TERESA TELLES GONÇALVES

DETERMINANTES DA OCUPAÇÃO DE ÁRVORES POR TÉRMITAS (INSECTA: ISOPTERA)

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-graduação em Entomologia, para obtenção do título de "Magister Scientiae".

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APROVADA: 29 de julho de 2005

Dr. Ronaldo Reis Júnior
(Conselheiro)

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Prof. Júlio Neil Cassa Louzada

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(Orientador)

Dedicatória

Aos meus pais,

Ruth Helena Telles da Silva
& Aloisio Antônio Gonçalves.

Deus está nas menores coisas e em nossos pensamentos mais íntimos. Existem ações que dignificam nossa existência perante Deus e o mantém dentro de nossos lares com constância. Uma dessas práticas é o amor, e outra é a busca diária da felicidade. Porém não a alegria frívola mas o sentimento amplo de receptividade aos entraves da vida com serenidade, e que se espalha em gestos generosos àqueles que estão à nossa volta. Ser receptivo é saber extrair dos momentos difíceis o significado educativo do não, isso clareia nossa mente tornando as soluções dos problemas mais simples, e nos fazendo compreender melhor a magnitude divina, o que possibilita uma vida em plena felicidade do espírito.

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Biografia

Teresa Telles Gonçalves, filha de Ruth Helena Telles da Silva e Aloisio Antônio Gonçalves, nasceu em Belo Horizonte, Minas Gerais, em 06 de dezembro de 1978.

Em julho de 2003, graduou-se em Engenharia Florestal, pela Universidade Federal de Lavras (UFLA), Lavras-MG. Durante o período de graduação, de 1999 a 2003, foi estagiária do Setor de Ecologia do Departamento de Ciências Biológicas da UFLA.

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Em julho de 2005, foi aprovada no processo de seleção do curso de Doutorado em Entomologia da UFV.

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Resumo

GONÇALVES, Teresa Telles, M.S., Universidade Federal de Viçosa, julho de 2005. **Determinantes da ocupação de árvores por térmitas (Insecta: Isoptera)** Orientador: Og Francisco Fonseca de Souza. Conselheiros: Ronaldo Reis Júnior e Sérvio Pontes Ribeiro.

Os cupins, ou térmitas, são organismos muito importantes para a manutenção de um ecossistema, agindo diretamente na decomposição da matéria orgânica e ciclagem de nutrientes. A despeito do considerável número de espécies de cupins que é capaz de se estabelecer em árvores, os fatores ecológicos determinando a exploração de árvores por cupins ainda não são bem conhecidos. Este trabalho teve como objetivo principal investigar os determinantes da ocupação de árvores em floresta tropical por térmitas, contribuindo com informações originais sobre cupins e sua relação com as árvores. Os dados foram coletados na área do Parque Estadual do Rio Doce, MG, Brasil e as amostras de cupins e formigas foram identificadas aos níveis de espécies ou gêneros. Especificamente foram testadas três hipóteses: *(i)* o aumento do tamanho e da complexidade de forma de crescimento de uma árvore, influenciam positivamente a presença e atividade dos cupins arborícolas; *(ii)* a presença de formigas afeta negativamente a atividade dos cupins arborícolas, seja por competição ou predação e *(iii)* cupins arborícolas são positivamente influenciados pelo aumento da quantidade de recursos potenciais existentes no chão, próximos à árvore hospedeira. Os resultados apotam que os três grupos de fatores estudados são importantes determinantes da exploração de árvores por cupins. Os padrões encontrados foram discutidos considerando-se a biologia de cupins, e de formigas quando envolvidas.

Abstract

GONÇALVES, Teresa Telles, M.S., Universidade Federal de Viçosa, july 2005. **Determinants of trees exploitation by termites (Insecta: Isoptera)** Adviser: Og Francisco Fonseca de Souza. Committee members: Ronaldo Reis Júnior and Sérvio Pontes Ribeiro.

Termites are important organisms involved in the maintainence of the ecossystems, acting directly in organic matter decomposition and in the nutrient cycling. Despite the well known diversity of termites capable of inhabiting arboreal enviroments, the ecological determinants of tree exploitation by termites remain largely unknown. The aim of this work was to investigate the determinants of tree exploitation in tropical forest by termites, contributing with primary information in the relationship between termite and trees. Data was collected in State Park of Rio Doce, MG, Brazil and the samples were indentified to the lowest possible taxonomic level. Specifically we tested three hipotheses: *(i)* the increment in tree size and growth form have a positive influence on arboreal termite presence and activity; *(ii)* the presence of ants have a negative effect on the activity of arboreal termites and *(iii)* arboreal termites are positively influenced by the increment of potencial resources amount in the ground level, below of the host trees. The results point that the three studied groups of factors are important determinants of tree exploitation by termites. The found patterns were discussed considering the biology of termite, and ants when involved.

1 Introdução Geral

1.1 Apresentação

A tese está dividida em seis seções. A seção 1, ou Introdução Geral, está dividida em duas subseções. A subseção 1 consta da presente apresentação, e a subseção 2 é uma pequena introdução, relacionando o grupo estudado e os fatos que embasaram o questionamento e o objetivo geral desse trabalho. As três seções subsequentes são três artigos, sendo que os dois primeiros já foram aceitos para a publicação na revista *Sociobiology*. A quinta seção é uma Conclusão Geral e a sexta consta das Referências Bibliográficas utilizada em toda a tese.

Especificamente foram testadas três das hipóteses levantadas na subseção 1.2 (Por que existem árvores não ocupadas por térmitas que sobem em árvores?): *(i)* o aumento do tamanho e da complexidade de forma de crescimento de uma árvore influenciam positivamente a presença e atividade dos cupins arborícolas; *(ii)* a presença de formigas afeta negativamente a atividade de cupins arborícolas, seja por competição ou predação; e *(iii)* cupins arborícolas são positivamente influenciados pelo aumento da quantidade de recursos potenciais existentes no chão, próximos à árvore hospedeira. Cada um dos artigos apresentados mostra o teste de uma das hipóteses acima.

1.2 Por que existem árvores não ocupadas por térmitas que sobem em árvores?

Térmitas ou cupins são insetos sociais da ordem Isoptera, que somam cerca de 2.860 espécies descritas. Estes são considerados organismos detritívoros, e um dos grupos de invertebrados mais importantes na decomposição da matéria orgânica (Black & Okwakol, 1997; Ohkuma, 2003) e ciclagem de nutrientes em ambientes naturais (Wood & Sands, 1978; Tayasu *et al.*, 1997). Mesmo sendo organismos geralmente associados ao solo, diversas espécies podem ser encontradas estabelecidas em árvores, incluindo espécies neotropicais (Constantino, 1999).

A denominação "cupim arborícola" é aplicada somente àquelas espécies que constróem seus ninhos em árvores, afixados em troncos ou galhos; e todas essas espécies pertencem à família Termitidae (Krishna & Weesner, 1969). Os cupins arborícolas brasileiros ocorrem em três subfamílias de Termitidae (Nasutitermitinae, Termitinae e Apicotermitinae) e em pelo menos sete gêneros (*Constrictotermes* Holmgren, *Nasutitermes* Dudley, *Armitermes* Wasmann, *Labiotermes* Holmgren, *Ruptitermes* Mathews, *Amitermes* Silvestri e *Microcerotermes* Silvestri) (Constantino, 1999). O hábito arborícola é muito mais expressivo e frequente na subfamília Nasutitermitinae (Noirot, 1969) e *Nasutitermes*, o gênero mais diverso do mundo, geralmente constrói ninhos em árvores (Constantino, 1999).

O hábito de nidificar em árvores é uma notória especialização que surgiu independentemente diversas vezes em Isoptera (Noirot, 1969). A estrutura dos ninhos arborícolas é muito similar à estrutura dos ninhos epígeos, ou montículo, sendo que a característica especial dos ninhos arborícolas é estar situado de forma destacada do solo, normalmente disposto nos troncos e nos galhos de árvores. Entretanto, mesmo localizados de forma destacada do solo, as colônias de cupins arborícolas geralmente apresentam uma ligação com o solo através de túneis descendentes (Noirot, 1969), o que sugere a existência de uma dependência entres esses insetos e o solo, seja para busca de alimentos ou de outros ítens necessários a sua sobrevivência.

A exploração de recursos por insetos sociais envolve um processo complexo, que inicia-se pela localização do recurso, seguida pela decisão de ocupação ou não deste recurso pelos demais indivíduos da colônia. Segundo Korb & Linsenmair (2001), a busca por recurso alimentar (forrageamento), se dá de forma coletiva em cupins, sendo geralmente realizado dentro de túneis construídos dentro ou sobre o substrato (solo ou madeira), existindo poucas espécies que realizam o forrageamento livre (Miura & Matsumoto, 1997).

A despeito do considerável número de éspécies de cupins que é capaz de se estabelecer em árvores, os fatores ecológicos locais, tais como interações biológicas e pressões do meio, que podem determinar a ocupação ou não de uma árvore por cupins ainda não são bem conhecidos. Entre outras interações biológicas, a pressão de predação, tanto de vertebrados quanto de invertebrados, pode ter um papel prepoderante sobre a atividade de cupins. Dentre os invertebrados, as formigas são os predadores mais ativos dos cupins e podem competir fortemente com os mesmos por espaço (Hölldobler & Wilson, 1990). Assim investigar a relação entre esses dois grupos de insetos, é imprescindível para a compreensão dos fatores que determinam a ocupação de árvores por térmitas.

Dentre as pressões exercidas pelo meio, estão a distribuição e a disponibilidade de recursos. As copas das florestas tropicais podem ser provedoras de recursos tanto alimentares quanto de nidificação para os cupins. Sendo que características da estrutura da árvore, como o número de galhos, pode influenciar diretamente na disponibilidade de sítios para alocação dos ninhos.

A celulose é o componente base da alimentação dos cupins e, sendo organismos detritívoros, eles consomem uma larga amplitude de ítens de origem vegetal morta, em vários estágios de decomposição (Donovan *et al.*, 2001). Assim, os ítens de consumo mais comuns desses insetos são pedaços de madeira morta, serrapilheira e matéria orgânica dissolvida em partículas de solo, e esses podem ser encontrados tanto em árvores quanto no chão das florestas.

