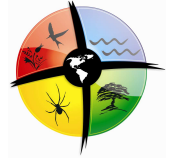




UNIVERSIDADE FEDERAL DE UBERLÂNDIA
INSTITUTO DE BIOLOGIA
PROGRAMA DE PÓS GRADUAÇÃO EM ECOLOGIA E
CONSERVAÇÃO DE RECURSOS NATURAIS



**ECOLOGIA DAS INTERAÇÕES ENTRE ARANHAS,
FORMIGAS E *Qualea multiflora* (VOCHYSIACEAE) NO
CERRADO: DIVERSIDADE E ABUNDÂNCIA DE
PREDADORES E SEUS IMPACTOS SOBRE HERBÍVOROS E
HERBIVORIA**

LARISSA NAHAS DOMINGUES

2011

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HERBIVORIA**

Dissertação apresentada à Universidade Federal de Uberlândia, como parte das exigências para obtenção do título de Mestre em Ecologia e Conservação de Recursos Naturais.

Orientador:

Prof. Dr. Kleber Del Claro

Coorientador:

Prof. Dr. Marcelo de Oliveira Gonzaga

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*Dedico este trabalho aos meus pais
Paulo Henrique e Anice, ao meu
irmão Paulo Júnior e ao meu
namorado Leonardo.*

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RESUMO

Domingues, Larissa Nahas. 2011. Ecologia das interações entre aranhas, formigas e *Qualea multiflora* (Vochysiaceae) no cerrado: diversidade e abundância de predadores e seus impactos sobre herbívoros e herbivoria. Dissertação de mestrado em Ecologia e Conservação de Recursos Naturais. UFU. Uberlândia-MG. 41p.

Aranhas e formigas estão entre os principais predadores de herbívoros em cadeias tróficas terrestres, podendo indiretamente beneficiar plantas. Várias espécies de plantas oferecem recursos alimentares e/ou abrigo para predadores e recebem proteção contra seus inimigos naturais, os herbívoros. O néctar extrafloral é um recurso alimentar líquido comumente encontrado em plantas do cerrado e atrai formigas e outros artrópodes, como aranhas por exemplo. No entanto, interações entre predadores, como competição e predação intraguilda podem influenciar sua capacidade de reduzir herbívoros e assim afetar o resultado final das interações com plantas. O presente estudo objetivou verificar se a presença ou ausência de predadores, como formigas e aranhas, afeta as taxas de herbivoria e o fitness de *Qualea multiflora* (Vochysiaceae), uma espécie arbórea comumente encontrada no cerrado e que possui nectários extraflorais pares na base do pecíolo e no pedúnculo dos botões. Verificou-se se há diferença nos efeitos desses dois grupos de predadores agindo em conjunto ou separadamente. Os experimentos de campo foram conduzidos em uma área de cerrado em Uberlândia, MG, no período de agosto de 2009 a maio de 2010. Em agosto de 2009, 60 indivíduos de *Q. multiflora*, similares e no mesmo estado fenológico, foram marcados e divididos por sorteio em quatro grupos de 15 indivíduos, sendo: *Controle* (plantas com livre acesso às aranhas e formigas); *Exclusão* (aranhas e formigas foram removidas das plantas); *Formigas* (somente aranhas foram removidas) e *Aranhas* (somente formigas foram removidas). Formigas foram excluídas por meio da aplicação de uma resina atóxica no caule das plantas (Tanglefoot) e aranhas foram excluídas manualmente a cada três dias. Todas as plantas foram inspecionadas três vezes ao mês durante todo o período de estudo, registrando a riqueza e abundância de herbívoros, formigas e aranhas. Uma vez ao mês eram registrados a porcentagem de área foliar perdida por herbivoria e ação de fungos e o número de galhas. Para avaliar o impacto dos predadores sobre a reprodução de *Q. multiflora*, foram contados os números de botões, frutos e sementes potencialmente viáveis produzidos por cada planta. No último mês dos experimentos os frutos foram coletados, medidos e pesados. Os resultados mostraram que a exclusão de um ou ambos os predadores causou um aumento na riqueza e abundância de herbívoros e na porcentagem de herbivoria das plantas. Houve sazonalidade evidente na abundância de formigas, aranhas e herbívoros. Foram observadas 21 espécies de formigas e 43 espécies de aranhas forrageando nas plantas durante o período de estudo. Houve maior riqueza e abundância de aranhas em plantas nas quais as formigas foram excluídas comparadas com as que as formigas estavam presentes. A riqueza e abundância de formigas não diferiram, entretanto, dependendo da presença ou ausência de aranhas. Não houve diferença entre número de botões, frutos e sementes produzidas, nem no comprimento e tamanho dos frutos entre os quatro grupos de plantas. Este estudo mostra a importância de se considerar os efeitos de todos os predadores e não somente de um grupo específico para avaliar proteção em plantas com nectários extraflorais.

