Effect of Tree Size and Growth Form on the Presence and Activity of Arboreal Termites (Insecta: Isoptera) in the Atlantic Rain Forest

by

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ABSTRACT

Despite the well known diversity of termites capable of inhabiting arboreal environments, the determinants of tree exploitation by termites remain largely unknown. Data collected on trees exploited by termites in Brazilian Atlantic rainforest, a hot spot of diversity, reveals that whereas termite presence on trees is positively related simply to tree size, termite activity within arboreal tunnels depends on tree size and growth form. This leads us to hypothesize that termites find large trees randomly but keep higher activity in large trees due to the availability of food and arboreal nesting sites.

Keywords: tree height, circumference at breast height, tree architecture, *Microcerotermes*, *Nasutitermes*, Isoptera.

INTRODUCTION

Termites are known as detritivorous organisms that have an enormous importance in the dynamics of natural forest ecosystems, being one of the most important groups involved in organic matter decomposition (Black & Okwakol 1997; Ohkuma 2003) and nutrient cycling (Wood & Sands 1978; Tayasu *et al.* 1997). Termites are generally associated to soil fauna but several species inhabit trees (Krishna & Weesner 1969), including several Neotropical species among which *Ruptitermes arboreus* Emerson, *Armitermes holmgreni* Snyder, *Constrictotermes cavifrons* Holmgren, *C. cyphergaster* Silvestri, *Labiotermmes labralis* Holmgren, some *Nasutitermes* Dudley and *Rotunditermes* Holmgren, *Armitermes excellens* Silvestri and species of the genus *Microcerotermes* Silvestri (Constantino 1999).

Little is known on the factors determining the exploitation of trees by termites but, for other insects, the size, growth form, and variety of above-ground parts of a tree seem to play an important role (Lawton

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1983; Strong *et al.* 1984). In fact, studies carried out on tropical forests have found that adult or large trees hold higher richness and abundance of herbivore insects than do saplings or trees that are in the understory or at the confluence of the canopy (Basset *et al.* 1992; Basset 2001; Barrios 2003). Accordingly, the height of the tree host affects the richness and abundance of immature Lepidoptera (Haysom & Coulson 1998), whereas the crown structure of neighboring trees determines the flight of the adults of these insects (Koike & Nagamitsu 2003).

Considering that the structure of a tree can affect the quantity and quality of resources and conditions offered to other insects, it is reasonable to assume that it will also affect termites. In fact, the structural simplicity of coconut trees was determined as a limiting factor for the settlement of termite nests, due to the lack of appendices on the stem (Leponce *et al.* 1997). Therefore, the objective of this work was to test the hypothesis that structural characteristics of adult trees affect the presence and activity of their associated arboreal termites.

MATERIALS & METHODS

Study area

The study was carried out in the Rio Doce State Park, Brazil, between January 15 and February 15 (summer season) of 2004. This park is the largest relict of Atlantic rain forest of Minas Gerais state, Southwestern, Brazil, and is **located between - S and - W.** To the East it is bordered by the river Doce and to the South by the Piracicaba river. This biome is one of the most important "hot-spots" of global biodiversity (Myers *et al.* 2000). The local altitude varies from 230 to 515 m above sea level (SOCT 1981). The area is characterized by the Aw Köppen climate type (Tropical warm semi-humid), with rainy season from October to March and dry season from April to September. Mean rainfall is 1480.3 mm/year and the **mean temperature C° (Gilhuis 1986)**. Vegetation is mainly stationary semideciduous (Lopes 1998), with a moderate to high percentage (20 to 50%) of deciduous trees (Veloso *et al.* 1991).

Definition of terms

We refer to "arboreal" as those termites (Insecta: Isoptera) that build earthen tunnels on living trees, such tunnels serving as a shelter for foragers. This is not a trivial definition of such termites, since most authors tend to (implicitly or not) use this term when referring to termites that do build nests on the tree (see Noirot & Darlington (2002) for a review on the nesting behavior of termites). However, since our data do not allow us to distinguish whether termites were searching for food, nesting on the tree, or merely using the tunnels as connections to other trees, we find it advisable to make such a warning in order to prevent any misconception.