O recurso alimentar dos cupins pode estar distribuído nas copas na forma de matéria orgânica em decomposição, na própria madeira constituínte das árvores, líquens e em epífitas. Segundo Basset *et al.* (2003), existe no conjunto de copas de árvores (dossel) das florestas tropicais e temperadas uma expressiva acumulação de matéria orgânica nas ramificações das árvores. Esse "entulho" provê habitat para uma diversa gama de microartrópodes. Consequentemente, o "entulho" ou "solo suspenso", como é chamado, presente acima do nível do solo é recurso alimentar em potencial para os cupins consumidores de serrapilheira.

A árvore é constituída de material vegetal e é como um todo, recurso alimentar em potencial, sendo que seus galhos mais antigos e em estágio de senescência serviriam de alimento para os cupins (principalmente cupins consumidores de madeira seca como os da família Kalotermitidae). As epífitas e as lianas são extremamente abundantes em florestas tropicais (Nieder *et al.*, 2001; Novotny *et al.*, 2003) e têm um forte efeito na distribuição e abundância de diversos artrópodes. A alta incidência de lianas e epífitas aumenta a heterogeneidade estrutural das copas e diminui o efeito climático nas mesmas, além de ser recurso em potencial para herbívoros (Stuntz *et al.*, 2003).

Considerando a potencialidade dos recursos a serem oferecidos por uma árvore e que as árvores são recursos potencialmente abundantes em uma floresta, e observando ainda que essas árvores, em uma floresta, podem estar ocupadas ou não por galerias de cupins, uma pergunta a se fazer é: Que fatores determinam a escolha de uma árvore pelos térmitas? Quais as condições e recursos devem estar reunidos nesta árvore, ou próximos à mesma, para que haja o estabelecimento e o sucesso da ocupação da mesma pelos cupins? E na tentativa de responder a essas questões formulamos as hipóteses a seguir.

1.2.1 Hipóteses

Em uma floresta, árvores são encontradas em abundância e são recursos em potencial para cupins. Assim, por que algumas árvores não são exploradas por cupins? Quais são os fatores que levam ao sucesso da utilização de uma árvore por cupins?

Uma árvore pode prover tanto local de nidificação como recursos alimentares para os cupins, e em uma floresta estas podem ser encontradas em duas situações:

(i) árvores que apresentam condições e recursos adequados e que, no entanto não são exploradas pelos cupins.

(ii) árvores que não são exploradas porque são rejeitadas pelos cupins.

Considerando as árvores da primeira situação *(i)*, podemos supor que:

(Hi.1) Existem árvores não exploradas por cupins porque existe uma oferta de árvores adequadas à exploração além da capacidade dispersiva e colonizadora dos mesmos.

Já na segunda situação, as árvores são rejeitadas por que não apresentam a reunião de condições e recursos adequados ao estabelecimento ou permanência dos cupins nas mesmas. Um fator de rejeição da árvore pelos cupins pode ser a inadequabilidade das condições físico-climáticas ou condições químicas e biológicas existentes na árvore. Os cupins são insetos de corpo mole e muito sensíveis a altas temperatura e dessecação. Assim um indivíduo de cupim pode rejeitar uma árvore quando o seu microclima não for favorável à sua ocorrência. Considerando que o microclima é altamente influenciado pelo grau de insolação, temperatura e umidade relativa do ar, podemos supor:

(Hii.1.1) O microclima (grau de insolação, temperatura e umidade relativa do ar) afetam a ocupação das árvores pelos cupins.

Uma árvore pode repelir ou então ser rejeitada por cupins caso apresente condições químicas e ou biológicas desfavoráveis. As diferentes espécies arbóreas possuem diferentes constituintes químicos. Entre as espécies arbóreas existe uma grande variação na proporção dos componentes químicos. Essa variação pode ocorrer na proporção dos compostos fundamentais (holoceluloses e lignina), na composição dos componentes secundários e na composição e concentração dos componentes minerais. Existem espécies arbóreas que possuem mais e outras que possuem menos componentes secundários, os extrativos. Os principais tipos de extrativos são os taninos, óleos voláteis, resinas, látex e alcalóides. Na casca de uma árvore, os extrativos podem representar de 20 a 40% do peso e alguns deles, como terpenóides, resinas ácidas e substâncias fenólicas, têm a função de "proteger" a árvore dos ataques de xilófagos, como fungos e insetos (Sjöstrom, 1993). Dos insetos, os xilófagos mais importantes são os cupins e os besouros. Dentre os fatores químicos que podem ser considerados fatores de rejeição estão a liberação de voláteis deletérios, ou a exudação de resinas que dificultem o acesso e a permanência de cupins na árvore. Assim:

(Hii.2.1) Espécies que sejam resinosas ou apresentem uma grande quantidade de extrativos, principalmente óleos voláteis, na casca são evitadas por cupins.

Dentre os fatores biológicos que podem influenciar na rejeição de uma árvore, a existência de organismos que interajam negativamente com cupins, seja como competidores ou como predadores, pode ser muito importante. As formigas são os invertebados predadores mais ativos e efetivos dos cupins. Existem pelo menos seis gêneros de formigas tropicais que são especializados em se alimentar de cupins (Wilson, 1971). Assim pode-se supor que:

(Hii.2.2) A presença de formigas nas árvores afeta negativamente a atividade dos cupins arborícolas, seja por competição ou predação.

Mesmo que as condições físico-climáticas, químicas e biológicas da árvore sejam aceitas pelos cupins, ainda assim esta pode ser rejeitada por não ser considerada adequada como recurso, seja para a nidificação ou para forrageamento. Dado que os ninhos de cupins são alocados em troncos e em galhos, e por serem estruturas pesadas, se a árvore não apresentar características de estrutura física adequadas para o estabelecimento de ninhos, ou seja, galhos de dimensões maiores (ramificações secundárias e terciárias), esta árvore pode ser rejeitada. Além disso, o número de ramificações também pode influenciar a quantidade de material que pode ser acumulado nessa árvore. Assim temos que:

(Hii.3.1) O aumento do número de ramificações secundárias e terciárias nas árvores favorece a taxa de ocupação dessas por cupins.

As pernas dos cupins são relativamente simples. Essas são constituídas terminalmente por *tarsi* que apresentam um número variável de junções curtas e uma porção final alongada com duas garras na região do *pretarsi* (Krishna & Weesner, 1969). Segundo Chapman (1991), em insetos de vida livre, as garras dos *pretarsi* são utilizadas para se agarrarem em superfícies com uma certa rugosidade; enquanto que, em superfícies lisas, um ponto de apoio pode ser obtido com o auxílio de adaptações morfológicas como os aróleos e os pulvinos, ou almofadas adesivas como apresentam os ortópteros e alguns heterópteros. Os cupins não possuem nenhuma dessas adaptações de aderência à superfície. Assim, as características de microestrutura de uma árvore, como a rugosidade da casca, seriam fatores limitantes ao acesso de cupins à árvore (cascas muito lisas são difíceis de serem escaladas). Por extensão:

(Hii.3.2) Quanto maior a rugosidade da casca maior é a ocorrência de cupins.

A árvore pode também ser inadequada quando não oferecer recursos alimentares suficientes ou qualitativamente aceitáveis pelos cupins. Isto é, os cupins podem rejeitar uma árvore quando a quantidade e qualidade dos recursos oferecidos por ela e no local onde se encontram forem absolutamente baixas, não justificando o esforço de explorá-las. A localização do alimento de térmitas arborícolas ainda não é bem definida e esses podem consumir uma variedade de ítens dispostos nas árvores e/ou no solo. Os cupins se alimentam basicamente de celulose, recurso que apresenta uma baixa relação Carbono/Nitrogênio; e dentre os hábitos alimentares de térmitas, está a ingestão de solo. Assim a proporção de nitrogênio orgânico existente no solo pode determinar a qualidade do mesmo. Considerando que exista pelo menos uma complementariedade entre os recursos oferecidos pela árvore e pelo solo, pode-se supor que:

(Hii.4.1) Árvores cujo solo adjacente apresentem maior proporção de nitrogênio orgânico são preferencialmente exploradas por cupins.

Já a quantidade de recursos pode ser entendida como o número de ítens de alimento oferecidos que são adequados ao consumo. Além da matéria orgânica dispersa no solo, a serrapilheira produzida em uma floresta também é uma fonte de alimento para os cupins. Segundo Abe & Matsumoto (1979) os cupins consomem 24 a 32 % das folhas que caem anualmente em uma floresta tropical na Malásia. A quantidade de troncos e galhos caídos também é recurso em potencial para os cupins. Assim:

(Hii.4.2) O aumento na quantidade de matéria orgânica existente no solo, na profundidade de serrapilheira e no número de galhos e troncos caídos, no solo abaixo de uma árvore, implicam em alta exploração dessa árvore por cupins.

