TERESA TELLES GONÇALVES MATHEWS

RISCOS E BENEFÍCIOS NA EXPLORAÇÃO DE RECURSOS POR CUPINS (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 *Doctor Scientiae*.

VIÇOSA
MINAS GERAIS - BRASIL
2009

Ficha catalográfica preparada pela Seção de Catalogação e Classificação da Biblioteca Central da UFV

T

M429r
2009

Mathews, Teresa Telles Gonçalves, 1978-
Riscos e benefícios na exploração de recursos por cupins (Insecta : Isoptera) / Teresa Telles Gonçalves Mathews. – Viçosa, MG, 2009.
xvi, 80f.: il. ; 29cm.

Texto em português e inglês.
Orientador: Og Francisco Fonseca de Souza.
Tese (doutorado) - Universidade Federal de Viçosa.
Referências bibliográficas: f. 68-80.

1. Térmita - Ecologia. 2. Inseto predador. 3. Aspereza de superfície. 4. Cascas. 5. Ecossistemas. 6. Glândulas exócrinas. 7. Térmita - Nutrição. I. Universidade Federal de Viçosa. II. Título.

CDD 22.ed. 595.736

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APROVADA: 06 de julho de 2009

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Dedicatória

Ao Nithin Mathews,

sempre presente!

De tudo resta o trajeto.
E o apredizado deixado por cada encontro,
Cada **pedra**, cada *curva*, cada alvorada.

Teresa.

Agradecimentos

Agradeço aos meus pais Ruth e Aloisio por tudo, sempre amorosos e confiantes!

Agradeço aos meus sogros, Moms e Pappa, todo o carinho, dedicação e apoio.

Minha gratidão ao Nithin, meu amor, meu amigo e meu esteio! Aquele que esteve presente em tudo, nas coletas, nas análises e nas revisões dos textos. Incansável em me lembrar a cada dia de que eu seria capaz de concluir essa jornada.

Aos amigos Djú, Eric, Fred, Cris, Amanda e Ronaldo, muito obrigada pelo carinho e atenção.

Agradeço ao professor Johan Billen pela acolhida generosa, pela oportunidade preciosa e pela quase surpresa!

Agradeço aos colegas e amigos do Laboratório de Entomologia da Universidade Católica de Leuven, Lien e Eric, Wim, An, Amèlie, Uli e Tom pela acolhida e por toda a experiência cultural que vivi entre maio de 2007 e maio de 2008. A An agradeço especialmente por providenciar os cortes necessários à microscopia de varredura. E a Lien e An por desvendarem pra mim todos mistérios das técnicas de seccionamento e por inúmeras vezes salvarem minhas lâminas, sempre esquecidas no “heating plate”.

À Iracenir Andrade dos Santos pela gentil colaboração na identificação das formigas.

Agradeço a todos os colegas da Termitologia! Ana, Alessandra, Cassiano, Daniela, Eloá, Fernanda, Marcela, Paulo e Andrea. Muito obrigada por toda ajuda, seja no campo na coleta de dados, seja no cotidiano do laboratório. Um obrigado especial à Ale, Cassiano, Dani e Eloá por terem lido e relido meus textos, sempre contribuindo com críticas valiosas. Agradeço ainda os

estagiários que passaram pelo laborátorio colaborando com a coletas de dados entre outros: José Hilário, Juliana e Raul.

Aos queridos prof. Eraldo R. Lima e Nerilda, pela amizade e carinho.

Ao prof. Ronaldo Reis-Jr, agradeço por sempre estar disposto a discutir e aconselhar sobre questões estatíticas, contribuíndo de maneira fundamental para a realização desse trabalho.

Mais uma vez exponho minha gratidão ao prof. Og F. F. DeSouza. Um mestre paciente e acessível, mas rigoroso. Agradeço-o ainda por confiar no meu trabalho e por me ensinar entre outros, a contar as palavras em uma frase!

À coordenação do programa de pós-graduação em Entomologia pela excelência, e à D. Paula e à Miriam pela cortesia e eficiência.

Agradeço ainda à Universidade Federal de Viçosa pela acolhida e estrutura cedida, e à CAPES pelo crédito depositado em mim com o financiamento e o incentivo nesses quatro anos.

Biografia

Teresa Telles Gonçalves Mathews, 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 agosto de 2005, iniciou o curso de Doutorado em Entomologia na UFV, defendendo tese em julho de 2009.

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Resumo

MATHEWS, Teresa Telles Gonçalves, D. Sc., Universidade Federal de Viçosa, julho de 2009. **Riscos e benefícios na exploração de recursos por cupins (Insecta: Isoptera)**. Orientador: Og Francisco Fonseca de Souza. Co-orientadores: Angelo Pallini, Eraldo Rodrigues Lima, Paulo Sérgio Fiúza e Simon Luke Elliot.

O objetivo dessa tese foi analisar os fatores determinantes da utilização de recursos por cupins, focando principalmente na variação da disponibilidade de recursos alimentares e de riscos locais de predação. Assim levantamos hipóteses embasadas na habilidade de cupins escolherem por utilizar ou não um determinado recurso potencial dependendo dessas condições em cada local. Os trabalhos foram desenvolvidos considerando dois grupos, cupins de solo e cupins arborícolas. Encontramos que (i) grupos de espécies de cupins que apresentam habilidades defensivas distintas respondem diferentemente à disponibilidade de recursos e ao risco de predação, (ii) a estrutura da casca de árvores é um fator limitante para a exploração das mesmas por cupins que sobem em árvores, e que (iii) cupins se estabelecem preferencialmente em árvores que estejam em locais com maior disponibilidade de recurso, disposto no solo adjacente às mesmas. Adicionalmente trazemos a descrição de uma nova glândula exócrina do tipo bicelular no tórax de cupins. Assim conclui-se que a exploração de recursos por cupins, sejam eles de solo ou arborícolas, baseia-se em decisões de utilização de um habitat ou recurso que dependem do balanço entre riscos e benefícios locais.

Abstract

MATHEWS, Teresa Telles Gonçalves, D. Sc., Universidade Federal de Viçosa, July, 2009. **Risks and benefits of resource exploitation by termites (Insecta: Isoptera)**. Adviser: Og Francisco Fonseca de Souza. Co-advisers: Angelo Pallini, Eraldo Rodrigues Lima, Paulo Sérgio Fiú- za and Simon Luke Elliot.

The main objective of this thesis was to investigate the determinant factors in resource exploitation by termites, with special atention to variation of local resource availability and predation risk. We proposed hypotheses which are based on differential use of resource items depending on these local conditions. Two groups of termites, soil and arboreal, were counted. The results show that: (i) termite species which present different defensive abilities respond differently to the balance between resource amount and risk of predation, (ii) the roughness of bark trees limits to tree exploitation by arboreal termites and (iii) tree exploitation by arboreal termites is affected by the quantity of potential resources on the ground below the host tree. Additionally a new exocrine structure on termites' thorax is decribed. In conclusion resource explotation by soil and arboreal termites depends on the balance between risks and benefits in each site.

1 Introdução Geral

1.1 Apresentação

O objetivo dessa tese foi analisar os fatores determinantes da utilização de recursos por cupins, focando principalmente na variação da disponibilidade de recursos alimentares e de riscos locais de predação. Assim levantamos hipóteses embasadas na habilidade de cupins escolherem por utilizar ou não um determinado recurso potencial dependendo dessas condições em cada local.

A tese está dividida em sete seções. A seção 1, ou Introdução Geral, está dividida em duas subseções. A subseção 1 consta da presente apresentação. A subseção 2 é uma pequena introdução, relacionando os insetos estudados e os fatores que determinam a utilização de um recurso alimentar em potencial. Além disso a subseção 2 aborda teoricamente como mecanismos decorrentes de interações biológicas hostis, originadas no aumento de recursos, podem determinar a riqueza local de espécies de cupins. As quatro seções subsequentes são compostas de um artigo cada, que tratam de maneira geral dos principais fatores que podem interferir na utilização de recursos por cupins.

O primeiro artigo nos trouxe um resultado inesperado que além de chamar a atenção para a importância de resultados não significativos, nos ajudou a responder a pergunta: por que a riqueza de espécies de cupins pode se correlacionar positiva ou negativamente com disponibilidade de recursos? Assim, levantamos a hipótese de que tal inconsistência a respeito da relação entre riqueza local de espécies de cupins e a disponibilidade de recursos advém de diferenças no balanço entre fatores que favorecem e que limitam cupins entre locais. Especificamente essa inconsistência pode ocorrer porque: (i) entre locais, o aumento do recurso pode teoricamente afetar a riqueza, positiva ou negativamente; (ii) o balanço entre os efeitos de recurso e risco de predação não é o mesmo entre locais; e porque (iii) diferentes locais apresentam diferentes composições de espécies e distintos grupos de espécies respondem diferentemente a esse balanço. Assim tal inconsistência ocorreria porque a resposta em cada local é dependente do grupo que ali predomina. Para isso testamos as seguintes predições: (i) a riqueza de espécies de cupim de um local depende da interação entre a disponibilidade de recursos e do risco de predação; e (ii) espécies de cupins defendidos por soldados são menos sensíveis à interação entre disponibilidade de recurso e risco de predação do que espécies de cupins sem soldados.

O segundo e terceiro artigos tratam do teste de duas hipótese levantadas apartir da pergunta “Por que existem árvores não ocupadas por térmitas que sobem em árvores?”. E mostram como a qualidade e a quantidade de recursos podem influenciar a ocorrência e atividade de cupins arborícolas. Especificamente testamos duas hipóteses, uma em cada artigo: *(i)* quanto maior a rugosidade da casca de uma árvore maior é a probabilidade de ocorrência de cupins; e *(ii)* cupins arborícolas são positivamente influenciados pelo aumento da quantidade de recursos potenciais existentes no chão, próximos à árvore hospedeira. O terceiro artigo foi realizado em colaboração com então estudante de iniciação científica Juliana Lins onde testamos a hipótese *(i)*. E o quarto artigo é a apresentação de uma nova versão do terceiro capítulo da minha tese de mestrado onde testamos a hipótese *(ii)*.

O quarto artigo é um exemplo de como tentivas frustradas do desenvolvimento de um projeto podem gerar resultados importantes. A idéia inicial era comparar a potencialidade defensiva de operários de cupins entre espécies que apresentam soldados com diferentes tipos de defesa a partir do desenvolvimento da glândula salivar dos operários. Por problemas metodológicos não foi possível realizar tal projeto mas nos deparamos com uma novidade. E assim esse trabalho trata da descrição de uma nova estrutura exócrina do tipo bicelular no tórax de cupins que está publicado no periódico Acta Zoológica volume 89, julho de 2009. Esse trabalho é fruto da colaboração entre o Laboratório de Termitologia da UFV e o Laboratório de Entomologia da Universidade Católica de Leuven, entre maio de 2007 e abril de 2008. Tal experiência foi realizada com a concessão de uma bolsa de estudos pela CAPES, no âmbito Programa de Doutorado no País com Estágio no Exterior.

Finalmente a sexta seção é uma Conclusão Geral, onde foram resumidos os principais resultados obtidos nos quatro artigos citados acima. E a sétima seção consta das Referências Bibliográficas utilizadas em toda a tese.

1.2 O uso de recursos alimentares por cupins

Térmitas ou cupins são insetos sociais da ordem Isoptera, que somam cerca de 2.860 espécies descritas (Constantino, 1999). Os recursos alimentares de térmitas são a madeira, seca ou em decomposição, serrapilheira, solo, micro-epífitas e fungos (Wood, 1978). A celulose é considerada a base nutricional de térmitas e esta pode ser obtida em materiais de origem vegetal nos seus vários estágios de degradação (Grassé, 1982; Donovan *et al.*, 2001). Os cupins, de uma forma geral, apresentam uma grande plasticidade na preferência alimentar (Darlington, 1994), porém poucas espécies consomem matéria vegetal viva e estas necessitam de complementar sua dieta com matéria orgânica morta ou em decomposição (Wood, 1978). Assim os cupins são considerados em geral como detritívoros. Além disso o substrato alimentar de muitas espécies não é bem conhecido (Eggleton & Tayasu, 2001) e a especificidade alimentar de cada espécie pode estar relacionada principalmente com o valor nutricional do ítem.

Devido a esse hábito detritívoro, os cupins são considerados organismos de extrema importância para manutenção dos ecossistemas tropicais (Black & Okwakol, 1997), participando de forma fundamental na ciclagem de matéria orgânica e de nutrientes (Wood & Sands, 1978). Além disso ser detritívoro traz diversas implicações particulares ao grupo, como por exmplo não influenciar diretamente a taxa de reposição do próprio alimento (DeSouza & Brown, 1994), diferentemente de predadores e ou consumidores primários (herbívoros). Isto é, os cupins ao se alimentarem não interferem na capacidade reprodutiva ou na sobrevivência do organismo/produto consumido.

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). O forrageamento em cupins é um processo complexo, que inicia-se pela localização do recurso, seguida pela decisão de ocupação ou não deste recurso pelos demais indivíduos da colônia. Para cupins que nidificam no próprio substrato alimentar, como as espécies da família Kalotermitidae e os cupins geófagos de ninhos subterrâneos (Krishna & Weesner, 1969), o custo de forrageamento tende a ser mínimo, mas em cupins que têm de buscar o alimento fora do ninho o forrageamento implica em um gasto de energia que pode representar um fator ecológico limitante importante (Eggleton & Tayasu, 2001). Adicionalmente a estratégia de forrageamento em térmitas não é igual para todas as espécies. Cupins de solo como *Reticulitermes santonensis*, na presença de um pedaço de madeira constróem galerias direcionadas ao recurso (Reinhard *et al.*, 1997), já o térmita arborícola *Constrictotermes cyphergaster*, quando chega ao solo, por intermédio de uma galeria descendente, emite trilhas de forrageamento de forma aletória (Sousa-Souto *et al.*, 1999).

Muitos fatores interferem no comportamento de forrageamento animal, impedindo que estes atinjam o máximo teórico de sua eficiência (Morse, 1980). Térmitas forrageiam coletivamente e fatores como risco de predação e disponibilidade de recurso são fundamentais na decisão de permanência ou abandono do local de forrageamento (Korb & Linsenmair, 2002).

