5% to 25% of the colony.

Jones *et al.* (1995) reported similar percentages for *P. corniceps* alates (1.5 - 9.8%) and soldiers (0.7 - 20.5%) from another location within Puerto Rico's subtropical dry forest life zone, Mona Island. It is worth noting that the slightly higher percentages of alates within the colonies sampled by Jones *et al.* (1995) could reflect the seasonal variability of alate occurrence within the nest. The dispersal of alates in the tropics generally occurs during a single rainy season (Nutting 1969). Colonies from Mona Island were collected in March, prior to the short rainy season that often occurs in this region during the month of May (Ewel & Whitmore 1973). The present study collected colonies in July, after this short rainy season, but before the extended wet season that lasts from August to November. Even though both studies collected *P. corniceps* alates just prior to

Table 5. Colony composition of *Procryptotermes corniceps*.

| Site[*] | Larvae | Pseudergates & Short Wing-pad Nymphs | Long Wing-pad Nymphs | Soldiers | Primary Reproductives | Eggs | Alates | Total |
|---|---|---|---|---|---|---|---|---|
| 7 | 0 | 5 | 0 | 2 (22.2%) | 2 | 1 | 0 | 9 |
| Guánica | 2 | 11 | 0 | 1 (6.3%) | 2 | 0 | 0 | 16 |
| Guánica | 8 | 56 | 0 | 3 (4.4%) | 2 | 0 | 0 | 69 |
| Guánica | 19 | 500 | 16 | 11 (2.0%) | 2 | 19 | 10 (1.8%) | 558 |
| Guánica | 14 | 177 | 0 | 10 (4.9%) | 2 | 0 | 0 | 203 |
| Guánica | 0 | 13 | 2 | 4 (20%) | 1 | 0 | 0 | 20 |
| Guánica | 0 | 73 | 9 | 9 (9.4%) | 1 | 0 | 4 (4.2%) | 96 |
| Guánica | 1 | 3 | 0 | 1 (16.7%) | 1 | 0 | 0 | 6 |
| 4 | 1 | 10 | 0 | 0 (0.0%)[†] | 2 | 10 | 0 | 13 |
| 4 | 10 | 456 | 0 | 20 (4.1%) | 2 | 3 | 0 | 488 |
| Guánica | 0 | 17 | 0 | 1 (5.0%) | 2 | 2 | 0 | 20 |
| Guánica | 0 | 6 | 0 | 1 (11.1%) | 2 | 0 | 0 | 9 |
| Guánica | 0 | 6 | 0 | 0 (0.0%)[†] | 2 | 3 | 0 | 8 |
| Guánica | 0 | 1 | 0 | 1 (25%) | 2 | 1 | 0 | 4 |
| Guánica | 2 | 30 | 0 | 5 (12.8%) | 2 | 1 | 0 | 39 |
| Guánica | 0 | 77 | 0 | 6 (7.1%) | 2 | 4 | 0 | 85 |
| Guánica | 3 | 69 | 8 | 7 (7.6%) | 2 | 1 | 3 (3.3%) | 92 |
| Guánica | 59 | 2186 | 89 | 36 (1.5%) | 2 | 31 | 22 (0.9%) | 2394 |

[*] See Figure 1 for site locations.

[†] Identification of colony can not be confirmed due to lack of soldiers.

a rainy season, the extent to which these alates disperse during each rainy season has not been described for this region. Thus, an accurate explanation of the discrepancy between the two studies may not be achieved until the seasonal flight pattern of *P. corniceps* alates is described for this region.

The largest termite encountered during the two summers of sampling was *Neotermes mona* (Banks). This species was originally described from Mona Island (Banks 1919) and has also been reported from Hispaniola (Dominican Republic) (Scheffrahn *et al.* 1994) and the Turks & Caicos (Grand Turk, Parrot Cay, and Providenciales) (Scheffrahn *et al.* 1990). This species was neither widespread nor common, occurring in only 4 of the 15 sites (sites 4, 7, 27, and 28; Figure 1) with densities that ranged from 104-208 nests/ha. Despite extensive searches on several occasions, this species was not located within Guánica Forest. Colonies of *N. mona* were collected exclusively from *L. leucocephala*. However, it has also been collected from *B. simaruba* and *Meliococcus bijugatus* (Jones *et al.* 1995).

*Incisitermes bequaerti* was collected on only one occasion (Guánica Forest), which yielded a density estimate of 35 nests/ha for that site (Table 3). This species has been reported from Bermuda, Cuba, Hispaniola (Dominican Republic), Mona, the Turks & Caicos (Grand Turk and Providenciales), and the US Virgin Islands (St. Croix and St. Thomas) (see Scheffrahn *et al.* 1994 for compilation of locality references). Another member of this genus, *I. snyderi*, has been reported from the subtropical dry forest life zone of Puerto Rico (Jones & Scheffrahn *unpublished*), but was not located during this study. Both *I. bequaerti* and *I. snyderi* have been listed as more common in the eastern dry forests of Puerto Rico than that of southern Puerto Rico (Jones & Scheffrahn *unpublished*). In addition, recent evidence indicates that *I. snyderi* may actually be *I. incisus* (Scheffrahn *pers. comm.*).

## *Rhinotermitidae*

*Heterotermes tenuis* (Hagen) and *Heterotermes convexinotatus* (Snyder) have both been reported to occur within the dry forests of southwestern Puerto Rico (Jones & Scheffrahn *unpublished*). However, differentiating between these two species often proves problematic considering the vagueness of Snyder's (1956) taxonomic key. It is still unclear whether these species represent a single extremely variable species or a complex of closely related distinct species (Scheffrahn *et al.* 1994). Therefore, species identifications for *Heterotermes* could not be accomplished, although they presumably are *H. tenuis* and *H. convexinotatus* (Snyder 1956).

*Heterotermes* spp. occurred at 13 of the 15 sites (at all sites except 27 and 36; Figure 1), being one of the most prevalent termites of the dry forest. Similarly, Jones and Scheffrahn (*unpublished*) report *Heterotermes* spp. as being the most abundant subterranean termites in the subtropical dry forest life zone of Puerto Rico. Nest densities ranged from 13-167/ha at all sites, but was consistently 13 nests/ha at the three sites within Guánica Forest (Table 3). However, these estimates should be interpreted with caution due to the difficulties in determining the extent of the foraging territories of individual colonies which likely extend to distances of 10 m or greater (Scheffrahn *pers. comm.*). For instance, these termites were often collected in SDW with galleries leading underground. If this situation occurred multiple times within the same 10m x 10m plot then these termites were treated as 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.

*Heterotermes* spp. were collected under rocks and in dead wood, including *Pisonia albida, Leucaena leucocephala,* and *Bursera simaruba*. Foraging groups of these species could often be located by scraping away the light brown tunnels that they construct on the surface of and within dead wood. These tunnels closely resembled those of *Parvitermes wolcotti* which are constructed out of soil (Snyder 1923).

### *Termitidae*

The only soldierless termite species of the subtropical dry forests of Puerto Rico belongs to the genus *Anoplotermes*. However, species identifications could not be assigned for this genus due to the absence of alates within the colonies encountered during sampling. Alates were collected once within the colony, but the species identification has not yet been designated (Scheffrahn *pers. comm.*). It is currently believed that the only species from this genus that occurs in Puerto Rico is *A. meridianus* Emerson (Snyder 1956, Jones & Scheffrahn *unpublished*). This species was present at 7 of the 15 sites (sites 2, 4, 5, 7, 28, 30 and Guánica N; Figure 1), and had nest densities in the range of 69-1000/ha. These densities may overestimate the abundance of this species because colonies were on occasion assumed to lie within the 2 m x 2 m plots when only foraging workers were found in the litter layer. Colonies of *Anoplotermes* sp. were not encountered during quantitative sampling at Guánica Forest, but were discovered during qualitative searches of the site. In addition to the litter layer, this species was also frequently found under rocks.

One of the smallest termites of Puerto Rico's dry forests is *Parvitermes wolcotti* (Snyder). This species was originally described from specimens collected at Boqueron, Puerto Rico (Snyder 1924), but has since been reported from the British Virgin Islands (Great Camanoe, Guana, Eustatia, Virgin Gorda) (Scheffrahn *et al.* 1994). This subterranean species occurred at 9 of the 15 sites (sites 4, 5, 7, 10, 27, 28, 30, and Guánica Forest sites S and N; Figure 1) with densities ranging from 69-500 nests/ha. At the three sites within Guánica Forest the range was 0-417 nests/ha (mean = 243) (Table 3). Once again, these estimates should be interpreted with caution as nothing is known of the foraging territory for this species. Colonies were located mostly under rocks, but foraging individuals were on occasion collected from dead wood, including *Pithecellobium unguis-cati*.

*P. wolcotti* workers and soldiers were also collected from soil tunnels and sheetings covering dead branches in the litter layer and SDW. These could easily be distinguished from the carton galleries of *Nasutitermes* spp. based on size and color. *P. wolcotti* tunnels were about half the width of the tunnels of *Nasutitermes* spp. and were light tan in color, while those of *Nasutitermes* spp. were dark brown. As mentioned earlier, it was impossible to distinguish *P. wolcotti* tunnels from those of *Heterotermes* spp. based upon visual inspection alone.

*Caribitermes discolor* had not been previously documented from the subtropical dry forest life zone of Puerto Rico. This species was recently reclassified from the genus *Parvitermes* to the new monotypic genus *Caribitermes* (Roisin 1996). *C. discolor* was collected on only two occasions, both within an area of Guánica Forest that has had minimal human disturbance over the past 60 years. These occurrences yielded a nest density of 208/ha for the relatively undisturbed site and an average density of 69 nests/ha for Guánica Forest (Table 3). This species is listed as common in Puerto Rico's subtropical moist forest, subtropical wet forest, subtropical rain forest, and lower montane wet forest life zones (Jones & Scheffrahn *unpublished*). During surveys within the subtropical wet forest life zone at El Verde, Puerto Rico, *C. discolor* foragers were found infesting one in six small (<5 cm diameter) dead branches on the forest floor (McMahan 1996). The environmental factors limiting the range of this species remain unclear. However, judging from its abundance in the other life zones, moisture probably plays a major role by limiting the colonization and initial breakdown of wood by other decomposers such as fungi, which may be a prerequisite for consumption by *C. discolor*.

One of the most prominent features of the dry forest are the arboreal nests of *Nasutitermes acajutlae* and *Nasutitermes costalis*. These nests ranged in density from 3.6-18/ha for *N. acajutlae* and 1.2-4.8/ha for *N. costalis* at the sites in which they were recorded during quantitative sampling. *N. acajutlae* was also more widespread than *N. costalis*, occurring at 13 of the 15 sites (at all sites except 10 and 40, Figure 1) while *N. costalis* only occurred at 7 sites (sites 2, 4, 7, 10, 16, 27, and Guánica S; Figure 1). Within Guánica Forest, *N. acajutlae* nest density ranged from 4.8-9.7/ha (mean = 6.5) (Table 3). *N. costalis* was not encountered in Guánica Forest while sampling along the belt transects, however, it was recorded during a qualitative search. Both *Nasutitermes* spp. have been reported from the subtropical dry, moist, and wet forest life zones of Puerto Rico (Jones & Scheffrahn *unpublished*). The above results contradict earlier reports (Martorell 1945, Wolcott 1948) that list *N. acajutlae* (=*N. creolina*) as scarce in Puerto Rico. Perhaps, *N. acajutlae* was often misidentified as *N. costalis* during these

Figure 3. Arboreal nest of *N. acajutlae* in *Tamarindus indica*.

earlier reports, as the two species are very similar. Their distinguishing characteristics (pilosity of soldier head capsule and abdominal tergites) can not be easily evaluated in the field.

In comparison to the dry forest life zone, the opposite trend in terms of *Nasutitermes* spp. abundance exists in the wet forest life zone of Puerto Rico. At El Verde *N. costalis* appears to be the common *Nasutitermes* sp. with a density of 4.5 nests/ha (McMahan 1996). *Nasutitermes acajutlae* has much lower nest densities at El Verde, with only 0.47 nests/ha. However, nests of *N. acajutlae* are generally much larger than those of *N. costalis*, a trend that is repeated in the dry forest life zone.

The size of the arboreal nests of *N. acajutlae* was often quite large, with some exceeding 1 m in height. In fact, this species builds arboreal nests that are among the largest known for termites (Thorne *et al.* 1994). Most large nests of *N. acajutlae* had an ellipsoid shape (Figure 3). The volume of *N. acajutlae* nests was significantly greater than those of *N. costalis* (Mann-Whitney: $U=161$, $n_1=5$, $n_2=36$, $P<0.0025$; Figure 4a). Nests of *N. costalis* generally did not exceed the size of a basketball in the dry forest.

Nest volume has been implemented as a way to estimate *Nasutitermes* spp. colony size by determining a termite density-nest volume relationship (Weigert 1970, Clarke & Garraway 1994). Applying a model created using *N. costalis* nests from the wet forest life zone (Weigert 1970) to dry forest nests yields colony sizes ranging from 9,600-79,000 individuals. Much higher colony sizes were estimated using the nest volumes of *N. costalis* from the wet forest, however, there is too little data to support any causal relationships between climatic variables and colony size. If this same model were applied to the nest volume estimates of *N. acajutlae*, colony size would range from 12,800-

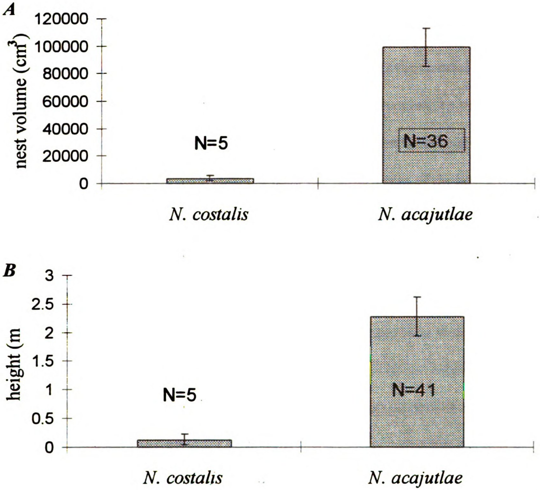

Figure 4. Nest characteristics of *Nasutitermes* spp., (A) nest volume and (B) height of the nest from ground. Vertical bars represent ±1 SE of the mean.

800,000 termites/nest. A similar analysis by Clarke and Garraway (1994) of *N. nigriceps* nests from mangrove forests in Jamaica yielded lower estimates of colony size (see below for taxonomic discussion of *N. nigriceps* and *N. acajutlae*).

Even though these models are being applied to other species and life zones, they may still be a relatively accurate way to obtain estimates of colony size for species that build carton nests. Their utility depends on whether colony size is mainly determined by characteristics of the species, physical properties of the nest, environmental variables, or some combination of these factors. If colony size is solely determined by the physical properties of the nest, then these models should be applicable to other regions as well as closely related species. One suggestion has been that surface area of the nest affects the overall rate at which oxygen and carbon dioxide can diffuse throughout the nest, thereby limiting the number of termites that can be accommodated within the nest (Weigert 1970).

Martorell (1945, 1941) lists 108 tree species that are affected by *N. costalis* in Puerto Rico. The present study did not include quantitative sampling to determine which tree species were being consumed by *Nasutitermes* spp., as only nest locations were recorded. *N. acajutlae* exhibited a preference for the tree species *Bucida buceras, Pisonia albida,* and *Pilosocereus royenii* for its nesting location, while there was not enough data to determine any preferences for *N. costalis* (Table 6).

Selection of the nesting site probably depends more on the size rather than the species of the supporting plant. The mean basal area of the stems supporting *N. acajutlae* nests was 0.039 $m^2$. The diameter of a single supporting stem needed to yield such a basal area is 22 cm. Considering that 95% of the trees in a reference site within Guánica Forest have a DBH less than 7.5 cm (Murphy & Lugo 1986), suitable nesting locations are

Table 6. Location of *Nasutitermes* spp. arboreal nests, including the frequency for each tree species or general position if not situated in a live tree.

| Location | Frequency<br>*N. acajutlae* | <br>*N. costalis* |
|---|---|---|
| *Bucida buceras* | 18 (25.7%) | |
| *Pisonia albida* | 9 (12.9%) | |
| *Pilosocereus royenii* | 7 (10.0%) | 1 (16.7%) |
| *Leucaena leucocephala* | 5 (7.1%) | 1 (16.7%) |
| *Clusia rosea* | 3 (4.3%) | |
| *Sweitenia mahogani* | 3 (4.3%) | |
| *Capparis hastata* | 2 (2.9%) | |
| combination of trees[†] | 2 (2.9%) | |
| dead tree (horizontal) | 2 (2.9%) | |
| *Erythroxylum areolatum* | 2 (2.9%) | |
| *Erythroxylum rotundifolium* | 2 (2.9%) | |
| *Leptocereus quadricostatus* | 2 (2.9%) | |
| *Acacia farnesiana* | 1 (1.4%) | |
| *Calyptranthes pallens* | 1 (1.4%) | |
| *Capparis cynophallophora* | 1 (1.4%) | 1 (16.7%) |
| *Coccoloba diversifolia* | 1 (1.4%) | |
| *Colubrina elliptica* | 1 (1.4%) | |
| *Delonix regia* | 1 (1.4%) | |
| *Ficus citrifolia* | 1 (1.4%) | |
| *Haematoxylum campechiaum* | 1 (1.4%) | |
| *Pictetia aculeata* | 1 (1.4%) | 1 (16.7%) |
| *Prosopis pallida* | 1 (1.4%) | |
| *Randia aculeata* | 1 (1.4%) | |
| *Tamarindus indica* | 1 (1.4%) | |
| on ground | 1 (1.4%) | |
| *Gymnanthes lucida* | | 1 (16.7%) |
| *Tabebuia heterohylla* | | 1 (16.7%) |
| **Total** | **70** | **6** |

[†] *Bursera simaruba*/*Zanthoxylum flavum* and *Bursera simaruba*/*Capparis flexuosa*/*Pithecellobium unguis-cati*.

limited to tree species capable of producing adequately large trunks and branches. The two most preferred trees, *B. buceras* (26%) and *P. albida* (13%), are also two of the most common large (>20cm DBH) tree species of the dry forest life zone. *Bursera simaruba* is another common tree of the dry forest life zone capable of exceeding 20 cm DBH, but its wood is very lightweight (specific gravity 0.29) and may not be able to support the very large nests of *N. acajutlae*. It also becomes evident after examining the tree preference data that these termites do not attack the tree in which their nest is situated, as the pipe-organ cactus (*Pilosocereus royenii*) is one of the most preferred species.