As hipóteses estão resumidas no fluxograma apresentado a seguir e o presente trabalho consistiu em testar as seguintes hipóteses derivadas da hipótese *(ii)*: *Hii.2.2, Hii.3.1, e Hii.4.2.*

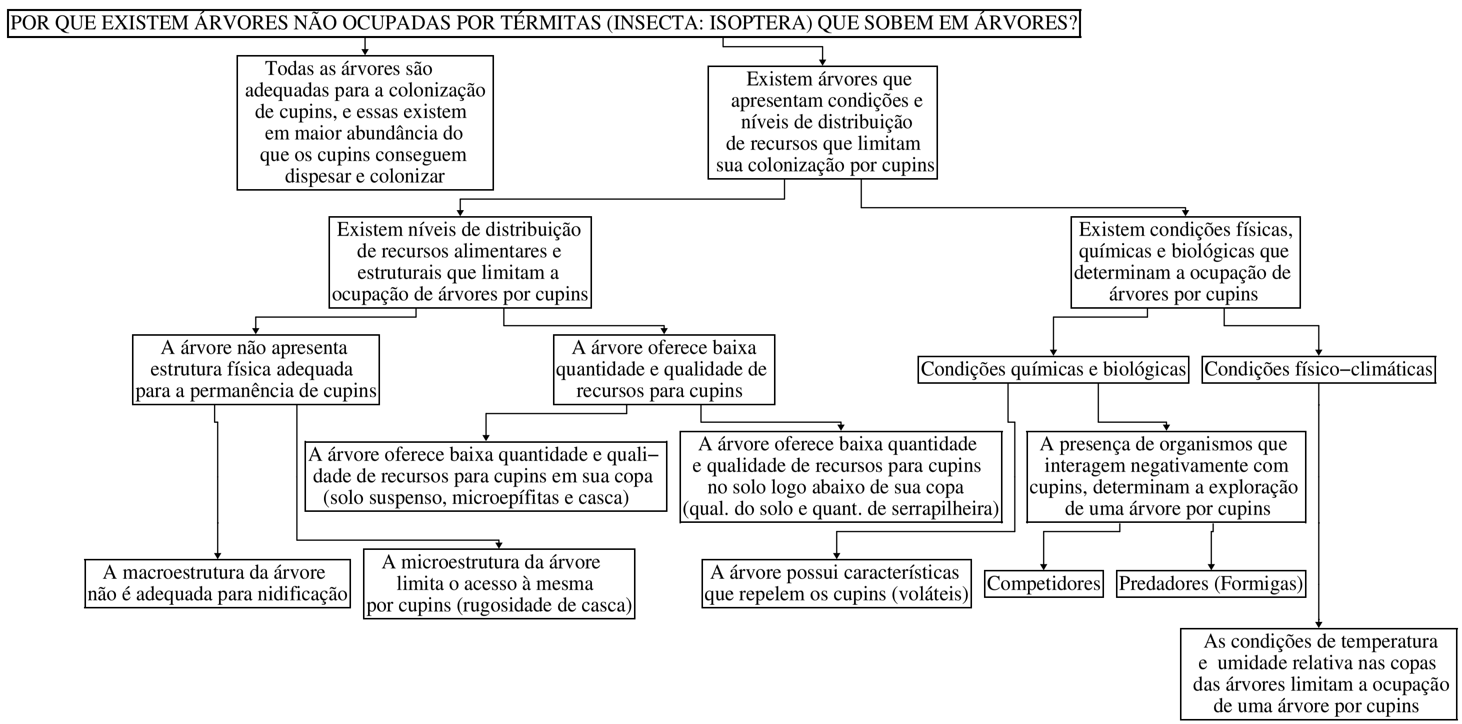

Figura 1: Principais fatores determinantes da ocupação de árvores por cupins.

2 Effect of tree size and growth form on the presence and activity of arboreal termites (Insecta: Isoptera) in Atlantic rain forest

Effect of tree size and growth form on the presence and activity of tree-inhabiting termites (Insecta:Isoptera) in Atlantic rain forest

Teresa Telles Gonçalves[1], Og DeSouza[2], Ronaldo Reis Júnior[2] and Sérvio Pontes Ribeiro[3],

Abstract

Despite the well known diversity of termites capable of inhabit 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.

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Efeito do tamanho e forma de crescimento de árvores na presença e atividade de cupins arborícolas (Insecta:Isoptera) em Floresta de Mata Atlântica

Teresa Telles Gonçalves[1], Og DeSouza[2], Ronaldo Reis Júnior[2] and Sérvio Pontes Ribeiro[3]

Resumo

Uma diversidade de espécies de cupins é capaz de se estabelecer em árvores, mas os fatores determinantes que limitam essa exploração ainda são muito pouco conhecidos. Dados coletados em árvores exploradas por cupins na Mata Atlântica brasileira, área considerada prioritária para a conservação da diversidade, revelam que enquanto a presença de cupins em árvores está positivamente relacionada simplesmente ao tamanho das árvores, a atividade de cupins dentro dos túneis encontrados nessas árvores depende tanto do tamanho quanto das características da forma de crescimento das mesmas. Isso nos leva a hipotetizar que cupins encontram árvores de maneira aleatória mas mantêm alta atividade em árvores grandes devido à disponibilidade de recurso alimentar e sítios de nidificação.

Palavras-chave: Altura da árvore, circunferência à altura do peito, arquitetura de árvores, *Microcerotermes*, *Nasutitermes*, Isoptera.

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2.1 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 (Noirot, 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).

There is few information 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, 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 understorey or at the influence of the canopy (Basset *et al.*, 1992; Basset, 2001; Barrios, 2003). Accordingly, the height of the tree host affects the richness and abundance of Lepdoptera immatures (Haysom & Coulson, 1998), whereas the crown structure of neighbouring 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. For instance, the structural simplicity of coconut trees was related 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.

2.2 Material & Methods

2.2.1 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 19°48′18" - 19°29′24" S and 42°38′30" - 42°28′18" W. To the East it is bordered by the river Doce and to the South by the Piracicaba river. This bioma 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 21.9° 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).

2.2.2 Terms definition

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 (implicitely or not) use this term when referring to termites that do build nests on the tree (see Noirot & Darlington (2000) for a review on the nesting behaviour of termites). However, since our data do not allow 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 the amount of individuals, was considered indicative that the tree was suitable enough to be used by them. On the other hand, the amount of termites within the tunnel, named here termite "activity", was taken as a surrogate of the degree of suitability of the tree to the termite.

2.2.3 Sampling design & Data collection

Sampling consisted in the evaluation of 69 trees with a minimum of 15 cm of circumference at 1.3 m from the soil (circumference at the 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 as to keep a minimum distance of 50 m to the forest edge.

Each tree was evaluated for presence and the absence of termite tunnels at 1.30 m from the 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 allowed catching additional soldiers, thereby guaranting secure identification of the species. This additional sample also allowed us to confirm that 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 architecture measurements, such as circumference at the breast height, shaft height, total height and number of secondary and tertiary ramifications, have been 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 “terciary” are those departing from secondary ones.

2.2.4 Data Analysis

All analysis were processed under R (R Development Core Team, 2005), using generalised 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):

$$Density\ of\ branches = \frac{(Secondary\ +\ Terciary\ ramifications)}{Crown\ height}$$

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_n) were the same used in the previous model, plus of the co-variate *Genus* and their interaction. Genus is a qualitative variable assuming one of the two values *Microcerotermes* or *Nasutitermes*. The full models used in hypotheses tests are therefore:

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

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

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.

2.3 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.

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

Subfamily	Morphospecie
Nasutitermitinae	*Nasutitermes corniger* Motschulsky
	Nasutitermes minor Holmgren
	Nasutitermes sp. 1
Termitinae	*Microcerotermes strunckii* Sorënsen

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.

The encounter of trees by termites was determined only by the increment of CBH ($F_{1,67}$ = 4.9187, P = 0.02657, Figure 2, Table 2). But the activity of termites was affected by all the variables measured and some interactions between them (Table 3).

Table 2: Analysis of deviance of the minimal adequate model showing the effect of circumference at the 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		

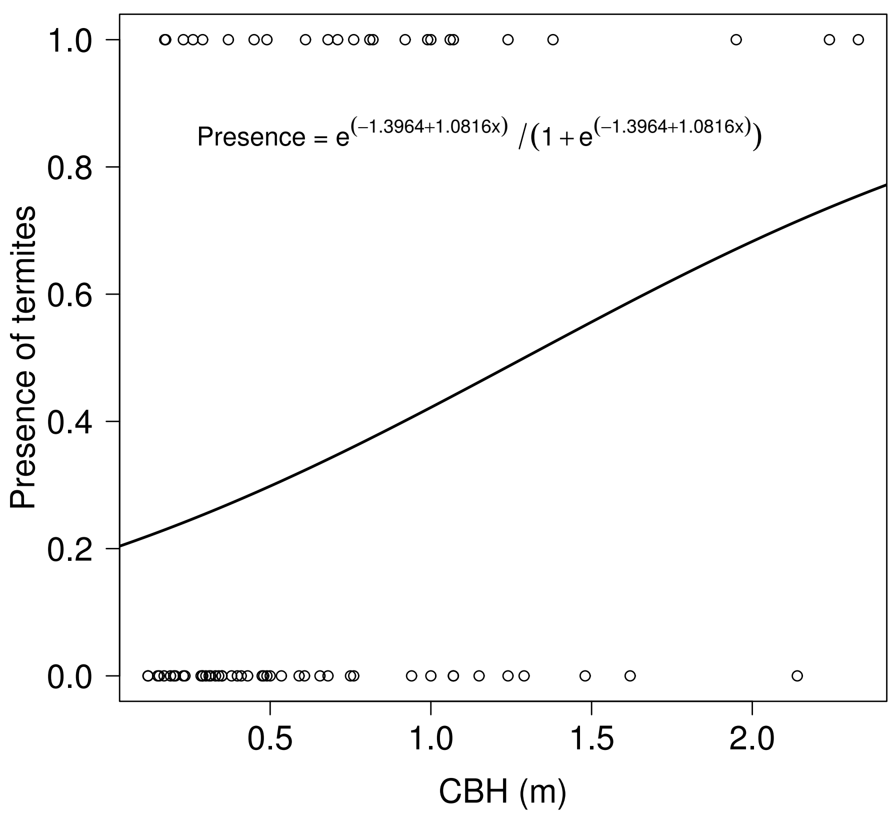

Figure 2: Relationship between CBH of trees and the presence of arboreal termites in State park of Rio Doce, MG, Brazil, 2004. Using generalised linear modelling with Binomial errors and logit link function. In axis y, 0 is absence of termites and 1 is presence.