A fuga parece ser a mais óbvia reação frente ao perigo, considerando a vulnerabilidade de um cupim. Segundo (Deligne *et al.*, 1981) a defesa em cupins não consiste de um único e bem definido tipo de mudança comportamental ou fisiológica, mas deve ser descrita como um conceito ecológico e funcional. Os mecanismos de defesa em cupins podem ser dividos em dois grupos, defesa química e mecânica (Krishna & Weesner, 1969). Em alguns casos, a defesa química possibilita que o cupim defenda-se do agressor sem o estabelecimento de um contato direto, já na defesa mecânica o contato é inevitável. Assim, como os mecanismos de defesa são diferentes, espera-se que o comportamento apresentado por esses diferentes grupos frente a situações de perigo, também o sejam. Sendo que tal variação de comportamento esteja relacionada às variações na morfológia das estruturas utilizadas para a percepção (sistema sensorial) e defesa dos cupins.

Concluindo, o sucesso de uma colônia dependerá da disponibilidade de recursos local e do risco relativo que cada colônia sofre para obtenção desse recurso. Sendo que a relatividade do risco é determinada crucialmente pela capacidade competitiva e defensiva de cada espécie.

1.2.1 Mecanismos decorrentes do aumento de recursos determinando a riqueza de especies local de cupins

Como padrão geral, o número de espécies coexistentes em um local apresenta uma relação positiva com a disponibilidade de recurso (Ricklefs & Schluter, 1993). Entretanto estudos recentes em ecologia de cupins, mostram que o aumento do recurso alimentar para cupins de um local pode resultar no aumento ou na diminuição da riqueza/atividade de cupins. Segundo Galbiati (2004) o aumento do número de iscas de papel higiênico resultou num maior número de espécies de cupins de solo capturadas, e que cupins ocuparam em maior proporção e mais rapidamente locais com um maior número de iscas (DeSouza *et al.*, in press). Adicionalmente o tamanho da árvore (Gonçalves *et al.*, 2005a) influencia positivamente a probabilidade de ocorrência de cupins arborícolas. Entretanto, Araújo *et al.* (2007) mostrou que o aumento da quantidade de serrapilheira no solo resultou na diminuição do número de espécies de cupins encontradas.

Estes resultados intrigantes, nos levam a crer que, além do aumento na disponibilidade de recursos outros fatores estariam regulando aspectos da comunidade de cupins de um local. Além da simples descrição de uma comunidade, como definir o número de espécies de um local, o grau de estruturação e a compreensão dos processos que a definem têm sido um dos principais focos dos estudos de ecologia de comunidades (Van Veen *et al.*, 2006). Dentre os diversos processos que podem definir essa dinâmica em uma comunidade, as interações biológicas entre indivíduos ou populações têm um papel fundamental. Segundo Morse (1980) as interações hostis existentes em uma comunidade, como predação e competição, exercem uma grande importância na determinação de padrões ecológicos. Considerando a sua importância na estruturação das comunidades, trataremos aqui apenas daqueles processos originados nas interações conflituosas entre indivíduos e ou populações biológicas (veja Figura 1).

O aumento da quantidade de um recurso potencial, alimentar ou de nidificação, pode teoricamente aumentar, diminuir ou não alterar a riqueza de espécies de cupins em uma comunidade. Quando o aumento do recurso corresponde ao aumento da disponibilidade de recurso alimentar no local (Figura 1, A), a comunidade de cupins pode responder pelo menos de duas maneiras: permitindo o aumento da abundância dos cupins pré-existente no local (Figura 1, B) ou favorecendo o estabelecimento/fundação de novas colônias (Figura 1, C). Sendo que o segundo evento pode implicar tanto no aumento do número de indivíduos como no aumento do número de espécies local, caso a fundação seja de uma espécie nova (Figura 1, D).

A maior concentração de indivíduos favorece o aumento de encontros e de interações entre os mesmos (Figura 1, E). Dentre as interações decorrentes do maior número de encontros entre os indivíduos, está a relação de competição (Figura 1, F). A competição é uma interação ecológica onde ambas as partes perdem, pois a disputa pela utilização de um recurso por dois indivíduos, ou grupo de indivíduos, gera desgastes para os dois lados, mesmo quando existe um vencedor. Competição em cupins figura-se principalmente pelo hábito territorialista das espécies (veja por exemplo Adams & Levins, 1987), já que a competição por exploração de alimentos parece improvável dada a alta abundância natural de seu alimento base, a celulose (Krishna & Weesner, 1969). Assim, o conflito gerado na defesa do território entre as colônias, intensificado pelo aumento populacional local, geraria uma taxa de perda de indivíduos ocasionando o enfraquecimento das colônias (Figura 1, G e H). Quando a perda de indivíduos é proporcional para todas as populações (Figura 1, I), a riqueza final após o aumento do recurso tende a ser a mesma (Figura 1, V). Entretanto se essa perda é desigual (Figura 1, T), diminuindo a equitabilidade da comunidade (balanço do número de indivíduos em cada população), a estrutura dessa comunidade é enfraquecida proporcionando o aumento da chance de uma extinção local (Figura 1, L), de origem determinística ou estocástica, que resultaria na diminuição da riqueza local de espécies de cupins (Figura 1, M). A diminuição da riqueza local, por sua vez, alivia a intensidade da competição (Figura 1, N), aumentando novamente a disponibilidade do alimento (Figura 1, A), e atribuindo ao processo a característica de ciclicidade.

Porém, o aumento do recurso pode corresponder também a um aumento na disponibilidade de sítios de nidificação, novos habitats ou novos itens alimentares (Figura 1, O) para cupins ou para outros organismos (por exemplo formigas; Campos *et al.*, 2003). Assim, esse evento pode favorecer o estabelecimento/fundação de novas colônias (Figura 1, C), o que implicaria no aumento da abundância ou riqueza local de cupins (Figura 1, D). Além disso, um aumento na disponibilidade de sítios de nidificação pode levar ao aumento da atividade de outros organismos, como por exemplo de predadores de cupins, sejam eles generalistas ou especialistas (Figura 1, P e Q). A presença de predadores atuando no local pode diminuir a atividade de cupins, seja porque os indivíduos são predados (perda de indivíduos; Figura 1, J) ou porque os cupins percebem a atividade dos predadores e fogem, abandonando o local (Figura 1, R e S). Considerando que essa perda de indivíduos pode ser proporcional ou desigual (Figura 1, K e T), dependendo do grau de especificidade do predador no local, a riqueza de espécies em uma comunidade de cupins pode não se alterar ou diminuir (Figura 1, V e M). E, no último caso, desencadeando o processo já descrito no parágrafo anterior. Já o abandono do local pode ser espacial ou temporal (Figura 1, S e V). O abandono espacial, causaria o mesmo efeito final sobre a estrutura da comunidade local acarretado pela perda de indivíduos, diminuição de riqueza (Figura 1, M). Já a fuga no tempo, como por exemplo uma mudança no comportamento forrageiro em alternância com o comportamento do predador, não alteraria de fato a riqueza de cupins do local (Figura 1, U).

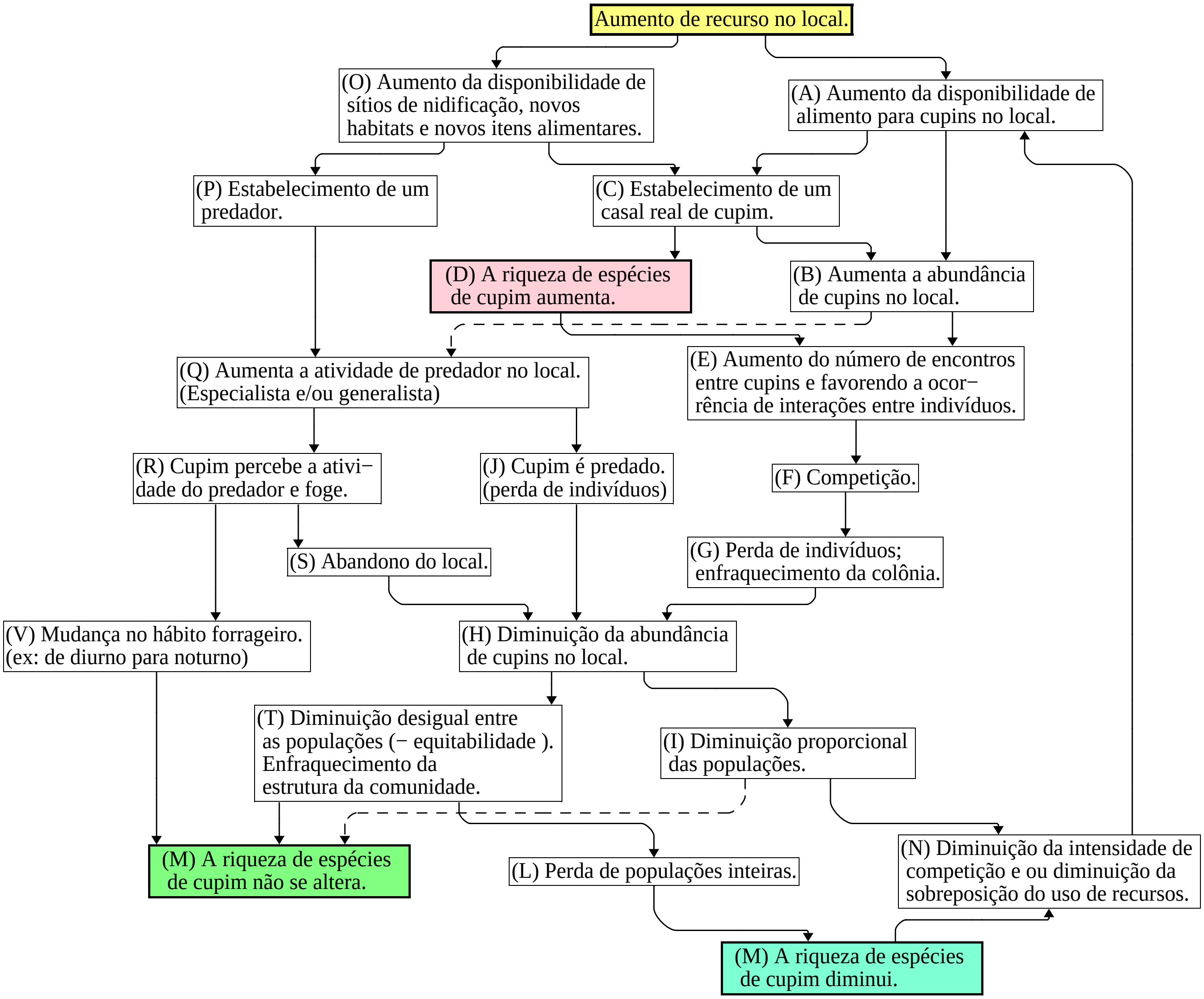

Figura 1: Processos ecológicos determinantes da riqueza local de espécies de cupins a partir do aumento de recursos. Os elementos destacados em cinza representam as três alterações possíveis na riqueza de espécies de cupins, devido ao aumento de recursos. Os diferentes estilos de linhas no diagrama são meramente ilustrativos, objetivando apenas facilitar a visualização.

2 Termite species richness non-response to resource availability: true or false?

Termite species richness non-response to resource availability: true or false?

Teresa Telles Gonçalves[1] and Og DeSouza[2],

Abstract

Generally the number of species that coexist in a certain site have a positive relationship to resource availability. However this is not always true: resource availability may also lead to reduction or no changes on termite richness. Among alleged reasons for the inconsistency in the reported responses of termite richness to resource availability, the interaction between resource availability and predation stand as fundamental. Therefore we hypothesize that such a inconsistency may arise from differences in the result of the balance of positive and negative effects, either from resource alone or from an interaction between resource and predation. Specifically, such an inconsistency may occur because: (i) among sites, resource increments may affect termite species richness either positively or negatively; (ii) the result of the balance between resource effects and predation effects among sites is not the same; and (iii) different sites may present distinct species composition, and such communities may respond differently to such a balance depending on inherent traits of the predominant group in the community. We inspected the effects of increasing resource amount and risk of predation on termite species richness at a local scale, testing the following predictions: (i) termite species richness respond to resource availability depending on the local risk of predation; (ii) termite species presenting soldier caste are less sensitive to the interaction of resource availability and risk of predation than soldierless termites species. Total termite richness was not related either to the interaction between resource amount and predation, or to any of these two factors alone. However the number of Apicotermitinae respond to an interaction between the two explanatory variables studied while non-Apicotermitinae species did not. The effect of counteracting of responses of each group might be a plausible explanation to the found pattern.

Keywords: ecology, predation, resource amount, balance of positive and negative effects

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2.1 Introduction

Generally the number of species that coexists in a certain site have a positive relationship to resource availability (Begon *et al.*, 2006; Ricklefs & Schluter, 1993). It seems that social insects follow this general pattern, as both ants and termites species richness may correlate positively to resource amount (Attignon *et al.*, 2005; Campos *et al.*, 2003; Ribas *et al.*, 2003; Eggleton, 2000). Even though, negative relationship between termite species richness and resource amount have also been reported (Araújo *et al.*, 2007).

Positive relationship between termite species richness and resource availability may take place when increased resource allows the settlement of more colonies in the site. Hence, the larger the number of colonies, the larger the probability that these colonies to belong to different species. Negative correlations between resource amount and termite species richness are not expected but are theoretically likely. Araújo *et al.* (2007) proposed three hypothesis that could explain this apparently unexpected result: as resource amount increases species richness diminishes because (i) another resource diminished; (ii) colonies retracted their foraging range, impairing sampling detection and hence producing pseudo-decrements in diversity; or (iii) predation risk increased. Thus resource increments could exert both positive and negative effects on termite species richness.

However termites' natural enviroments will always present both resources and predators. Thus local termite species richness might be the result of the counteract of these two factors, rather than the result of the effect of resource alone. That is, termite species richness varies from place to place because in some cases the effects of resource is stronger than predation and in others the opposite occurs. Hence the number of termite species of one site might be defined by the balance of these two factors.

Therefore we hypothesize that the inconsistency in the reported response of termite richness to resource availability may arise from differences in the result of the balance of positive and negative effects, either from resource alone or from an interaction between resource and predation. Specifically, such an inconsistency may occur because: (i) among sites, resource increments may affect termite species richness either positively or negatively; (ii) the result of the balance between resource effects and predation effects among sites is not the same; and because (iii) different sites may present distinct species composition, hence such communities may respond differently to such a balance depending on inherent traits of the predominant group in the community (e.g. one community where the number of soldierless termite species is higher than the number of soldier defended termite species may be more sensitive to predators activity than a community where the opposite occurs).

Hence, we propose to inspect the effects of increasing resource amount and risk of predation on termite species richness at a local scale, testing the following predictions: (i) termite species richness respond to resource availability depending on the local risk of predation; (ii) termite species presenting soldier caste are less sensitive to the interaction of resource availability and risk of predation than soldierless termites species.