The average height of the nest off the ground was another variable that was significantly different between the two *Nasutitermes* spp. *N. acajutlae* nests were located at greater heights in trees than the nests of *N. costalis* (Mann-Whitney: $U=190.5$, $n_1=5$, $n_2=41$, $P<0.0005$; Figure 4b). Three out of the five *N. costalis* nests recorded were located on the ground. Their nests have also been reported occurring on the ground in Puerto Rico's rain forests (Weigert 1970) and in the Turks & Caicos Islands (Scheffrahn *et al.* 1990). It is unclear why this species seems to be limited to the ground, although moisture requirements may be a major factor in subtropical dry forest life zones.

*N. acajutlae* represents a recent taxonomic revision by Thorne *et al.* (1994) that is still being questioned by some Caribbean termite taxonomists (Jones & Scheffrahn *unpublished*). Previously this species was designated as *N. nigriceps* (Haldeman) by Snyder (1956). The current designation is based on the following morphological characteristics of the soldier: (1) pilosity of the head capsule, (2) indentation shape on the anterior margin of the pronotum, and (3) the presence of bristles on regions flanking the postmentum (Thorne *et al.* 1994). Thorne *et al.* (1994) proposed an eastern distribution throughout the Caribbean for *N. acajutlae* (Puerto Rico east and south to Trinidad, and Guyana) and a western distribution for *N. nigriceps* (Jamaica, Cayman Islands, Mexico south to Panama). Even though the issue is yet to be resolved, *N. acajutlae* was the name chosen to represent this species in this paper as it coincides with the current literature (Scheffrahn *et al.* 1994).

In conclusion, very little is known about the termites of Puerto Rico's subtropical dry forest life zone. With a few exceptions, previous knowledge of these termites was limited to the comments and observations listed in their original descriptions. This chapter summarized the data and observations that were collected during a quantitative survey of these termites throughout the dry forest life zone. A species was recorded that is new to this life zone, while a previously documented species occurrence was not confirmed. Nest densities were reported for the first time from a representative subtropical dry forest, Guanica Forest, providing new insight into termite community structure for this type of ecosystem. The drywood termite, *P. corniceps*, exhibited a colony composition and diet similar to previous findings (Jones & Scheffrahn 1995, Jones *et al.* 1995). A comparison of *Nasutitermes* spp. revealed many differences in terms of nest size, location, and abundance. *Nasutitermes acajutlae* was more common than its congener *N. costalis* in the subtropical dry forests of southwestern Puerto Rico, a result which contradicts earlier reports (Martorell 1945, Wolcott 1948).

# CHAPTER TWO

## Environmental Influences on the Distribution and Abundance Termite Species in a Subtropical Dry Forest

There are a multitude of environmental factors that affect the activity, distribution, and population density of termites. Of these factors, temperature, moisture, and availability of a food source have been implicated as major contributors (Lee & Wood 1971, Ueckert *et al.* 1976, Davis & Kamble 1994, Leponce *et al.* 1995, Cabrera & Rust 1996, Pearce 1997). In addition, certain structural characteristics of the habitat can greatly influence these variables, resulting in a diverse array of microhabitat conditions. For instance, temperature extremes experienced by termites are influenced by their ability to move underground or build soil runways, the amount of shade provided by various vegetation types (Sands 1965), and the presence of objects on the soil surface (i.e., rocks and litter) which provide a thermal shadow in the soil below (Lee & Wood 1971, Ettershank *et al.* 1980, Pearce 1997).

The subtropical dry forest life zone of Puerto Rico has a mean annual temperature of 25.1°C, a ratio of potential evapotranspiration to precipitation that exceeds unity, and soils that exhibit moisture deficits 10 months out of the year (Murphy & Lugo 1986). Suitable habitat for termites in this hot, dry environment may be limited to areas where enough cover exists to provide refugia from high temperatures and allow the retention of moisture in the soil for relatively extended periods.

Termites have differing temperature and moisture tolerances, which can vary among genera and families as well as at the species level (Pearce 1997). For instance, termites in the family Kalotermitidae build their nests in sound dry wood and do not require contact with the soil. Their nesting location combined with their resistance to desiccation (Pearce 1997) would suggest that Kalotermitids are not going to be affected by soil moisture deficits as much as other termites.

The objective of this chapter is to determine whether structural variables of the habitat that influence its temperature and moisture levels can also affect termite distributions in a subtropical dry forest. The knowledge gained from such an investigation coupled with a landscape-level analysis (Chapter 3) is of great importance to conservation planning. Knowledge of species' habitat requirements or preferences can be used to limit the extent of area in a landscape considered as 'suitable' and can therefore focus efforts towards habitats with greater conservation value (Scott *et al.* 1993). The value of such habitat studies increases when the variables that affect the distribution of a species can be detected by remote sensing (i.e., percent canopy cover, vegetation type) or determined from pre-existing spatially referenced data sources (i.e., soil type, elevation, aspect).

Another area of conservation planning involves the use of indicator groups to predict the occurrence of a wide range of other unrelated groups in order to pinpoint diversity 'hotspots'(Kremen 1992, Pearson & Cassola 1992, Kremen 1994, Beccaloni & Gaston 1995, Abensperg-Traun et al. 1996a). The determination of a potential indicator group is accomplished by looking for a group of organisms (e.g., butterflies, tiger beetles) whose species richness is correlated with that of a number of other groups of organisms. While it is not the objective of this chapter to make a case for termites as biodiversity indicators (they do not fit the criteria established by Pearson & Cassola 1992), it would still be useful for conservation purposes to determine whether the diversity of the termite community is correlated to the diversity of other communities of the dry forest life zone. Therefore, this chapter also investigates whether any correlations exist between termite species richness and the species richness of plant and lizard communities.

## MATERIALS & METHODS

### *The Study Region*

The southwestern portion of Puerto Rico includes the majority of the island's subtropical dry forest life zone. This region extends east along the south coast approximately 120 km from the southwest corner of the island (Figure 1) and reaches between 3 and 20 km inland, depending on local topography (Ewel & Whitmore 1973). Although there is considerable temporal variability, annual precipitation ranges from 600 mm in the west of the dry forest life zone to about 1,000 mm in the east.

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 in 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 associations. Three sites within Guánica Forest were selected in order to obtain baseline data for termite communities in a relatively undisturbed, contiguous subtropical dry forest. In addition, twelve forest fragments of various sizes (Figure 1) were randomly selected for study from a total of 40 sites in which the vegetation composition and structure had previously been documented (Ramjohn *et al. unpublished*; Appendix A). A more complete description of the study sites, Guánica

Forest, as well as the dry forest life zone of Puerto Rico can be found in the main Introduction of this thesis.

### *Nest Density*

A quantitative survey of the termites of the southwestern dry forests of Puerto Rico was conducted during the summer months of 1997 (May, June, and July) and 1998 (July and August). The location of the sampling plots (10 m x 10 m) was determined by randomly selecting points on a grid overlay of the aerial photos of each site. Large fragments (>10 ha) and sites within Guánica Forest were stratified using four aspect categories (N-, S-,E-, W-facing slopes) and one category for ravine areas. The number of samples selected from each category was largely determined by the proportion of the total area that each represented.

The total number of samples taken from each site was largely a function of area; the number of samples increased as the area of the site increased (Table 2). However, due to the amount of time required for each sample (between 1 and 2 hours on average to search a plot) it was impossible to achieve a constant proportion of area sampled across all sites (Table 2). Ultimately, the determination of the number of samples taken from each site was based on maximizing the number of sites that could be sampled with the given time constraints while maintaining some degree of consistency for the proportion of area sampled.

The abundance of termites was determined by exhaustively searching three 2 m x 2 m subplots which were randomly selected within each 10 m x 10 m plot. The majority of termite species encountered build relatively small nests and have foraging territories that generally did not extend beyond the boundary of the 2 m x 2 m subplot. For these species, the total number of nests recorded from the three nested 2 m x 2 m subplots was used as a measure their abundance. For termite species that forage great distances (>10 m), the three nested 2 m x 2 m subplots may lie entirely within the foraging territory of a single colony (Scheffrahn *pers. comm.*). Multiple occurrences of such species (e.g., *Heterotermes* spp., *Nasutitermes* spp.) within the same 10 m x 10 m plot were treated as foragers from the same colony, and only one colony was recorded for the entire plot.

### *Habitat Variables*

Associations between termites and characteristics of the habitat were examined on two spatial scales. The present study collected habitat structural data within randomly selected 10 m x 10 m plots located within the forest fragments. The composition and structure of the plant communities within the twelve forest fragment study sites was previously described by Ramjohn *et al.* (*unpublished*) (see Appendix A) as part of a related study and was incorporated into this study to investigate the effects of habitat structure on termite communities at a spatial scale greater than the 10 m x 10 m plots. In addition, associations between termite and lizard species richness were also examined using the forest fragment as the sampling unit.

#### *10 m x 10 m Plots*

A number of variables describing habitat structure and composition were recorded for each 10 m x 10 m plot. A compass was used to determine the primary aspect of the plot using eight direction categories (N, NE, E, SE, S, SW, W, NW) and one category for plots that were located on flat terrain. The canopy of each plot was classified by visual inspection as either open (<33% cover), partially open (34-66%) or closed (67-100%). For relatively short canopies (< 4 m), canopy height was measured with a 2 m measuring stick held at a known height above the ground. Canopy height for taller tracts of forest had to be estimated by visual inspection. Species richness of the woody vegetation (tree, shrub, and vine) within a plot was accomplished by thoroughly searching each plot and recording the number of species present.

Other variables that were estimated for each plot include the percentage of rock covering the ground and the average depth of the litter layer. The percentage of the substrate within a plot covered by rock outcroppings was estimated by visual inspection. Litter depth was measured by vertically inserting a metric ruler into the litter layer until it reached the soil surface. Measurements were taken at five random locations within the plot to obtain an average litter depth.

Spearman's rank correlation was used to examine the associations between the diversity and abundance of termites and the following habitat variables: canopy height, percent rock, litter depth, and the species richness of woody vegetation. The percentage of rock was arcsine transformed in order to approach an underlying normal distribution (Zar 1984). Correlations were performed between the habitat variables and termite species richness as well as with the individual densities of the most abundant termite species from each of the three families. Limiting the analysis to only the most abundant species in each family was necessary because the rare occurrence of other species precluded determination of any patterns in their distributions.

The abundances of termite species which nest in similar locations were pooled (see Table 7) and included in the correlation analysis in order to determine whether any associations exist between these groups and the habitat variables. Drywood termites refer to species belonging to the family Kalotermitidae. These species excavate their nest within their food source, dead wood that can either be on the ground or still standing. The subterranean group includes termites from the families Rhinotermitidae and Termitidae. These species construct their nests within the soil but may forage above ground. The arboreal group consists of two species from the family Termitidae which build carton nests on the exterior of trees.

Table 7. The termite groupings used in determining associations with habitat variables.

| Group | Species Included |
|---|---|
| Drywood termites | *Incisitermes bequaerti*<br>*Neotermes mona*<br>*Procryptotermes corniceps* |
| Subterranean termites | *Anoplotermes* sp.<br>*Caribitermes discolor*<br>*Heterotermes* spp.<br>*Parvitermes wolcotti* |
| Arboreal termites | *Nasutitermes acajutlae*<br>*Nasutitermes costalis* |

In order to evaluate whether aspect or canopy cover has any influence on the species richness of termite communities or the abundance of individual termite species, a Kruskal-Wallis nonparametric analysis of variance (ANOVA) was performed. The combined total abundance of the species within each of the groups (Table 7) was also analyzed using the Kruskal-Wallis ANOVA. In all cases with significant ANOVAs, multiple comparisons were made with Tukey's Honestly Significant Difference (HSD). In addition, the diversity and abundance data from plots on primarily north-facing slopes (N, NE, NW) were grouped together in order to make the comparison with termite communities on south-facing slopes (S, SE, SW). In general, north-facing slopes in Puerto Rico's dry forest life zone receive more precipitation than south-facing slopes (Ewel & Whitmore 1973) which may affect the distribution of termites in this region.

### *Forest Fragments*

Plant species composition as well as vegetative structural data for the twelve sites were acquired from Ramjohn *et al.* (*unpublished*) (see Appendix A). The species richness of the lizard community within the study sites was obtained from K. Genet (*pers. comm.*). The vegetation data were collected during the previous two years as well as the same year that the termite and lizard data were collected.

Pearson correlation was used to examine individual associations between termite community attributes (e.g., species richness and individual abundances) and characteristics of the plant community. The vegetation variables included in the analysis were: (1) number of plant species, (2) number of tree species, (3) number of stems/ha greater than 1 cm DBH, (4) number of stems/ha greater than 2.5 cm, (5) number of stems/ha greater than 5 cm, and (6) mean basal area ($m^2$/ha). In addition, associations between termite richness and the species richness of plants, trees, and lizards within forest fragments were examined using Pearson correlation.

Table 8. Mean number of nests/ha for individual termite species at the 12 forest fragments and the reference site (Guánica Forest). SE = standard error.

| | | **Species** | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | *P. corniceps* | | *P. wolcotti* | | *Heterotermes* spp. | | *N. mona* | | *I. bequaetri* | |
| **site** | **area (ha)** | **mean** | **(SE)** | **mean** | **(SE)** | **mean** | **(SE)** | **mean** | **(SE)** | **mean** | **(SE)** |
| 40 | 0.006 | 0.00 | 0.00 | 0.00 | 0.00 | 166.67 | ** | 0.00 | 0.00 | 0.00 | 0.00 |
| 36 | 0.06 | 4375.00 | 1875.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 30 | 0.26 | 500.00 | 500.00 | 500.00 | 500.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 27 | 0.69 | 2083.33 | 1262.56 | 208.33 | 208.33 | 0.00 | 0.00 | 208.33 | 208.33 | 0.00 | 0.00 |
| 28 | 2.0 | 1250.00 | 652.79 | 0.00 | 0.00 | 0.00 | 0.00 | 208.33 | 208.33 | 0.00 | 0.00 |
| 13 | 3.1 | 3750.00 | 1393.30 | 0.00 | 0.00 | 50.00 | 28.87 | 0.00 | 0.00 | 0.00 | 0.00 |
| 16 | 3.4 | 1666.67 | 1243.67 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 10 | 6.3 | 0.00 | 0.00 | 0.00 | 0.00 | 50.00 | 28.87 | 0.00 | 0.00 | 0.00 | 0.00 |
| 7 | 33.6 | 729.17 | 318.48 | 312.50 | 172.40 | 37.50 | 18.30 | 104.17 | 104.17 | 0.00 | 0.00 |
| 5 | 97.1 | 833.33 | 199.20 | 69.44 | 69.44 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 4 | 136.8 | 972.22 | 401.85 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 2 | 854.1 | 625.00 | 270.49 | 0.00 | 0.00 | 33.33 | 14.21 | 0.00 | 0.00 | 0.00 | 0.00 |
| C | 3724 | 1041.67 | 751.16 | 0.00 | 0.00 | 12.50 | 12.50 | 0.00 | 0.00 | 0.00 | 0.00 |
| S | 3724 | 3437.50 | 925.34 | 312.50 | 172.40 | 12.50 | 12.50 | 0.00 | 0.00 | 0.00 | 0.00 |
| N | 3724 | 2187.50 | 607.78 | 416.67 | 194.27 | 12.50 | 12.50 | 0.00 | 0.00 | 104.17 | 104.17 |
| Guánica | 3724 | 2222.22 | 454.71 | 243.06 | 87.90 | 12.50 | 6.90 | 0.00 | 0.00 | 34.72 | 34.72 |

Table 8. cont'd

| | | **Species** | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | *Anoplotermes* sp. | | *C. discolor* | | *N. acajutlae* | | *N. costalis* | | unknown specimens | |
| **site** | **area (ha)** | **mean** | **(SE)** | **mean** | **(SE)** | **mean** | **(SE)** | **mean** | **(SE)** | **mean** | **(SE)** |
| 40 | 0.006 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | ** | 0.00 | ** | 0.00 | 0.00 |
| 36 | 0.06 | 0.00 | 0.00 | 0.00 | 0.00 | 17.97 | ** | 0.00 | ** | 0.00 | 0.00 |
| 30 | 0.26 | 1000.00 | 612.37 | 0.00 | 0.00 | 3.90 | ** | 0.00 | ** | 500.00 | 500.00 |
| 27 | 0.69 | 0.00 | 0.00 | 0.00 | 0.00 | 4.76 | 4.76 | 4.76 | 4.76 | 0.00 | 0.00 |
| 28 | 2.0 | 0.00 | 0.00 | 0.00 | 0.00 | 4.76 | 4.76 | 0.00 | 0.00 | 0.00 | 0.00 |
| 13 | 3.1 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 625.00 | 326.40 |
| 16 | 3.4 | 0.00 | 0.00 | 0.00 | 0.00 | 4.55 | 4.55 | 4.55 | 4.55 | 416.67 | 280.92 |
| 10 | 6.3 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 208.33 | 208.33 |
| 7 | 33.6 | 208.33 | 144.08 | 0.00 | 0.00 | 4.84 | 2.75 | 3.23 | 2.26 | 520.83 | 211.70 |
| 5 | 97.1 | 69.44 | 69.44 | 0.00 | 0.00 | 3.57 | 2.04 | 0.00 | 0.00 | 208.33 | 116.79 |
| 4 | 136.8 | 0.00 | 0.00 | 0.00 | 0.00 | 4.76 | 2.34 | 0.00 | 0.00 | 208.33 | 116.79 |
| 2 | 854.1 | 69.44 | 69.44 | 0.00 | 0.00 | 4.76 | 2.34 | 1.19 | 1.19 | 277.78 | 132.80 |
| C | 3724 | 0.00 | 0.00 | 0.00 | 0.00 | 4.84 | 2.75 | 0.00 | 0.00 | 104.17 | 104.17 |
| S | 3724 | 0.00 | 0.00 | 208.33 | 144.08 | 9.68 | 3.79 | 0.00 | 0.00 | 104.17 | 104.17 |
| N | 3724 | 0.00 | 0.00 | 0.00 | 0.00 | 4.84 | 2.75 | 0.00 | 0.00 | 0.00 | 0.00 |
| Guánica | 3724 | 0.00 | 0.00 | 69.44 | 48.76 | 6.45 | 1.81 | 0.00 | 0.00 | 69.44 | 48.76 |

** Standard error could not be determined because density estimate is based on a search of the entire site.

Note: Standard errors which equal their mean reflect estimates for which there was only one nest sampled in the entire site.