2.4 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, Figure 2). Trees presenting large circumference are necessarily more conspicuous and have more probability of being found because (i) occupy more

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

Source of variation	df	χ^2	P
MAM	8	34.36	$3.45e^{-05}$
Density of branches	1	3.25	0.071
Total height	1	24.62	$6.98e^{-07}$
CBH	1	13.70	$2.14e^{-04}$
Genus	1	6.48	0.011
Density of branches : Total height	1	0.05	0.821
Density of branches : CBH	1	15.43	$8.56e^{-05}$
Total height : CBH	1	19.89	$8.20e^{-06}$
Density of branches : Total height : CBH	1	5.34	0.021
Error	15		
Total	23		

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 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 (Sousa-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 individuals 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 larger (Table 3, Figure 3). Data on the effect of tree characteristics upon its termite activity are scarce, limiting our conclusions, but Jones & Gathorne-Hardy (1995) 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.

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 generalised linear modelling with Negative Binomial errors and log link function.

Variables	Estimate	Std. Error	z value	Pr(>|z|)
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

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 "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 (2000) 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.*

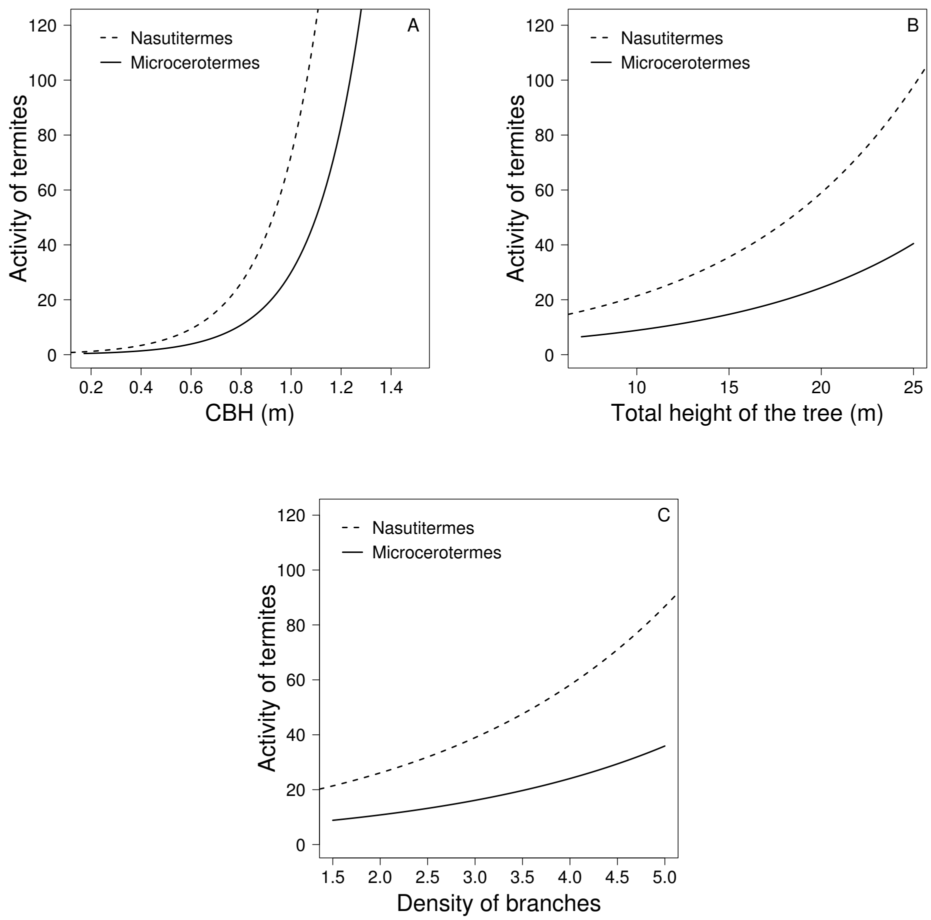

Figure 3: Expected relationship between termite activity of the two collected genera and the tree architectural variables considered, where x in graphic **A** is circumference at breast height (CBH), **B** tree total height and **C** density of branches. Termite activity exponencially increased when 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.

Besides promoting increased availability of food, such an accumulation of 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 optimize their foraging, choosing shorter routes between their nest and the food resource (Ydenberg & Schimid-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 favouring the maintenance and growth of termite colonies and, hence, promoting higher termite activity.

Our data do not allow 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 pursuing 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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3 Predation and interference competition between ants and arboreal termites

Predation and interference competition between ants and arboreal termites

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Abstract

One of the most apparent biological interactions affecting termites is predation by vertebrates and invertebrates. Ants are the most important predators of other invertebrates and are the most active and effective predators of termites. Also, ants and termites might heavily compete for nesting space. Considering the potential of ants as competitors and predators of termites and the scarce knowledge of how they interact we tested the effects of the presence of ants on the activity of arboreal termites. Predatory ants had a negative effect on arboreal termite activity, and non-predatory ants had no effect. Specialised predatory ants are an important disturbance factor in resource exploitation by termites. Perhaps competition with non-predatory ants did not occur in our study because the foraging territories of ants and termites maybe do not overlap. Hence, it is clear that predation has a big impact on activity of termites, but the role of competition in shaping termite communities still needs further study, especially the competitive interaction between termites and ants.

Keywords: arboreal termites, asymetrical interactions, determinants of tree exploitation, *Microcerotermes*, *Nasutitermes*, Isoptera.

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Predação e competição por interferência entre formigas e cupins arborícolas

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Resumo

Cupins são importantemente influenciados pela ação de predação, tanto de vertebrados quanto de invertebrados. As formigas são os predadores mais importantes de outros invertebrados e os mais ativos predadores dos cupins, pdendo também competir fortemente com os mesmos por espaço. Considerando esse potencial competidor e predador das formigas e a escassez de informação a respeito da interação existente entre formigas e cupins, nós testamos o efeito da presença de formigas sobre a atividade de cupins arborícolas. Formigas predadoras tiveram um efeito negativo sobre a atividade de cupins, enquanto formigas não-predadoras não apresentaram nenhum efeito. Formigas predadoras, são um importante fator limitante para a exploração de recursos por cupins. A competição por espaço prevista não ocorreu neste trabalho talvez porque os territórios de formigas e cupins não se sobrepõe. Assim, sugerimos que a predação é um importante fator determinando a atividade dos cupins arborícolas, mas o papel da competição sobre a comunidade dos mesmos ainda não é claro, necessitando de mais estudos, focando especialmente a interação competitiva entre cupins e formigas.

Palavras-chave: cupins arborícolas, interações assimétricas, determinates da exploração de árvores, *Microcerotermes*, *Nasutitermes*, Isoptera.

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3.1 Introduction

Besides being affected by the availability and quality of resources, resource use also depends on habitat structure (Bell *et al.*, 1991; Cornell & Lawton, 1992) and biological interactions (Begon *et al.*, 1990; Chesson, 2002). Likewise, resource use by termites is affected by resource quantity (Waller & La Fage, 1987; Waller, 1988; Hedlund & Henderson, 1999), resource quality (Miura & Matsumoto, 1997, 1998; Traniello & Leuthoud 2002) and biological interactions, such as predation by vertebrates and invertebrates (Abensperg-Traun, 1998) and competition, specifically for foraging territories (Adams & Levins, 1987; Leponce *et al.*, 1997).

Ants are the most important predators of other invertebrates and are the most active and effective predators of termites, and a major factor of termite mortality (Abe & Darlington, 1985), existing at least six genera of ants that are specialised in termite predation (Wilson, 1971). In fact, risk of predation by ants is an important factor affecting resource exploitation by termites (Korb & Linsenmair, 2002).

Besides predation, competition may also determine resource use by termites. Competition for space can occur among conspecific or heterospecific and between termites and non-termites. Territoriality is an important and widespread form of asymmetric competition (Adams, 2001) and is very common among termites (Adams & Levins, 1987; Jones & Trosset, 1991; Thorne & Haverty, 1991) including arboreal termite species (Leponce, 1997; Leponce *et al.*, 1999). Especially considering that termites and ants are both eusocial, live in colonies and have similar needs for nesting space, ants are expected to be important competitors for space with termites, particularly termites living in trees. Indeed, it is known that ants and termites may compete for nesting sites, especially on leaves and twigs (Hölldobler & Wilson, 1990). Several species of termites, including various neotropical species (Constantino, 1999), inhabit trees (Noirot, 1969). And arboreal-nesting ants are able to dislodge mature termite colonies from trees by progressively invading the nests (Leponce *et al.*, 1999). Further indications for competition between ants and termites in trees comes from a study of the fauna associated with canopy epiphytes (Ellwood *et al.*, 2002), showing that termites and ants never co-occured inside small-sized epiphytes.

Little is known on the determinants of tree exploitation by termites, and besides some architectural aspects of trees (Gonçalves *et al.*, 2005a), biological interactions, particularly with ants, seem to be an important determinant of termite activity, especially because ants are the dominant arthropod family in lowland tropical forest canopies (Tobin, 1995). Considering the potential of ants as competitors and predators of termites and the lack of knowledge of the interactions between ants and termites (Leponce *et al.*, 1999), we tested the effects of presence of ants on tree exploitation by termites. Specifically we tested the hipothesis that the presence of ants have a negative effect on the activity (number of termite individuals active inside the tunnels, see methods) of arboreal termites, either for competition or predation.

3.2 Material & Methods

3.2.1 Study area

The study was carried out in the Rio Doce State Park, Minas Gerais, southwestern Brazil, between January 15 and February 15 (summer season) of 2004. This park is the largest relict of Atlantic coastal rain forest in the state of Minas Gerais (35.976 ha), and is located between 19°48′18” - 19°29′24”S and 42°38′30” - 42°28′18”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 characterised by the Aw Köppen climate type (Tropical warm semi-humid), a rainy season from October to March and a dry season from April to September. Mean rainfall is 1480.3 mm/year and the mean temperature 21.9° 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).

3.2.2 Definition of terms

“Arboreal termites” were defined as termites 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 (implicitely or not) use this term when referring to termites that do build nests on the tree (see Noirot & Darlington (2000) for a review on the nesting behaviour of termites). However, because our data do not allow 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. “Termite activity” is the amount of termites within the tunnel, which was taken as a surrogate of the degree of suitability of the tree to the termite.

3.2.3 Sampling design & Data collection

We sampled 23 trees with a minimum circumference at breast height (1.3 m from the soil), of 15 cm. The trees were situated 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 arbitrarily selected, but a minimum distance of 50 m from the forest edge was kept for minimize edge effects.