2.2 Material & Methods

2.2.1 Study area

The study was carried out in seven different sites which are remanescents of Atlantic forest in the surroundings of Viçosa, MG, southeastern of Brazil. The data were collected during the months of April 2006 and of April and May 2007. The mean monthly temperatures and the accumulated rainfall during months of the study were $20,7\,^{\circ}\mathrm{C}$ and 56mm in April 2006; and $19,3\,^{\circ}\mathrm{C}$ and 58mm in April and May 2007. The mean temperature and the accumulated rainfall during the years of the study were $20,1\,^{\circ}\mathrm{C}$ and 1.188,8mm in 2006; and $16\,^{\circ}\mathrm{C}$ and 987,3 mm in 2007.

According to Veloso *et al.* (1991) the original vegetation in the region, is classified as Seasonal Semidecidual Montana Forest, which belongs to the Atlantic forest Bioma. The regional landscape has been drastically changed due to the development of agricultural activities and urban expansions. Nowadays this landscape is dominated by crop plantations and pastures fields where numerous fragments of primary and secondary forest of different ages are found.

2.2.2 Sampling design

Eight collecting points of 16 m^2 of area (4m × 4m), hereafter called 'grid' (Figure 2), were defined in all seven sites. In total 56 grids ($896m^2$) were sampled. The grids were distant from each other 15m minimum. In each grid it was evaluated the risk of predation, availability of resources, and species richness of termites. In all grids both termite sampling and the risk of predation experiment were carried during the highest temperatures of the day (between 10:00 am and 15:00 Pm).

2.2.3 Resource amount

A soil portion of soil (10cm × 10cm × 10cm) was collected in the central area of each grid where a square of 0,5m × 0,5m (Figure 2) was delimited. These soil samples were processed and analyzed in the Lab of Soil Analysis of UFV to quantify the amounts of total Carbon and Nitrogen. This quantification was used as a surrogate of the quantity of feeding resources available for termites.

2.2.4 Risk of predation

The risk of predation in each grid, was estimated by measuring the number of living termite baits attacked by predators. This kind of bait has been largely used to evaluate the pattern of predation by ants (Freitas & Oliveira, 1996; Cogni *et al.*, 2003). To build each bait, the dorsal region of the abdomen of a termite was attached to a toothpick with glue (tenaz, Loctite Brazil Ltd) (Cogni *et al.*, 2003). The toothpicks were cut and scratched with

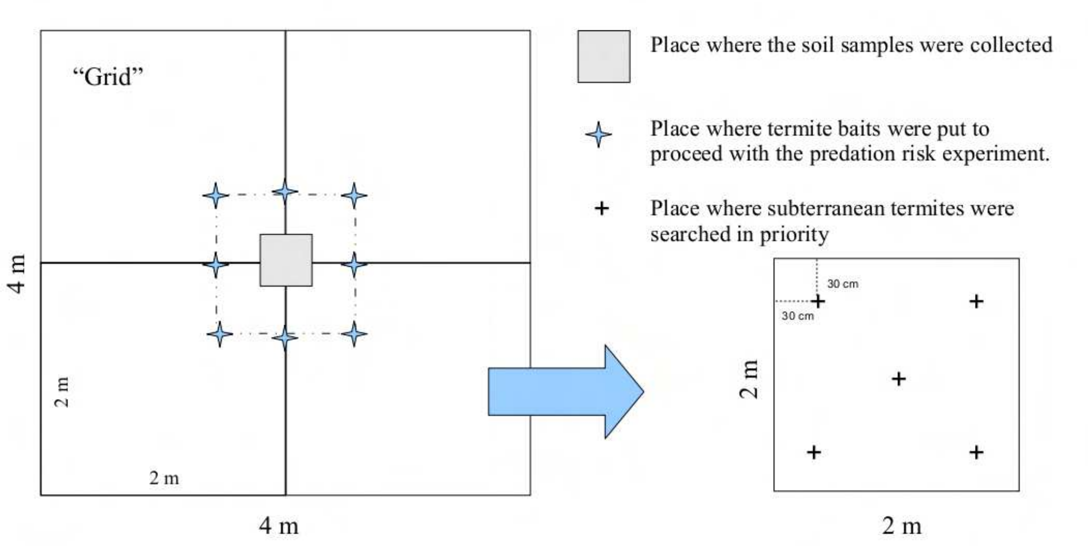

Figure 2: Schematic drawing of the sampling area.

sand paper in one of the tips, where the living termite was glued. Each termite bait was introduced in the soil aiming that the termite body would be as close as possible to the litter surface, to ease the access of the termites by predators.

In order to standardize the size and the odour of the baits, all termite individuals used were workers (3rd instar or older) of *Cornitermes cumulans* of the same colony. *C. cumulans* was chosen simply because they build epigeic nests, what allows to assure that the all individuals used belonged from the same colony.

This experiment was carried out in each of the 56 studied grids. In the central portion of each grid it was delimited a square of 1m × 1m where eight termite baits were placed equally distant from each other (Figure 2). The total number termite baits used in this study was 448 (8 × 56). Immediately after placing all the eight termite baits the observation started. Each group of eight termite baits was observed by two people at the same time during 40 minutes, where each person observed 4 neighboring baits. Every predator which attacked a termite bait was collected, put in bottle containing 80% alcohol, labeled and posteriorly identified. Each attacked bait, or the rests of it, was removed to guarantee that each bait was observed only once. A bait was considered to be attacked when it was bite, eaten or captured by one predator.

The risk of predation test was carried 24 hours before the termite sampling. This period was established to allow termites to get back to normal activity after human disturbance and the possible increased predator activity, caused by the exposition of termite baits. The risk of predation was thus estimated by the number of baits attacked in each grid. The identification of the collected ants was confirmed by comparison to specimens from the Ants Collection of the Lab of Community Ecology of the Federal University of Viçosa, Brazil.

2.2.5 Termite sampling

In order to make the sampling activity easier and standardized, each grid, was subdivided in four subgrids of $4m^2$ of area (2m × 2m) (Figure 2). Termites were manually sampled respecting a collecting effort proposed by Jones & Eggleton (2000). Each subgrid (2m × 2m) took 24 min to inspected by a single collector (0.16m/min.collector). The termites sampling was performed with the help of gardening shovels, plastic trays and entomological forceps. Since it is known that the termites which are soil foragers are largely abundant in the region, the first collection trials were performed in the soil. For such, in each subgrid, 5 soil samples of 24 cm^2 of area and 10 cm of depth (20 holes/grid) were taken to search for subterranean termites in prior. Four of these soil samples were taken from approximately 30 cm of the subgrids corners and one from the middle of the subgrid area (Figure 2). After collecting termites from such soil samples then the collector would search for termites in existent epigeous nests, fallen branches, litter, trees, and tunnels in the subgrid area, always respecting the mentioned time period of collecting effort. Termites were kept in 80% alcohol, labeled and identified. 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.

Attempting to minimize the effects of human disturbance in termite activity right before their sampling, the delimitation of each grid area, its subdivision, the risk of predation experiment and the sampling of soil used in the estimation of local resource amount, were done one day before. Additionally termites were sampled preferentially in the same period of hours that the experiment of the risk of predation was performed, minimizing the difference of light and temperature conditions in the measurement of the activity of both groups here studied, termites and their potential predators.

2.2.6 Data Analysis

To verify the proposed hypothesis, the following specific predictions were tested: (i) termite species richness respond to resource availability depending on the local risk of predation, (ii) termite species presenting soldier caste (non-Apicotermitinae) are less sensitive to the interaction of resource availability and risk of predation than soldierless termites species (Apicotermitinae).

All analysis were done with R (R Development Core Team, 2008), with generalized linear models (glm), followed by analysis of residues to check for the suitability of error distribution and for model adjustment. The minimum adequate models (MAM) were obtained by extracting non-significant terms (p>0.05) from the full models composed by the variables and their interactions. Non-significant terms, as single variables or lower interactions levels, were kept in the MAM when corresponding to a significant interaction term. In the models, a plus sign (+) denotes the addition of a variable to the model whereas an asterisk (*) means addition and an statistical interaction between variables. In all full models a blocking term (site) was added to distinguish between the seven sites studied. The full models used to test the proposed predictions are therefore:

$$Termite\ richness \sim site + C * N * predation\ risk \tag{1}$$

$$Apicotermitinae\ richness \sim site + C * N * predation\ risk \tag{2}$$

$$Non\ Apicotermitinae\ richness \sim site + C * N * predation\ risk \tag{3}$$

2.3 Results

Termites collected belong to the family Termitidae and comprise 4 subfamilies, 20 genera, 14 species and 16 morphospecies (Table 1). The Apicotermitinae group was represented by 10 different taxon and were 42% of the collected species per grid from a mean of 6.95 species per grid. 93.4 % of the species were found on soil samples. All the organisms observed attacking the termite baits in the risk of predation experiment were ants. The ants collected belong to 4 subfamilies, 9 genera, 6 species and 10 morphospecies (Table 2).

Total species richness of termites was not related to the interaction between resources amount and risk of predation (Table 3). Neither to resource amount or risk of predation alone. The hypotheses that the balance between resource amount and risk of predation affect distinct groups of termite species (Apicotermitinae and non-Apicotermitinae) in different ways was supported. Apicotermitinae species richness respond to the interaction between resource amount and risk of predation, while non-Apicotermitinae species richness does not respond. The number of Apicotermitinae species decreases with the increase of risk of predation when the amount of availabe carbon in soil is low. And the number of Apicotermitinae species increases when the amount of carbon in soil is high, disregarding augmentation in risk of predation (Table 4 and Figure 3).

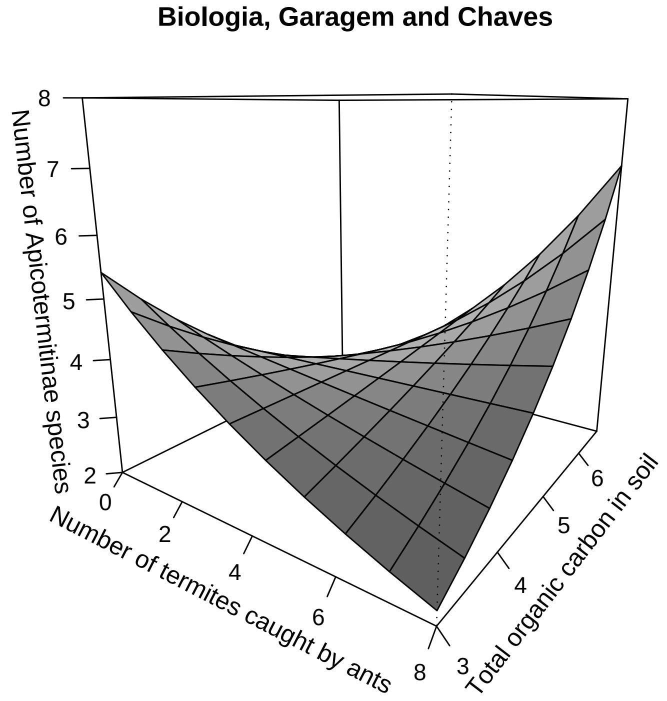

Figure 3: Effect of the interaction between the activity of predatory ants and the availability of total carbon in soil on the species richness of Apicotermitinae termites, Viçosa - MG. Brasil.

Table 1: List of the termite (morpho)species and their respective subfamily and feeding habit recorded in seven forest remanescents in the surrounding of Viçosa, MG, Brazil May 2006 and April/May 2007. Feeding habit definition follow Donovan *et al.* (2001), DeSouza & Brown (1994) as well as the observations made in this study. In the absence of full match at species level, the habit definition follows the most referred feeding habit for the respective genus. Termites were identified according to Constantino (1999) and Mathews (1977).

Subfamily	Species	Donovan *et al.*	DeSouza & Brown	This study
Termitinae	*Dentispicotermes cupiporanga*	soil	-	soil
	Dihoplotermes inusitatus	-	-	soil
	Neocapritermes opacus	-	-	soil/litter/wood
Syntermitinae	*Armitermes* sp.1	-	-	soil
	Cornitermes cumulans	litter/wood	litter	wood
	Cornitermes sp.1	litter/wood	litter	wood
	Cyrilliotermes cupim	soil	soil	soil
	Ibitermes curupira	-	-	soil
	Labiotermes sp.1	soil	soil	soil
	Labiotermes sp.2	soil	soil	soil
	Procornitermes lespesii	soil (upper layers)	-	soil/litter/wood
	Syntermes dirus	-	litter	soil
Nasutitermitinae	*Atlantitermes osborni*	-	soil	soil
	Diversitermes castaniceps	-	-	soil/litter/wood
	Nasutitermes jaraguae	litter/wood	wood	soil/wood
	Nasutitermes rotundatus	litter/wood	wood	soil/wood
	Nasutitermes sp.1	litter/wood	wood	soil
	Nasutitermes sp.2	litter/wood	wood	soil/wood/ arboreal gallerie
	Nasutitermes sp.3	litter/wood	wood	soil
	Subulitermes sp.1	-	soil	soil/litter
Apicotermitinae	*Anoplotermes* sp.1	soil	-	soil/litter
	Anoplotermes sp.2	soil	soil	soil/wood/ arboreal gallerie
	Anoplotermes sp.4	soil	soil	soil
	Anoplotermes sp.5	soil	soil	soil/litter
	Anoplotermes sp.6	soil	soil	soil/wood/dung
	Anoplotermes sp.7	soil	soil	soil/wood
	Anoplotermes sp.8	soil	soil	soil
	Aparatermes abbreviatus	-	-	soil
	Grigiotermes sp.1	soil	-	soil
	Ruptitermes silvestrii	-	-	soil

Table 2: List of the ant species collected in the event of the risk of predation experiment in seven forest remanescents in the surrounding of Viçosa, MG, Brazil May 2006 and April/May 2007.