The mere "presence" of termites in tunnels, regardless of the number of individuals, was considered indicative that the tree was suitable enough to be used by them. On the other hand, the number of termites within a tunnel, named here termite "activity", was taken as a surrogate of the degree of suitability of the tree to the termite.

Sampling design & Data collection

Sampling consisted of the evaluation of 69 trees with a minimum of 15 cm of circumference at 1.3 m from the soil (circumference at breast height, CBH). Trees were located in four regions of the Park, known as the Mata do Gambá, Mata do Macuco-Lagoinha, Mata da Tereza and Mata do Vinhático. Trees were selected that were a minimum distance of 50 m from the forest edge.

Each tree was evaluated for presence or absence of termite tunnels at 1.30 m from soil level. Termite activity was accessed by simultaneously interrupting both extremities of a 15 cm long portion of the tunnel and capturing all termites found therein. Further inspection on the remainder of the tunnel resulted in catching additional soldiers, thereby guaranteeing secure identification of the species. This additional sample also allowed us to confirm that the tunnels were actually being used by termites, in the event that the activity inside the inspected portion of tunnel was momentarily zero. We did not sample tunnels built *inside* wood. Termites were kept in 80% alcohol, labeled and identified to genus and morphospecies. The identification was confirmed by comparison to specimens from the Section of Termitology of the Entomological Museum of the Federal University of Viçosa, Brazil, where voucher specimens are deposited.

Tree architectural measurements, such as the circumference at breast height, shaft height, total height and number of secondary and tertiary ramifications, were taken using a 50 m long measuring tape. Trees were climbed using the single rope technique (Moffet & Lowman 1995). Ramifications originating from the trunk are called "secondary" whereas "tertiary" are those departing from secondary ones.

Data Analysis

All analysis were processed under R (R Development Core Team 2005), using generalized linear models (glm), followed by analysis of residues to check for the suitability of error distribution and for model adjustment. Minimum adequate model (MAM) was obtained by extracting non-significant terms ($p < 0.05$) from the full model composed by all the variables and their interaction.

The hypothesis that the architectural characteristics of a tree affects the presence of termites on trees, was tested using a model whose binary response variable y assumed the value one, when active tunnels were detected on the tree trunk and zero when there were no tunnels or when they were abandoned. Explanatory variables used were: *Density of branches*, *Total height* and *Circumference at breast height (CBH)*.

Density of branches is the ratio of the sum of secondary and tertiary ramifications to crown height (m):

$$Density\ of\ branches = \frac{Secondary + Tertiary\ ramifications}{Crown\ height}$$

The effect of tree architecture on termite activity was tested using a model whose response variable (y) was the activity of termites on the tree (= number of termites inside a 15 cm long portion of the tunnel), and the explanatory variables (x) were the same used in the previous model, plus the co-variate *Genus* and their interaction. Genus is a qualitative variable assuming one of the two values *Microcerotermes* and *Nasutitermes*. The full models used in hypotheses tests are therefore:

$$\begin{aligned} Presence\ \&\ Absence\ of\ termites = \\ Density\ of\ branches + Total\ height + CBH + \\ Density\ of\ branches : Total\ height + \\ Density\ of\ branches : CBH + \\ Total\ height : CBH + \\ Density\ of\ branches : Total\ height : CBH \end{aligned} \qquad (1)$$

$$\begin{aligned} Activity\ of\ termites = \\ Density\ of\ branches + \\ Total\ height + CBH + Genus + \\ Density\ of\ branches : Total\ height + \\ Density\ of\ branches : CBH + \\ Density\ of\ branches : Genus + \\ Total\ height : Genus + CBH : Genus + \\ Total\ height : CBH + \\ Density\ of\ branches : Total\ height : CBH \end{aligned} \qquad (2)$$

In the models, a plus sign (+) denotes the addition of a variable to the model whereas a colon (:) means an statistical interaction between variables. Error distribution was Binomial and Negative Binomial for models (1) and (2) with logit and log link functions respectively.