Tunnels with active termites were present in all trees. 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 allowed catching additional soldiers, thereby guaranting secure identification of the species. These aditional inspections also allowed us to confirm that tunnels were used by termites, when no termites were encountered in the 15 cm long portion of the tunnel. Termites were put in 80% alcohol, labeled and identified to genus or morphospecies. The identification was confirmed by comparison to specimens from the section of termitology of the Entomological Museum of the Federal University of Viçosa, where voucher specimens are deposited.

Trees were climbed using the single rope technique (Moffet & Lowman, 1995) and ants were collected from tree crowns using an entomological umbrella. The ants were identified to species and morphospecies where appropriated, by comparison to specimens from Community Ecology Laboratory of the Federal University of Viçosa. The feeding habits of the ants were determined according to Brown-Jr (2000). And ants specimens are deposited in the Entomological reference collection of federal University of Ouro Preto.

3.2.4 Data Analysis

All analyses were processed under R (R Development Core Team, 2005). We tested whether ants had a negative effect on activity of arboreal termites using a generalised linear model (*Termite activity = Ants + Termite genus*), followed by analysis of residues to check for the error distribution and model adjustment. A minimal adequate model (MAM) was obtained by extracting non-significant terms ($p > 0.05$) from the full model and difference between levels of the categorical explanatory variable *ants* were tested through a *posteriori* contrast procedures (Crawley, 2002). In the presented full model

(*Termite activity* = *Ants* + *Termite genus*), *Ants* is a categorical variable with three levels: presence of predatory ants; presence of non-predatory ants; and absence of ants. The variable *Termite genus* is also categorical, identifying the genus of the termites (*Microcerotermes* or *Nasutitermes*). The error distribution used was negative binomial with log link function.

3.3 Results

We found four termite morphospecies of the family Termitidae, comprising two subfamilies and two genera (Table 5), and 40 ant morphospecies of 12 genera from six subfamilies (Table 6). Among the genera of ants, four were essentially predatory ants: *Ectatomma* Fr. Smith; *Gnamptogenys* Roger; *Pachycondyla* Fr. Smith; and *Pseudomyrmex* Lund Hölldobler & Wilson (1990); Brown-Jr (2000).

Table 5: List of the morphospecies of arboreal termites collected in the State Park of Rio Doce, Minas Gerais, Brazil, 2004.

Subfamily	Morphospecie
Nasutitermitinae	*Nasutitermes corniger* Motschulsky
	Nasutitermes minor Holmgren
	Nasutitermes sp. 1
Termitinae	*Microcerotermes strunckii* Sorënsen

The activity of termites was influenced by the presence of ants (Table 7, Figure 4). Compared to the absence of ants, termite activity was lower in the presence of predatory ants (χ^2_1 = 6.11, P = 0.0134, Figure 4), whereas non-predatory ants did not affect arboreal termite activity (χ^2_1 = 0.77, P = 0.3814). Colonies of the genus *Nasutitermes* were more active than colonies of the genus *Microcerotermes* (Table 7, Figure 4).

3.4 Discussion

We hypothesized that ants may have negative effects on termite activity through predation and through competition for space. Our results show that predatory ants, but not non-predatory ants, have a negative effect on termite activity (Table 7, Figure 4), suggesting that predation is an important source of disturbance of termite activity, but competion is not. Nevertheless, we

Table 6: List of the morphospecies of ants collected with an entomological umbrella in the State Park of Rio Doce, Minas Gerais, Brazil, 2004.

Subfamily	Morphospecie
Dolichoderinae	*Azteca* sp. 1, sp. 2
	Dolichoderus sp. 1, sp. 2, sp. 3, sp. 4
Ectatominae	*Ectatoma tuberculatum* Olivier
	Gnamptogenys sp. 1
Formicinae	*Camponotus sericeiventris* GuZrin
	Camponotus sp. 1, sp. 2, sp. 3, sp. 4,
	Camponotus sp. 5, sp. 6, sp. 7, sp. 8, sp. 9
Myrmicinae	*Cephalotes atratus* Linnaeus
	Cephalotes borgmeieri Kempf
	Cephalotes sp. 1
	Crematogaster sp. 1, sp. 2, sp. 3, sp. 4
	Lepthotorax sp. 1, sp. 2
	Procryptocerus sp. 1, sp. 2
	Trachymyrmex sp. 1
Ponerinae	*Pachychondyla magnifica* Borgmeier
	Pachychondyla sp. 1, sp. 2, sp. 3
Pseudomyrmecinae	*Pseudomyrmex* sp. 1
	Pseudomyrmex sp. 2, sp. 3, sp. 4, sp. 5, sp. 6

cannot rule out that predatory ants species also competed for space with termites.

The coevolutionary relationship between termites and ants dates back more than 100 million years, with ants mostly acting as aggressors and termites as victims (Hölldobler & Wilson, 1990). A majority of ant species prey on termites if given the opportunity and some ant genera are specialised in termite predation (Wilson, 1971), including the collected *Pachychondyla* Smith (Table 6). The strategies of termite capture by ants are diverse. There is a guild of specialised predators ponerine ants which organise raids on termites mounds, whereas other ants hunt solitary or steal eggs and nymphs from the colonies (Hölldobler & Wilson, 1990). Yet other ant species, like *Megaponera foetens* Fabricius, only attack termites on the surface (Hölldobler & Wilson, 1990), whereas doryline ants attack underground nests (Darlington, 1985). The raid strategy seems to be the most important factor on termite colony

Table 7: Analysis of deviance of the minimal adequate model (MAM) showing the effect of ants (predatory, non-predatory and absence) on the activity of arboreal termite genera (*Microcerotermes* and *Nasutitermes*), using a generalised linear model and Negative Binomial errors and log link function. Contrasts between levels of the variable ants are denoted by *vs*.

Source of variation	df	χ^2	P
MAM	2	12.35	0.002
Termite genus	1	7.92	0.005
Ants	1	7.42	0.006
predatory ants *vs* ants absent	1	6.11	0.013
non-predatory ants *vs* ants absent	1	0.77	0.381
predatory ants *vs* non-predatory ants	1	7.68	0.006
Error	20		
Total	22		

survival and is especially adopted by *Pachychondyla* Smith (Acosta-Avalos & Esquivel, 2001).

The specialised predatory ants are an important disturbance factor in resource exploitation by termites. Especially doryline ants and *Megaponera foetens* Fabricius can prey high proportions of the foraging population and production of termite colonies (Lepage & Darlington, 2002). Thus, our results comes to confirm the important pressure that ants exert on termites as predators.

It is surprising that we found such strong effects of predatory ants on termite activity, whereas we did not find effects of competition, because competition between ants and termites is considered much more common than predation (Sennepin, 1996). Competition for space, which has often been reported between ants and termites (Hölldobler & Wilson, 1990; Sennepin, 1996; Leponce *et al.*, 1999), seems not to occur in our study; we found no relationship between non-predatory ants and termite activity (Table 7). Thus, why is competition for space with ants not of importance for arboreal termites?

Perhaps termites and ants do not compete for space because their foraging territories do not overlap. Termites are cryptic organisms, generally foraging in protected environments (Noirot, 1969), and seldom leave the shelter of their tunnels and nests (Leponce *et al.*, 1999), whereas ants possess quite

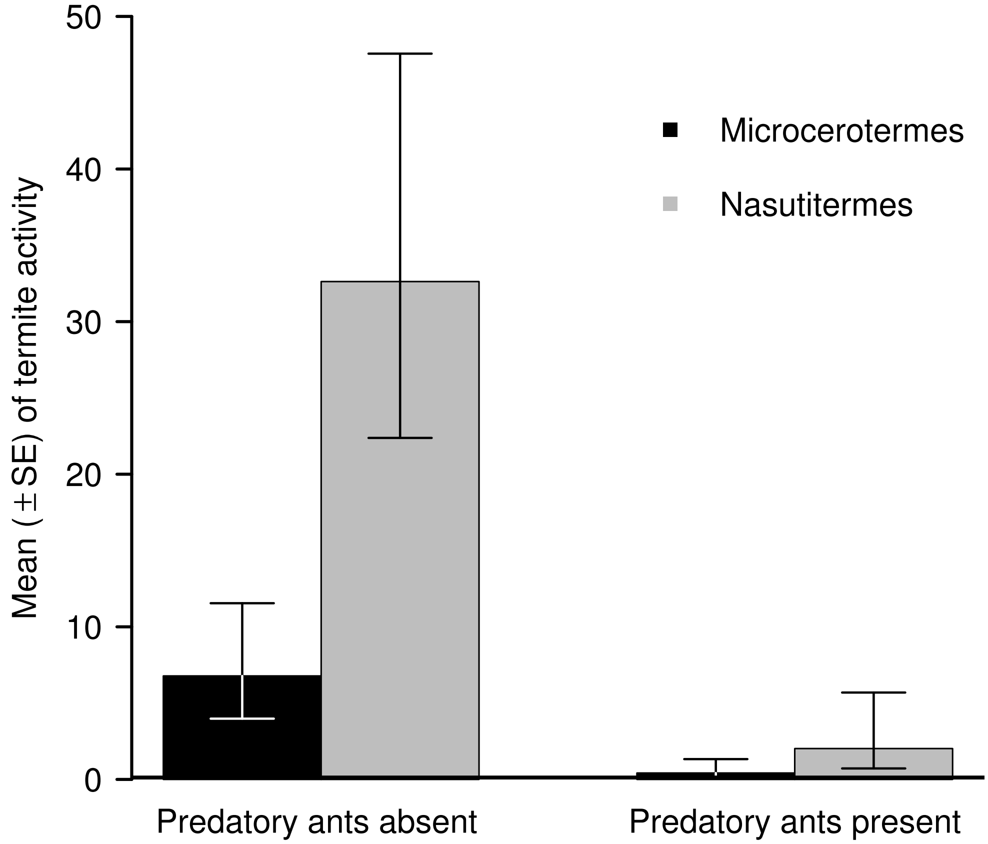

Figure 4: Effect of the presence of predatory ants on the activity of arboreal termites (*Microcerotermes* and *Nasutitermes*). Bars were grouped following the statistical contrasts of Table 7, in which the effect of non-predatory ants does not differ from the effect of ants absent, and these differ from the effect of predatory ants. Therefore, bars grouped under the term "predatory ants absent" refer to samples without ants plus samples with only non-predatory ants.

diverse foraging strategies. Although on the same tree, the foraging territories of ants and termites maybe separated in space, circumventing contact between them and avoiding competitive battles.