Subfamily	Species
Ectatomminae	*Ectatomma edentatum*
	Gnamptogenys striatula
Formicinae	*Brachymyrmex* sp.1
	Camponotus (myrmothrix) rufipes
Myrmicinae	*Crematogaster* sp.1
	Pheidole (G-fallax) sp.1
	Pheidole (G-fallax) sp.2
	Pheidole sp.3
	Pheidole sp.4
	Pheidole sp.5
	Solenopsis sp.1
	Solenopsis sp.2
	Solenopsis sp.3
Ponerinae	*Odontomachus chelifer*
	Odontomachus meinerti
	Pachychondyla striata

Table 3: Analysis of deviance of the minimal adequate model showing the effect of the interaction between the activity of predatory ants and the availability of total carbon in soil on the species richness of termites, Viçosa - MG. Brasil, using glm with Poisson errors and log link function. The full model tested was *Termite richness = site + C * N * predation risk.*

Source of variation	df	Variance	$P(>\chi^2)$
MAM	13		<0.01
site	6	28.128	<0.01
Error	42		
Total	55		

Table 4: Analysis of deviance of the minimal adequate model showing the effect of the interaction between the activity of predatory ants and the availability of total carbon in soil on the species richness of Apicotermitinae termites, Viçosa - MG. Brasil, using glm with Quasipoisson errors and log link function. The site variable here refer to the two groups of sites after contrasting. The full model tested was *Apicotermitinae richness = site + C * N * predation risk*.

Source of variation	df	Variance	$P(>\chi^2)$
MAM	4	39.589	<0.01
site	1	8.139	<0.01
C	1	2.654	0.012
predation risk	1	0.402	0.327
C:predation risk	1	3.822	<0.01
Error	51		
Total	55		

Table 5: Analysis of deviance of the minimal adequate model showing the effect of the interaction between the activity of predatory ants and the availability of total carbon in soil on the species richness of non-Apicotermitinae termites, Viçosa - MG. Brasil, using glm with Poisson errors and log link function. The full model tested was *Non Apicotermitinae richness = site + C * N * predation risk*.

Source of variation	df	Variance	$P(>\chi^2)$
MAM	13		0.017
site	6	15.525	0.017
Error	42		
Total	55		

2.4 Discussion

Why are the reported responses of termite species richness to resource availability sometimes positive and sometimes negative?

We accepted the hypothesis that the inconsistency in the reported response of termite richness to resource availability may occur because distinct functional groups respond differently to a balance between resource availability and risk of predation. Our results demonstrate that the two groups of termites studied have different responses to the interaction of resource availability and risk of predation. While Apicotermitinae species richness was determined by an interaction of resource amount and risk of predation (Table 4 and Figure 3), non-Apicotermitinae species richness was not (Table 5). Additionally, Apicotermitinae species are less prone to coexist where resources is scarce and the risk of predation is high, i.e. where resource aquisition would not pay the costs of defense. Such a response of Apicotermitinae species richness to the interaction of resource amount and risk of predation may thus denounce, the sensitiveness of such group to predators.

Besides the strong effect of the interaction of resource amount and risk of predation on Apicotermitinae species richness, such response varied between groups of sites. The mean number of Apicotermitinae species in Biologia, Garagem and Chaves is higher than the mean number of Apicotermitinae species in Nico, Zootecnia, Paraiso A and B (Table 4 and Figure 3). Thus, the inconsistency in the reported response of termite richness to resource availability may also arise from differences in the effect of the balance between resource and predation effects among sites. Therefore, termite species richness is sometimes positively correlated to resource increments and sometimes negatively either because: (i) distinct functional groups respond differently to the balance between resource availability and risk of predation; (ii) or because the effect of such a balance among sites is not the same.

Why total termite species richness is not related to resource availability and risk of predation?

In opposition to our expectation, total termite species richness neither respond to an interaction between resource availability and risk of predation nor to any of the measured variables alone (Table 3). Rather than rare, nonsignificant relationships between animal species richness and resource availability are often found (Begon *et al.*, 2006; Mittelbach *et al.*, 2001), though rarely discussed. Nonsignificant relationships between resource and species diversity may arise from the counteract of two forces. The positive effect of increments in resource availability would be nulled by the negative effect of increments in risk of predation on the total species richness. Alternatively such a counteracting effect may be occurring in another level because increases of resource amount may affect distinct groups of termites in different ways. That is, the same combination of resource amount and predators activity in one local may affect some species in one way and other species in another way, depending on inherent features of such groups. Accordingly, Johnson & Isaac (2009) alleged that ground-dwelling marsupial species are more likely to suffer declines and extinction than similar sized arboreal marsupial species because ground-dwelling marsupial species suffer more predation. If we had found that the two studied termite groups responded in opposing ways, such an explanation would be straightforward. Even though, the found nonsignificancy when the groups are lumped together may still be explained by such a mechanisms because the mean number non-Apicotermitinae species in one sample was higher than Apicotermitinae species. Thus the predominance of the non-Apicotermitinae group in the community would conceal the response of the Apicotermitinae group. In fact, in a community where Apicotermitinae species represented 60% of the collected species, DeSouza *et al.* (2009) found that risk of predation by ants is determinant in resource use by termites. Hence the nonsignificant found result may be a consequence of the species composition of the community.

Why non-Apicotermitinae species richness does not respond to the interaction of risk of predation and resource availability?

Non-Apicotermitinae species are likely to be less sensitive to predation than Apiotermitinae species either because of their inherent defensive abilities (presence of the soldier caste) or because non-Apicotermitinae species generally present numerous colonies (among the collected non-Apicotermitinae genera the mean number of individuals per nest range from 34.000 to more than 1 milion; Lepage & Darlington (2000)). Thus, the risk of predation is relatively low to non-Apicotermitinae species as more individuals in the colony lower the risk of it to be extinct and so smaller the chance of exclusion of such species at the site.

Why risk of predation exert contrasting effects on Apicotermitinae species richness?

Predation exerting contrasting effects on species richness is not a novelty (Begon *et al.*, 2006). We observed that Apicotermitinae species richness decreases with high risk of predation when resource is scarce and increases when resource is abundant. Such an interaction may occur because when resource is scarce the effect of high risk of predation in lowering abundance may demote rare species to extinct. But when resource is abundant, predators may prevent single species from monopolizing the resources (Paine, 1966) and so favour the coexistence of more species.

Conclusion

We warn to the problem of neglecting nonsignificative results or even of dismissing of such results. Such a problem occurs because researchers either tend not to publish the nonsignificative results or they do not discuss the possible mechanisms that had led to such a pattern. In this matter, our paper may be an example of how nonsignificative results may hide valuable information and thus lead to missinterpretations. The nonsignificant relationship found in this work might be not explained as a result of the counteracts of the two evaluated forces - resource availability and risk of predation. However at the group perspective this explanation is shown to be plausible, as the effects of the counteraction between resource and predation was not equal to all termite groups of species. Thus, despite the fact that all termites are social, detritivorous and do fit into a single order, they seem to respond differently to the offer of resource and risk of predation. Therefore, to unveil mechanisms linked to resource use and termite species richness, termites should be grouped according to specific traits such as defense mechanism and specific feeding habit.

Acknowledgements

TTG was supported by a CAPES PhD studentship and ODS is supported by Brazilian National Council (CNPq, Fellowship #306 081/2007-5, research support 485460/2007-6) and by FAPEMIG (APQ-4627-5.03/07). We are also thankful to the members of the Termitology Lab, Ana Paula A. Araújo, Alessandra Marins, Daniela F. Florencio, Cassiano S. Rosa, Fernanda S. Araújo, Marcela M. de Lima, Rodigo Krüger and Raul for all their help with the field work. We are enormously indebted to Ana Paula A. Araújo for the termite identification. We are very grateful to Iracenir Andrade for the ants identification. This is contribution # nnn from the Termitology Lab (http://www.isoptera.ufv.br), at Federal University of Viçosa, Brasil (UFV). This paper is part of TTG's PhD thesis presented to UFV. This paper has been entirely produced using Free Software (Linux, LaTeX, Kile, Xemacs, R).

3 Bark roughness ruling presence and activity of arboreal termites (Isoptera: Termitidae) on trees

Bark roughness ruling presence and activity of arboreal termites (Isoptera: Termitidae) on trees

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Abstract

In tropical forests, tree may present from smooth to irregulary fissured barks. Such a diversity of roughness is known to play an important role on the the amount of species and biomass of invertebrates supported on the bark of a tree. Arboreal termites may use the bark of tree as a highway, where they have to walk up and down between canopy and ground. Besides two claws termites workers and soldiers have no morphological adaptation such as arolia on their *tarsi* to walk on smooth surfaces. Hence, we explore such an idea using termites (Insecta: Isoptera) in a field experiment, investigating whether bark roughness would (i) affect the proneness to find termite galleries on tree trunks and (ii) limit termite activity on such trunks. Data were collected in a semidecidous forest in the domains of the Brazilian Atlantic forest, Minas Gerais State. We evaluated 66 trees which were exploited, not simultaneously, by termite species of two Termitidae genera: Nasutitermes and Microcerotermes. The chance to find an active arboreal termite gallery on a tree trunk increases with higher values of the bark roughness index but termite activity is not related to such an index. We argue that rougher barks have a positive effect on arboreal termite occurrence either because they favour termites' coming and going on the trees; or because they are a surrogate for the resources provided by such trees.

Keywords: Isoptera, Microcerotermes, Nasutitermes, arboreal termite, tree bark structure, determinants of tree exploitation, Quadrat-method, uniform and aggregate

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3.1 Introduction

Termites are social insects majorly associated to soil enviroment. Despite that, there are several termite species which inhabit the forest canopies (Constantino, 1999). Such species, generally referred as "arboreal termites", build their nests hanged on trees' branches or trunks (Noirot, 1970). Efforts to clear the factors constraining tree exploitation by termites have been made and nowadays it is known that predation risk (Gonçalves *et al.*, 2005b; Leponce *et al.*, 1999), and "macrostructural" features of trees such as size (Gonçalves *et al.*, 2005a; Jones & Gathorne-Hardy, 1995) and number of branches (Gonçalves *et al.*, 2005a) are important determinants of tree exploitation by termites. However, information on the effect of "microstrutural" features of trees, such as bark roughness, that may rule the exploitation of trees by termites, remain largely unknown.

The bark is indeed an important component of forest and woodland ecosystems (Majer *et al.*, 2003) and, besides protecting the trees in various ways, it serves as shelter and as source of nutrition for many animals, plants, fungi and lichens. In tropical forests, trees may present high morphological diversity of barks which can vary from smooth to irregulary fissured ones. Such a diversity of traits is known to play an important role on the number of species and the biomass of invertebrates supported on the bark of a tree (Halula *et al.*, 2000; Nicolai, 1989, 1993).

For arboreal termites the bark of a tree acts as a highway, where they have to walk in their up and down movement between canopy and ground. Such a movement may be far from trivial. Besides two claws (Krishna & Weesner, 1969) termites workers and soldiers have no morphological adaptation such as arolia on their *tarsi* and are inefficient to climb smooth vertical surfaces (Crosland *et al.*, 2005). Thus, it is plausible to hypothesize that bark roughness affects the exploitation of trees by termites. Here, we explore such an idea using termites (Insecta: Isoptera) in a field experiment, investigating whether bark roughness would (i) affect the proneness to find termite galleries on tree trunks and (ii) limit termite activity on such trunks. Our rationale is that, to exploit a tree, termites must attach galleries on it. To build galleries on the tree's trunk, termite require barks rough enough to the attachment of their morphologically simple tarsi as well as of their buiding materials. That is, barks can not be totally smooth, but must present a certain level of roughness on which termites could hold fast and where their constructs could adhere. Accordingly, past the critical roughness limit, termite activity should increase steadily, possibly up to a certain value where it levels off.

3.2 Material & Methods

3.2.1 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 continuous remnant of semideciduous Atlantic rain forest of Minas Gerais state (35.976ha), Southeastern, Brazil, and is located between 19°48'18" - 19°29'24" S and 42°38'30" - 42°28'18" W. To the East the park is bordered by the river Doce and to the South by the Piracicaba river. The local altitude varies from 230 to 515 m above sea level (SOCT- Sistema Operacional de Ciência e Tecnologia, 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 yearly mean temperature is 21.9° C (Gilhuis, 1986). Vegetation is mainly seasonal semideciduous (Lopes, 1998), with a moderate to high percentage (20 to 50%) of deciduous trees (Veloso *et al.*, 1991).

3.2.2 Sampling design & Data Collection

The study was conducted in four sites in the Park, known as the Mata do Gambá, Mata do Macuco-Lagoinha, Mata da Tereza and Mata do Vinhático.

All trees evaluated in this study were at least 50 m distance from the forest edge.

One 4 cm^2 portion of bark was collected from each of the 66 trees presenting a minimum of 15 cm of circumference at 1.30 m from the soil (circumference at the breast height, CBH). Each tree was evaluated for the presence or the absence of termite galleries at 1.30 m from the soil level. To access termite activity we simultaneously interrupted both extremities of a 15 cm long portion of the gallery and captured all termites found therein. Further inspection on the remainder of the gallery allowed catching additional soldiers, thereby guarantying secure identification of the species. This additional sample also allowed us to confirm that galleries were actually being used by termites, whenever the event that the activity inside the inspected portion of gallery was momentarily zero. We did not sample galleries built *inside* wood. Termites were kept in 80% alcohol, labeled and identified. The identification was confirmed by comparison to specimens from the Section of Termitology of the Entomological Museum of the Federal University of Viçosa (http://www.insecta.ufv.br/museu), Brazil, where voucher specimens are deposited.