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Single-linkage cluster analysis (SYSTAT version 8.0) measuring euclidean distance was performed using the composition and structure of the plant community at each site (see Appendix A). The resulting dendrogram was then compared to another cluster analysis created using the abundance data for the termites present at each site (Table 8) in order to determine whether vegetative characteristics of the habitat influence the structure and composition of termite communities in forest fragments. If the two dendrograms exhibited similar groupings then it was speculated that the structure of the two communities being compared was some how interrelated. Sites were not included in the cluster analysis if they did not have a complete set of both termite and plant community data. For example, site 40 could not be included in the analysis because mean basal area was not reported for this site (Ramjohn *et al. unpublished*).

## RESULTS

### *10 m x 10 m Plots*

Nine (32%) of the 28 correlations between the termite diversity and abundance measures and the habitat variables were statistically significant (Table 9). The height of the canopy accounted for the majority of these significant correlations. However, all of the significant associations between the termite and habitat variables were weak; none of the habitat variables explained more than 12% of the variation in any of the termite abundance and diversity measures. There were no significant correlations between the species richness of woody vegetation and the termite variables.

The amount of canopy cover had a significant effect on the distribution of certain termite species within the study sites (Figure 5). The abundance of *P. wolcotti*, arboreal species, and termite species richness were greatest in areas that had a closed canopy. In addition, a number of other termite abundance measures exhibited marginally significant ($P<0.10$) differences between the three canopy levels. These include the abundance of *P. corniceps* (Kruskal-Wallis: H = 5.734, P = 0.057), subterranean termites (H = 5.413, P = 0.067), and drywood termites (H = 5.498, P = 0.064). In all of the above cases, the greatest abundance was in areas that had a closed canopy.

Table 9. Spearman's rank correlation coefficients ($r_s$) between termite diversity and abundance estimates and habitat variables within the 10 m x 10 m plots (N = 88 plots). $^{*}$ = $P < 0.01$, $^{**}$ = $P < 0.005$, ns = $P > 0.05$.

| Termite Variables | Structural Variables | | | |
|---|---|---|---|---|
| | Canopy Height | % Rock | Litter Depth | Woody Vegetation Species Richness |
| *Procryptotermes corniceps* | 0.228 | ns | ns | ns |
| *Parvitermes wolcotti* | 0.342$^{**}$ | ns | 0.282$^{*}$ | ns |
| *Heterotermes* spp. | ns | ns | ns | ns |
| Subterranean termites | 0.305$^{**}$ | ns | 0.224 | 0.217 |
| Arboreal termites | ns | ns | ns | ns |
| Drywood termites | 0.222 | ns | ns | ns |
| Termite species richness | 0.250 | ns | 0.216 | ns |

There were no significant differences in any of the termite diversity and abundance measures between the eight aspect categories. There were also no statistically significant differences when the termite data from predominantly north- and south-facing slopes were compared.

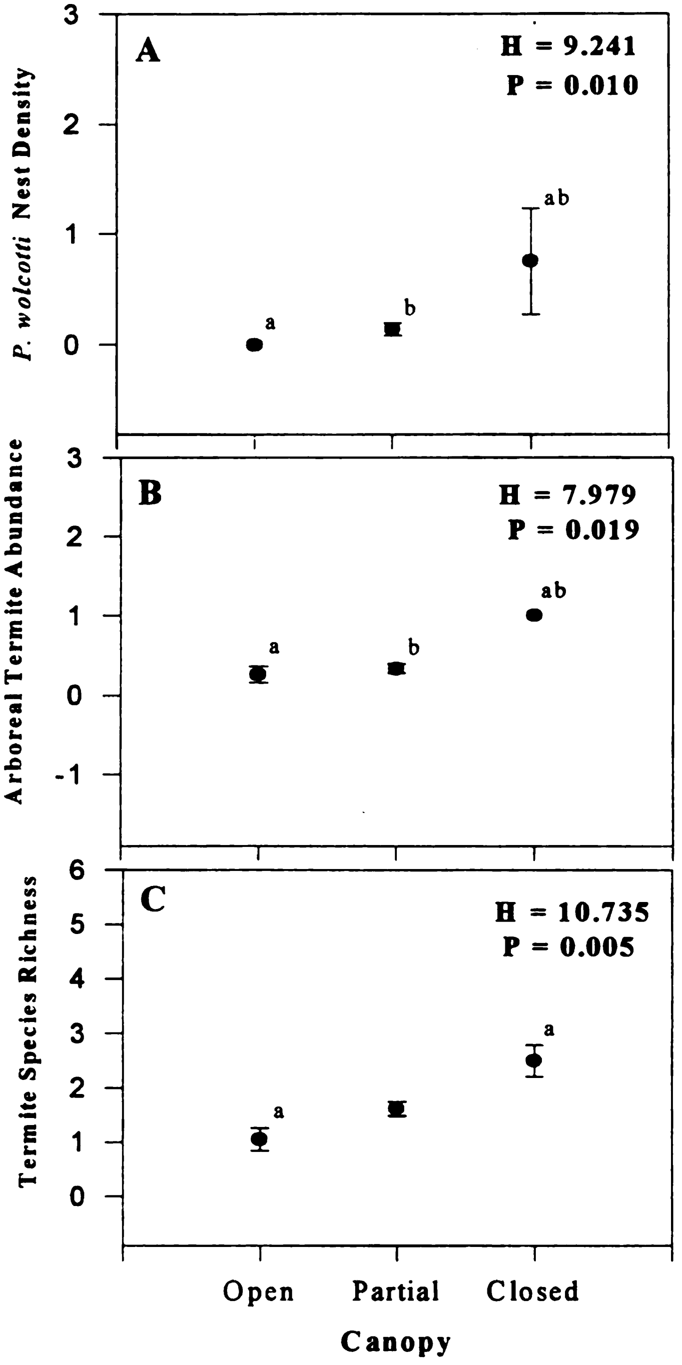


Figure 5. Mean (± SE) (A) abundance of *P. wolcotti*, (B) abundance of arboreal termite species, and (C) termite species richness within the three canopy categories. Points within a graph with at least one of the same superscripts are significantly different ($P < 0.05$, Tukey's HSD). See text for canopy category definitions. (N = 88 plots)

### *Forest Fragments*

When forest fragments were utilized as the sampling unit, termite species richness and the abundance of *Neotermes mona* were the only two termite variables that exhibited significant correlations with characteristics of the plant community (Table 10). All the significant correlations were relatively strong, each explaining more than 35% of the variance. The two most widespread species, *Procryptotermes corniceps* and *Nasutitermes acajutlae*, were not significantly correlated with any of the plant community variables. Termite species richness, in addition to the significant associations with the number of plant and tree species, was also significantly correlated with lizard species richness (Figure 6).

The two resulting dendrograms produced by the cluster analysis of plant and termite community data exhibited distinct groups of fragments (Figure 7). The cluster analysis of the plant data revealed two large groups, one group consisting of sites 2, 5, 7, 27, and 28, and a second group consisting of sites 4, 10, 13, 16, 30, and 36. Examining the dendrogram produced by the termite data reveals a large group consisting of sites 2, 4, 5, 7, 10, 16, 27, 28, and 30, and a much smaller group consisting of sites 13 and 36 (Figure 7). Therefore, it appears that the combination of plant community variables included in this analysis do not greatly influence the structure of the termite community in a subtropical dry forest ecosystem.

Table 10. Pearson correlation coefficients (r) between termite diversity and abundance estimates and characteristics of the plant community within forest fragments (N = 12 fragments). * = P < 0.01, ** = P < 0.005, ns = P > 0.05.

| Termite Variables | Plant Sp. Richness | Tree Sp. Richness | No. Stems/ha >1 cm | No. Stems/ha >2.5 cm | No. Stems/ha >5 cm | Mean Basal Area ($m^2/ha$) |
|---|---|---|---|---|---|---|
| *Anoplotermes* sp. | ns | ns | ns | ns | ns | ns |
| *Heterotermes* spp. | ns | ns | ns | ns | ns | ns |
| *Neotermes mona* | ns | ns | ns | 0.756** | 0.694 | ns |
| *N. acajutlae* | ns | ns | ns | ns | ns | ns |
| *N. costalis* | ns | ns | ns | ns | ns | ns |
| *P. wolcotti* | ns | ns | ns | ns | ns | ns |
| *P. corniceps* | ns | ns | ns | ns | ns | ns |
| Species Richness | 0.741* | 0.678 | 0.608 | ns | ns | ns |

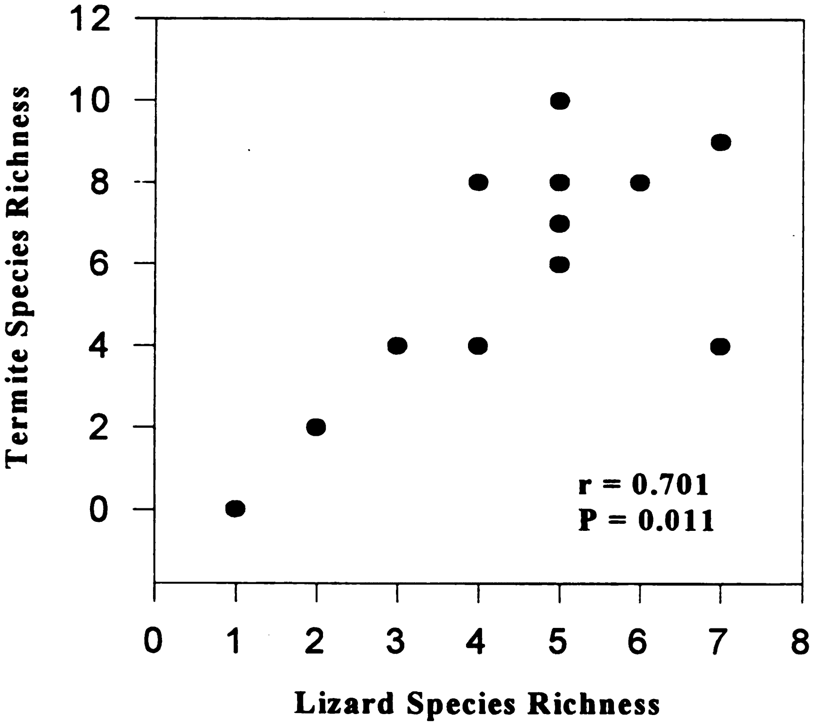


Figure 6. Association between termite and lizard species richness among forest fragments.

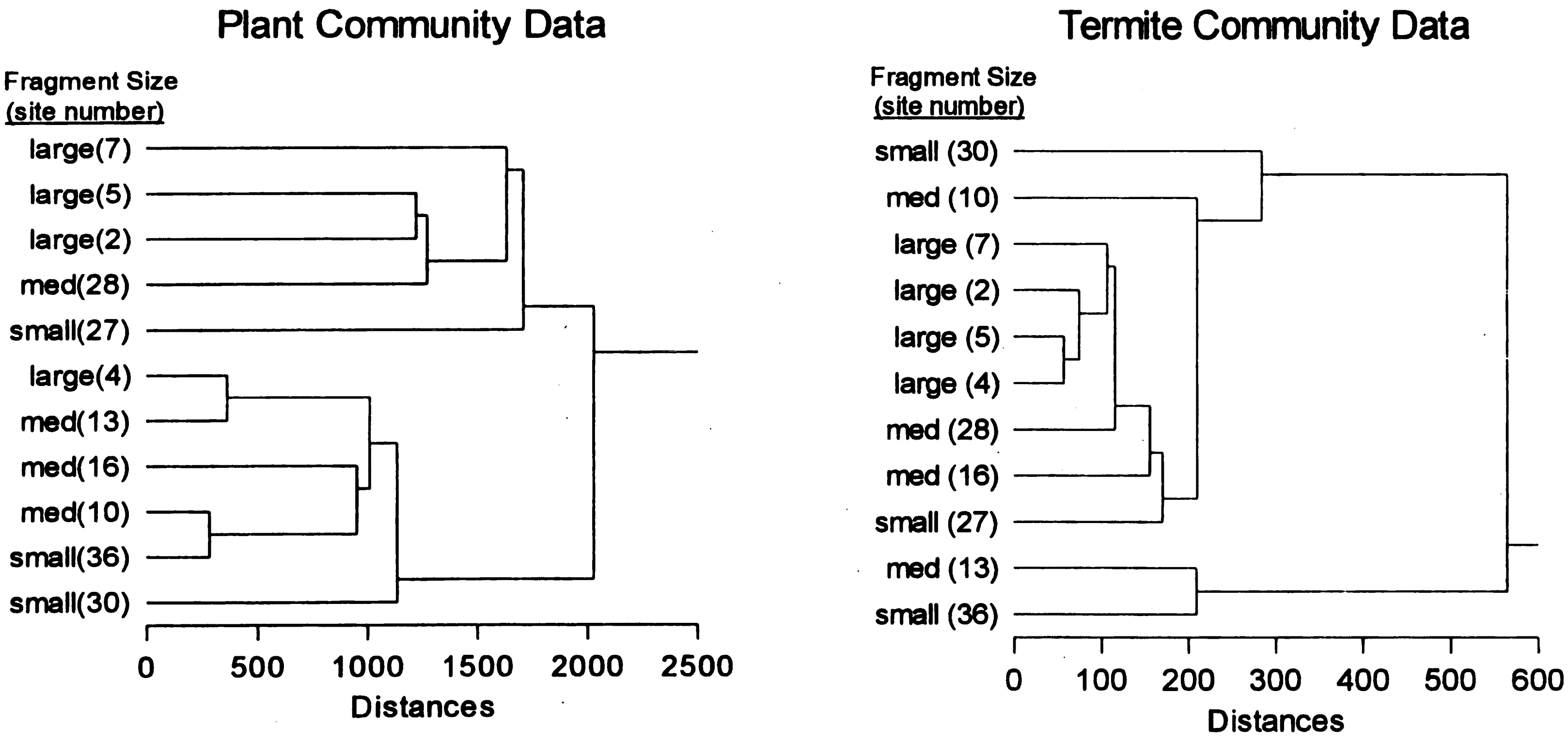


Figure 7. Dendrograms constructed using plant community variables and termite community variables from eleven of the forest fragment sites.

# DISCUSSION

## *Termite Diversity*

The diversity of termites in the subtropical dry forests of Puerto Rico appears to be influenced by certain characteristics of the habitat which may be important for providing cover in this water-limited environment. Termite species richness increased with litter depth, canopy height, and the amount of cover provided by the forest canopy. It is difficult to determine whether these results are due to the increased amount of shade provided by the canopy (and litter for subterranean species), the relative degree of disturbance these sites have experienced, or if these two factors are inextricably linked. For instance, the height of the canopy is probably a good reflection of the amount of time since the forest was last cut or burnt, while the amount of canopy cover may indicate the current degree of disturbance at a site (e.g., fencepost harvesting). Litter would also be more developed in older, less disturbed tracts of forest. In fact, litter depth and canopy height have the strongest association of all the correlations examined ($r_s = 0.583$, $P < 0.001$). Clearly, a more rigorous approach is needed to determine the causal agent of these observed patterns.

Examination of the associations with plant variables on the scale of entire forest fragments revealed that termite species richness increased with the number of stems/ha that had a diameter at breast height (DBH) greater than 1 cm. In addition to serving as a food source, trees and their dead branches serve as a substrate in which certain termite species construct their nests. For instance, drywood termites build their nests in dead branches and standing dead wood while the *Nasutitermes* spp. construct large carton nests on the exterior of trees. Therefore, as the density of stems greater than 1 cm DBH increases the amount of suitable habitat for drywood termites increases. However, the large carton nests of *Nasutitermes* spp. require stems much greater than 1 cm DBH to provide adequate support (see Chapter 1). Overall, the increase in termite species richness is likely due to the combination of the increase in suitable habitat for drywood termites and the increase in the amount of potential food for other termite species.

Even without knowing the causal factors, these results still have implications for establishing conservation priorities. Tracts of closed canopy forest with relatively high stem densities support the richest communities of termites and should therefore be given the highest priority for conserving these species. Other factors such as aspect, amount of rock, and mean basal area are not major associates of termite diversity and therefore do not warrant as much attention if conservation of termites is the main goal of a management plan.