Besides competing for foraging territories, ants and termites are known to compete for nesting sites (Hölldobler & Wilson, 1990), an aspect that was not supported by our data. This maybe due to the low number of termite nests observed (in five out of the 23 observed trees), suggesting that termites do not use the trees of our study for nest or that nest construction had not started yet.

Ants and termites also may interact in non-antagonistic ways, such as in commensalism, mutualism and inquilinism (Hölldobler & Wilson, 1990; Leponce *et al.*, 1999). Our results show no evidence for commensalism and mutualism because the effect of the presence of non-predatory ants was the same as that of the absence of ants (Table 7). Also, the lack of interaction between non-predatory ants and termites may be due to the fact that the large majority of ant species in forest canopies consists of inconspicuous species with small colonies and limited foraging territories (Tobin, 1995), which probably do not disturb termite activity.

Besides a strong effect of predatory ants on termite activity, activity levels also varied with the genus of termites. The activity of *Microcerotermes* was lower than *Nasutitermes* (Table 7, Figure 4). Thus, despite the equal response of the two studied termite genera to the presence predatory ants, termite *taxa* differ in the intensity of that response.

Our results show that the presence of predatory ants decreases the activity of arboreal termite colonies and no evidence was found for any effect of competition. It is known that competitive interactions between termites are determinants of termite community structure (Adams & Levins, 1987; Jones & Trosset, 1991; Thorne & Haverty, 1991; Leponce *et al.*, 1997, 1999). Termites and ants do not completely compete for resources because termites are mostly detritivorous (Wood & Sands, 1978; Grassé, 1982) and ants are not (Hölldobler & Wilson, 1990; Agosti *et al.*, 2000). And that may be a reason for the absence of compettion! If the resources are less used, the competition may not occur. Thus, we suggest that competition with "real" food competitors, could be more important than competition for space *per se*, and that the presence of predatory ants can be an important local factor limiting resource use of arboreal termites in tropical rainforest enviroments.

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4 Ground resource use by arboreal termites

Ground resource use by arboreal termites

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Abstract

Termites are detritivorous and one of the most important invertebrates involved in organic matter decomposition and nutrient cycling. These insects are commonly associated to soil fauna but there are various species that inhabit trees. Being detritivorous, termites feed on a wide range of dead plant material at various decomposition stages as litter, dead-wood and organic matter dispersed in soil. These items can be found lodged in tree canopy but it is in the ground level that they are more abundant. Thus, considering that arboreal termites generally present tunnels connecting their colonies to the ground environment, added to the large availability of resources on this enviroment (compared to that lodged on trees) leaded us to hipothesize that besides being installed on trees, arboreal termites are positivelly influenced by the increment of potential resources n the ground level. Our results have shown that presence and activity of arboreal termites are related to ground components. The dependence of arboreal termites on the ground were discussed considering their need of resources to nest building, food suply or simply to connect a termite colony from one tree to another.

Keywords: Canopy, litter, soil organic carbon, *Microcerotermes*, *Nasutitermes*, Isoptera.

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Uso de potenciais recursos de solo por cupins arborícolas

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Resumo

Cupins são detritívoros e um dos invertebrados mais importantes na decomposição da matéria orgânica e ciclagem de nutrientes. Esses insetos são comumente associados à fauna de solo mas existe um considerável número de espécies que é capaz de se estabelecer em árvores. Sendo detritívoros, os térmitas consomem uma larga amplitude de itens de origem vegetal morta, em vários estágio de decomposição, como serrapilheira, madeira morta e matéria orgânica dispersa no solo. Esses itens podem ser encontrados localizados nas copas das árvores mas é no nível do chão de uma floresta que são encontrados em maior abundência. Assim, considerando que colônias de cupins arborícolas geralmente apresentam túneis interligando a árvore e o solo, e que a abundância dos potenciais itens de recurso de cupins e relativamaente maior no nível do solo do que nas copas de árvore, hipotetizamos que cupins arborícolas são positivamente influenciados pelo aumento da disponibilidade de potenciais recursos que estejam dispostos no chão. Os resultados mostram que a presença e atividade de cupins arborícolas está relacionada à componentes do nível do chão. Os resultados foram discutidos considerando-se a necessidades desses insetos em captar recursos no chão para a contrução de seus ninhos, suprimento alimentar ou simplesmente para conectar a colônia de uma árvore a outra.

Palavras-chave: Dossel, serrapilheira, carbono orgânico do solo, *Microcerotermes*, *Nasutitermes*, Isoptera.

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4.1 Introduction

Termites are essentially detritivorous, 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 feed on a wide range of dead plant material at various decomposition stages (Donovan *et al.*, 2001), and their commonest food items are litter, dead-wood and organic matter dispersed in the soil. These resources are largelly distributed in forests floor but also can be found on the trees, lodged on the branches bifurcations or insides epiphytes (Ellwood *et al.*, 2002; Noirot & Darlington, 2000; Basset *et al.*, 2003; Davies *et al.*, 2003).

Because termites are detritivorous, they are generally associated to soil fauna. However, there are several termite species that inhabit trees, and this arboreal nesting habit is a remarkable specialization, which is restricted to Termitidae and very frequent in Nasutitermitinae subfamily (Noirot, 1969). Information on the factors determing exploitation of trees by termites are scarce but tree size and growth form (Gonçalves *et al.*, 2005a) and presence of predatory ants (Gonçalves *et al.*, 2005b), seems to play an important role. Besides biological interactions and habitat structure, termites have a strong tendency of feeding on locals presenting higher availability of resources, as material for nesting construction and food items. In fact, termites preferencially use paths that presents higher quantity of food (number of paper baits) (Araújo et al., in prep.). Jones & Gathorne-Hardy (1995) suggested that *Hospitalitermes* forage in larger trees, because these trees may suport higher amounts of food.

The foraging range of arboreal termites and feeding habits, are not well known. There are reports of arboreal termites foraging on ground (Sousa-Souto *et al.*, 1999) and in the tree canopies (Jones & Gathorne-Hardy, 1995; Miura & Matsumoto, 1997, 1998). The search for resources by termites generally occur inside tunnels, existing just a few species which are open-air foragers (Miura & Matsumoto, 1997). These tunnels serve as shelters (Costa-Leonardo, 2002), and can be construct *inside* or *on* the substrate (wood or soil), depending on the termite specie (Noirot, 1969).

Termitidae species that inhabit trees, generally present tunnels on the tree barks, and always present tunnels connecting their arboreal colonies to the ground environment (Noirot, 1969). Thus, this canopy-ground connection, added to the large availability of resources on the ground enviroment (compared to that deposited on the trees) leaded us to hipothesize that despite being installed on trees, arboreal termites are positivelly influenced by the increase in the amount of potential resources in the ground level, below the host trees.

4.2 Material & Methods

4.2.1 Study area

The study was carried out in the Rio Doce State Park, Minas Gerais, southwestern Brazil, between January 15 and February 15 (summer season) of 2004. This park is the largest relict of Atlantic coastal rain forest in the state of Minas Gerais (35.976 ha), and is located between 19°48′18” - 19°29′24”S and 42°38′30” - 42°28′18”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 characterised by the Aw Köppen climate type (Tropical warm semi-humid), a rainy season from October to March and a dry season from April to September. Mean rainfall is 1480.3 mm/year and the mean temperature 21.9° 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).

4.2.2 Terms definition

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 (implicitely or not) use this term when referring to termites that do build nests on the tree (see Noirot & Darlington (2000) for a review on the nesting behaviour of termites). However, since our data do not allow to distinguish whether termites were searching for food, nesting on the tree, or merely using the tunnels as connections to others trees, we find advisable to make such a warning in order to prevent any misconception.

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

4.2.3 Sampling design & Data collection

Sampling consisted in the evaluation of 70 trees with a minimum of 15 cm of circumference at 1.3 m from the soil (circumference at the 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 as to keep a minimum distance of 50 m to the forest edge, to avoid edge effects.

Each tree was evaluated for presence and the absence of termite tunnels at 1.30 m from the 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 allowed catching additional soldiers, thereby guaranting secure identification of the species. This additional sample also allowed us to confirm that 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.

The soil was sampled, beneath the tree, from 0 to 10 cm of depth, air-dried and passed trough a 0.5 mm sieve. The percentage of *Total organic carbon* was determined by hot oxidation with potassium dichromate and titration with ammoniac ferrous sulphate, according to Walkley & Black (1934). The *Litter depth* is the mean of ground litter thickness from four points that were 20 cm distant from the tree trunk (North, South, East and West; determined with a compassing), which were measured using an iron ruler. And the *Length of fallen branches*, is the sum of the linnear length of the fallen branches, with a minimum diameter of 10 cm, found inside a plot of 1 m^2 next to the tree trunk. It was obtained using a measuring tape.

4.2.4 Data Analysis

All analysis were processed under R (R Development Core Team, 2005), using generalised 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. Non-significant terms, as single variables or lower interactions levels, were kept in the MAM when belonging to a significant interaction term.