3.2.3 Measurement of bark roughness

To evaluate the degree of bark roughness, all bark pieces were imprinted on paper by scratching a piece of carbon paper on the bark surface with the help of a pencil (Figure 4). Three imprints have been produced from each piece of bark. Such imprints were then eletronically scanned to produce a digital image, at 2000 dpi. The sharpest among the three images obtained was selected to proceed to bark roughness measurements. After that, the digital image of each piece of bark was cropped to 1000 x 1000 pixels of area. The images were manipulated using GIMP (GNU Image Manipulation Program - http://www.gimp.org) in order to have black and white images (Figure 4). Bark crests are indicated by the black portions in the image and bark crevices are represented by the white portions. Such images were then converted into 1000 x 1000 matrices, composed by zero and one (Figure 4), where zero represented the black pixels, and one represented the white pixels in the edited image. The matrices were obtained using the script *img2txt* from the R package Rt4bio (http://sourceforge.net/projects/rt4bio/). Finally, an index of roughness of bark was calculated from each matrix. This index was processed under R (R Development Core Team, 2008) using the quadrat-based method (Crawley, 2007). The quadrat-based method test for spatial randomness of individuals (here black pixels) in quadrat areas. The quadrat-based method is describe in the following steps:

1. Calculation of the number of black pixels of each 1000 x 1000 pixels black and white image (quadrat).
2. Calculation of the area of a sub-quadrat need to fit one black pixel per sub-quadrat if the distribution of black pixels in the quadrat was uniform (Figure 5 B).
3. Placement of the sub-quadrats over the original image to proceed the measurement of the mean and the variance of the number of black pixels in the sub-quadrats (Figure 5 C).
4. Determination of the distribution of black pixels in each quadrat, which is given by the variance over the mean number of black pixels distribuited on the correspondent areas of sub-quadrats on the quadrat (Equation 4). Where the higher ratio of variance/mean, more aggregated is the distribution of the black points and thus rougher is the bark.

$$Index\ of\ bark\ roughness \;=\; \frac{variance}{mean} \tag{4}$$

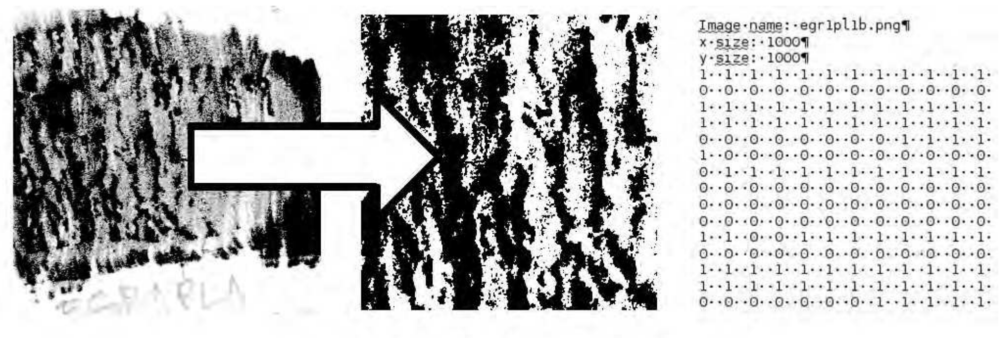

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Figure 4: Schematic ilustration on the routine to obtain the index of bark roughness. (right) Result from the imprint procedure performed in one portion of bark. (center) Black and white image with 1000 x 1000 pixels of size , converted from the image imprinted from the portion of bark. (left) Portion of the matrix obtained from the black and white image, the black pixels are here represented by 0 and the white pixels by 1.

3.2.4 Data Analysis

Statiscal analysis was used to check whether the bark roughness index would affect the proneness of termites galleries occurrence and the termite activity therein such galleries on trees. All analysis were done with R (R Development Core Team, 2008), using generalized linear models (glm). Modelling proceeded by building full models, including the above parameters and their interactions when possible. The hypothesis that bark roughness affects

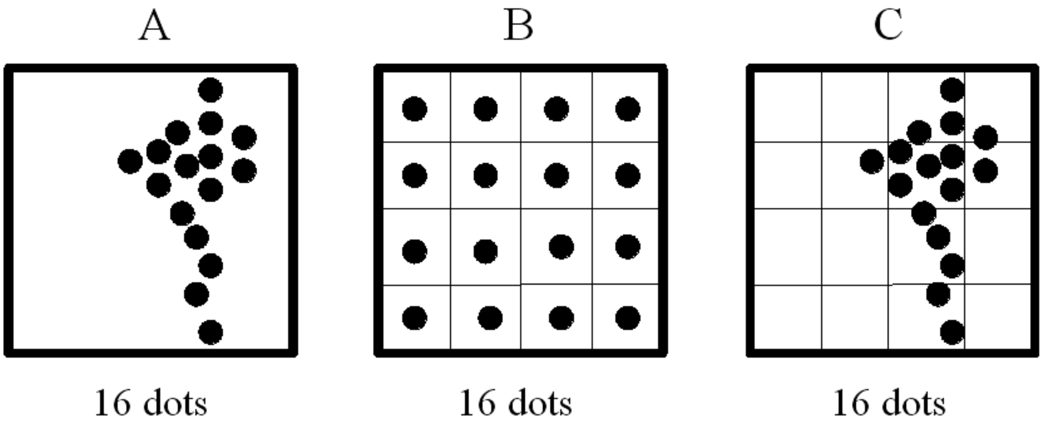

Figure 5: Schematic ilustration on the routine to calculate the index of bark roughness. (right) Drawing of a schematic result from the imprint procedure performed in one portion of bark. (center) Drawing showing the fit of one black pixel per sub-quadrat if the distribution of black pixels in the quadrat was uniform. (left) Drawing showing the placement of the sub-quadrats over the schematic original drawing to proceed the measurement of the mean and the variance of the number of black pixels in the sub-quadrats.

the presence of termite galleries on the tree, was tested using a model whose binary response variable y assumed the value one when active galleries were detected on the tree trunk, and zero when there were no galleries or when they were abandoned. The index of bark roughness (Equation 4) was used as the explanatory variable. On its turn, the hypothesis that the bark roughness affects arboreal termite activity was tested using a model whose response variable (y) was the number of termites inside a 15 cm long portion of the gallery, a surrogate for termite activity. As explanatory variables we used the index of bark roughness plus of the co-variate *genus*. *Genus* is a qualitative variable assuming one of the two values *Microcerotermes* or *Nasutitermes*. This was needed to prevent the term "bark roughness" to spuriously capture statistical significance due to differences in termite activity atributable to *genus* solely. To proceed with the test of this hypothesis only trees holding termite active galleries were taken in to account. The full models used are therefore:

$$\textit{Presence of termites} \sim \textit{index of bark roughness} \tag{5}$$

$$\textit{Activity of termites} \sim \textit{index of bark roughness} * \textit{genus} \tag{6}$$

In the models, an asterisk sign (*) denotes both addition and interaction of the variables in the model. Error distribution was Binomial for the model described in equation 5 and Negative Binomial for the model described in equation 6 with logit and log link functions, respectively. Model simplification, was performed by backward term extraction, removing one term at a time. Terms returned to the model if their removal provoked a change of deviance with P <0.05.

3.3 Results

Termites collected belong to the family Termitidae and comprise two subfamilies, two genera, three species and one morphospecie (Table 6). Out of the 66 evaluated trees, 23 held active galleries, whereas five held inactive termite galleries. The remaining 38 trees did not show any sign of termite presence. Termite nests were directly spotted on 4 out the 23 trees containing active galleries. Among those, only one tree held two nests, whereas the others held single nests. The maximum distance of the nests to the ground observed was 15 meters, the average distance was 10.91 meters, and the minimum distance was 7.35 meters. The maximum value of bark roughness index obtained was of 6.93, the mean value was 1.99 and minimum value was 0.27.

The hypothesis that bark roughness affects termite sucess in exploiting trees was confirmed. The rougher is the bark, the more likely to find termites on the tree (χ^2_1 =4.986; P=0,026, n=66, Figure 6). According to the final statistical models achieved, proneness to termite occurence on trees is related to bark roughness according to the logistic equation $log(\frac{p}{q}) = -1.52+0.4348* bri$, where $(\frac{p}{q})$ is the odds ratio of presence/absence and the bri is the trait bark roughness index as defined in the Material & Methods section. When we back-transform this odds ratio to the "probability of termite occurrence", such an equation gives Figure 6. The inflection point of this curve is bark roughness =3.5, and represents the value where the probability of termite occurrence, p, is 50%. That is, the probability of termite occurence on trees drops below 50% for trees presenting bark roughness index below 3.5. Bark roughness, however, did not affect the activity of termites within the galleries on the trunk (χ^2_1 =0.6385; P=0,42, n=23).

Table 6: List of the termite species of the sampled on trees in State Park of Rio Doce, MG, Brazil 2004.

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

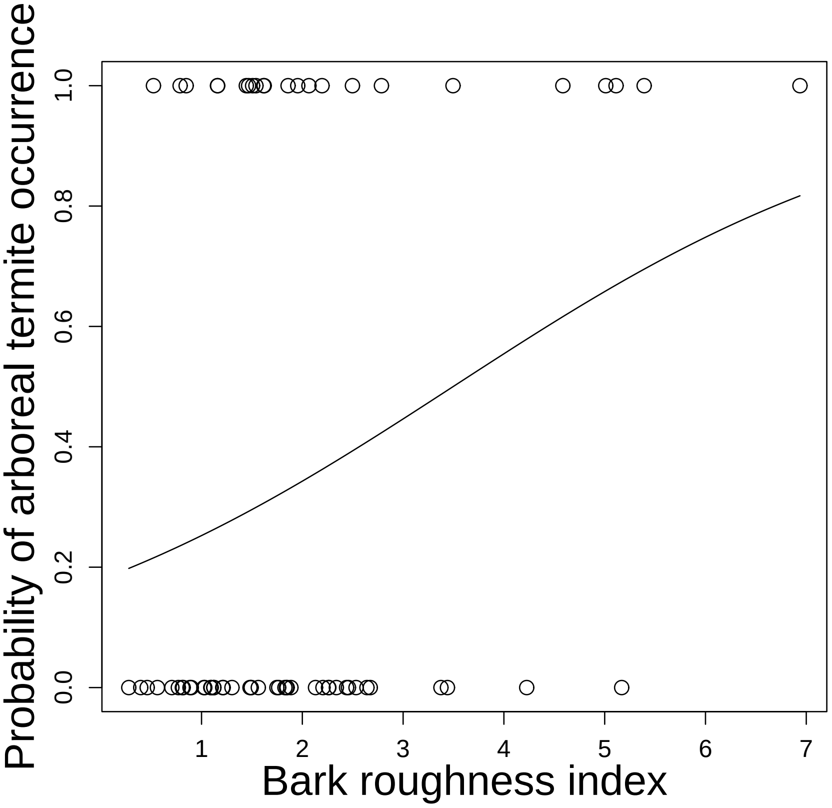

Figure 6: The effect of bark roughness on the probability of finding termites on trees in State Park of rio doce, MG, Brazil. The higher the value of bark roughness index the rougher the tree bark. See Material & Methods for details.

3.4 Discussion

Insects crawl vertical surfaces with the help of special morphological structures present on their tarsi: the claws, arolia, and pulvilli. Claws allow gripping on rough surfaces while arolia and pulvilli present hairs which adhere to smooth surfaces (Chapman, 1991). The workers and soldiers of the termite species studied here, as with in all other Termitidae (Crosland *et al.*, 2005), do not present arolia nor pulvilli in their *tarsi*. Therefore, they may experience trouble when trying to climb trees whose barks are excessively smooth.

Such a morphological feature of termite *tarsi* could be the proximal cause of the results achieved here. Cracks could ease termite grip onto barks, and this could be the underlying mechanism for the positive effect of bark roughness on the chance to find an active termite gallery on a tree trunk (Figure 6). Moreover, there seems to be a critical value of bark roughness above which the likelyhood to find termites exploiting a tree exceeds 50% (χ^2_1= 4.986; P= 0,026, n= 66). That is, trees are prone to be exploited by termites providing their bark roughness exceeds a given threshold.

Interestingly enough, termite activity within such galleries was not affected by bark roughness, contrarily to our expectancies (χ^2_1= 0.6385; P= 0,42, n= 23). This indicates that once galleries are built, bark irregularity does not provide further ease to termite doings. Bark roughness, therefore, seems crucial for termite establishment on trees, but not for everyday colony dynamics.

This intriging pattern may, at a first glance, appear conflicting: how come the positive effect of bark irregularity on arboreal termite is vanished after galleries are built? One possible explanation would be that, by paving the galleries' floor, termites may turn any bark irregularity into an optimized texture. If this is so, all barks are made alike after the roughness threshold is overcome and, hence, termite activity should not vary above this limit. Apart from a better grip for termites themselves, rough barks can also favour adhesion of building materials, thereby providing better attachment of galleries and nests. This could also explain the absence of effects of bark texture on termite activity. That is, if the main problem is to attach galleries and nests, there is no reason to suspect increased activity after the threshold of roughness is overcome and the attachment problem is solved.

An alternative interpretation would be that termites may be related to bark roughness indirectly; this trait indicating the resources available on the tree. In fact, trees presenting rough barks are suitable to the attachment of epiphytes (Male & Roberts, 2005) and lichens (Ranius *et al.*, 2008), which are known to be important source of nutrition for some arboreal termites (Miura & Matsumoto, 1998). Additionally, bark roughness could indicate the tree's age, since older trees are prone to present barks with deeper crevices (Ranius *et al.*, 2008). Older trees hold older barks, and barks are dead tissue. It follows that, for a given tree species, the rougher its bark the longer it have entered decomposition processes and the closer it could be to termite needs. Older trees are also larger, and the larger the tree the more likely that it will hold termites (Gonçalves *et al.*, 2005a; Jones & Gathorne-Hardy, 1995).

In summary, bark roughness could indicate to termites that the tree holds resources in suitable quantity and/or quality. This would call for an ultimate cause: how would termites 'know' that bark roughness indicates anything? The answer to such a question is beyond the scope of our experiment, but current evidence allows some conjectures on the matter. Providing that surface irregularity is an essential condition to trigger termite building behaviour (Lee *et al.*, 2008), one could think that such a trait was selected in response to tree's suitability associated to bark roughness.

Concluding, arboreal termites respond positively to rougher barks, as opposed to smoother ones, because trees presenting such barks (i) offer a better grip, being hence easier to be exploited and (ii) hold suitable resources to these insects.

Acknowledgements

This paper has been produced within the Field Course on Canopy Ecology (FCO-CGP 2004), with financial support from PROFIX/CNPq (# 540552/2001-1), PELD/CNPq (# 520026/98-8), British Embassy, and FAPEMIG (# CRA 1041/04). TTG was supported by a CAPES PhD studentship and ODS is supported by Brazilian National Council (CNPq, Fellowship #306 081/2007-5, research support 485460/2007-6) and by FAPEMIG (APQ-4627-5.03/07). FAPEMIG provided to RRJ a Post-doctoral grant (# CRA 00083/04) and to JL a undergraduated grant (# CRA 1041/04????). We are indebted to the Administration of the Rio Doce State Park/IEF; to the field crew, F.S. Neves, J.P. Soares, R.I. Campos, R.F. Ferreira and W.D. da Rocha; and to the Rio Doce State Park climbers, Canela and Rogério; for optimizing the whole sample process. Special thanks to Duca for all the help. We thank very much to Prof. Reginaldo Constantino for confirmation on the termite identification. Thanks very much to C. S. Rosa, A. Marins, E. S. Varga and D. F. Florêncio, whose critical comments significantly improved the manuscript. This is contribution # nnn from the Termitology Lab (http://www.isoptera.ufv.br), at Federal University of Viçosa, Brasil (UFV). This paper is part of TTG's PhD thesis presented to UFV. This paper has been entirely produced using Free Software (Linux, LaTeX, Kile, Xemacs, R).