RESULTS

Termites collected belonged to Termitidae family and comprised two subfamilies, two genera and four morphospecies (Table 1). Out of the 69 evaluated trees, 25 held active tunnels, whereas 6 held inactive termite tunnels. The remaining trees did not show any sign of termite presence.

Termite nests were directly spotted on five out of the 25 trees containing active tunnels. Among those, only one tree held two nests, whereas the others held single nests. The maximum height of the observed nests was 16.9 meters, the average height was 11.91 meters, and the minimum height was 7.35 meters above ground.

Table 1. List of the morphospecies of the sampled arboreal termites in State Park of Rio Doce, MG, Brazil 2004.

Subfamily	Morphospecies
Nasutitermitinae	*Nasutitermes kemneri* Snyder & Emerson
	Nasutitermes sp. 1, sp. 2
Termitinae	*Microcerotermes* cf. *exiguus* Hagen

The encounter of trees by termites was determined only by the increment of CBH (F = 4.9187, P = 0.02657, Fig. 1, Table 2). But the activity of termites was affected by all the variables measured and some interactions between them (Table 3).

DISCUSSION

The size, growth form, and variety of above-ground parts of a tree affect the presence and the activity of termites, and this varied with the genus of termites. The mere presence of termites on a tree is determined only by tree size as represented by its circumference at breast height (CBH) (Table 2, Fig. 1). Trees presenting large circumference are necessarily more conspicuous and have more probability of being found because (*i*) occupy more space and/or (*ii*) are older and therefore have been in the environment for a longer time. This, coupled to the low ability of termites to control their flight (Nutting 1969), lead us to conclude that alates find trees randomly. That is, upon a swarm, alates

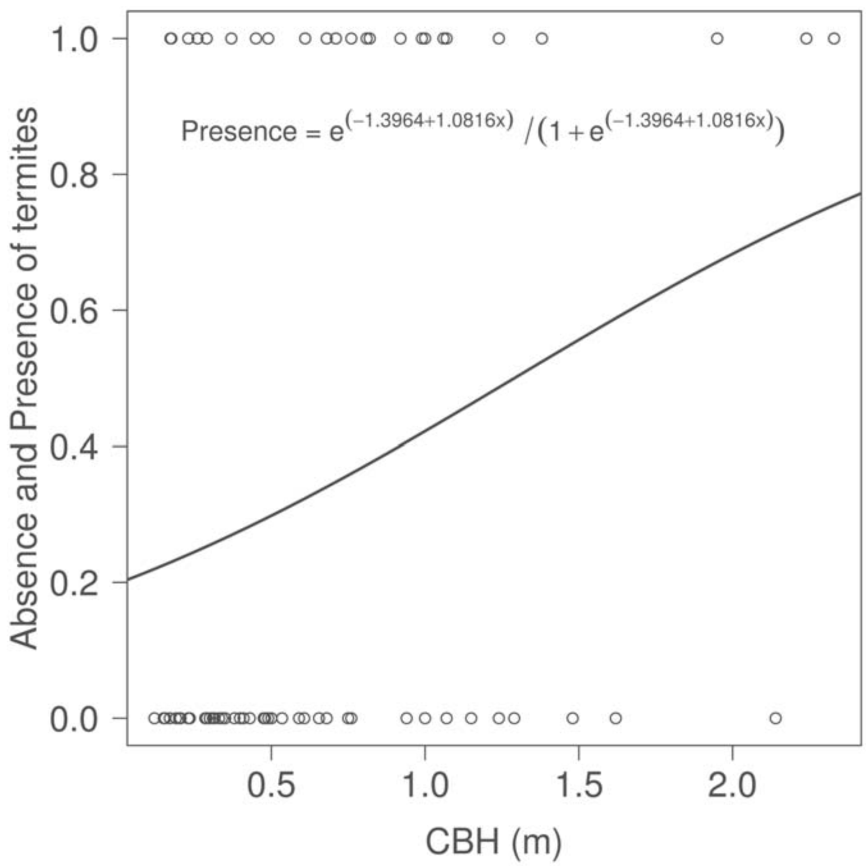

Fig. 1. Relationship between CBH of trees and the presence and absence of arboreal termites in State park of Rio Doce, MG, Brazil, 2004. Using generalized linear modelling with Binomial errors and logit link function. In axis y, 0 is absence of termites and 1 is presence.

land on large trees not because such trees have been selected, but simply because the wind has blown termites against them. Moreover, this may occur also for foragers, since, at least for the arboreal species *Constrictotermes cyphergaster* Silvestri, food search begins without a directional pattern (Souto *et al.* 1999). Thus larger trees are more prone to be found by termites, and this seems not to be due to any intrinsic quality of the tree.