The hypothesis that resources from the ground affect the presence of arboreal termites, 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: the percentage of soil *Total organic carbon*, mean of ground *Litter depth* and sum of the length of *Fallen branches* from 1 m^2 ground area, under the tree. The effect of these variables on arboreal 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), where the explanatory variables (x_n) were the same used in the previous model, plus of the co-variate *Genus* and their interaction. *Genus* is a qualitative variable assuming one of the two values *Microcerotermes* or *Nasutitermes*. The full models used in hypotheses tests are therefore:

$$\begin{aligned} \textit{Presence of termites} &= \textit{Total organic carbon} + \\ &\quad \textit{Litter depth} + \textit{Fallen branches} + \\ &\quad \textit{Total organic carbon} : \textit{Litter depth} + \\ &\quad \textit{Total organic carbon} : \textit{Fallen branches} + \\ &\quad \textit{Litter depth} : \textit{Fallen branches} + \\ &\quad \textit{Total organic carbon} : \textit{Litter depth} : \textit{Fallen branches} \end{aligned} \tag{3}$$

$$\begin{aligned} \textit{Activity of termites} &= \textit{Total organic carbon} + \\ &\quad \textit{Litter depth} + \textit{Fallen branches} + \textit{Genus} + \\ &\quad \textit{Total organic carbon} : \textit{Litter depth} + \\ &\quad \textit{Total organic carbon} : \textit{Fallen branches} + \\ &\quad \textit{Litter depth} : \textit{Fallen branches} + \\ &\quad \textit{Total organic carbon} : \textit{Genus} + \\ &\quad \textit{Litter depth} : \textit{Genus} + \textit{Fallen branches} : \textit{Genus} + \\ &\quad \textit{Total organic carbon} : \textit{Litter depth} : \textit{Fallen branches} + \\ &\quad \textit{Fallen branches} : \textit{Litter depth} : \textit{Genus} + \\ &\quad \textit{Fallen branches} : \textit{Total organic carbon} : \textit{Genus} + \\ &\quad \textit{Total organic carbon} : \textit{Litter depth} : \textit{Genus} + \\ &\quad \textit{Total organic carbon} : \textit{Litter depth} : \textit{Fallen branches} : \textit{Genus} \end{aligned} \tag{4}$$

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 (3) and (4) with logit and log link functions respectively.

4.3 Results

Termites collected belong to the family Termitidae and comprise two subfamilies, two genera and four morphospecies (Table 8). Out of the 70 evaluated trees, 25 held active tunnels, whereas six held inactive termite tunnels. The remaining trees did not show any sign of termite presence.

Table 8: List of the morphospecies of the sampled arboreal termites in State Park of Rio Doce, MG, Brazil 2004.

Subfamily	Morphospecie
Nasutitermitinae	*Nasutitermes corniger* Motschulsky
	Nasutitermes minor Holmgren
	Nasutitermes sp. 1
Termitinae	*Microcerotermes strunckii* Sorënsen

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 m, the average 11.91 m, and the minimum height was 7.35 m above ground.

The presence of termites was affected by the three evaluated variables, with interaction between litter depth and fallen branches (Table 9). Our results show that the increment of total organic carbon in soil and litter depth had a positive effect on the presence of arboreal termite (Figure 5, C). However, increases in fallen branches had a negative effect on the presence of arboreal termite both isolated or associated to total organic carbon and litter depth (Figure 5, A and B). Also, litter depth, while isolated, had a positive effect on termite presence, if in association to fallen branches presents a negative synergic effect (Figure 5, A).

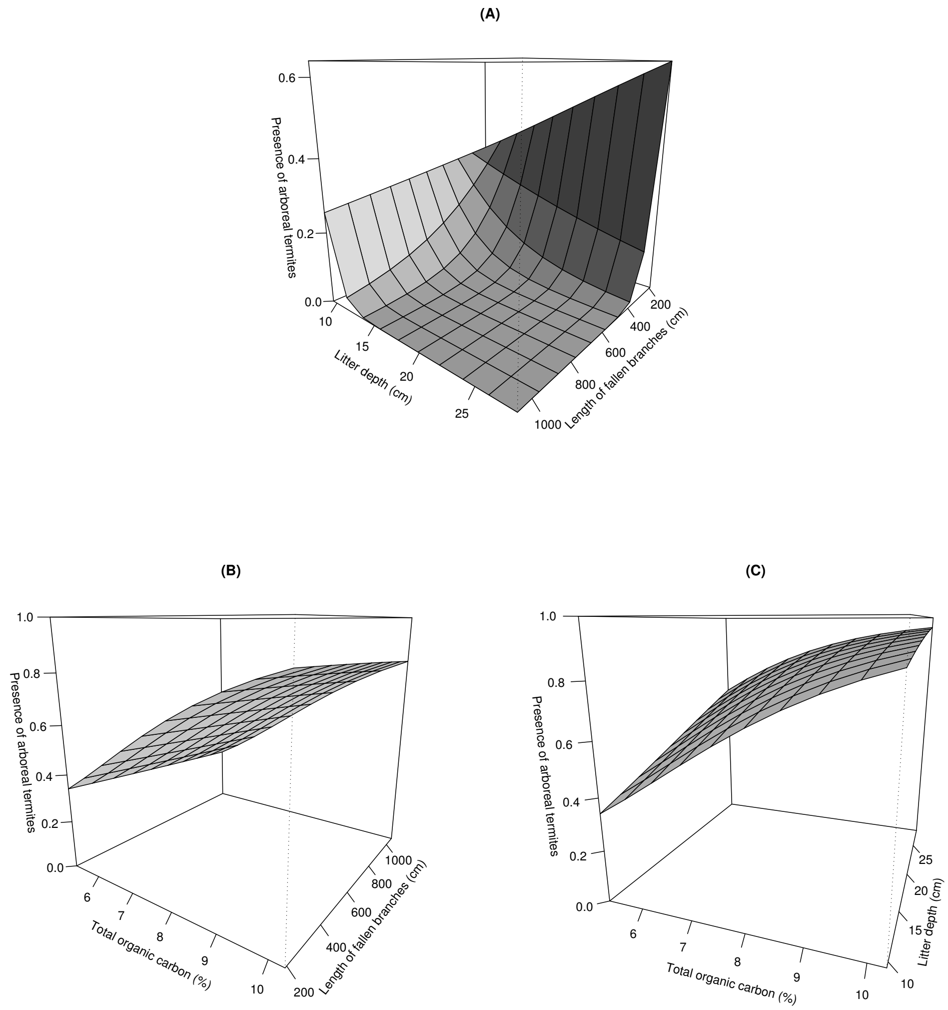

Figure 5: Relationship between the evaluated ground components, sum of the length of fallen branches (cm/m^2), mean of litter depth (cm) and soil total organic carbon (%), and the presence of arboreal termites in State park of Rio Doce, MG, Brazil, 2004. Using generalised linear modelling with Binomial errors and logit link function. In axis y, 0 is absence of termites and 1 is presence. While two variables varied in x and z axes the third was kept in its average. Notice that *Length of fallen branches* axis in graphic **A** increases from rigth to left. Curves were built from the parameters in Table 10.

Table 9: Analysis of deviance of the minimal adequate model showing the effect of the measured ground resources, sum of the length of fallen branches (cm/m^2), mean of litter depth (cm) and soil total organic carbon (%), on arboreal termite presence, using glm with Binomial errors and logit link function.

Source of variation	df	χ^2	P
MAM	4	21.882	<0.01
Total organic carbon	1	10.128	0.001
Litter depth	1	4.837	0.028
Length of fallen branches	1	0.059	0.809
Litter depth : Length of fallen branches	1	6.859	0.009
Error	65		
Total	69		

Table 10: Estimated parameters for the minimal adequate model showing the effect of sum of the length of fallen branches (cm/m^2), mean of litter depth (cm) and soil total organic carbon (%) on arboreal termite presence, using generalised linear modelling with Binomial errors and logit link function.

Variables	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	-6.3143809	1.6255475	-3.884	<0.01
Length of fallen branches	0.0120037	0.0057475	2.089	<0.05
Litter depth	0.3174563	0.1226903	2.587	<0.01
Total organic carbon	0.5180070	0.1618955	3.200	<0.01
Litter depth : Length of fallen branches	-0.0013140	0.0005604	-2.345	<0.05

The activity of termites was affected by the four evaluated variables, with some interactions between them (Table 11). Our results show that the increment of total organic carbon in soil and litter depth had a positive effect on termite activity (Figure 6, E and F). However, increases in fallen branches had a negative effect on the activity (Figure 6, A and B) of the both termite genus, except in sites presenting high percentage of total organic carbon in soil; which had a supplantative effect, favoring both presence and the activity of arboreal termites (Figure 5, B and Figure 6, C and D). As shown for termite presence, the associated effect of litter depth and fallen branches presents a negative synergic effect (Figure 6, A and B) decreasing termite activity.