4 Use of ground resources by arboreal termites (Isoptera:Termitidae)

Use of ground resources by arboreal termites (Isoptera:Termitidae)

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Abstract

Termites are known to act directly on organic matter decomposition and nutrient cycling, and therefore are important organisms to the maintenance of ecosystems functionality. Despite being majorly associated to the soil fauna several termites species inhabit arboreal environments. Nevertheless the ecological determinants of tree exploitation by termites remain largely unknown. Arboreal termites always present galleries connecting their nests to the ground. And besides being provided in the trees crowns it is on the ground that most of termites feeding resources are largely abundant. Thus we tested the hypothesis that the exploitation of trees by arboreal termites is affected by the amount of potential resources on the ground below hosts trees. Data were collected in a semidecidous forest in the domains of the Brazilian Atlantic forest, Minas Gerais State. We evaluated 70 trees which were exploited, not simultaneously, by termite species of two Termitidae genera: Nasutitermes and Microcerotermes. As hypothesized, we found that the availability of potential resource items on the ground were important determinants of tree exploitation by these termite species. It is therefore plausible to suspect that, despite inhabinting colonies apparently detached from the ground habbitat, arboreal termites can be constrained by ground traits - rather than only canopy traits.

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

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4.1 Introduction

Termites are generally associated to soil fauna and are basically detritivorous. They feed on a wide range of dead plant material (cellulose) in various stages of decomposition (Donovan *et al.*, 2001), which is largely distributed on the forest floor. Despite the apparent availability of this resource on the forest floor, there are several termite species that inhabit forest canopies. Such species, generally referred to as "arboreal termites", build their nests hanging from tree branches or trunks (Noirot, 1970).

The habit of hanging the nest on trees brings to the arboreal termite species several benefits. It allows for instance, arboreal termites to escape from enemies such as ground dwelling ant and mammal predators (Deligne *et al.*, 1981), or even to escape from natural catastrophes such as fires and floodings. Furthermore, on trees termites can find food items like lichens and microepiphytes (Jones & Gathorne-Hardy, 1995; Miura & Matsumoto, 1997), which are rich in nitrogen (Miura & Matsumoto, 1997), an element essential to termite growth and reproduction (Brent & Traniello, 2002).

Despite providing food and promoting relief from predation by ground dwelling animals, the arboreal habit may also impose some risks. A tree and its branches, are susceptible, for instance, to falls that could kill the colony. Moreover, although virtually free from ground dwelling competitors and predators, arboreal termites still face predation risk and competition for space and/or food in the tree canopy. Indeed, it has been shown that the presence of predatory ants in the canopy negatively affects the activity of arboreal termites activity (Gonçalves *et al.*, 2005b). Additionally territoriality often occurs among arboreal termite species (Levings & Adams, 1984; Leponce, 1997; Leponce *et al.*, 1999) and even between termites and other insects. For example tree-nesting ants are able to dislodge mature termite colonies from trees by progressively invading the nests (Leponce *et al.*, 1999). Beyond all such disadvantages, it is on the forest floor that termite's feeding resources are relatively more abundant; a fact that arboreal termites seem not to neglect.

In fact, Termitidae species that inhabit trees, always construct tunnels connecting their arboreal colonies to the ground environment (Noirot, 1970). For instance *Microcerotermes parvus* nests in dead trees and maintains communication with the soil through galleries, though which the workers may reach branches which have fallen onto the floor, or branches in neighboring trees (Noirot, 1970). Also, arboreal termite species are reported to forage both on the ground (Jones *et al.*, 1998; Sousa-Souto *et al.*, 1999), and on tree branches (Jones & Gathorne-Hardy, 1995; Miura & Matsumoto, 1997, 1998).

However, besides the evidences of connection between the tree and the forest floor, the effects exerted by the ground elements on tree exploitation by arboreal termites remain unknown. Thus, supported by (i) the alleged ability of arboreal termites species of foraging on the ground, (ii) the widespread occurrence of canopy-ground connections, and (iii) the large availability of potential resources on the ground coupled with their relative lower availability up on the tree, we pose the hypothesis that tree exploitation by arboreal termites is positively affected by the amount of ground resources below such a tree. We thus tested the prediction that the availability of potential feeding resources for termites (like branches, litter and soil organic matter), on the ground level beneath trees increases the likelihood of the presence of arboreal termites on trees.

4.2 Material & Methods

4.2.1 Study area

The study was carried out in the Rio Doce State Park, Minas Gerais, Southeastern Brazil, between January 15 and February 15 (summer) of 2004. This park is the largest continuous remnant of semideciduous Atlantic rain forest in the state of Minas Gerais (35.976 ha), and is located between $19°48'18"$ - $19°29'24"S$ and $42°38'30"$ - $42°28'18"W$. Its eastern border is defined by the Doce river and its northern boder by the Piracicaba river, while it is also bordered by eucalyptus plantations, pastures and urban areas elsewhere. The 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 a rainy season from October to March and a dry season from April to September. Mean rainfall is 1480 mm/year and the mean annual temperature 21.9° C (Gilhuis, 1986). Vegetation is mainly semideciduous (Lopes, 1998), with a moderate to high percentage (20 to 50%) of deciduous trees (Veloso *et al.*, 1991).

4.2.2 Definition of terms

Hereafter, we refer to "arboreal" as those termites that build earthen galleries on trunks of living trees, such galleries serving as protection for foragers. This is not a trivial definition of such termites, as most authors tend to (implicitly or not) use this term when referring to termites which build their nests on the tree (see Noirot & Darlington, 2000 for a review on the nesting behaviour of termites). However, our data do not allow us to distinguish if the termites were actually inhabiting the particular tree from which they were collected or a neighbour.

Moreover, the "presence" of termites in tunnels, regardless the amount of individuals, was considered indicative that the tree was suitable enough to be used by them.

4.2.3 Sampling design & Data collection

Sampling consisted of the evaluation of 70 trees with at least 15 cm of circumference at breast height (CBH, 1.3 m from the soil). Trees were located in four sites in the Park, known as the Mata do Gambá, Mata do Macuco-Lagoinha, Mata da Tereza and Mata do Vinhático, which represented a comprehensible range of geomorphological traits and forest physionomies in the park. All trees evaluated in this study were at least 50 m distance from the forest edge.

Each tree was evaluated for the presence or absence of termite galleries at 1.30 m from the soil level. We also inspected each gallery to confirm that tunnels were actually being used by termites and to collect these. The termites found therein were collected to identify the termite species. We did not sample galleries built *inside* wood. Termites were kept in 80% alcohol, labeled and identified. 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.

Soil samples were taken beneath each tree, between 0 to 10 cm of depth, and were air-dried and passed through a 0.5 mm sieve. The percentage of total organic carbon (toc) was determined by hot oxidation with potassium dichromate and titration with ammoniac ferrous sulphate, according to Mendonça & Matos (2005). Litter depth (ld) was taken as the mean ground litter thickness from four points that were 20 cm distant from the tree trunk (North, South, East and West; determined with a compass). Length of fallen branches (lfb), was the sum of the linear length of the fallen branches with a minimum circumference of 10 cm, found inside a squared plot of 1 m^2 next to the tree trunk. It was obtained using a measuring tape.

4.2.4 Data Analysis

All analyses were done using R (R Development Core Team, 2008), with generalized linear models (glm), followed by analysis of residuals to check for the suitability of error distribution and for model adjustment. The 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 correponding to a significant interaction term.

The prediction that the availability of resources on the ground level beneath trees increases the likelihood of the presence of arboreal termites on trees, was tested using a model whose binary response variable y took the value 1, 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 (toc), mean ground litter depth (ld) and the sum of the length of fallen branches (lfb) from 1 m^2 area, under the tree. The full model used in those hypotheses tests are therefore:

$$Presence\ of\ termites \quad \sim \quad toc * ld * lfb \tag{7}$$

In the models, an asterisk sign (*) denotes the addition of a variable to the model and a statistical interaction between the variables. Error distribution used was Binomial with logit functions.

4.3 Results

Termites collected belong to the family Termitidae and comprise two subfamilies, two genera, three species (*Microcerotermes strunckii*, *Nasutitermes corniger* and *N. minor*) and one morphospecies (*N.* sp.1). Out of the 70 evaluated trees of 13 families (Table 8), 25 held active galleries, whereas 6 held inactive termite galleries. The remaining trees did not show any sign of termite presence. Termite species never co-occurred in the same tree. Termite nests were directly spotted on 5 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 hypothesis that the amount of ground resources affects arboreal termite occurrence on trees was supported. Termite occurrence is correlated positively with total organic carbon in soil (Table 7, Figure 7). Additionaly according to the final model achieved (Table 7) there is a combination of litter depth and length of fallen branches amounts at which termite occurrence on trees is highest (Figure 8). Thus, arboreal termites are more prone to occur on trees where, on the ground below, termites find high amounts of total organic carbon in soil, and high amounts of litter combined to low quantities of branches.

Table 7: 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 (toc)	1	10.128	0.001
Litter depth (ld)	1	4.837	0.028
Length of fallen branches (lfb)	1	0.059	0.809
Litter depth (ld) : Length of fallen branches (lfb)	1	6.859	0.009
Error	65		
Total	69		

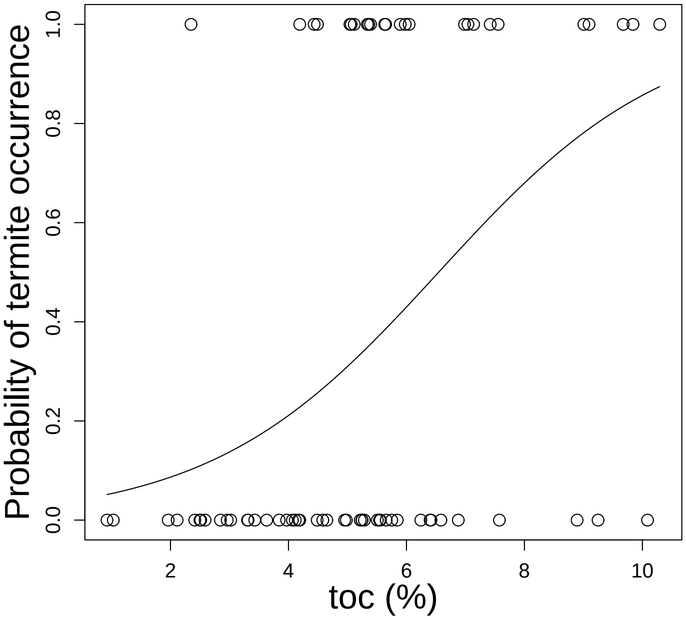

Figure 7: Relationship between (toc) soil total organic carbon (%), and the probability of arboreal termites occurrence in State park of Rio Doce, MG, Brazil, 2004. Using generalized linear modeling with Binomial errors and logit link function. In axis y (right), 0 is the lack of probability of arboreal termites occurrence and 1 is 100% of probability of arboreal termites occurrence. While toc varied in x, (lfb) sum of the length of fallen branches (cm/m^2), (ld) mean of litter depth (cm) were kept in its average. Curves were built according to the main following equation: $\textit{Probability of arboreal termite occurrence} = -6.3143809 + 0.0120037 \cdot lfb + 0.3174563 \cdot ld + 0.5180070 \cdot toc - 0.0013140 \cdot lfb \cdot ld$ transformed by the anti-logit function $\dfrac{e^{equation}}{1 + e^{equation}}$.

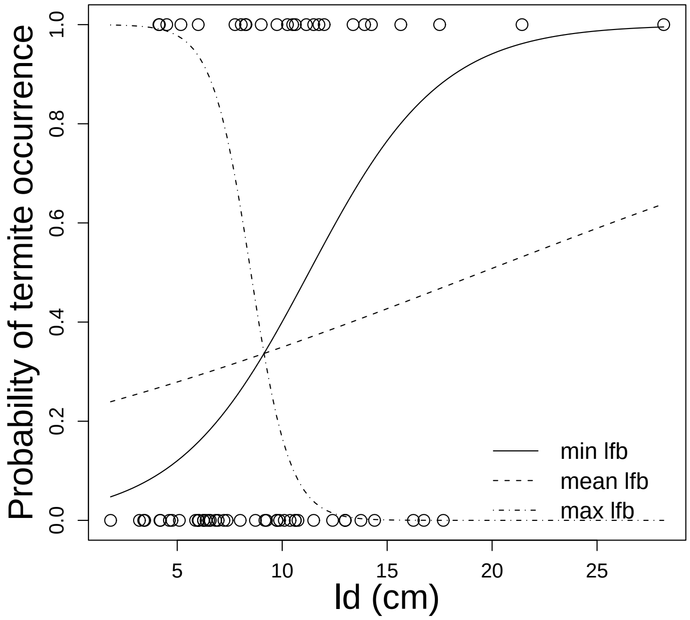

Figure 8: Relationship between (ld) mean of litter depth (cm) and the probability of arboreal termites occurrence in State park of Rio Doce, MG, Brazil, 2004. Using generalized linear modeling with Binomial errors and logit link function. In axis y (right), 0 is the lack of probability of arboreal termites occurrence and 1 is 100% of probability of arboreal termites occurrence. While ld varied in x, curves for min, mean and max of lfb were built. The explanatory variable toc was kept in its average. Curves were built according to the main following equation: $\textit{Probability of arboreal termite occurrence} = -6.3143809 + 0.0120037 \cdot lfb + 0.3174563 \cdot ld + 0.5180070 \cdot toc - 0.0013140 \cdot lfb \cdot ld$ transformed by the anti-logit function $\frac{e^{equation}}{1 + e^{equation}}$.

Table 8: List of arboreal termite species occurence on the evaluated trees species in State Park of Rio Doce, MG, Brazil 2004. The found termite species are *Microcerotermes strunckii*, *Nasutitermes corniger*, *Nasutitermes minor* and a non identified species of the genus *Nasutitermes*.