The amount of readily available food is another consideration when trying to elucidate the factors that affect the distribution and abundance of termites. However, termite species feed on a wide variety of plant material which makes the quantification of food availability for all the termites present within a habitat a rather difficult task. For instance, termites may eat wood (living or dead), herbaceous plant material, plant litter, humus, fungi, or dung, depending on the species in question (Lee & Wood 1971). While the variety of diets exhibited by the termites of southwest Puerto Rico was not as diverse as the list above, as all of them primarily feed on dead wood, there was variability in the condition and type of wood that each preferred (Chapter 1). For example, *P. corniceps* fed on tree species with a wide variety of densities while *Heterotermes* spp. seemed to prefer only lightweight woods. In addition, *P. wolcotti* and *C. discolor* primarily fed on wood that was in an advanced state of decay (*pers. obs.*). Therefore, quantification of the food source for all of the species that comprise the entire termite community would need to consider the type of wood as well as its stage of decomposition.

In addition to the difficulties associated with quantifying the availability of all the various types and conditions of wood, the task of measuring the volume of wood litter has traditionally been problematic (Warren & Olsen 1964). In attempts to make the process of estimating the amount of wood litter reasonably accurate and less time consuming, a number of line-intersect sampling methods have been introduced (Warren & Olsen 1964, Van Wagner 1968, De Vries 1974). However, these techniques fail to include standing dead wood and are still time consuming if the habitat contains dense understory vegetation which is characteristic of the subtropical dry forests of southwestern Puerto Rico. The above considerations led to the omission of food availability as a measured variable from the present study.

The data from the 10 m x 10 m plots produced an insignificant correlation between the species richness of termites and woody vegetation, lending support to the notion that species-rich areas ('diversity hotspots') frequently do not coincide for different taxa (Prendergast *et al.* 1993, Pimm & Lawton 1998, van Jaarsveld *et al.* 1998). However, significant correlations between the species richness of termites, plants, trees, and lizards were obtained when data from entire forest fragments were pooled. These results coincide with another study that investigated patterns of species richness for a variety of taxa. Abensperg-Traun *et al.* (1996a) found significant associations between the species richness of termites and other taxa (plants, lizards, scorpions) in *Eucalyptus* woodlands of the central wheatbelt region of Western Australia. The contrasting results obtained in this study depending on whether data from the 10 m x 10 m plots or entire forest fragments were used illustrates the importance of selecting the appropriate spatial scale on which to conduct investigations of this nature. Obviously, the appropriate scale of the study will depend on the research question being asked. Clearly, if selecting areas to designate as biodiversity reserves is the main goal of a project, then examining patterns of species richness among forest fragments is more appropriate than examining these same patterns among 10 m x 10 m plots.

### *Termite Abundance*

Only a few species were influenced by the habitat characteristics that were measured in this study. Canopy height and the amount of canopy cover were the most important habitat variables affecting termite abundance. The nest density of *Procryptotermes corniceps* and *Parvitermes wolcotti* both increased with canopy height. Again, canopy height may just be a surrogate measure of disturbance, reflecting the time since the forest was last cleared. The abundance of *P. wolcotti* and arboreal termites was also greatest in areas that had a closed canopy. Tracts of closed canopy forest tended to be mature stands with large trees, perhaps explaining why arboreal termites were found in these areas at a greater frequency (see Chapter 1 for a discussion of tree size preferences). Similarly, Leponce *et al.* (1995) demonstrated that the proportion of trees occupied by arboreal termite colonies and average nest volume was greater in dense coconut plantations than in open or standard plantations. The authors suggested that these results were mainly the effect of varying sun exposure and density of available resources among the three plantation types.

The subterranean termite *P. wolcotti* and the combined abundances of all subterranean species exhibited a positive relationship with litter depth. These results may reflect a reliance on cover at the soil surface for providing a thermal shadow, however, there were no significant correlations with percent rock (a more effective barrier of solar radiation). Once again, the observed association may reflect the influence of disturbance on these termite species, assuming that areas with more developed litter layers are less disturbed. In fact, the relationship between litter depth and the abundance of subterranean species may have no biological significance at all, and could merely be a spurious correlation.

The only species that exhibited significant associations with the plant variables measured for entire forest fragments was the drywood termite *Neotermes mona*. This was the largest species encountered during the sampling period of this study and was only collected from standing dead wood that had a DBH of at least 3 cm. Due to its large size, *N. mona* may not be able to excavate nests out of wood that has a DBH less than 2.5 cm. Therefore, as the density of larger stems (> 2.5 cm) increases, there is a concomitant increase in the abundance of *N. mona*. However, this rationale is not supported within the other drywood termite species. The most abundant drywood species in southwest Puerto Rico, *P. corniceps*, did not exhibit any significant relationships with the stem density data.

The composition and structure of the plant community within subtropical dry forest fragments does not appear to influence the overall structure of the termite community. The comparison of the two dendrograms did not reveal any patterns which would indicate that a certain type of plant community supports a termite community distinct from those within other plant communities. This type of analysis was not the ideal way to compare these two sets of variables, however, the extremely low sample size (12 fragments) precluded the use of more sophisticated multivariate analyses.

In summary, litter depth, height of the canopy, tree stem density, and the amount of cover within a habitat are important characteristics that influence the diversity of termite communities and abundance of certain termite species. While it cannot be determined from this study whether the observed patterns are due to the effects of shading, disturbance, availability of nesting substrate, or some other unmeasured factor, the results still have implications for determining conservation priorities. The availability of food is another major factor to consider when trying to determine the environmental variables that affect the distribution and abundance of termites. However, this variable is difficult to quantify in the subtropical dry forests of Puerto Rico and thus was not included in this analysis. The notion of 'diversity hotspots' is supported by the significant correlations between termite, plant, tree, and lizard species richness when forest fragments were used as the sampling unit. Due to their scarcity, it was impossible to determine any relationships between the abundance of rare species and habitat variables. The information gained from this habitat analysis will nonetheless provide guidance for refining and focusing a landscape-level applications.

# CHAPTER THREE

## Contrasting Responses of Termite Community Composition and Wood Decomposition to Habitat Fragmentation in a Subtropical Dry Forest

The fragmentation of terrestrial ecosystems currently represents one of the leading threats to biological diversity (Wilcox & Murphy 1985, Saunders *et al.* 1991,Turner 1996, Laurance & Bierregaard 1997). While the majority of studies thus far have supported this assessment by demonstrating declines in variables such as species richness and densities of individual species within fragments (Turner 1996), it is becoming evident that not all native species are adversely affected by the fragmentation of their habitat (Robinson *et al.* 1992, Margules *et al.* 1994). Once such species have been identified, the traits that confer resilience to fragmentation can be ascertained, thus contributing to the development of a framework concerning species responses to fragmentation. Though often neglected, this approach should prove just as beneficial as determining the traits which render species susceptible to local population decline and extinction (Didham *et al.* 1998).

The preponderance of fragmentation studies focusing on vertebrates (especially birds and mammals) has led to the development of generalizations concerning the relationship between specific traits and responses to fragmentation. For example, species that are large-bodied, poor dispersers, rare, or intolerant of disturbed conditions are particularly predisposed to local extinction as a result of habitat fragmentation (Turner 1996, Laurance *et al.* 1997). However, due to the limited number of studies investigating invertebrate responses to fragmentation, it has not yet been determined whether such broad generalities can be extended to this group of organisms.

Considering the importance of arthropods in ecosystem functions such as nutrient cycling, pollination, and seed parasitism (Janzen 1987), it is surprising that there has not been more of an emphasis on determining their response to fragmentation until recently. Over the past decade there has been a dramatic increase in the number of studies investigating the effects of fragmentation on arthropods (e.g., Klein 1989, Aizen & Feinsinger 1994a, Fonseca de Souza & Brown 1994, Margules *et al.* 1994, Daily & Ehrlich 1995, Brown & Hutchings 1997, Didham 1997, Weishampel *et al.* 1997, Didham *et al.* 1998). However, only a few of these studies have actually measured the effects of habitat fragmentation on the ecosystem processes mediated by the organisms under investigation (e.g., Klein 1989, Aizen & Feinsinger 1994b, 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 (Robinson *et al.* 1992, Didham *et al.* 1996).

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 & Sands 1978, Wood & Johnson 1986). The importance of termites as decomposers of organic material in savanna ecosystems has been confirmed (Wood & Sands 1978, Collins 1981, Holt 1990, Jones 1990); although high termite biomass in tropical forests implies a critical role in decomposition, their significance in these regions has yet to be quantified (Wood & Johnson 1986). In addition to their contribution to ecosystem processes, termites also have negative impacts as highly destructive pests of residential, agricultural, and silvicultural interests (Wood 1978, Wood & Pearce 1991, Pearce 1997).

Given the significant role of termites in essential ecosystem processes, it is imperative for the development of conservation and management guidelines for fragmented landscapes to determine the impacts of habitat fragmentation on these communities. 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, Wood *et al.* 1982, Eggleton *et al.* 1995) and more sensitive to fragmentation than litter-feeders and 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 to the time of the study. In order to allow sufficient time for faunal relaxation, the process whereby the number of species inhabiting an area approaches some dynamic equilibrium between colonization and extinction rates (Diamond 1972, 1973, Terbourgh 1974), studies need to focus on areas that have been disturbed or fragmented for decades not years. 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 their favorable climate and productive soils, the dry forests of Puerto Rico represent an ecosystem that has been historically impacted through human activities (Murphy & Lugo 1986). As a result, the landscape currently resembles a mosaic dominated by agriculture and urban developments with interspersed patches of natural vegetation. These patches of habitat have been isolated for many decades (at least 60 years), therefore making them 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 of varying sizes are distinct from those in a relatively undisturbed tract of contiguous dry forest, (2) the minimum fragment area required to support subsets (50 and 75%) of the termite community found in the reference site, (3) how the composition and structure of termite communities vary relative to characteristics of fragments and their surrounding landscape, (3) the impact of fragmentation on an important ecosystem function: wood decomposition, and (4) the relative importance of termites in the decomposition of wood within a subtropical dry forest ecosystem. In addition, this study examines what is currently known about the biology of the termites native to the subtropical dry forests of Puerto Rico in an attempt to determine the traits which may account for the observed responses to fragmentation.

## MATERIALS & METHODS

### *The Study Region*

The southwestern portion of Puerto Rico comprises the majority of the island's subtropical dry forest life zone (*sensu* Holdridge 1967) (Figure 1). This region extends east along the south coast approximately 120 km from the southwest corner of the island and reaches between 3 and 20 km inland, depending on local topography (Ewel & Whitmore 1973). 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. 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 associations.

This study was conducted in the southwestern coastal region of Puerto Rico (approximately 18°N and 66°35'W to 66°12'W). Twelve forest fragments (Figure 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;* Appendix A). 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 11). All sites were located within a few kilometers of the coast and to the west of the city of Ponce. In addition, three sites within Guánica Forest were selected in order to obtain baseline data for termite communities in a subtropical dry forest (Figure 8). These sites within Guánica Forest include a coastal scrub forest and upland deciduous forests on north- and south-facing slopes.

### *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 the reference site (Figure 8). Polygons were delineated from the aerial photographs by tracing their outlines onto mylar overlays. Each polygon was assigned to one of nine

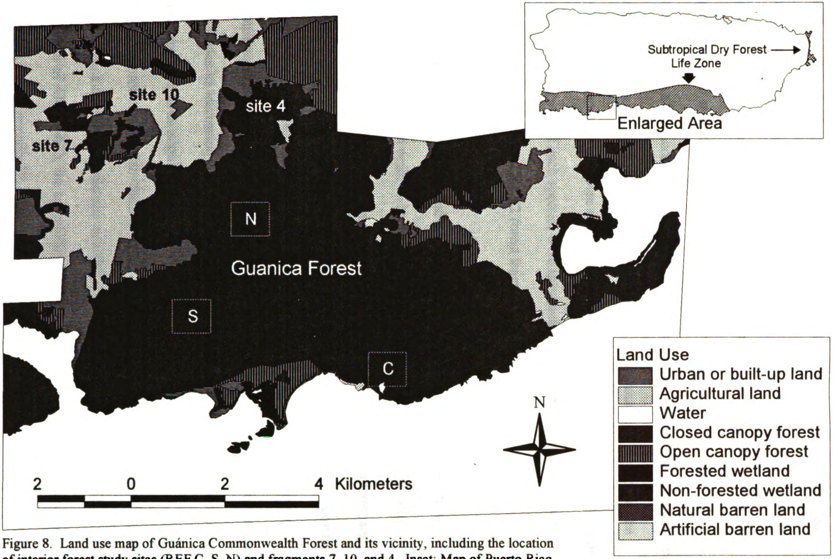


Figure 8. Land use map of Guánica Commonwealth Forest and its vicinity, including the location of interior forest study sites (REF C, S, N) and fragments 7, 10, and 4. Inset: Map of Puerto Rico illustrating the extent of the subtropical dry forest life zone on the island.

land-use classes using the criteria specified in Lugo *et al.* (1996). Photointerpreted polygons were then digitized into the ARC/INFO version 7.1 geographic information system (GIS) package. Once topology was constructed, the digitized data were then geroreferenced and transformed into Universal Tranverse Mercator (UTM) Grid Zone 19 coordinates to allow accurate measurements and overlay with other geographic data sets. Adjacent coverages were subsequently edgematched and permanently linked via the MAPJOIN command. Attribute data, including land-use classes, termite species richness, and the nest density of each species, were then assigned to each polygon in order to create a final useable coverage of the 12 forest fragments, the reference site, and their surroundings.

A number of fragment and landscape characteristics were determined from the completed coverage in order to investigate spatial patterns of termite species richness and abundance. Fragment characteristics included in this study were area, perimeter, and compactness (Table 11). 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 perfectly circular polygon), 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, a number of landscape variables were examined. Using the BUFFER command of ARC/INFO, the surrounding area within 1000 m of the study sites was delineated (see Appendix D). This new polygon coverage was then overlaid with land-use in order to create a new coverage from which queries could be performed concerning the

Table 11. Selected fragment and landscape characteristics of the twelve study sites and the reference site (Guánica Forest).

| Site-ID[†] | Area (ha) | Perimeter (m) | Patch Compactness | Distance to Nearest Forest Fragment (m) | Primary Aspect |
|---|---|---|---|---|---|
| Small: | | | | | |
| 40 | 0.006 | 27 | 0.9989 | 392 | S |
| 36 | 0.06 | 92 | 0.9010 | 110 | S |
| 30 | 0.26 | 226 | 0.7911 | 364 | E |
| 27 | 0.69 | 408 | 0.7191 | 10 | W |
| Medium: | | | | | |
| 28 | 2.0 | 835 | 0.5978 | 7.5 | E |
| 13 | 3.1 | 919 | 0.6821 | 20 | Flat |
| 16 | 3.4 | 832 | 0.7868 | 278 | E + S |
| 10 | 6.3 | 1723 | 0.5182 | 15 | N |
| Large: | | | | | |
| 7 | 33.6 | 3517 | 0.5846 | 10 | All |
| 5 | 97.1 | 5258 | 0.6641 | 30 | All |
| 4 | 136.8 | 7562 | 0.5482 | 10 | All |
| 2 | 854.1 | 23277 | 0.4451 | 20 | All |
| Guánica[*] | 3724 | 47885 | 0.4518 | | All |

[†] from Ramjohn *et al.* (*unpublished*); see Appendix A.

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

landscape within 1 km of the site. Within this specified area, 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, and (6) percentage of urban land-use. 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 reproductives exhibiting positive phototactic behavior during nocturnal flights (Nutting 1969). The distance to the nearest closed canopy forest fragment was also measured in order to characterize the isolation of the study sites.

The influence of land-use directly adjacent to the fragments was assessed by calculating the percentage of the study site perimeter comprised by each land-use. Only the major types of land-use (closed forest, open forest, urban, and agriculture) were investigated, as the other land-use types rarely occurred adjacent to the study sites. Water, artificial barren land, natural barren land, and forested wetland were only adjacent to two sites each, while non-forested wetland was not adjacent to any of the study sites. Closed canopy forest separated only by a road from the study sites was considered adjacent.

### *Termite Sampling*

A quantitative survey of the termites of the southwestern dry forests of Puerto Rico 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 regimes were necessary to obtain accurate estimates of abundance. Two species (*Nasutitermes costalis* and *Nasuititermes acajutlae*) build large, conspicuous arboreal nests and were sampled using 100 m x 10 m belt transects. The location for establishing the 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 samples selected from each category was largely determined by the proportion of the total area that each category represented.

The remainder of the termites have less conspicuous nesting locations such as within small pieces of wood or underneath rocks and logs. Nest abundance for these species was determined by exhaustively searching 2 m x 2 m plots randomly selected from within the first 10 m segment of the belt transect. All dead wood within the plot, including standing dead wood (SDW) and attached dead branches up to a height of 2 m, was sampled for termites. 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 ('site walks') were necessary in order to document species that were not detected within the samples. These searches were used only to supplement the species richness data for the sites (Table 2).

Whenever possible, soldiers and winged reproductives (alates) were collected from each colony and field 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 original descriptions of Snyder (1923, 1924, 1929) and taxonomic key (Snyder 1956).

Abundance estimates for each species represent nest densities (# nests/ha), 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 wolcotti, Caribitermes discolor*) as nothing is known of the foraging territory for these species. The abundance estimates for these species may therefore be positively biased.