However our results also show that the parameters determining the encounter of trees by termites do not guarantee the success of their colonies. If one considers the activity of termites (= number of individu-

Table 2. Analysis of deviance of the minimal adequate model showing the effect of circumference at breast height on arboreal termite presence, using glm and Binomial errors and logit link function.

Source of variation	df	F	P
MAM	1	4.9187	0.02657
CBH	1	4.9187	0.02657
Error	67		
Total	68		

als inside a tunnel, see Material & Methods) as a measure of this success, one can say that the success of a termite colony does not rely only on variables linked to the size of trees but also on variables that represent its growth form. That is, colonies of termites, will keep more individuals active inside the tunnels, when the tree size (CBH and total height) and the concentration of big branches (density of branches) are bigger (Table 3, Fig. 2). Data on the effect of tree characteristics upon its termite activity are scarce, limiting our conclusions, but Jones & Gathorne-Hardy observed a similar pattern, where *Hospitalitermes hospitalis* Haviland colonies prefer to forage in larger circumference trees. These authors consider that larger circumference trees are preferred because they present a larger superficial area, providing a higher accumulation of food resource.

Our results seem to point to the same direction. The joint effect of density of branches, circumference at breast height, and total tree size (Table 3) could be thought as a surrogate for the availability of termite feeding resources. The more tree branching, the higher the number of bifurcations where organic matter, alone or within epiphytes, can accumulate in the tree crown, and hence the larger the amount of

Table 3. Analysis of deviance of the minimal adequate model showing the effect of circumference at breast height, total height and density of branches on arboreal termite activity, using generalized linear modelling with Negative Binomial errors and log link function.

Source of variation	d	χ^2	P
MAM	8	34.36	3.45
Density of branches	1	3.25	0.071
Total height	1	24.62	6.98
CBH	1	13.70	2.14
Genus	1	6.48	0.011
Density of branches : Total height	1	0.05	0.821
Density of branches : CBH	1	15.43	8.56
Total height : CBH	1	19.89	8.20
Density of branches : Total height : CBH	1	5.34	0.021
Error	15		
Total	23		