Palavras-chave: nectários extraflorais; predadores; herbívoros; cerrado; relações mutualísticas.

ABSTRACT

Domingues, Larissa Nahas. 2011. Ecology of interactions among spiders, ants and *Qualea multiflora* (Vochysiaceae) in cerrado: diversity and abundance of predators and their impact on herbivores and herbivory. MSc.thesis. UFU. Uberlândia-MG. 41p.

Spiders and ants are among the main predators of herbivores in terrestrial trophic chains, and can indirectly benefit plants. Several plant species offer feeding resources and/or shelter to predators which provide protection against their natural enemies. The extrafloral nectar is a liquid feeding resource common in cerrado plants that attract ants and other arthropods, such as spiders for example. However, interactions between predators such as intraguild competition and predation can influence their ability to reduce herbivores and affect the final results of interactions with plants. The present study aimed to determine the impact of the spiders and ants' fauna on herbivory and reproduction of *Qualea multiflora* (Vochysiaceae), a tree specie common in cerrado bearing paired extrafloral nectaries on the stem next to the insertion of the leaves, and on the bud pedicels. It was verified if there is difference in the effects of these two groups of predators when act jointly or separately. The field experiments were conducted in a cerrado area in Uberlandia, MG, between August 2009 and May 2010. In August 2009, 60 individuals of *Q. multiflora*, similar and in the same phenological state, were tagged and raffled off in four groups of 15 individuals: *Control* (plants with free access to spiders and ants); *Exclusion* (spiders and ants were removed from the plants); *Ants* (only spiders were removed) and *Spiders* (only ants were removed). Ants were excluded by covering the trunk with a lay of sticky resin (Tanglefoot) and spiders were excluded manually every three days. All plants were inspected three times per month from August 2009 to May 2010. In each inspection were registered the richness and abundance of herbivores, ants and spiders. Leaf area loss due to herbivory and action of mould, and gall infestation were registered monthly. To assess the predators impact on reproduction of *Q. multiflora* were counted the number of floral buds, fruits and potentially viable seeds produced by each plant. In the last month of experiments, all fruits were collected, measured and weighted. The results showed that the removal of one or both types of predators resulted in a significant increase in richness and abundance of herbivores and herbivory level in plants. There was evident seasonality in abundance of ants, spiders and herbivores. It were observed 21 ant species and 43 spider species foraging in the plants during the study. There was a higher richness and abundance of spiders in plants without ants. The richness and abundance of ants did not differ depending on the presence or absence of spiders. There was not difference in number of buds, fruits and seeds produced, or in the length and weight of fruits among the four treatments. This study shows the importance of consider the effects of all predators and not only a specific group to assess protection in extrafloral nectary-bearing plants.

1. INTRODUÇÃO GERAL

Interações entre formigas e plantas

As formigas estão entre os insetos mais abundantes nos ambientes terrestres (Rico-Gray & Oliveira 2007). Estima-se que possam representar de 10 a 15% da biomassa animal em muitos ecossistemas (Beattie & Hughes 2002). Dessa forma, ocupam uma variedade de nichos ecológicos e posição chave nas cadeias tróficas, por interagir com uma série de organismos (Leal 2005). Na maioria dos ambientes terrestres, estão entre os principais predadores de outros insetos e pequenos invertebrados (Hölldobler & Wilson 1990; Floren *et al.* 2002). Forrageiam extensamente na vegetação (Oliveira & Freitas 2004) e muitos taxa mantém relações mutualísticas obrigatórias ou facultativas com diversas espécies de angiospermas (Oliveira & Pie 1998).