### *Sample Size*

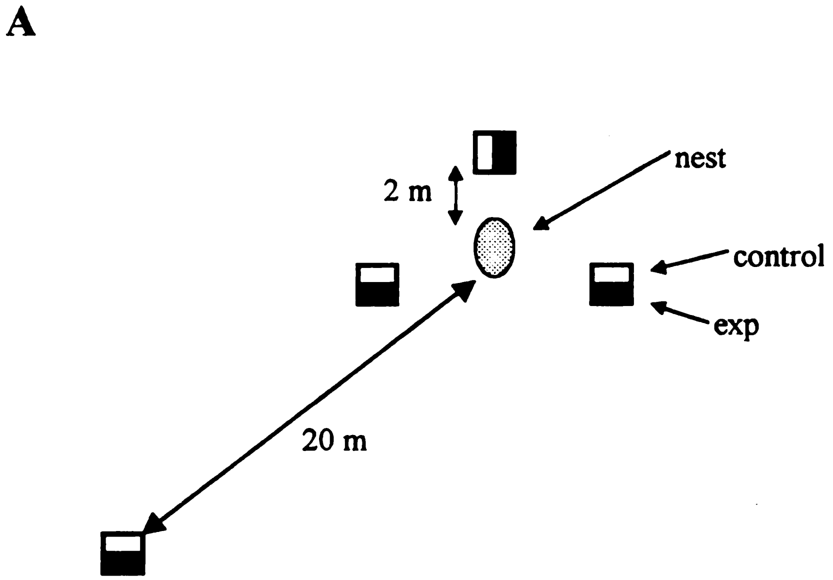
The total number of samples taken from each site was largely a function of area; the number of samples increased as the area of the site increased (Table 2). However, due to the amount of time required for each sample (between 1 and 2 hours on average to search a plot) it was impossible to achieve a constant proportion of area sampled across all sites (Table 2). Ultimately, the determination of the number of samples taken from each site was based on maximizing the number of sites that could be sampled with the given time constraints while maintaining some degree of consistency for the proportion of area sampled. In order to evaluate the effectiveness of this sampling design, species accumulation and performance curves were constructed for each site using data from the 2m x 2m plots. The mean nest density for one of the most common species in the region, *Procryptotermes corniceps*, was used to create the performance curves.

### *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 species, *Leucaena leucocephala* (Leguminosae: Mimosoideae), was collected. This species is very abundant throughout the dry forests of Puerto Rico and is probably the only tree species common to all of the study sites. The relatively hard, heavy wood (specific gravity 0.7) has traditionally only had uses as fuelwood in Puerto Rico (Little & Wadsworth 1964), although this species has tremendous value in reforestation projects in other regions.

The collected 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 ± SE, 1545 ± 42 g), while the estimates of initial dry weight ranged from 639 to 1637 g (mean ± SE, 1108 ± 32 g).

Two types of bundles were assembled, an experimental and control bundle. The wood in the control bundle was wrapped in a fine aluminum mesh (1 mm) in order to exclude termites and other macroinvertebrate decomposers. Experimental bundles were constructed with a wider mesh (5 mm) that would not prevent invertebrates from attacking the wood inside. The two mesh treatments were used in order to ascertain the relative role of termites and other smaller invertebrates in the decomposition of wood. Bundles were placed in pairs (control and experimental) around the large nests of the common arboreal termite, *Nasutitermes acajutlae*, at one site in each of the three size categories (<1 ha, 1-10 ha, >10 ha) and at two locations within the reference site (Guánica



B

| | Size Categories | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | <1 ha | | | | 1-10 ha | | | | >10 ha | | | | reference site | | | |
| | Away | | Near | | Away | | Near | | Away | | Near | | Away | | Near | |
| Nest A: | C | E | C | E | C | E | C | E | C | E | C | E | C | E | C | E |
| | C | E | C | E | C | E | C | E | C | E | C | E | C | E | C | E |
| | C | E | C | E | C | E | C | E | C | E | C | E | C | E | C | E |
| Nest B: | | | | | | | | | | | | | C | E | C | E |
| | | | | | | | | | | | | | C | E | C | E |
| | | | | | | | | | | | | | | | C | E |

Figure 9. Design summary of wood decomposition study. (A) Arrangement of wood bundles around *N. acajutlae* arboreal nests. (B) Sample size and design for each of the study sites. C = control bundle, E = experimental bundle.

Forest). Three replicates (3 pairs) were placed within 2 m of the base of the tree which supported the nest and were equidistant from each other (Figure 9a). In addition, three replicates were placed approximately 20 m from the nest, making sure that they were not near other *Nasutitermes* spp. colonies (Figure 9a). This stratification of the sampling units was an attempt to account for the contribution made by the patchily distributed and numerically dominant *N. acajutlae* (see Chapter 1) as well as the contribution made by other invertebrates to the decomposition of wood. A total of 58 bundles were assembled and placed in the field (see Figure 9b for experimental design).

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. In addition, the condition of the wood from each size category (log, branch, twig) within the bundle was noted.

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 weren't 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 and 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.

### *Analyses*

In order to determine whether termite communities in forest fragments were distinct from those in the reference site, 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) ANOVA was 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. To determine if community structure varied relative to area of the fragment, a single-linkage cluster analysis (SYSTAT, version 8.0) measuring euclidean distance was used to compare individual species densities among the sites (Table 8). The resulting dendrogram was then examined in order to determine if termite communities clustered together according to size category.

Inspection of the species richness data allowed the determination of the minimum fragment area required to support subsets of the termite community found in the reference site. The proportion of the reference site species composition represented by the species richness of each fragment was calculated. The subsets were arbitrarily set at 50 and 75 % of the species richness within the reference site.

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 in order to convert its positively skewed distribution into a symmetrical one and percentage data were arcsine transformed in order to approach a normal distribution (Zar 1984). Multiple regression was also used to generate predictive models of termite species richness and individual termite densities for the four most abundant species.

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, reference). 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 evidence 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

## *Sampling Effectiveness*

The species accumulation curves indicated that some sites were more adequately sampled than others (Appendix C). However, the majority of sites were adequately sampled in terms of termite species richness by thoroughly searching 2 m x 2 m plots. The only sites which did not demonstrate a clear plateau in their species accumulation curves were sites 7, 27, and 28.

Examination of the performance curves revealed that even though a large proportion of the small (< 1 ha) sites was sampled (Table 2), the estimates of *P. corniceps* abundance may not be as accurate as those obtained from larger sites (Appendix B). For instance, the mean nest density at site 36 was still fluctuating widely from sample to sample at the end of the curve. In general, increasing the number of samples as the area of a site increased resulted in more reliable estimates of *P. corniceps* abundance. However, the tremendous number of samples required to obtain relatively accurate density estimates becomes evident when examining the performance curve for all reference sites combined (Appendix B). Approximately 50 samples (200 $m^2$ area sampled) were required before the cumulative mean density of *P. corniceps* became insensitive to fluctuations in the data.

The abundance estimates for the remainder of the termite species in this study was not as reliable as the abundance estimates obtained for *P. corniceps*. Due to their low frequency of occurrence, performance curves for the other termite species never reached a point where the cumulative mean was insensitive to fluctuations in the data. For example, even with all the reference sites combined (96 samples total), the cumulative mean nest

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

| | <1 ha | | | | 1-10 ha | | | | >10 ha | | | | reference site[†] | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | 40 | 36 | 30 | 27 | 28 | 13 | 16 | 10 | 7 | 5 | 4 | 2 | C | S | N | T |
| **Family Kalotermitidae** | | | | | | | | | | | | | | | | |
| *Incisitermes bequaerti* | | | | | | | | | | | | | | | X | X |
| *Neotermes mona* | | | | X | X | | | | X | | P | | | | | |
| *Procryptotermes corniceps* | | X | X | X | X | X | X | P | X | X | X | X | X | X | X | X |
| **Family Rhinotermitidae** | | | | | | | | | | | | | | | | |
| *Heterotermes* spp.[††] | X | | P | | P | X | P | X | X | P | P | X | X | X | X | X |
| **Family Termitidae** | | | | | | | | | | | | | | | | |
| *Anoplotermes* sp. | | | X | | P | | | | X | X | P | X | | | P | P |
| *Caribitermes discolor* | | | | | | | | | | | | | | X | | X |
| *Nasutitermes costalis* | | | | X | | | X | X | X | | X | X | | P | | P |
| *Nasutitermes acajutlae* | | X | X | X | X | X | X | | X | X | X | X | X | X | X | X |
| *Parvitermes wolcotti* | | | 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 |

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[†] C = coastal scrub site; S = upland deciduous forest on predominantly south-facing slope; N = upland deciduous forest on predominantly north-facing slope; T = total of all three reference sites.

[††] *H. tenuis* and *H. convexinotatus* have both been documented within the dry forests of southwestern Puerto Rico (Jones & Scheffrahn *unpublished*), but could not be distinguished in this study. Thus, individuals exhibiting traits of this genus were treated as one species for the purposes of this analysis.

density for *Incisitermes bequaerti* would double with the addition of 1 nest in a subsequent sample (Figure 2).

### *Comparison of Reference and Fragment Communities*

A total of 9 species from 8 genera and 3 families were encountered during this study (Table 12). Only one species (*Neotermes mona*) was not detected within the reference site and all but two species (*Caribitermes discolor* and *Incisitermes bequaerti*) were represented in the fragments. Of the seven species present in the fragments, all were represented in each of the size categories (Table 12). Species richness was not significantly different between the <1 ha, 1-10 ha, >10 ha, and reference forest sites ($P = 0.152$, ANOVA; $P = 0.173$, 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).

Cluster analysis did not group termite communities according to the size categories (Figure 10). In fact, none of the small, medium, or contiguous forest sites clustered with other sites within the same category. Large fragments exhibited a partial clustering of three out of the four sites with a contiguous forest site included in the group. The minimum distance occurred between a large fragment and a contiguous forest site (coastal scrub). The grouping pattern of the dendrogram did not change when the densities of specimens that were unable to be identified were included in the analysis, only the euclidean distances varied between the two dendrograms.

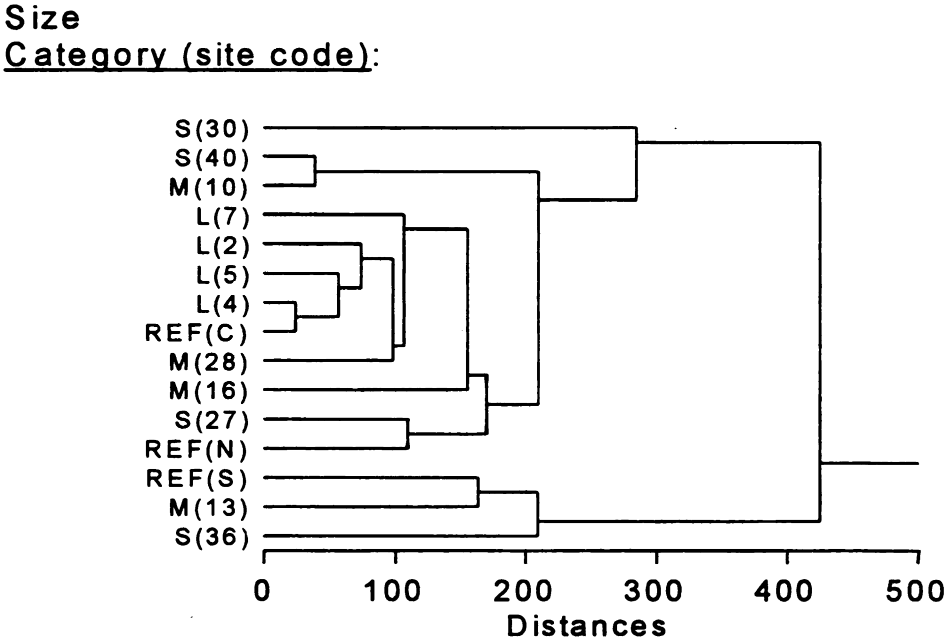

Figure 10. Dendrogram of site similarities based on termite densities from the small (S), medium (M), and large (L) fragments and the reference sites (REF C, S, N).

*Minimum Fragment Area*

The minimum fragment area required to support 50 and 75% of the species composition in the reference site was 0.256 ha (site 30) and 1.985 ha (site 28), respectively (Figure 11). A fragment area of 3.4 ha or more consistently supported at least 50 % of the reference termite community. There was no area threshold at which the fragments surveyed in this study consistently supported 75% of the termite community found in the reference site.

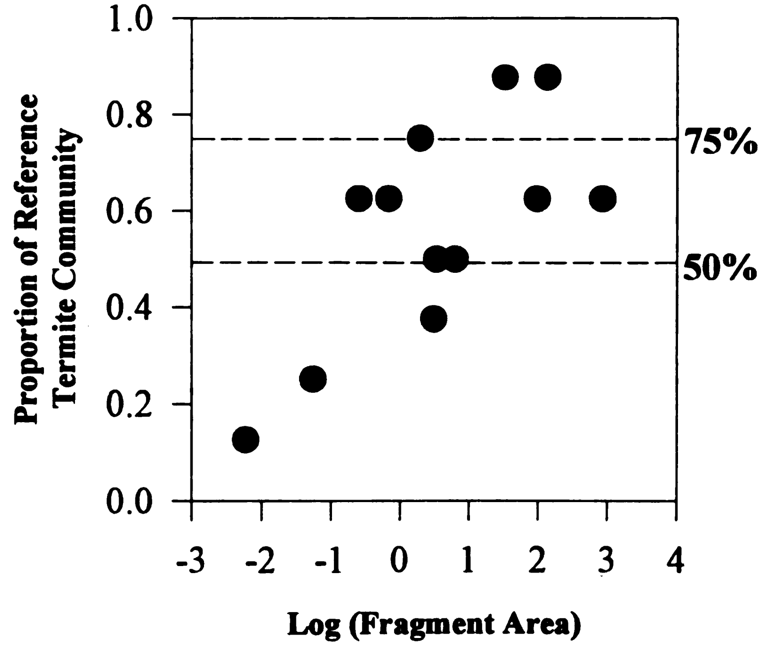

Figure 11. Graph summarizing the fragment area required to support proportional subsets of the termite community found in the reference site.

### *Fragment and Landscape Characteristics*

The majority of correlations between termite and fragment variables were not statistically significant (Table 13). 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 therefore should be treated as one fragment characteristic rather than two separate ones.

Table 13. Pearson correlation coefficients (r) among termite diversity and abundance (no. nests/ha) measures and fragment characteristics. $^{*}$ $P < 0.05$

| Termite Variables | Area | Perimeter | Compactness |
|---|---|---|---|
| *Anoplotermes* sp. | -0.141 | -0.100 | 0.127 |
| *Heterotermes* spp. | -0.422 | -0.060 | 0.365 |
| *Nasutitermes acajutlae* | -0.179 | -0.029 | 0.261 |
| *Nasutitermes costalis* | 0.086 | -0.046 | -0.001 |
| *Neotermes mona* | -0.070 | -0.219 | -0.151 |
| *Parvitermes wolcotti* | -0.113 | -0.201 | 0.088 |
| *Procryptotermes corniceps* | -0.238 | -0.262 | 0.291 |
| species richness | 0.710$^{*}$ | 0.305 | -0.728$^{*}$ |

Only three (5%) of the 56 correlations between termite diversity and abundance variables and landscape characteristics were statistically significant (Table 14). The percentage of open forest and total forest in the surrounding landscape was positively correlated with *N. acajutlae* and *P. corniceps* abundance, respectively. None of the landscape variables were significantly correlated with termite species richness. In addition, one (3%) of the 32 correlations between the measured termite variables and percentage of

Table 14. Pearson correlation coefficients (r) among termite diversity and abundance (no. nests/ha) measures and landscape characteristics. * $P < 0.05$

| Termite | Landscape Attributes† | | | | | | |
|---|---|---|---|---|---|---|---|
| Variables | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| *Anoplotermes* sp. | 0.484 | -0.454 | -0.213 | -0.252 | -0.372 | -0.546 | 0.566 |
| *Heterotermes* spp. | 0.410 | 0.101 | 0.147 | -0.232 | -0.036 | -0.106 | 0.301 |
| *Nasutitermes acajutlae* | -0.090 | -0.014 | -0.412 | 0.585* | 0.027 | 0.225 | -0.110 |
| *Nasutitermes costalis* | -0.026 | 0.053 | -0.369 | 0.028 | -0.273 | -0.267 | -0.100 |
| *Neotermes mona* | -0.372 | 0.492 | -0.035 | 0.510 | 0.265 | -0.148 | 0.080 |
| *Parvitermes wolcotti* | 0.275 | -0.348 | -0.337 | -0.057 | -0.358 | -0.573 | 0.646* |
| *Procryptotermes corniceps* | -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).

Table 15. Pearson correlation coefficients (r) between termite diversity and abundance (no. nests/ha) measures and the percentage of the study site perimeter occupied by the four major land-use types. *$P < 0.05$

| | Adjacent Land-Use | | | |
|---|---|---|---|---|
| Termite Variable | Closed Forest | Open Forest | Urban | Agriculture |
| *Anoplotermes* sp. | -0.308 | -0.226 | -0.239 | 0.484 |
| *Heterotermes* spp. | -0.139 | -0.236 | -0.155 | 0.413 |
| *Nasutitermes acajutlae* | -0.302 | -0.184 | -0.220 | 0.331 |
| *Nasutitermes costalis* | 0.135 | 0.232 | 0.029 | -0.334 |
| *Neotermes mona* | 0.145 | 0.597* | -0.360 | -0.357 |
| *Parvitermes wolcotti* | -0.137 | 0.084 | -0.272 | 0.345 |
| *Procryptotermes corniceps* | 0.177 | 0.188 | -0.422 | 0.131 |
| species richness | 0.092 | 0.387 | 0.390 | -0.499 |

adjacent land-use types was statistically significant (Table 15). Multiple regression analysis yielded no models that included more than one significant fragment or landscape variable for predicting termite species richness, *P. corniceps* abundance, *P. wolcotti* abundance, *Heterotermes* spp. abundance, or *N. acajutlae* abundance.