Plant family	Plant species	*M. strunckii*	*N. corniger*	*N. minor*	*N.* sp. 1
Anacardiaceae	*Astronium grasyolens*		x		
	Spondios dulcis		x		
Anonaceae	*Guatteria* sp. 1				
	Guatteria sp. 2				
	Rollynia sp. 1				
	Rollynia sp. 2				
Bombacaceae	*Pseudobombax* sp. 1		x		
Cecropiaceae	*Pourouma guianensis*				
Chrysobalanaceae	*Licania runthiana*				
Clusiaceae	*Vismia* sp. 1				
Euphorbiaceae	*Aparisthmium cordatum*	x			
	non-identified 1				
Fabaceae	*Anadenanthera colubrina*			x	
	Anadenanthera macrocarpa				
	Balizia sp. 1			x	
	Dalbergia foliolosa			x	
	Dalbergia nigra		x		
	Dalbergia sp. 1				
	Machaerium brasiliense	x	x		
	Machaerium caratinganum				
	Platypodium elegans				
	Sclerobium rugosum	x		x	
	Sclerobium sp. 1	x			
	Zollernia glabra				
	non-identified 1	x			
	non-identified 2				
Flacourtiaceae	*Caesaria arborea*				
	Caesaria sp. 1				
Humiriaceae	*Humiriastrum villosum*			x	
Lauracea	*Nectandra* sp. 1			x	
	Ocotea brachybotrya				
	Ocotea sp. 1				
	Ocotea sp. 2				
Malpighiaceae	*Byrsonima sericera*				x
Meliaceae	*Guarea guidonia*				
	Guarea kunthiana				
	Guarea macrophylla		x		
	Trichilla silvatica		x		
	Trichilla sp. 1				
Moraceae	*Sorocea guilleminiana*				
Myrtaceae	*Myrcia fallax*				
	Psidium sp. 1				
Nyctaginaceae	*Adradaea floribunda*				
Olacaceae	*Tetrastylidium grandifolium*	x			
Rubiaceae	*Amaisua corybosa*				
Sapotaceae	*Chrysophyllum imperiale*		x		
	Pouteria torta				
	Pouteria sp. 1				
Violaceae	*Rinorea guianensis*				
non-identified 3					
non-identified 4					

4.4 Discussion

Termite occurrence on trees was correlated positively with carbon in soil and there was a combination such that occurrence highest at high amounts of leaf litter and low amounts of branches. This is in accord with our hypothesis, and such a result sets –by experimental evidence– previous suspected links between arboreal termites and the ground environment. That is, the ground components under trees seem not to be ignored by arboreal termites and seem to be determinant for tree exploitation by such insects.

Whether or not this correlation reveals a strict dependence of arboreal termites on the tree's substrate is open to discussion. On the one hand, if termites sampled here were inhabiting the tree, they could use the galleries as downward ducts to (i) collect ground resources or (ii) to search for resources up on another tree. On the other hand, if these termites were not inhabiting the tree where they were collected, the galleries could function as upward conduits for foragers aiming for resources located up that particular tree. Strictly speaking, this last option is the same as item (ii) above, but predicts the settlement of the colony on a tree different from the one where the samples have been taken.

Our data do not allow to distinguish whether or not termites were actually inhabiting the tree from which they were collected. Hence, we cannot state categorically that the foragers found within the galleries on the tree bark aimed to climb down or up the tree. One could think that the correlation we found between termites and ground resources would rule out the possibility that termites where climbing up the tree. However, as we shall see below, ground resource traits may modulate any of these alternatives.

Let us consider the hypothesis that arboreal termites were using their galleries downwardly. If this is so, they could either be looking for food or building materials not available on the tree. Interestingly enough, the genera studied here (*Microcerotermes* and *Nasutitermes*) are said to rely largely on wood as both, food (Donovan *et al.*, 2001) and building material (Weesner, 1960; Constantino, 1999; Noirot & Darlington, 2000), and wooden items are not scarce on a tree. Accordingly, negative correlation was found between termites and high amounts of *length of fallen branches*, which amongst the resource studied *length of fallen branches* is the one closest to wood. Hence this correlation may implicate that termites are not searching for feeding or building wooden resources below the tree.

Conversely, *leaf litter depth* and *total carbon in soil* correlate positively with the proneness of termite occurrence on the tree, and this coincidence does not seem accidental, as leaf litter is the main source of soil carbon. Considering the xylophagous habit commented above, one could readily dismiss such a correlation as indicative of foraging. We warn, however, that this could be a hasty conclusion. Despite largely dependent on wooden food, *Microcerotermes* and *Nasutitermes* belong to a guild whose members may feed even on highly humified substrates (Donovan *et al.*, 2001). Soil organic matter (of which total carbon stands as a suitable surrogate) would not seem, therefore, too unlikely to be taken as food by termites from this group. Moreover, the soil organic matter's low carbon-to-nitrogen ratio (C/N) resembles more the ratio found in termites' body, than the C/N ratio of vegetable tissues. It is tempting to suggest that a not-so-strict xylophagous termite could rely on such a resource as a supplementary diet. Of course, these are highly conjectural ideas that would need further research before any formal statement is put forward.

In summary, if arboreal termites use their galleries to climb down the tree, they do not appear to do so in search of the wood accumulated below such a tree. Our results allow suspictions that such a move downwards would aim for supplementary diet in the form of soil organic matter.

An alternative hypothesis is that arboreal termites were using their galleries to climb up the tree, foraging for regular food items or other specific and nutritional richer food items, such as micro-epiphytes and lichens (Jones & Gathorne-Hardy, 1995; Miura & Matsumoto, 1997, 1998). Indeed, this is a plausible explanation as we directly spotted termite nests only on five trees of the 25 housing active galleries, which suggests that the evaluated trees were exploiting areas rather than nesting sites. This seems to agree with Roisin *et al.* (2006) who stated that the two genera of arboreal termite studied here are long-distance foragers: they could live on a tree and forage on another one. Soil carbon would then be used by termites as a surrogate of tree's quality, because richer soils would allegedly sustain larger trees, and those would accumulate more lichens on their trunks as well as more epiphytes and litter on their forks (Gonçalves *et al.*, 2005a).

Concluding, despite not allowing to distinguish whether arboreal termites build galleries to climb down or up the tree, our study shows that ground elements do affect termite occurrence on trees. Termites use such elements either directly as source of supplementary diet or as a surrogate of the suitability of the tree as a foraging site.

Acknowledgements

This paper has been produced within the Field Course on Canopy Ecology (FCO-CGP 2004), with financial support from PROFIX/CNPq (# 540552/2001-1), PELD/CNPq (# 520026/98-8), British Embassy, and FAPEMIG (# CRA 1041/04).TTG was supported by a CAPES PhD studentship and ODS is supported by Brazilian National Council (CNPq, Fellowship #306 081/2007-5, research support 485460/2007-6) and by FAPEMIG (APQ-4627-5.03/07). RRJ was supported by a Post-doctoral grant from FAPEMIG (# CRA 00083/04). We are indebted to the Administration of the Rio Doce State Park/IEF; to the field crew, F.S. Neves, J.P. Soares, R.I.Campos, R.F. Ferreira and W.D. da Rocha; and to the Rio Doce State Park climbers, Canela and Rogério; for optimizing the whole sample process. Special thanks to Duca for all the help. Thanks to the lab of Soil Organic

Matter and Residues/UFV for the structural support. We thank very much to Prof. Reginaldo Constantino for confirmation on the termite identification and to Glauco and F. S. Araújo for plant identification. Thanks very much to M. M Lima and S. L. Elliot, whose critical comments significantly improved the manuscript. This is contribution # nnn from the Termitology Lab (http://www.isoptera.ufv.br), at Federal University of Viçosa, Brasil (UFV). This paper is part of TTG's PhD thesis presented to UFV. This paper has been entirely produced using Free Software (Linux, LaTeX, Kile, Xemacs, R).

5 A novel exocrine structure of the bicellular unit type in the thorax of termites[3]

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[3] Artigo publicado no periódico Acta Zoologica (Stockholm), vol. 89

A novel exocrine structure of the bicellular unit type in the thorax of termites

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Abstract

Studying the thorax of some Termitidae species, we found two pairs of hitherto unknown lateral glands in the meso- and metathorax of both workers and soldiers, that we here describe. The glands consist of distinct clusters of class 3 secretory cells accompanied by their duct cells, located in the upper lateral portion of the thoracic wall. Ultrastructural observations reveal numerous mitochondria, a well developed Golgi apparatus and vesicular smooth endoplasmic reticulum, indicating a cytoplasm in intensive metabolic activity. The gland is reported to occur in *Microcerotermes strunckii*, *Cornitermes cumulans*, and *Nasutitermes minor*, three species comprising an interesting morpho-behavioural gradient, respectively, from only mechanical, to mechanical-chemical, to only chemical defense system. The extent of such a gradient allows speculations that this gland would be related to the general needs of termites, rather than some specificities of a single group. We warn, however, that complementary studies are needed, before any conclusions are drawn on this matter.

Keywords: Exocrine glands, Cornitermes, Microcerotermes, Nasutitermes, ultrastructure

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5.1 Introduction

The fascinating life of social insects has since long attracted the attention of man. One of the characteristics of these insects is the amazing development of their exocrine system, the secretions of which play an essential role in many aspects of social life (Billen, 2006). Among the social insects, however, it is surprising to see the relatively limited number of exocrine glands that have been described in termites, compared to the considerably higher variety of the exocrine system in the social Hymenoptera. Termites can have a total of 17 glands (Table 9), while approx. 70 glands form the overall exocrine repertoire of ants. A possible reason for this may be found in differences in the communication system between both groups, where social Hymenoptera to a very considerable extent rely on pheromonal substances (and hence possess the glandular equipment for producing these (Billen & Morgan, 1998), while in termites acoustical signals can play an important role (Kirchner *et al.*, 1994; Röhrig *et al.*, 1999; Evans *et al.*, 2007). The lower number of exocrine glands in the termites definitely is not due to an eventual lack of attention, as several termitologists have produced extensive and thorough studies on the isopteran exocrine apparatus (e.g. Pasteels, 1965; Noirot, 1970; Noirot & Quennedey, 1974, 1991; Deligne *et al.*, 1981; Leis & Sbrenna, 1983; Sbrenna & Leis, 1983; Costa-Leonardo & DeSalvo, 1987; Soares & Costa-Leonardo, 2002; Costa-Leonardo, 1994, 2004; Sobotnik *et al.*, 2003; Quennedey, 1984, 1998; Quennedey *et al.*, 2004, 2008). Finding novel glands in termites therefore does not happen frequently. Studying the thorax of some Termitidae species, however, we found two pairs of hitherto unknown lateral glands in the meso- and metathorax of both workers and soldiers, that we here describe as a 17^th exocrine structure of termites.

Table 9: Survey of the known exocrine glands of termites, listed from head to abdomen, with indication of the cellular organization according to the classification of Noirot and Quennedey (1974), and corresponding references. For the dehiscent gland, no precise information about its class allocation is available.

	Gland	Class	References
1	Epidermal tegumental glands	1	Sobotnik *et al.*, 2003
2	Bicellular unit tegumental glands	3	Leis & Sbrenna, 1983; Sbrenna & Leis, 1983; Sobotnik *et al.*, 2003
3	Frontal gland	1,3	Noirot, 1969; Deligne *et al.*, 1981; Costa-Leonardo & DeSalvo, 1987
4	Labral gland	3	Mao & Henderson, 2006
5	Cibarial gland	1	Quennedey, 1984
6	Mandibular base gland	3	Quennedey, 1984
7	Mandibular gland	3	Noirot, 1969
8	Labial (salivary) gland	1	Pasteels, 1965; Noirot, 1969
9	Tarsomere glands	3	Bacchus, 1979; Soares & Costa-Leonardo, 2002
10	Tibial gland	3	Bacchus, 1979; Soares & Costa-Leonardo, 2002
11	**Lateral thoracic glands**	**3**	**this article**
12	Dehiscent gland	?	Costa-Leonardo, 2004
13	Tergal glands	1,2,3	Noirot, 1969; Wall, 1969; Quennedey, 1975; Ampion & Quennedey, 1981; Bordereau *et al.*, 2002
14	Sternal glands	1,2,3	Pasteels, 1965; Noirot, 1969; Quennedey, 1975; Quennedey *et al.*, 2008
15	Posterior sternal glands	3	Quennedey *et al.*, 2004, 2008
16	Spermathecal gland	3	Costa-Leonardo & Patricio, 2005; Raina *et al.*, 2007
17	Pleural abdominal glands	3	Ampion, 1980

5.2 Material & Methods

The termite species here investigated are *Cornitermes cumulans* (Kollar), *Microcerotermes strunckii* (Sörensen) and *Nasutitermes minor* (Holmgren). *M. strunckii* specimens were collected in Sete Lagoas, MG, Brazil; *C. cumulans* and *N. minor* specimens were collected in Viçosa, MG, Brazil. Head-thorax and thorax portions of workers specimens of the three species were fixed in cold 2% glutaraldehyde, buffered at pH 7.3 with 50 mM Na-cacodylate and 150 mM saccharose. Also the thorax of M. strunckii and N. minor soldiers was studied. Postfixation was done in 2% osmium tetroxide in the same buffer, followed by dehydration in a graded acetone series. Tissues were embedded in Araldite and sectioned with a Reichert OmU2 microtome. Semithin sections of 1 μm were stained with methylene blue and thionin and viewed in an Olympus BX-51 microscope. Double stained thin sections of 70 nm were examined in a Zeiss EM900 electron microscope. Workers and soldiers of M. strunckii were also prepared for scanning microscopy, the individuals were critical point dried using a CPD 030 instrument. The dried samples were mounted on aluminium stubs using Leit-C and coated with gold with a SPI-ModuleTM Sputter Coater. Images were obtained with a Jeol JSM-6360.

5.3 Results

Semithin transversal sections through the thorax of both workers and soldiers of *M. strunckii* and *N. minor* and of *C. cumulans* workers show an obvious paired glandular structure, located in the upper lateral portion of both the meso- and metathorax, just below the meso- and metanotum, respectively (Fig. 9A).

Each of these four novel lateral thoracic glands consists of a distinct cluster with an estimated number of approx. 100 glandular units. Among the studied species, the size of the gland varies in the meso- and metathorax. The thickness in the mesothorax varies from 15-40 μm for *M. strunckii*, it measures approx. 20 μm in *N. minor* and approx. 35 μm in *C. cumulans*. In the metathorax, the thickness varies from 10-30 μm for *M. strunckii*, from 10-25 μm for *N. minor* and is approx. 20 μm for *C. cumulans*. The width (in dorsoventral direction) in the mesothorax ranges from 80-120 μm for *M. strunckii*, from 35-60 μm for *N. minor* and is approx. 80 μm for *C. cumulans*. In the metathorax, the width varies from 100-140 μm for *M. strunckii*, from 85-140 μm for *N. minor* and is approx. 200 μm for *C. cumulans*. The length (in anterior/posterior direction) for *M. strunckii* ranges from 180-190 μm in the mesothorax and from 100-200 μm in the metathorax.

Scanning electron microscopy (Fig. 9B,C) of workers and soldiers of *M. strunckii* revealed the presence of numerous pores with a diameter of approx. 0.5 μm, that occur on the entire surface of the lateral region of the thorax. Most pores occur on top of a small nipple-like elevation (Fig. 9C). Additionally, scanning microscopy revealed the presence of hairs associated with the cuticle covering the gland region (Fig. 9C).