Algumas plantas mantêm relações íntimas e específicas com formigas, possuindo estruturas especializadas para sua nidificação (domáceas) e sendo, portanto, habitadas por colônias durante a maior parte de sua vida. Tais plantas são chamadas mirmecófitas (Webber *et al.* 2007) e podem oferecer além das domáceas, outros recursos, como néctar extrafloral e corpúsculos alimentares (Heil & Mckey 2003). Um exemplo clássico deste tipo de relação é a estabelecida entre formigas do gênero *Pseudomyrmex* e plantas do gênero *Acacia*. As formigas nidificam em cavidades pré-existentes nos espinhos dessas plantas, recebendo, portanto, refúgio, além de recursos alimentares oferecidos pela planta hospedeira, como néctar foliar e corpúsculos de Beltian. Com o constante patrulhamento das formigas, as plantas ganham proteção contra a ação de insetos fitófagos (Janzen 1966). Outro exemplo de mirmecófito é *Tococa guianensis* (Melastomataceae), uma espécie comumente encontrada em matas ciliares e de galeria, que possui domáceas localizadas na base foliar ou entre a folha e o pecíolo. Moraes (2006) demonstrou que na ausência de formigas obrigatórias, essas plantas apresentam maiores índices de herbivoria. Nos biomas tropicais, interações entre formigas e mirmecófitas são comuns (Hölldobler & Wilson 1990). Por exemplo, na região amazônica são conhecidas cerca de 230 espécies de mirmecófitas (Benson 1985). Além de fornecer proteção contra herbívoros, formigas podem beneficiar suas hospedeiras pela grande quantidade de detritos (exúvia, larvas e operárias mortas, restos de presas) deixados no interior das domáceas. As plantas frequentemente possuem adaptações específicas para absorção de nutrientes a partir destes detritos (Treseder *et al.* 1995).

Embora haja vários exemplos de mirmecófitas, na maioria das plantas, os mutualismos são mediados somente pelo fornecimento de recompensas alimentares a várias espécies de formigas que nidificam em outros lugares que não a própria planta (Koptur 1992). Tais

plantas, chamadas mirmecófilas, atraem formigas principalmente com produção de néctar extrafloral ou indiretamente através de hemípteros produtores de honeydew, e ganham proteção de uma facultativa e oportunista comunidade de formigas (Rosumek *et al.* 2009). Uma vez que os custos das associações formiga-hemíptero podem ou não ser compensados pelos benefícios que estas formigas conferem às plantas repelindo outros herbívoros, as associações formiga-planta mediadas por hemípteros são extremamente facultativas, oportunistas e variáveis (Rico-Gray & Oliveira 2007). Em geral, as associações formiga-planta baseadas em néctar extrafloral tendem a ser mais generalizadas enquanto as envolvendo domáceas e corpúsculos alimentares tendem a ser mais especializadas (Rico-Gray & Oliveira 2007). Isso ocorre porque o néctar extrafloral é uma fonte alimentar que atrai alta diversidade de taxa (Oliveira & Brandão 1991).

O néctar extrafloral é secretado por glândulas especializadas, os nectários extraflorais (NEFs), que não estão associadas diretamente com a polinização (Bentley 1977). Essa substância pode conter açúcares, aminoácidos, proteínas, lipídeos e outros compostos orgânicos (Oliveira & Pie 1998). Comparado ao néctar floral, frequentemente apresenta maior concentração de açúcar (Wäckers 2005). Plantas com nectários extraflorais são diversas e abundantes em vários biomas (Heil & Mckey 2003) e atraem grande diversidade de formigas (Oliveira & Brandão 1991), as quais podem ter seu valor adaptativo aumentado com o consumo de néctar (Byk & Del-Claro 2010). Muitos estudos têm demonstrado que formigas visitantes destes nectários promovem redução na herbivoria e aumento do sucesso reprodutivo das plantas (e.g. Koptur 1979, 1984; Ferreira 1993; Del-Claro *et al.* 1996; Oliveira 1997; Oliveira *et al.* 1999). Outros estudos, no entanto, não detectaram tal efeito (e.g. O'Dowd & Catchpole 1983; Rashbrook *et al.* 1992; Mody & Linsenmair 2004). Tais exemplos podem constituir exceções ou simplesmente refletir a grande variação temporal e espacial prevista para mutualismos de proteção oportunísticos (Heil & Mckey 2003).