### *Wood Decomposition*

Even though invertebrates were not excluded from 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 ($T = -0.391$, $df = 56$, $P > 0.05$). 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 the reference site than they did in any of the fragment size categories (all $P < 0.05$, Dunnett's test; Figure 12a). In addition, control bundles in the 1-10 ha site exhibited significantly reduced levels of wood decomposition compared to the reference site ($P = 0.007$, Dunnett's test; Figure 12b).

Identification of the invertebrates collected from the wood bundles revealed an invertebrate community composed of 5 classes and at least 13 distinct orders (Table 16). Coleoptera was the most diverse group with 10 identified families and 12

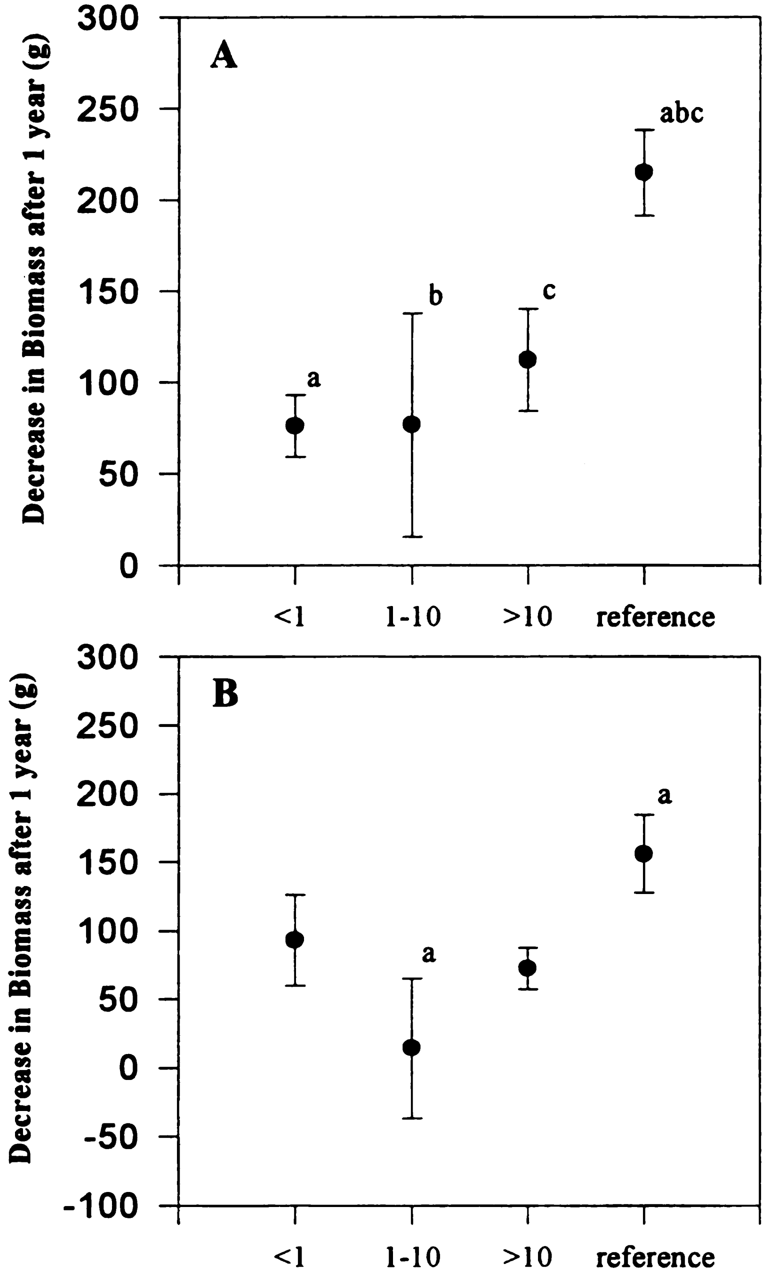

Figure 12. Mean (± SE) loss of biomass from (A) experimental and (B) control bundles at the <1 ha, 1-10 ha, >10 ha, and reference forest study sites. Points within a graph with at least one of the same superscripts are significantly different ($P < 0.05$, Dunnett's test).

Table 16. List of taxa collected from wood bundles including their frequency (the no. of bundles in which they were found), location within the bundles, and indication of whether or not they consume wood.

| Taxa | No. of bundles (%) | Location[†] | Wood Consumer |
|---|---|---|---|
| Class Malacostraca | | | |
| Isopoda | 2 (3.4%) | M, B, L | — |
| Class Arachnida | | | |
| Acari | 3 (5.2%) | B, L | — |
| Aranaea | 15(25.9%) | M, L | — |
| Scorpionida: species A | 26(44.8%) | M, T, B, L | — |
| species B | 1 (1.7%) | L | — |
| Whip Scorpion | 2 (3.4%) | M | — |
| Class Diplopoda | 4 (6.9%) | M | — |
| Class Chilopoda | 15(25.9%) | M, T, B, L | — |
| Class Insecta | | | |
| Coleoptera: | | | |
| Anthribidae | 1 (1.7%) | B | + |
| Buprestidae | 1 (1.7%) | M | + |
| Bostrichidae | 2 (3.4%) | M, T | + |
| Cerambycidae: | | | |
| Cerambycinae (adult) | 3 (5.2%) | M, T, B | — |
| " (pupa) | 5 (8.6%) | T, B | — |
| " (larvae) | 18(31%) | T, B, L | + |
| Cryptophagidae | 1 (1.7%) | M | — |
| Cucujidae | 30(51.7%) | T, B, L | — |
| Curculionidae | 1 (1.7%) | M | — |
| Erotylidae | 2 (3.4%) | L | — |
| Scolytidae | 17(29.3%) | T, B, L | + |
| Tenebrionidae: adult A | 9 (15.5%) | M, L | ? |
| adult B | 3 (5.2%) | M | ? |
| unk. larvae | 4 (6.9%) | L | ? |
| unknown adult #1 | 3 (5.2%) | M, B | ? |

Table 16. cont'd

| Taxa | No. of bundles (%) | Location† | Wood Consumer |
|---|---|---|---|
| unknown immature #1 | 1 (1.7%) | B, L | ? |
| unknown immature #2 | 36(62.1%) | T, B, L | ? |
| unknown immature #3 | 1 (1.7%) | T | ? |
| unknown immature #4 | 1 (1.7%) | L | ? |
| unknown immature #5 | 1 (1.7%) | T | ? |
| unknown immature #6 | 1 (1.7%) | B | ? |
| unknown immature #7 | 1 (1.7%) | T | ? |
| unknown immature #8 | 1 (1.7%) | B | ? |
| unknown immature #9 | 1 (1.7%) | B | ? |
| unknown immature # 10 | 1 (1.7%) | T | ? |
| unknown immature # 11 | 1 (1.7%) | T | ? |
| Embioptera | 7 (12.1%) | T, B, L | + |
| Hemiptera: Heteroptera | 1 (1.7%) | M | – |
| Hymenoptera: Formicidae: species A | 9 (15.5%) | T, B, L | – |
| species B | 1 (1.7%) | M, T | – |
| Isoptera: Rhinotermitidae | | | |
| *Heterotermes* spp. | 23(39.6%) | M, T, B, L | + |
| Termitidae | | | |
| *Nasutitermes acajutlae* | 17(29.3%) | M, T, B, L | + |
| *Parvitermes wolcotti* | 3 (5.2%) | T, B, L | + |
| Thysanura | 6 (10.3%) | M, T, B | – |
| unknown insect # 1 | 31(53.5%) | T, B, L | ? |
| unknown insect # 2 | 1 (1.7%) | M | ? |
| Fungi | 31(53.5%) | T, B, L | + |

† M= within mesh of bundles, T = twigs (1-2 cm diameter), B = branches (2-4 cm diameter), L = Log (4-6 cm diameter)

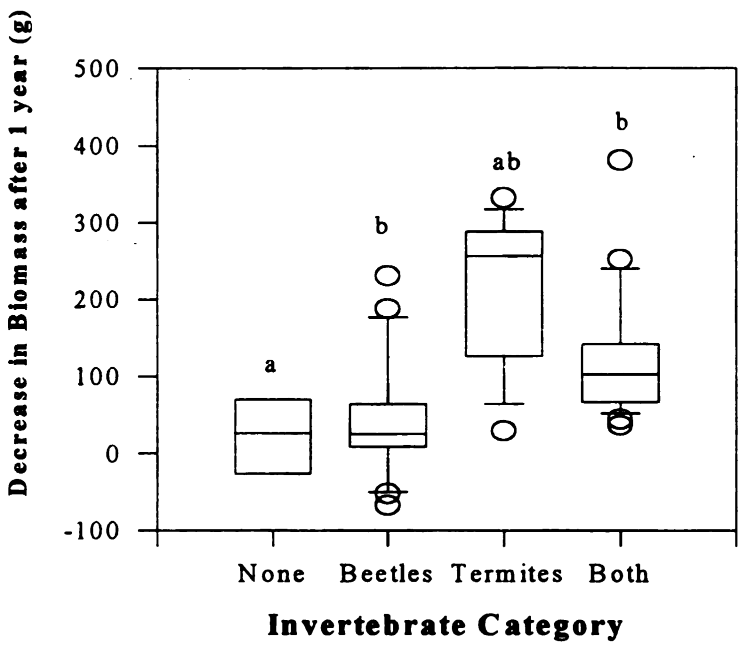

Figure 13. Boxplots of reductions in wood bundle biomass categorized by the presence/absence and relative amount of the two major wood-feeding invertebrate groups encountered in this analysis. None = no major decomposer activity (group 1). Horizontal lines show the 10th, 25th, 75th, and 90th percentiles increasing up the ordinate. 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).

species 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 there frequency of occurrence and abundance in the wood bundles (Table 16).

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; Figure 13). 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 Community Response to Fragmentation*

The composition and structure of termite communities did not differ distinctly between dry forest fragments and contiguous forest. Forest fragments and contiguous forest were not significantly different in terms of species richness or abundance of individual species compared in the context of the entire termite community. Cluster analysis revealed no separation of the reference forest sites from fragments, and grouping patterns among the fragments were only apparent with the large sites.

There are a multitude of possible mechanisms explaining 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 (Scheffrahn *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 areas, perhaps these alternate land-uses do not serve as effective barriers of 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 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 (Grassé 1942, 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 it is plausible to suggest that alates could traverse the distances separating the forest fragments surveyed in 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 possible 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 (directly adjacent or within 1 km) 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 supported the most diverse termite assemblages (see Chapter 2: Figure 5), 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, Moen 1974, Grace 1977), or an indirect consequence of elevated evapotranspiration coupled with reduced humidity and increased desiccation (Tranquillini 1979, Lovejoy *et al.* 1986) may increase available food resources for wood-feeding termites. Since the majority of the termites encountered in this study fed predominantly on wood (Chapter 1), these species might be expected to increase in abundance at the edge or in very small fragments. Although there were no significant correlations, it is still interesting to note that the abundance of six of the seven species occurring within the fragments exhibited a negative relationship with fragment area (Table 13). 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 and 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 (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).

It is not clear 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.

Termites and social insects in general may be more vulnerable to stochastic extinctions than they appear based on numbers of individuals. The reproductive division of labor within colonies means that the effective population size may be small even though the number of individuals is great (Pamilo & Crozier 1997). Considering the extensive foraging territories maintained by some species (e.g., *Nasutitermes* spp., *Heterotermes* spp.), the effective population size may be very low within fragments due to the limited number of colonies they can support. This suggests that immigration probably has a significant role in maintaining population viability for such species (Wright & Hubbell 1983).

One of the most frequently implicated traits believed to confer resilience to the various impacts of fragmentation is generality (Willis 1979, Aizen & Feinsinger 1994a, Margules *et al.* 1994, Turner 1996). Polyphagy seems to be the rule rather than the exception among the termites (Lee & Wood 1971, Wood & Johnson 1986). The most prevalent species among the fragments in this study, *P. corniceps*, consumed wood from a number of trees, shrubs, and vines which spanned a broad range of densities (see Chapter 1: Table 4). While there were insufficient data to determine whether the rest of the species in this study were generalists, there was no evidence proving otherwise.

The two species not represented in the fragments were rare even in the contiguous reference forest. *C. discolor* and *I. bequarti* were detected in less than 2% of the samples.

Failure to detect these species within the fragments may be the result of inadequate sampling. However, another rare species, *N. mona*, was found at three of the fragments, two of which had only 12 samples taken at each. A possible reason for *C. discolor* absence 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 sampled within 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, Lugo *et al.* 1996).

Previous studies of the effects of forest fragmentation on termite communities have yielded differing results than those of the present study. Fonseca de Souza and 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 wheatbelt region of western Australia also demonstrated significant declines in termite species richness as a result of habitat disturbance and fragmentation (Abensperg-Traun *et al.* 1996b).

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.

### *Effects of Fragmentation on the Decomposition of Wood*

Rates of wood decomposition 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 reference 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 the reference forest sites were beyond the area of altered microclimatic conditions associated with the forest edge.

Examining the invertebrate decomposer data reveals that bundles classified as predominantly attacked by termites were mostly from the reference site. Conversely, bundles classified as predominantly attacked by beetles were mostly from the fragments. Considering the relative contributions made by beetles and termites (Figure 13), 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 (sites 2, 16, 30, and ref S) reveals highly disparate termite communities among these sites (Figure 10). 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 reference site, whereas the fragments only supported one or two of these species (Table 17). In fact, the species that was found in the most bundles, *Heterotermes* spp., was not even present in the two sites which exhibited the lowest decomposition rates. An experimental design which encompasses more study sites is needed to resolve the conflicting responses to fragmentation exhibited by the termite community and wood decomposition.

Table 17. The mean density (no. nests/ ha) of the three termite species contributing to the decomposition of wood within the bundles at the four study sites.

| site | area (ha) | *Parvitermes wolcotti* | *Heterotermes* spp. | *Nasutitermes acajutlae* |
|---|---|---|---|---|
| 30 | 0.26 | 500 | 0 | 3.9 |
| 16 | 3.41 | 0 | 0 | 4.6 |
| 2 | 854.11 | 0 | 33.3 | 4.8 |
| ref S | 3724.75 | 312.5 | 12.5 | 9.7 |
| No. of bundles attacked | | 3 | 23 | 17 |

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.

### *Conservation Priorities*

In general, termite species richness increased relative to fragment area, suggesting that large fragments should receive the highest priority when considering which areas to protect and manage. The protection of large fragments will also be required in order to preserve species which may be sensitive to forest fragmentation (e.g., *C. discolor*). However, fragments as small as 0.3 ha are able to support relatively diverse assemblages of termites and should also be incorporated into landscape level management strategies. The percentage of statistically significant relationships between termite community attributes and landscape characteristics was low (less than 5% without being corrected for multiple comparisons). Therefore, no recommendations can be made concerning the surrounding landscape of forest fragments. These results should be interpreted with caution due to the limited number of sites investigated and the low variability among the sites with respect to their surrounding landscapes (i.e., three of the twelve sites were completely surrounded by agriculture), which may preclude determination of existing relationships.

### *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 controlled by 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 functions necessitates 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.

# APPENDIX A

Compositional and structural data for the vegetation at 40 subtropical dry forest fragments located throughout southwestern Puerto Rico and three forest types within Guánica Commonwealth Forest (from Ramjohn *et al. unpublished*). Sites included in the present study are in **bold** print.

| Site | Area | Plant Species Richness | Tree Species Richness | No. of Stems/ha | | | Mean Basal Area ($m^2$/ha) |
|---|---|---|---|---|---|---|---|
| | | | | >1cm | >2.5cm | >5cm | |
| 1 | 750 | 173 | 87 | 24825 | 8600 | 1550 | 17.5 |
| **2** | **854** | **128** | **67** | **18800** | **7600** | **2160** | **18.4** |
| 3 | 98 | | | | | | 28.8 |
| **4** | **137** | **153** | **73** | **11861** | **5687** | **1357** | **16.5** |
| **5** | **97** | **152** | **79** | **21680** | **7120** | **2840** | **30.7** |
| 6 | 68.1 | 96 | 40 | 4600 | 2733 | 1200 | 17.9 |
| **7** | **33.6** | **149** | **61** | **25400** | **8600** | **2760** | **26.1** |
| 8 | 9.4 | 102 | 42 | 8333 | 4600 | 2900 | 23.0 |
| 9 | 5.9 | 51 | 26 | 35840 | 4960 | 160 | 9.5 |
| **10** | **6.3** | **101** | **42** | **8067** | **3800** | **1667** | **17.0** |
| 11 | 3.1 | 108 | 52 | 12250 | 6300 | 1450 | 23.3 |
| 12 | 3 | 82 | 33 | 11752 | 5214 | 1239 | 13.1 |
| **13** | **3.1** | **69** | **31** | **11371** | **5029** | **1029** | **9.5** |
| 14 | 2.7 | 84 | 46 | 12800 | 6050 | 1700 | 15.4 |
| 15 | 2.1 | 71 | 25 | 13244 | 4790 | 2647 | 23.0 |
| **16** | **3.4** | **69** | **34** | **10100** | **2900** | **967** | **11.7** |
| 17 | 1.7 | 59 | 38 | 16867 | 2467 | 267 | 5.1 |
| 18 | 1.5 | 84 | 37 | 24686 | 9543 | 1600 | 17.8 |
| 19 | 1.5 | 62 | 27 | 6400 | 4700 | 2250 | 23.7 |
| 20 | 1.5 | 47 | 16 | 5300 | 3750 | 1900 | 14.8 |
| 21 | 1.2 | 104 | 40 | 6067 | 3933 | 1133 | 10.9 |
| 22 | 1.2 | 70 | 44 | 25543 | 4571 | 800 | 12.5 |
| 23 | 1 | 65 | 23 | 5143 | 3000 | 2000 | |
| 24 | 1 | 30 | 13 | 6800 | 3600 | 700 | 10.2 |
| 25 | 0.98 | 98 | 46 | 10200 | 5300 | 2800 | 20.8 |
| 26 | 0.9 | 74 | 27 | 7479 | 4790 | 2647 | 14.1 |
| **27** | **0.7** | **71** | **27** | **17067** | **10267** | **6333** | **33.3** |
| **28** | **2** | **68** | **31** | **15840** | **8240** | **2880** | **16.5** |
| 29 | 0.2 | 44 | 22 | 9467 | 6400 | 3600 | |
| **30** | **0.26** | **76** | **36** | **5134** | **2723** | **804** | **15.7** |
| 31 | 0.11 | 63 | 34 | | | | |
| 32 | 0.1 | 41 | 15 | | | | |