At the cell level, the gland is formed by bicellular units according to class 3 in the standard classification of Noirot & Quennedey (1974). A transverse section of a lateral thoracic gland shows between 5 and 10 secretory cells (Fig. 10A). They have a diameter of approx. 10 μm and are characterized by rather pale and rounded nuclei with a diameter of approx. 5 μm. In between the secretory cells are duct cells, that contain a dark and more irregularly shaped nucleus that occupies nearly the entire duct cell volume (Fig. 10A). The secretory cell contains an end apparatus with a central cuticular duct, surrounded by irregular microvilli (Fig. 10B). In the cytoplasm surrounding the end apparatus, we find numerous mitochondria, a well developed Golgi apparatus and vesicular smooth endoplasmic reticulum (Fig. 10C). The cuticular ducts have a diameter of approx. 0.5 μm, that generally open as pores in the centre of the nipple-like elevations through the outer thoracic tegument (Fig. 10D,E).

The basic cell arrangement of both glands pairs does not differ among the studied species, neither between workers and soldiers. However, in all species, the metathoracic cell clusters present a more linear shape when compared to the mesothoracic glandular region, which is more ellipsoid in shape.

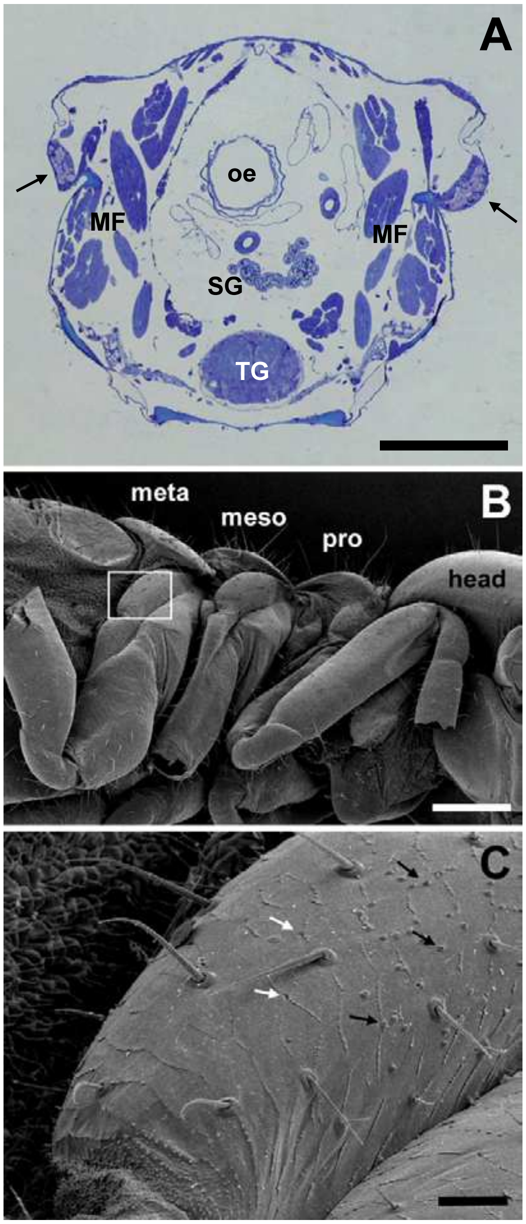

Figure 9: A. Transverse semithin section through the mesothorax of a *M. strunckii* worker showing the position of the lateral thoracic glands (arrows). Scale bar 100 μm. MF: muscle fibres; oe: oesophagus; SG: salivary gland; TG: mesothoracic ganglion. B. Scanning electron micrograph of the thorax of a *M. strunckii* worker, frame indicates position of lateral metathoracic gland. Scale bar 200 μm. C. SEM detail of Fig. 9B, showing pores and hairs in the region of the metathoracic lateral gland of a *M. strunckii* worker. Some pores open through the flat cuticle (white arrows), but the majority open through the centre of the nipple-like elevations (black arrows). Scale bar 20 μm.

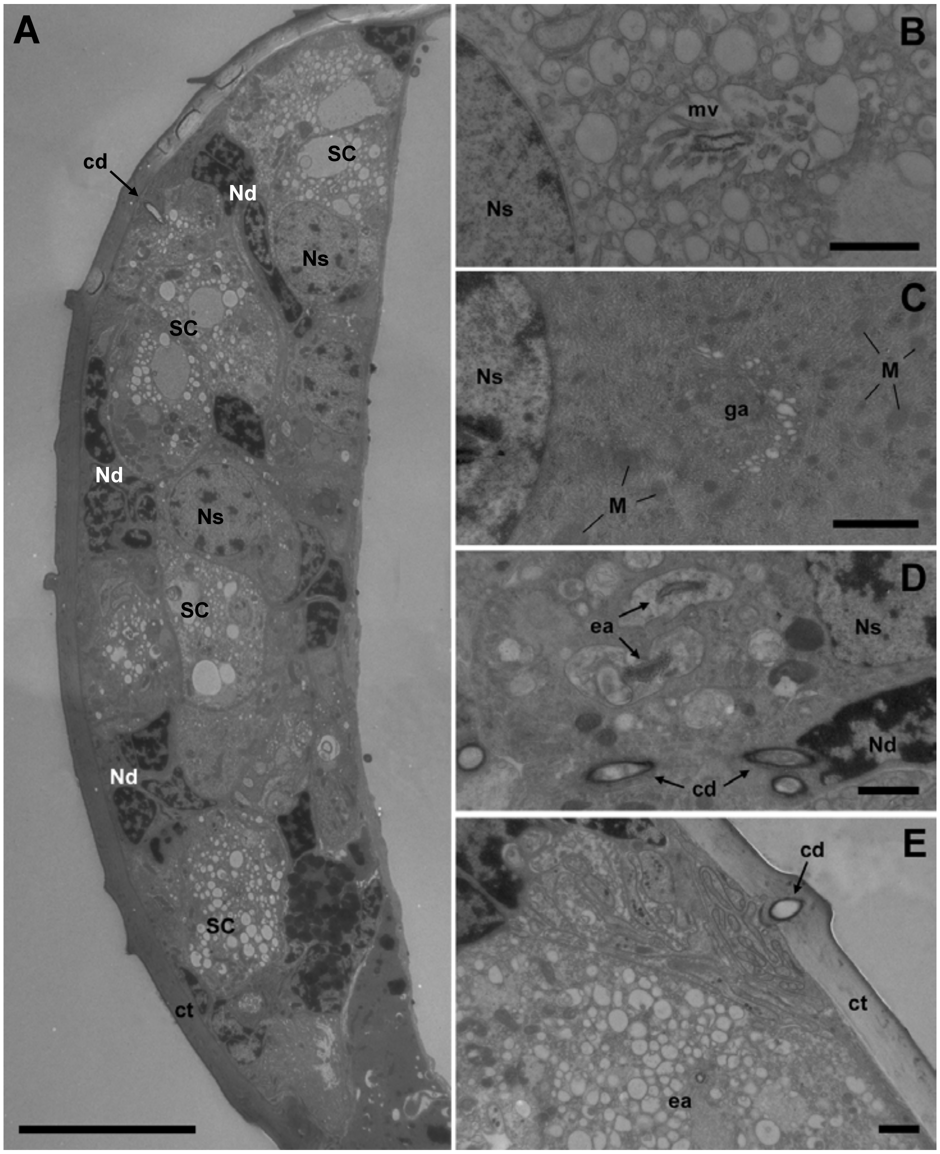

Figure 10: A. Electron micrograph showing a transverse section through the mesothoracic lateral gland of a *M. strunckii* worker, showing densely packed secretory cells (SC) and duct cells. Scale bar 10 μm. B. Electron micrograph of end apparatus in mesothorax of *M. strunckii* soldier. Scale bar 1 μm. C. Detail of cytoplasm in metathoracic gland cell of *C. cumulans* worker with Golgi apparatus (ga) and densely packed smooth endoplasmic reticulum. Scale bar 1 μm. D. View of duct cells in metathorax of *M. strunckii* worker. Scale bar 1 μm. E. Opening of duct cell on top of nipple-like elevation through tegumental cuticle in metathorax of *M. strunckii* worker. Scale bar 1 μm. cd: cuticular duct, ct: cuticle, ea: end apparatus, M: mitochondria; mv: microvilli, Nd: nucleus of duct cell, Ns: nucleus of secretory cell.

5.4 Discussion

The paired lateral glands in the meso- and metathorax of the termite species studied in this article represent hitherto unknown exocrine structures for this insect group (Table 9). In 1993, Costa-Leonardo already described mainly dorsally occurring oenocyte clusters in the three thoracic as well as the various abdominal segments of soldiers of *Cornitermes cumulans*. Their clustered appearance much resembles that of the meso- and metathoracic lateral glands we here report, but the cellular organization is different. The general structural organization of the glands now described clearly corresponds with class 3 (Noirot & Quennedey, 1974), with bicellular units each comprising a secretory cell and its accompanying duct cell. Secretroy cells of this class 3 display the very characteristic end apparatus (which is a cuticular continuation of the duct cell, surrounded by a microvillar sheath), but which does not occur in oenocytes. In their 1991 paper, Noirot & Quennedey updated their 1974 pioneer paper by considering the oenocytes homologous with class 2 epidermal glands. The oenocyte clusters reported by Costa-Leonardo (1993) in *C. cumulans* soldiers therefore may be similar to the glands we presently describe, but their assignment as class 3 exocrine glands seems to have been overlooked.

If the legs are not taken into account (Billen, 2008), exocrine glands in the thorax of social insects are less numerous than in the head and abdomen. The salivary (= labial) gland in the prothorax is a common structure for all social insects, while the metapleural gland in the mesothorax is found in ants only (Hölldobler & Engel-Siegel, 1984). In ants of the genus *Diacamma*, a peculiar gland occurs inside the gemmae (Peeters & Billen, 1991), that appear as vestigial wing buds of the mesothorax (Baratte *et al.*, 2006). These gemmae, however, are structurally very different from the region of the thoracic lateral glands in termites.

Tegumental glands of the bicellular unit type (class 3 following Noirot & Quennedey, 1974) with a scattered distribution over the body are known for ants (Gobin *et al.*, 2003) and bees (Guerino & de Oliveira, 2002), and have also been reported for termites (Leis & Sbrenna, 1983; Sbrenna & Leis, 1983). In *Kalotermes flavicollis*, they occur in the head, thorax and abdomen as scattered single units or in groups of two or three (Sbrenna & Leis, 1983), but without a specific distribution pattern (Leis & Sbrenna, 1983). This is in contrast with the two pairs of lateral thoracic glands that we describe here, as these represent very distinct clusters of class 3 glandular units, rather than clustered oenocytes (= class 2) as reported by (Costa-Leonardo, 1993). The two pairs of this novel gland have the same structural appearance, and are also similar in workers and soldiers. With a well developed smooth endoplasmic reticulum and Golgi apparatus, the general ultrastructural organization of these novel lateral thoracic glands is in line with that of the tegumental glands in *Kalotermes flavicollis* (Sbrenna & Leis, 1983) and with the subepithelial gland in ants (Gobin *et al.*, 2003). This cytoplasmic composition of the secretory cells is indicative for a non-proteinaceous secretion.

The function of the lateral thoracic glands as yet remains unknown, although the non-proteinaceous nature of the secretion may correspond with a pheromonal role. Termites do not rely as extensively on chemical communication as ants do. However, chemical communication in termites is also essential for the maintenance of their social life (Costa Leonardo, 2006), including several aspects such as nestmate recognition (Marins & DeSouza, 2008), defence (Deligne *et al.*, 1981; Quennedey, 1984) and recruitment and resource exploitation (Reinhard *et al.*, 1997; Reinhard & Kaib, 2001). The presence of hairs and sensillae associated with the cuticle in the gland region may support that the secretion produced by the lateral thoracic glands is involved in chemical communication, as these also has been reported to be associated with other termite glands involved in chemical communication, as the sternal gland (Costa Leonardo, 2006).

Alternatively, the non-proteinaceous secretions from these glands could contribute to the chemical profile of the cuticular surface, and hence play an important role in nestmate recognition. In fact, nestmate recognition supposedly through body-to-body contact (and hence sharing cuticular hydrocarbons), has been hypothesized to be the key for the survival of grouped individuals of *Cornitermes cumulans* (DeSouza *et al.*, 2001) and *Nasutitermes aquilinus* (Miramontes & DeSouza, 1996), a species and a genus reported here to possess these thoracic glands. However, a complementary study of the thoracic glands' function is needed for any further conclusions. Finally, it is worth noting that such glands are reported here for genera representing two very diverse subfamilies (Termitinae and Nasutitermitinae) inside the Neotropical Termitidae. Moreover, the three genera studied here comprise an interesting morphological gradient, from only mechanical (*Microcerotermes*), to a mixed chemical-mechanical (*Cornitermes*), and finally only chemical (*Nasutitermes*) defense apparatus. The extent of these diverse taxonomical and morpho-behavioural realms may indicate that such a gland is widespread in termites and that it would have a function related to the general needs of termites as a whole, rather than some function specific of a single group.

Acknowledgements

We are very grateful to An Vandoren for her skillful assistance in making sections for electron microscopy and to Alex Vrijdaghs for his help in scanning microscopy. We are also thankful to Alessandra Marins, Daniela Faria Florencio and Nithin Mathews for all their help. TTG was supported by a CAPES PhD studentship and ODS by a CNPq Fellowship (#306 081/2007-5). This research was supported through grant G.0699.08 from the Flemish Fund for Scientific Research and CAPES/PDEE (BEX 5151/06-6). This is contribution N° 39 of the Lab of Termitology (http://www.isoptera.ufv.br).

6 Conclusão Geral

Resumindo os resultados mostram que:

1. Grupos de espécies de cupins que apresentam habilidades defensivas distintas respondem diferentemente à disponibilidade de recursos e ao risco de predação.
2. A estrutura da casca de árvores é um fator limitante para a exploração das mesmas por cupins que sobem em árvores.
3. Cupins se estabelecem preferencialmente em árvores que estejam em locais com maior disponibilidade de recurso, disposto no solo adjacente às mesmas.

Assim conclui-se que a exploração de recursos por cupins, sejam eles de solo ou arborícolas, baseia-se em decisões de utilização de um habitat ou recurso. E essas decisões dependem do balanço entre riscos e benefícios locais ou seja da disponibilidade de alimento, do risco ambiental relativo de exploração do recurso, e de limitaçãoes estruturais para acessibilidade dos recursos.

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