Os resultados das associações entre formigas e plantas mediadas por nectários extraflorais podem variar, por exemplo, de acordo com o tipo de habitat (e.g. Cogni *et al.* 2003), identidade das formigas associadas (Horvitz & Schemske 1984) e suscetibilidade dos herbívoros à predação por formigas (Oliveira & Pie 1998). Condições abióticas influenciam pressão de herbivoria, taxas de visitação de formigas ou ambos (de la Fuente & Marquis 1999; Wirth & Leal 2001), determinando variações nos custos e benefícios dessas associações para plantas (Di Giusto *et al.* 2001) Assim, há uma forte condicionalidade nas relações mutualísticas entre formigas e plantas com NEFs (Del-Claro 2004).

Interações entre aranhas e plantas

Aranhas compreendem um grupo megadiverso, com 41.719 espécies descritas até o momento (Platnick 2010). São amplamente distribuídas em praticamente todos os ambientes ecológicos e particularmente abundantes em áreas de rica vegetação (Foelix 1996). Como predadores generalistas, atacam primariamente insetos, mas também outros artrópodes, incluindo aranhas (Wise 1993). Há ainda registros de predação de vertebrados (como pequenos peixes e girinos) por determinadas aranhas (Foelix 1996). São capazes de exercer forte controle topo-base sobre populações de herbívoros (Sanders & Platner 2007), sendo consideradas de valor econômico devido à sua habilidade em suprimir pestes em agroecossistemas (revisão em Sunderland 1999; Romero 2007). Apresentam uma variedade de estratégias de forrageamento, o que possibilita sua classificação em guildas (e.g. Uetz *et al.* 1999). Em geral, as famílias de aranhas que compõem as guildas das caçadoras por espreita (e.g. Salticidae, Oxyopidae), por emboscada (e.g. Thomisidae) e corredoras na vegetação (e.g. Anyphaenidae) são as mais comumente encontradas na vegetação (Romero & Vasconcellos-Neto 2007a).

Aranhas interagem com plantas indiretamente, pois estas proporcionam substrato para forrageamento, refúgio e construção de teias (Gunnarsson 1990). Uma vez que variações na complexidade estrutural e arquitetura das plantas determinam diferenças na disponibilidade de sítios para forrageamento, esconderijo de predadores, acasalamento e oviposição, essas são consideradas importantes variáveis que influenciam a distribuição e abundância de aranhas (Souza 2007). Por exemplo, Souza & Martins (2005) encontraram relação positiva entre a abundância de aranhas e a densidade de folhas em ramos de sete espécies de plantas em uma área de cerrado. Heikkinen & MacMahon (2004) fizeram experimentos utilizando modelos de arbustos e constataram que a altura e orientação de ramos influenciam a distribuição de guildas de aranhas. Características da arquitetura de inflorescências também podem ser importantes para explicar abundância de aranhas. Souza (1999) encontrou relação positiva entre o número total destes predadores e número total de flores, número de flores abertas e tamanho das flores em 14 espécies de plantas em área de cerrado.