# APPENDIX A (cont'd)

| Site | Area | Plant Species Richness | Tree Species Richness | No. of Stems/ha >1cm | No. of Stems/ha >2.5cm | No. of Stems/ha >5cm | Mean Basal Area ($m^2$/ha) |
|---|---|---|---|---|---|---|---|
| 33 | 0.09 | 27 | 7 | 4900 | 2100 | 1000 | 5.6 |
| 34 | 0.07 | 58 | 22 | 2257 | 1285 | 771 | 25.4 |
| 35 | 0.07 | 46 | 18 | 12661 | 8257 | 4771 | 23.0 |
| **36** | **0.06** | **70** | **32** | **7717** | **3696** | **1087** | **19.4** |
| 37 | 0.02 | 29 | 12 | 2750 | 1800 | 1500 | |
| 38 | 0.01 | 17 | 6 | 20583 | 9750 | 2833 | |
| 39 | 0.01 | 28 | 10 | 10900 | 5300 | 3200 | |
| **40** | **0.006** | **21** | 7 | **7000** | **5000** | **3833** | |
| **Guánica Forest**[†]**:** | | | | | | | |
| Semi-evergreen forest | | | | 11275 | 5125 | 1800 | 20.5 |
| Deciduous forest | | | | 24857 | 9857 | 1905 | 16.9 |
| Scrub forest | | | | 18133 | 8733 | 4467 | 25.8 |

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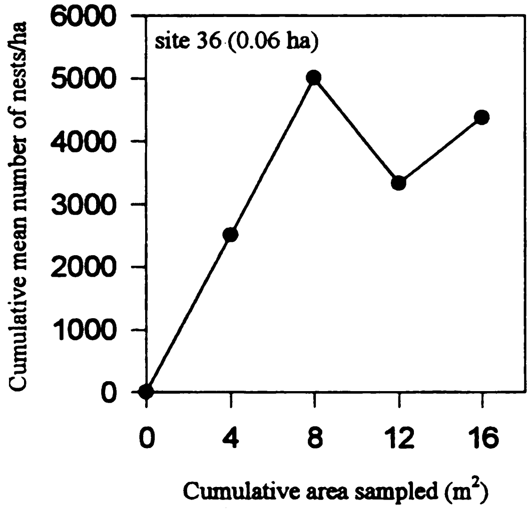
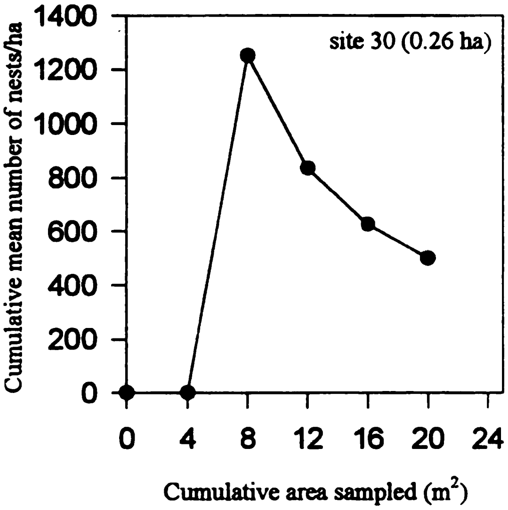
[†] Richness data not available.

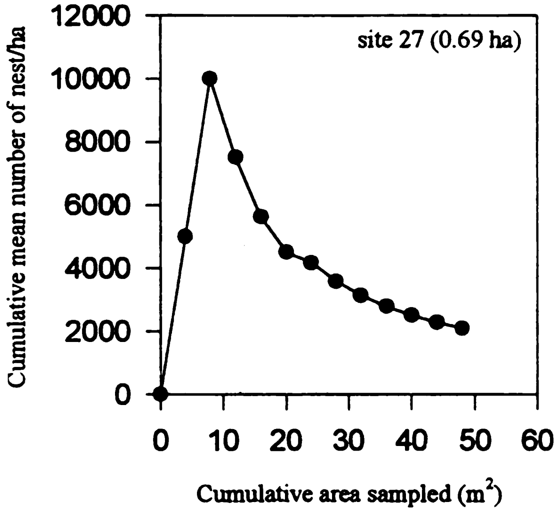
# APPENDIX B

Performance curves for *Procryptotermes corniceps* nest density (# nests/ha) at the 12 forest fragments and reference site (Guánica Forest). Sites where *P. corniceps* was not detected by the plot sampling procedure have not been included.

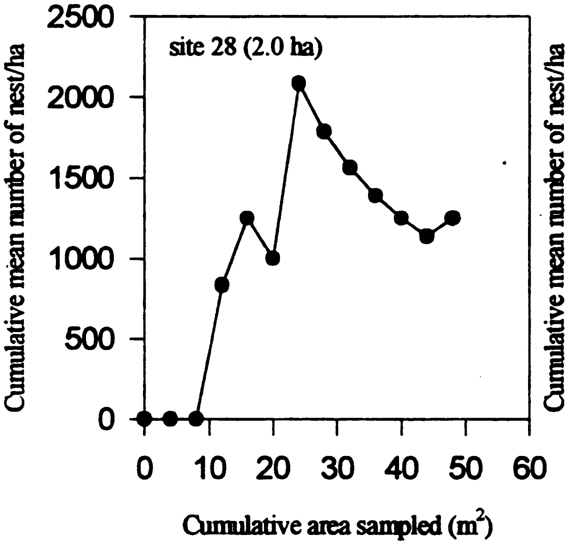
**Small (< 1 ha) Fragments:**

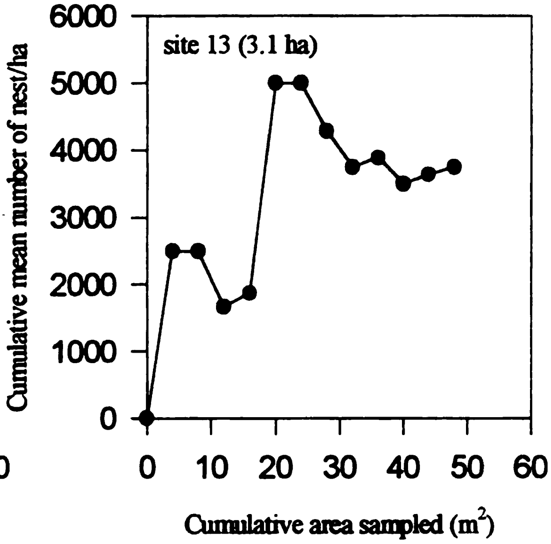


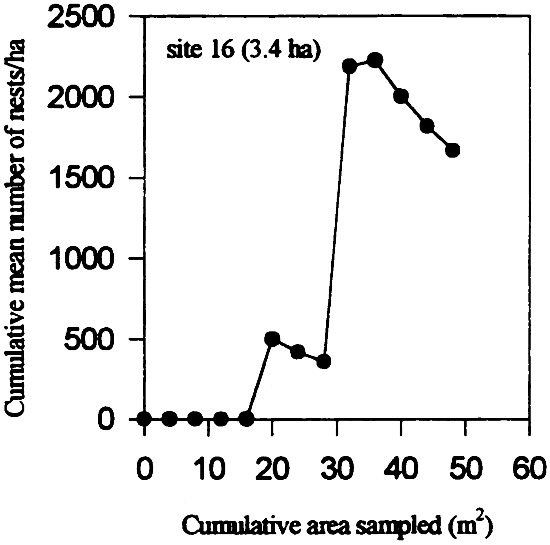




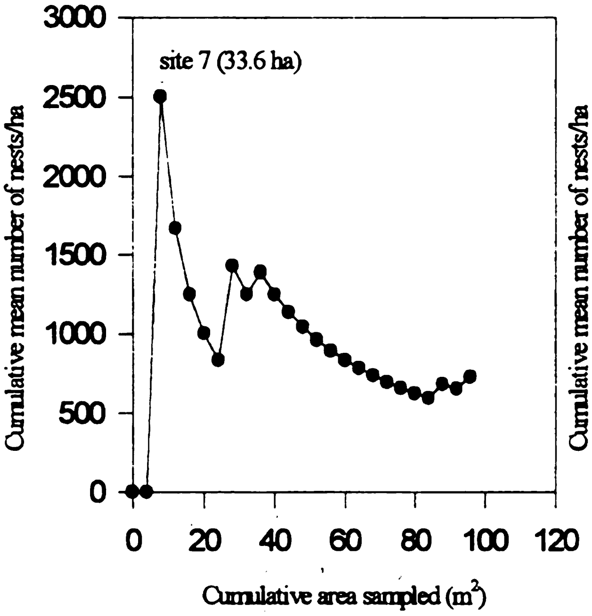
**Medium (1-10 ha) Fragments:**

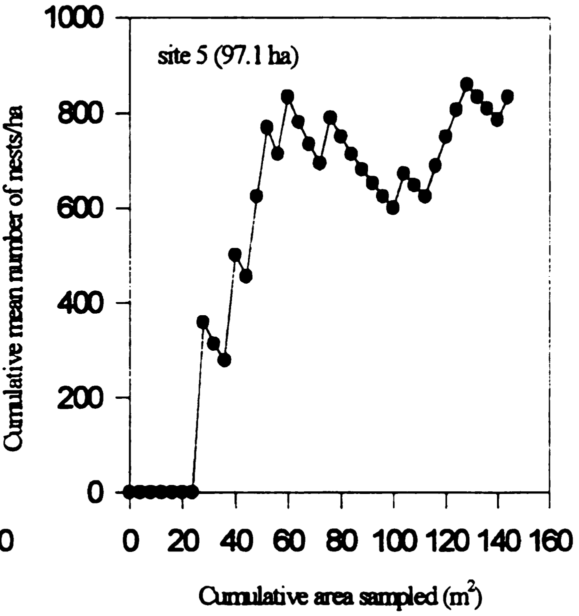


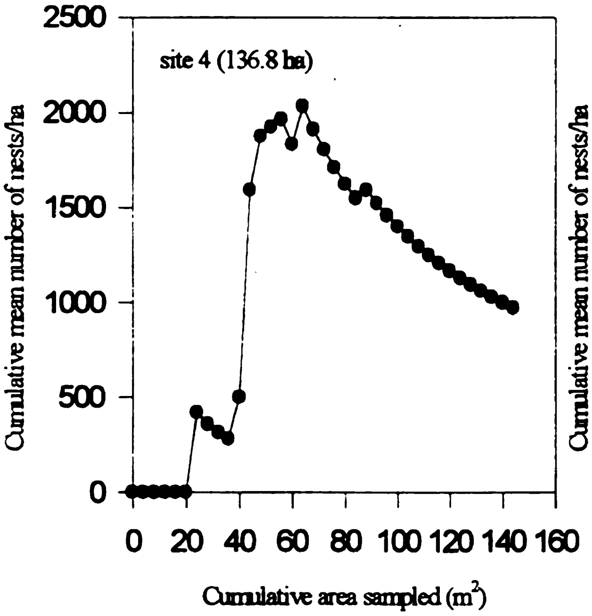


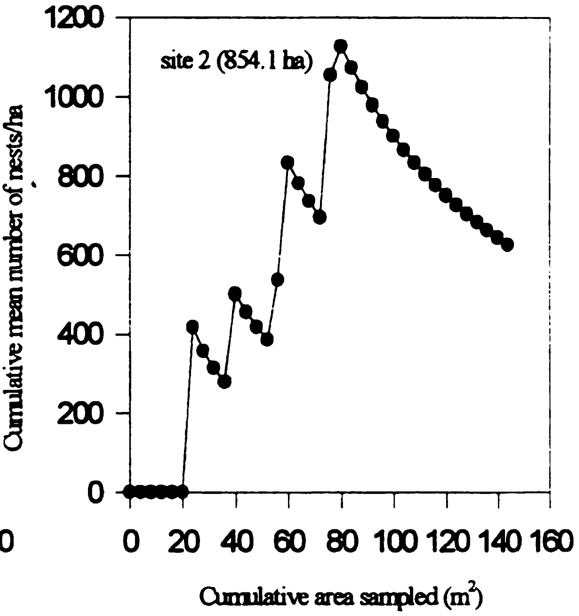


**Large (> 10 ha) Fragments:**

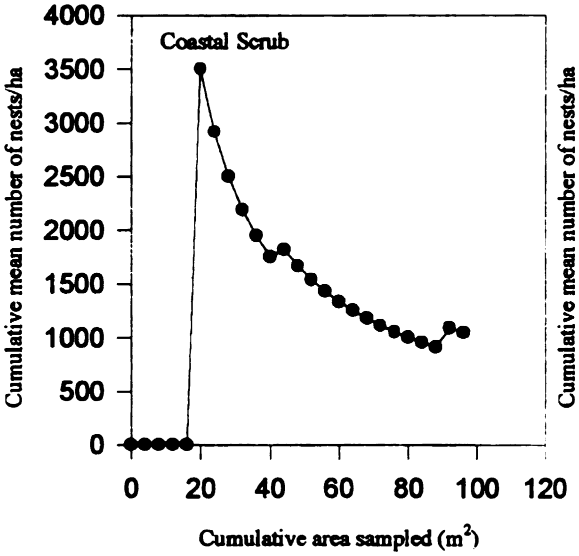


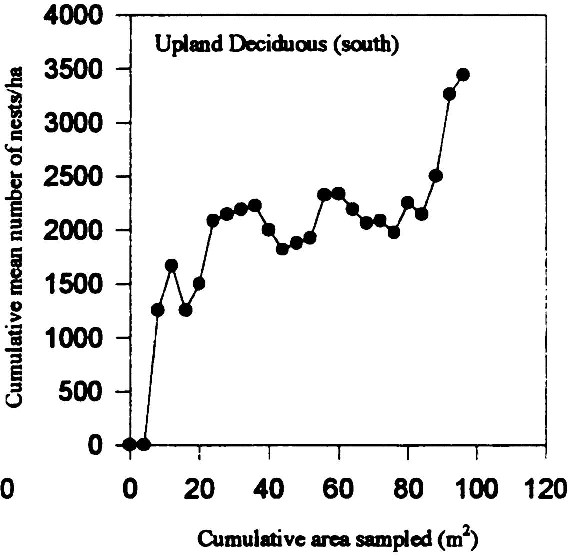


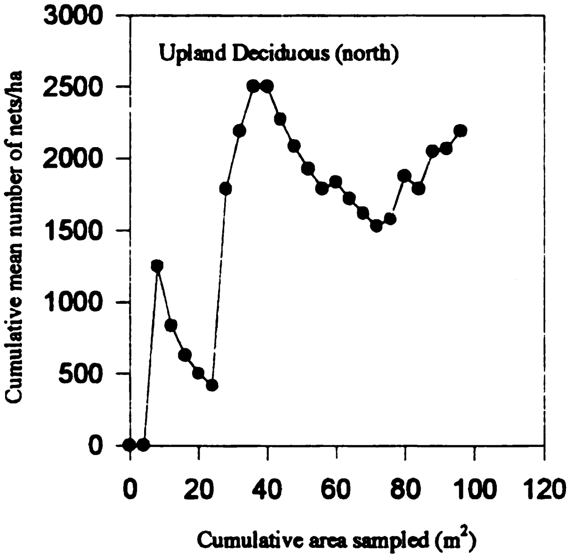


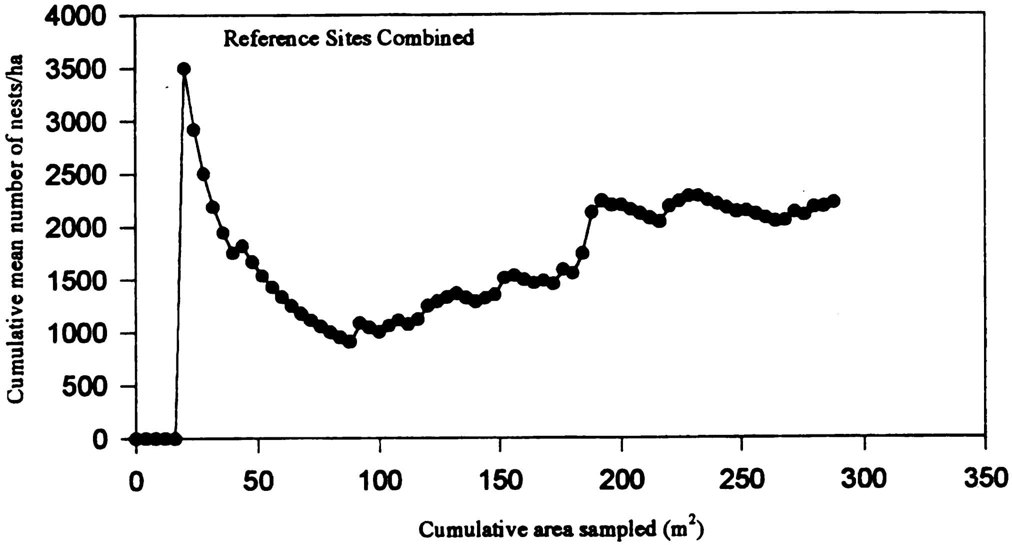


## Reference Site (Guánica Forest):





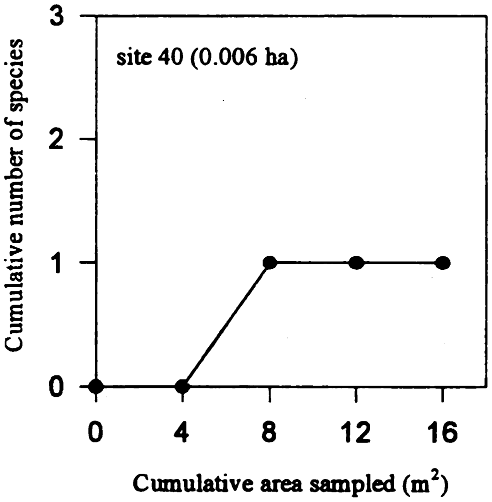


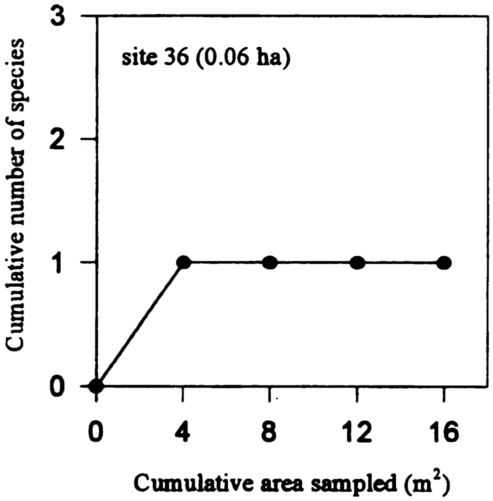

Reference Sites Combined
Cumulative mean number of nests/ha
4000
3500
3000
2500
2000
1500
1000
500
0
0
50
100
150
200
250
300
350
Cumulative area sampled (m²)