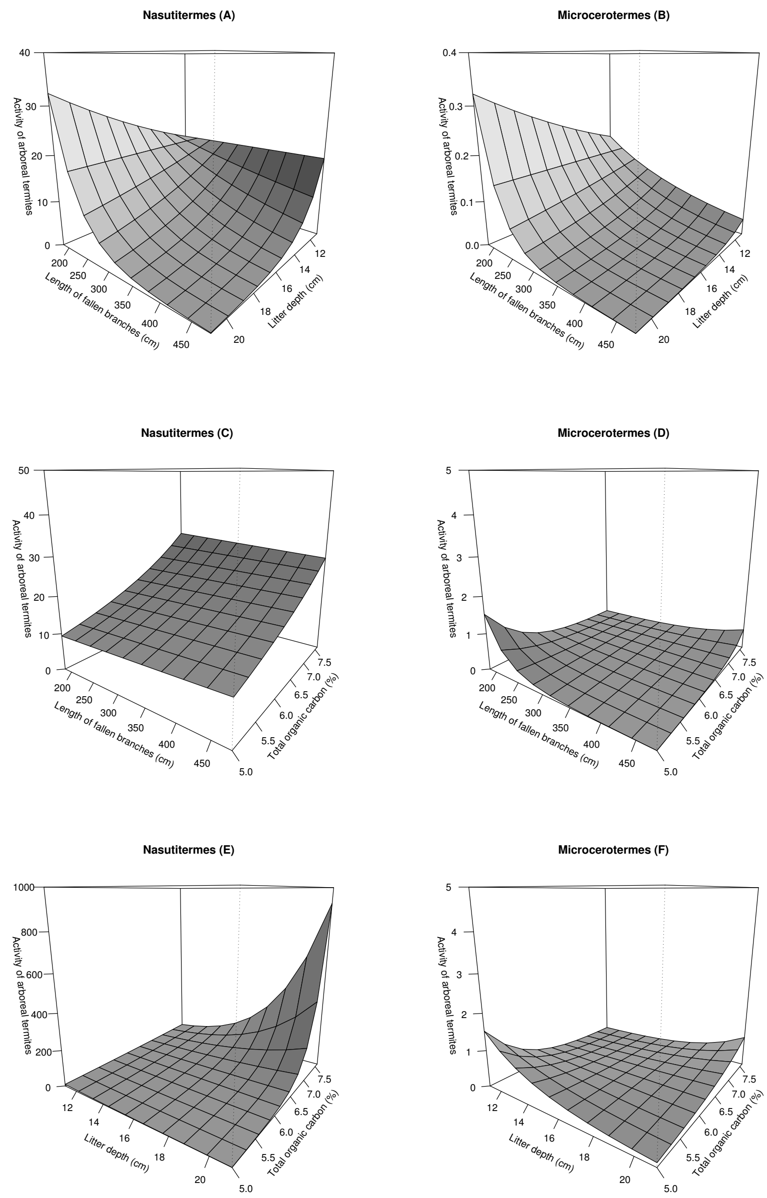

Figure 6: Relationship between the evaluated ground components, sum of the length of fallen branches (cm/m^2), mean of litter depth (cm) and soil total organic carbon (%) and the activity of arboreal termites in State park of Rio Doce, MG, Brazil, 2004. Using generalised linear modelling with Negative Binomial errors and log link function. While two variables varied in x and z axes the third was kept in its average.Curves were built from the parameters in Table 12

Table 11: Analysis of deviance of the minimal adequate model showing the effect of the measured ground resources, sum of the length of fallen branches (cm/m^2), mean of litter depth (cm) and soil total organic carbon (%), on arboreal termite activity, using glm with Negative Binomial errors and log link function.

Source of variation	df	χ^2	P
MAM	11	22.228	0.023
Total organic carbon	1	4.424	0.035
Litter depth	1	2.886	0.089
Length of fallen branches	1	2.433	0.119
Genus	1	2.916	0.088
Litter depth : Length of fallen branches	1	1.659	0.198
Total organic carbon : Length of fallen branches	1	0.005	0.943
Total organic carbon : Litter depth	1	4.607	0.032
Length of fallen branches : Genus	1	2.329	0.127
Total organic carbon : Genus	1	0.132	0.716
Total organic carbon : Litter depth : Length of fallen branches	1	4.398	0.036
Total organic carbon : Length of fallen branches : Genus	1	6.368	0.012
Error	13		
Total	24		

Table 12: Estimated parameters for the minimal adequate model showing the effect of sum of the length of fallen branches (cm/m^2), mean of litter depth (cm) and soil total organic carbon (%) on arboreal termite activity, using generalised linear modelling with Negative Binomial errors and log link function.

Variables	Estimate	Std. Error	z value	$Pr(>\vert z\vert)$
Microcerotermes	52.6200	13.9100	3.784	<0.01
Nasutitermes	-25.1400	11.9600	-2.103	<0.05
Length of fallen branches	-0.1530	0.0443	-3.449	<0.01
Litter depth	-2.5130	0.7214	-3.484	<0.01
Total organic carbon	-9.0650	2.5040	-3.620	<0.01
Length of fallen branches : Nasutitermes	0.0919	0.0364	2.520	<0.05
Total organic carbon : Nasutitermes	4.4880	2.0900	2.147	<0.05
Length of fallen branches : Litter depth	0.0057	0.0020	2.736	<0.01
Total organic carbon : Length of fallen branches	0.0263	0.0073	3.574	<0.01
Total organic carbon : Litter depth	0.4580	0.1263	3.626	<0.01
Total organic carbon : Length of fallen branches : Nasutitermes	-0.0135	0.0055	-2.420	<0.05
Total organic carbon : Litter depth : Length of fallen branches	-0.0011	0.0003	-3.119	<0.01

The activity response to ground resources availability, of the termite genera studied, were specially different in intensity: *Microcerotermes* had a lower response in scale and showed low response to the compensatory effect of total organic carbon. *Microcerotermes* also seems to be more demanding than *Nasutitermes*, needing a higher percentage of soil organic matter to justify activity directioned to ground level, and they are less prone to forage in ground areas which present higher debris accumulation (Figure 6, D and F).

Additionally, total organic carbon in soil seems to be more preponderant to termite ground activity than debris elements. In Figure 6, we see that litter depth and fallen branches, only promote more expressive changes in termite ground activity if the percentage of organic carbon in soil is kept constant (Figure 6, A and B).

4.4 Discussion

As hypothesized, our results have shown that presence and activity of arboreal termites are related to ground components. And supported by the fact that arboreal termites always present tunnels linking canopy and soil (Noirot, 1969), we may conclude that there is a strong connection between arboreal termites and ground environment. This important connection may be due to the arboreal termite need of soil to nest building, food supply or simply to connect the termite colony from one tree to another.

Termite nest building materials are particles of soil and wood, and faecal material, which in the construction process are moistened and joined by the "saliva" (CostaLeonardo, 2002; Noirot & Darlington, 2000). The proportion of nest construction materials are very variable among species, where faecal material is preponderantly used in arboreal carton nests and humus-feeders nests (Noirot & Darlington, 2000). Both studied genera are known to build carton nests (Weesner, 1960; Constantino, 1999), and besides soil particles being an important material in the construction of the epigeal nests outer part (Noirot & Darlington, 2000), in carton nests this component may play a minor role. Thorne *et al.* (1996) found a high organic matter content (88.3 to 96%) in *Nasutitermes* nest material and suggests that little, if any, soil or sand is incorporated in these termites nest constructions. Thus, considering the abundance of soil material and its low request to carton nests building, the connection between ground and arboreal termites maybe is more related to colony nourishment needs than to structural ones.

Information on the feeding habits of arboreal termites are scarce. However the commonest food items of termites are litter, dead-wood and organic matter dispersed in soil. About 51% of all Isoptera genera and 62% of Termitidae present soil-feeding habits (Noirot, 1992), and since being found on trees, lodged on the branches bifurcations or inside epiphytes (Ellwood *et al.*, 2002; Noirot & Darlington, 2000; Davies *et al.*, 2003), it is on the ground level that these resources are more abundant. Our results show that both genera studied, even in different scales, are favored by the increase of the percentage of organic carbon in soil and litter amount, but are unfavored by the increase of fallen branches (Figure 6). Termites show a dominance, in terms of taxonomic diversity and in some cases biomass, towards more humified food items (Donovan *et al.*, 2001). Considering that the measured variables represent different stages of decomposition of the same basic resource (cellulose) and that fallen branches are the beginning and organic carbon in soil the end, of this humification gradient, we can easily understand why termites are favored in high percentages of soil organic carbon. Also, branches are more difficult to consume, due to its hardness and to the remaining presence of natural toxic components as terpens and phenolic substances, which have the function of protect the plants from insects and fungus attacks (Sjöstrom, 1993). Additionally, termite avoidance of branches, can occur because they are potential shelters to many organisms, including ants which are the most active and effective termite predators (Abe & Darlington, 1985; Hölldobler & Wilson, 1990; Gonçalves *et al.*, 2005b). However, we cannot make any conclusions because we did not sample ants in the debris or any termite ground foraging observations. Then, further experiments must be done to elucidate the negative interaction between the increase in ground branches amount and termite tree exploitation.

Besides foraging for food on ground level, termites may forage for others trees, searching for specific and nutritially richer food items, as micro-epiphytes and lichens (Jones & Gathorne-Hardy, 1995; Miura & Matsumoto, 1997, 1998). The tree environment is space limited and patchy compared to ground environment, and in the process of the expansion of the foraging area, termite access from one tree to another can occur through canopy branches or through ground. Adams & Levins (1987) found that the connections between the trees, from a flooded area, affect strongly mangrove termites. But, in non-flooded areas, termites may forage on floor searching for another tree, and thus, the presence of adequable food items in ground level may increase their success, being an alternative of consume when the other tree found is not available or too far, being not suitable in terms of energy/cost relationship for the colony.

Our data do not allow to distinguish which of the proposed assumptions for the tested hipotheses are true. But it is clear that besides keeping their colony detached from the ground, arboreal termites are dependent and influenced by ground elements. That seems to us that the most probably explanation turns around on the ground role as a provider of food resources to arboreal termites. The different response found between *Microcerotermes* and *Nasutitermes* can be supported in some differences of their biological characteristics. The different scales shown are probably correlated to the smaller colonies of *Microcerotermes* (Leponce *et al.*, 1997). Also *Microcerotermes* presents a lower proportion of soldiers (Noirot & Darlington, 2000), being more susceptible to the dangers hidden in the ground debris.

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5 Conclusão Geral

Concluímos que a ocupação (1) e a exploração (2) de determinadas árvores em detrimento de outras por cupins pode ter origem nas três hipóteses testadas:

1. Os cupins preferencialmente se estabelecem em árvores de grande porte, possivelmente devido a fatores aleatórios, onde árvores maiores são mais conspícuas e mais facilmente localizadas pelos cupins. Cupins se estabelecem também, preferencialmente em árvores que estejam em locais com maior disponibilidade de recurso, seja disposto em suas copas ou no solo adjacente às mesmas, que possam assegurar o sucesso inicial da formação da colônia.

2. Por outro lado, a exploração de uma árvore por cupins, parece não ser aleatório. Cupins parecem ter mais sucesso, ou se apresentarem mais ativos, em árvores que apresentem menor relação custo/benefício, seja por estarem em locais com maior abundância de recursos de nidificação (densidade de galhos) ou alimentar (quantidade de serrapilheira e matéria orgânica no solo), ou por se apresentarem como ambientes com menor risco de predação (ausência de formigas predadoras).

Adicionalmente, os fatores testados podem determinar a estrutura da comunidade de cupins arborícolas e devem ser levados em consideração durante o planejamento de áreas que visem a conservação e manutenção dos mesmos em ecossistemas naturais.

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