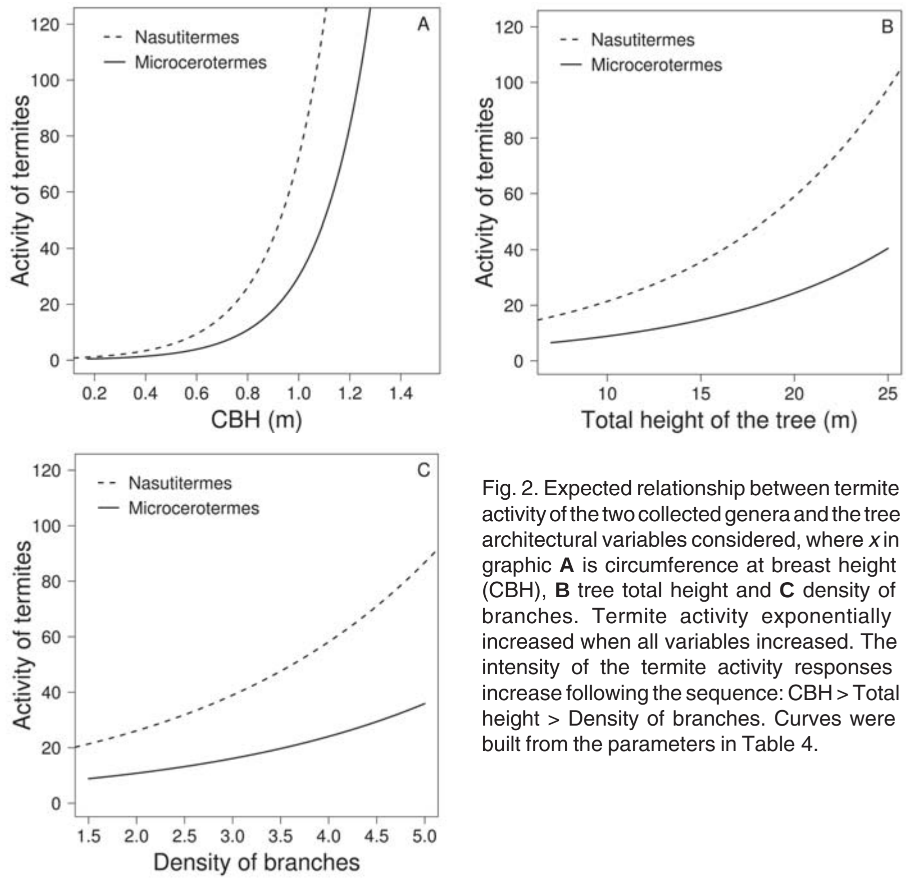

Fig. 2. Expected relationship between termite activity of the two collected genera and the tree architectural variables considered, where *x* in graphic **A** is circumference at breast height (CBH), **B** tree total height and **C** density of branches. Termite activity exponentially increased when all variables increased. The intensity of the termite activity responses increase following the sequence: CBH > Total height > Density of branches. Curves were built from the parameters in Table 4.

"suspended soil". Similarly, larger trees would hold larger amounts of "suspended soil", because there is more space to do so, and also because, by holding more foliage, such trees would produce more debris.

Recent studies have shown that termites profit a lot from such an accumulation of organic matter in tree crowns. Ellwood *et al.* (2002) investigating the debris inside canopy epiphytes found that termites were one of the most numerous organisms using this kind of resource. Similarly Davies *et al.* (2003) recorded the soil feeding termite *Anoplotermes parvus* inside canopy epiphytes, whereas Noirot & Darlington stressed the importance of "suspended soil" as a potential feeding resource for the arboreal nester hummus feeding termites from the genera *Procubitermes, Labiotermes* and some *Anoplotermes*. Besides promoting increased availability of food, such an accumulation of

Table 4: Estimated parameters for the minimal adequate model showing the effect of circumference at the breast height (CBH), total height and density of branches on arboreal termite activity, using generalized linear modelling with Negative Binomial errors and log link function.

Variables	Estimate	Std. Error	z value	Pr(>lZl)
Microcerotermes	-6.55653	1.55854	-4.207	<0.01
Nasutitermes	0.88222	0.35893	2.458	<0.05
Density of branches	1.05333	0.27004	3.901	<0.01
Total height	0.50940	0.09651	5.278	<0.01
CBH	6.54091	1.65092	3.962	<0.01
Density of branches : Total height	-0.13488	0.04071	-3.313	<0.01
Density of branches : CBH	-0.43197	0.99179	-0.436	>0.05
Total height : CBH	-0.40721	0.09456	-4.306	<0.01
Density of branches : Total height : CBH	0.13416	0.05706	2.351	<0.05

debris can also shorten the distance between the arboreal nest and the food resource otherwise found down in the soil, thereby reducing foraging costs. In fact social insects, are capable of optimizing their foraging, choosing shorter routes between their nest and the food resource (Ydenberg & Schimi-Hempel 1994), and termites are known to choose sites richer in food (Waller & La Fage 1987; Waller 1988; Hedlund & Henderson 1999). One could yet hypothesize that trees being large and holding high branch density are stable habitats, thereby favoring the maintenance and growth of termite colonies and, hence, promoting higher termite activity. Our data do not allow us to distinguish which of these hypotheses are true. In view of the paucity of data on the relationship between termites and trees we refrain to pursue them any further, before specific experiments are carried out. In spite of that, our data allow us to state that whereas termite presence on trees is positively related simply to tree size, termite activity within arboreal tunnels depends on tree size and growth form.

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