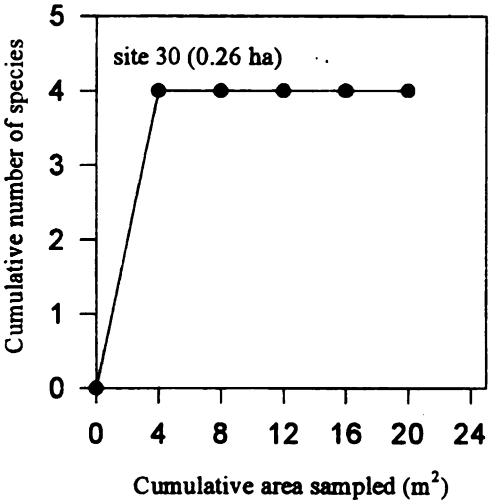
# APPENDIX C

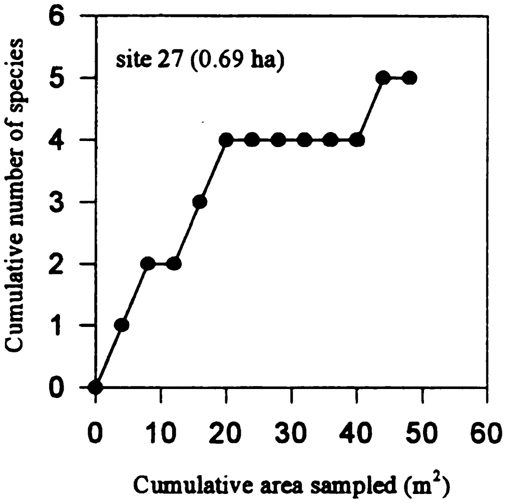
Species accumulation curves for the 2 m x 2 m plots at the 12 forest fragments and reference site (Guánica Forest).

**Small (< 1 ha) Fragments:**

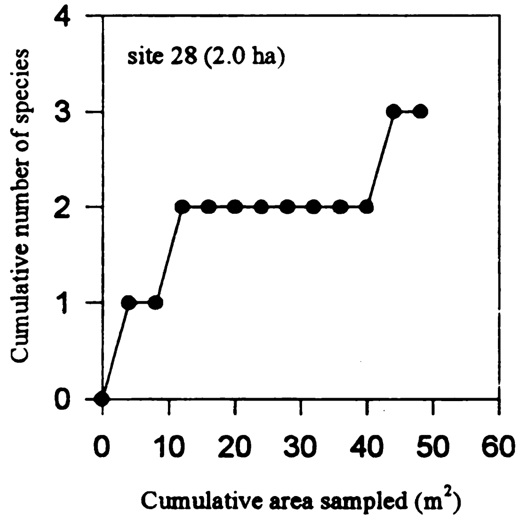


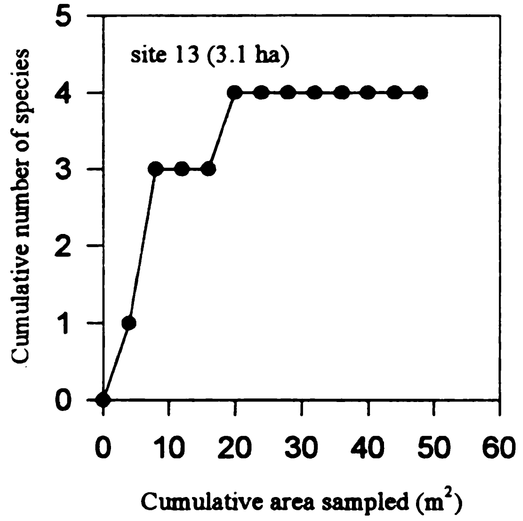


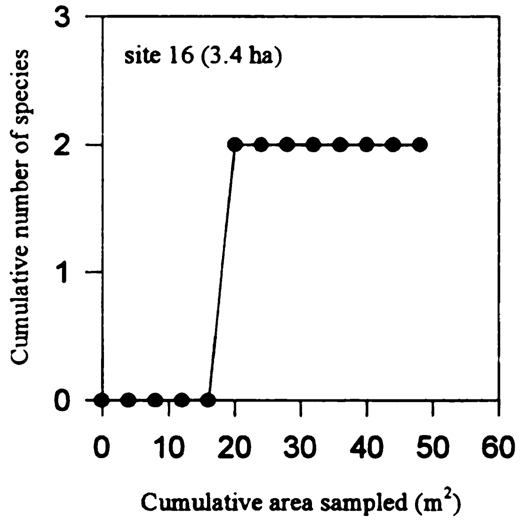


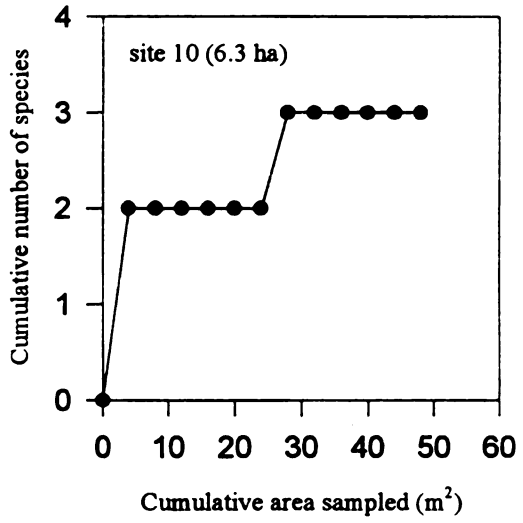


## Medium (1-10 ha) Fragments:

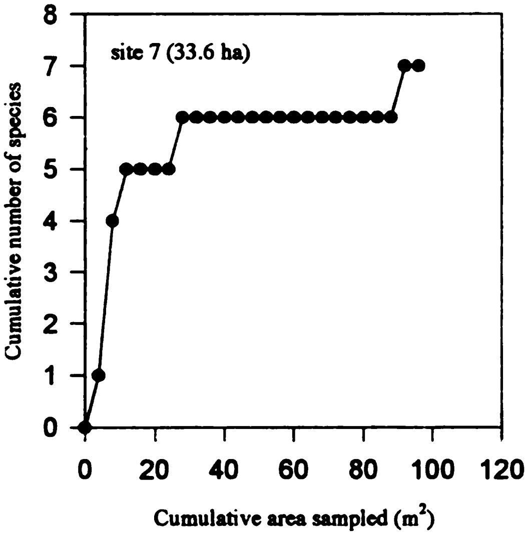


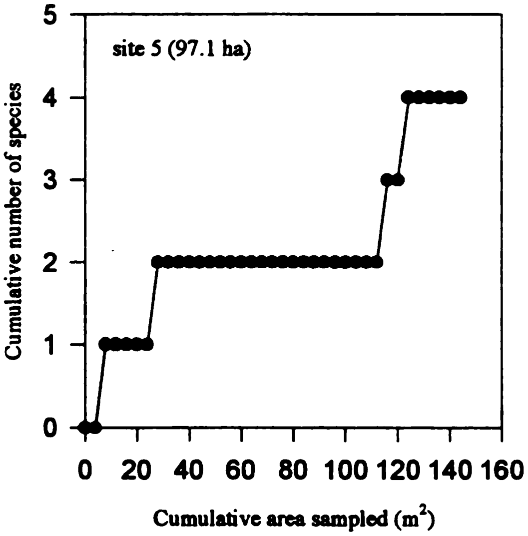


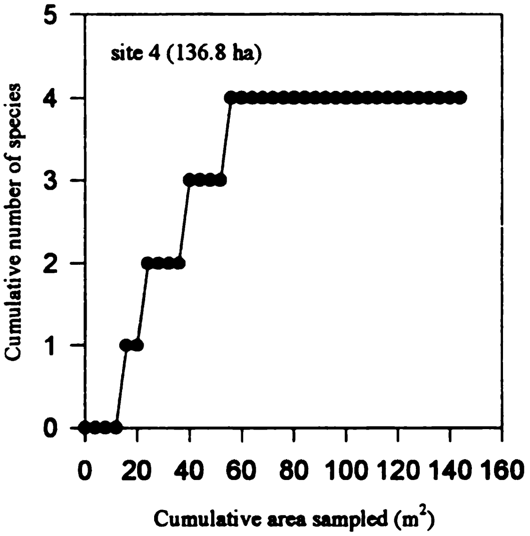


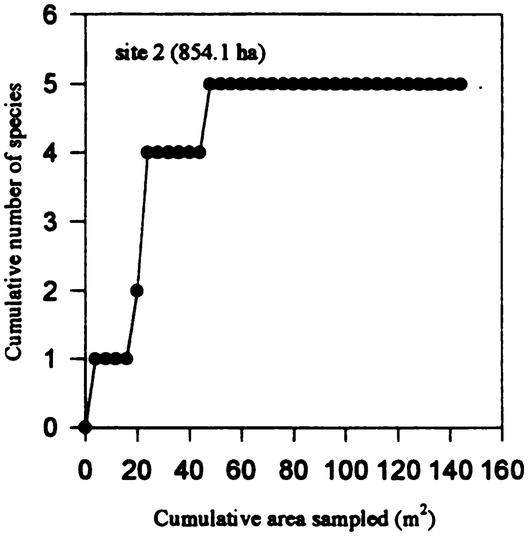


## Large (> 10 ha) Fragments:

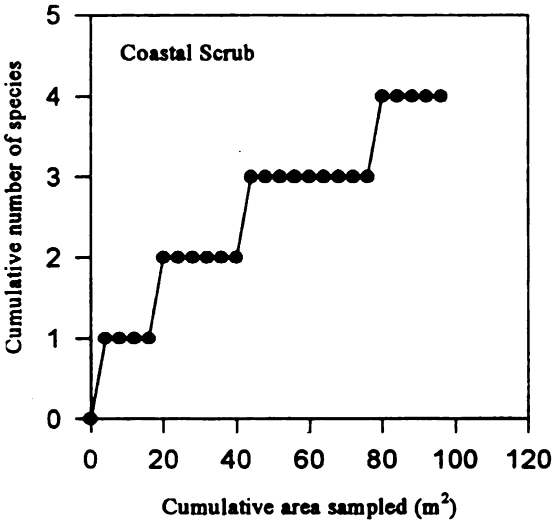


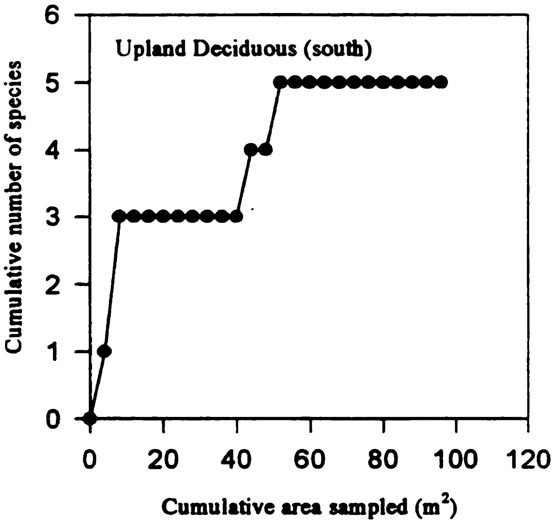


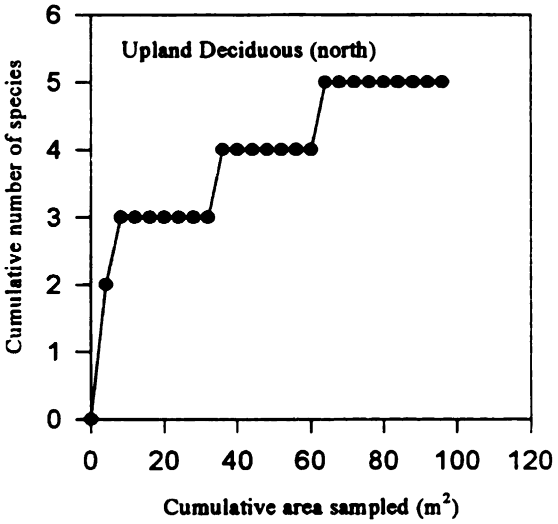


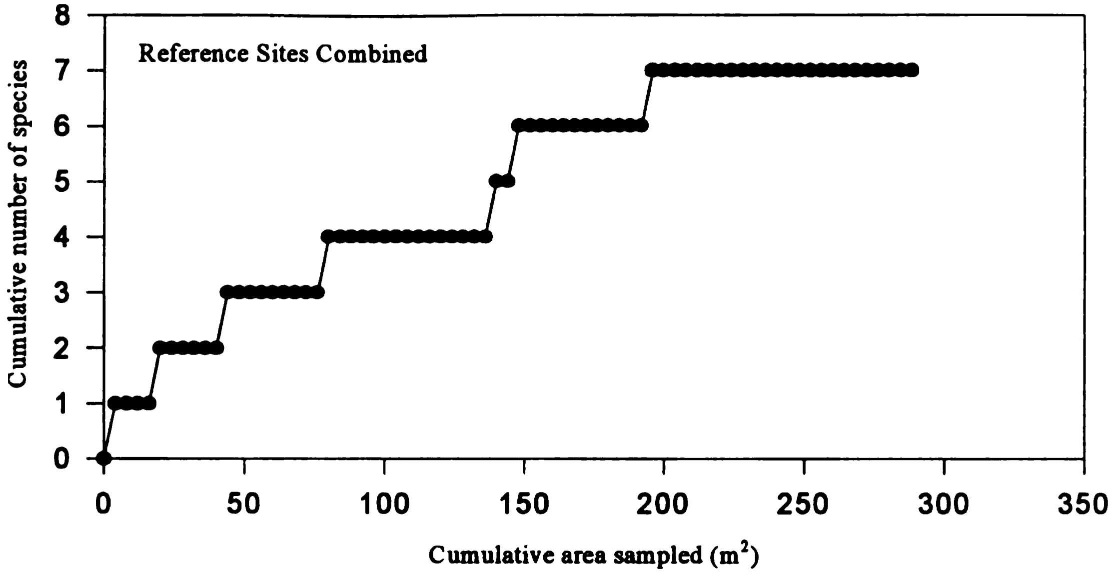


**Reference Site (Guánica Forest):**



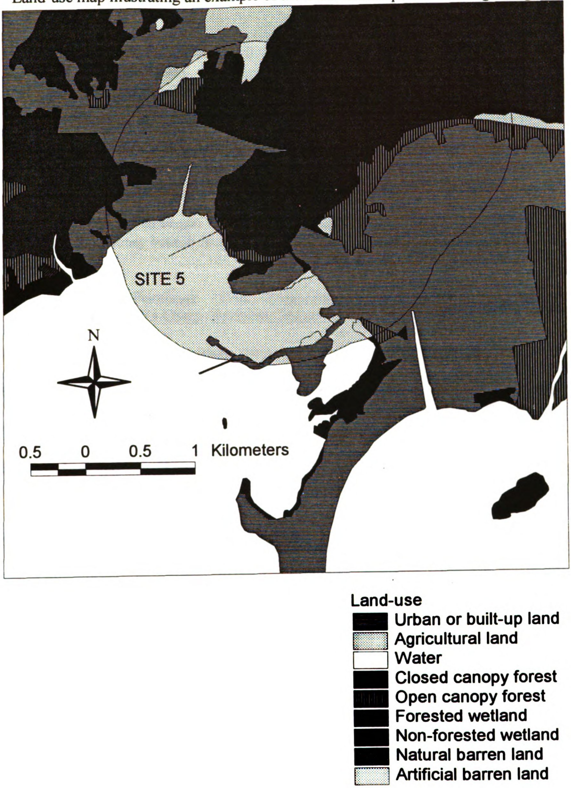





Reference Sites Combined
Cumulative number of species
0
1
2
3
4
5
6
7
8
0
50
100
150
200
250
300
350
Cumulative area sampled (m2)

# APPENDIX D

Land-use map illustrating an example of the 1 km landscape surrounding a fragment.



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