Associações específicas entre aranhas e plantas são pouco conhecidas, mas há exemplos que sugerem preferência desses aracnídeos por determinadas características e/ou espécies de plantas. Por exemplo, Vasconcellos-Neto *et al.* (2006) constataram que aranhas do gênero *Peucetia* (Oxyopidae) ocorrem em plantas com tricomas glandulares, provavelmente devido à maior facilidade de capturar presas nessas estruturas. Outro exemplo

é *Psecas chapoda* (Salticidae) que ocorre quase exclusivamente em *Bromelia balansae* (Bromeliaceae), passando todo o seu ciclo reprodutivo sobre a planta. As folhas da bromélia possuem arquitetura em forma de rosetas, possibilitando locais de proteção contra dessecação e inimigos naturais (Romero & Vasconcellos-Neto 2005).

Como predadores extremamente diversos e abundantes que forrageiam na vegetação, aranhas tem o potencial de indiretamente aumentar o valor adaptativo das plantas que visitam, por meio da diminuição de herbívoros e conseqüentemente, herbivoria. Uma série de estudos demonstram tal efeito benéfico da presença de aranhas em plantas. Por exemplo, Romero & Vasconcellos-Neto (2004) constataram que *Misumenops argenteus* (Thomisidae) reduziu a abundância de herbívoros em *Trichogoniopsis adenantha* (Asteraceae). Em *Dipteryx oleifera* (Fabaceae), menores níveis de herbivoria, maior crescimento de plântulas e melhor sobrevivência foram relacionados à presença de aranhas (Ruiz *et al.* 2009). Alguns estudos demonstram efeitos negativos da presença desses predadores para plantas. Geralmente nestes casos, as aranhas atacam espécies que mantêm relações mutualísticas com as plantas, como polinizadores ou outros predadores (veja exemplos em Romero & Vasconcellos-Neto 2007b).

Apesar de serem quase exclusivamente carnívoras, alguns estudos têm mostrado que néctar pode ser uma importante fonte de energia para aranhas (e.g Jackson *et al.* 2001; Taylor & Pfannenstiel 2008 e referências neles). Assim, a presença de néctar extrafloral pode mediar interações mutualísticas entre aranhas e plantas. Ruhren & Handel (1999) encontraram correlação positiva entre a presença de salticídeos que se alimentavam de néctar extrafloral e o número de frutos e sementes produzidos em *Chamaecrista nictitans* (Fabaceae). Whitney (2004) constatou aumento na produção de sementes em *Acacia ligulata* (Fabaceae) contendo ninhos da aranha subsocial *Phryganoporus candidus* (Desidae). Apesar das análises impossibilitarem a conclusão de que o néctar extrafloral é uma importante recompensa para essa espécie de aranha, o número de colônias por planta e volume do ninho foram maiores em *Acacia ligulata* do que em outras hospedeiras sem nectários extraflorais.

Cerrado

O cerrado é a paisagem dominante do Brasil central (Goodland & Pollard 1973). Faz fronteira ao norte com a Floresta Amazônica, ao sul e sudeste com a Floresta Atlântica e ao nordeste com a Caatinga (Oliveira & Marquis 2002). Com uma área total de aproximadamente dois milhões de quilômetros quadrados, ocupa cerca de 22% do território

brasileiro (Oliveira-Filho & Ratter 2002). A vegetação do cerrado apresenta ampla variação, abrangendo desde áreas abertas com uma esparsa cobertura de arbustos e pequenas árvores, até áreas mais fechadas com árvores atingindo de 12 a 15 metros de altura (Ratter *et al.* 1997). O clima é subtropical caracterizado por um verão chuvoso (de outubro a março) e um inverno seco (de abril a setembro), onde eventos de fogo podem ocorrer. A temperatura média anual varia de 18 a 28 °C e a precipitação de 800 a 2000 mm (Oliveira-Filho & Ratter 2002).

Dentre as savanas tropicais, o cerrado é a mais diversa tanto em fauna como em flora (Oliveira-Filho & Ratter 2002). É sugerido que sua heterogeneidade espacial é um fator determinante para essa enorme diversidade de espécies de animais e plantas (Machado *et al.* 2004). No entanto, é também um bioma altamente ameaçado, devido ao seu alto potencial para agricultura e pecuária (Klink & Machado 2005). Estes fatos contribuíram para que o cerrado fosse inserido na lista dos “hot spots” mundiais com prioridade de conservação (Myers *et al.* 2000). Plantas com nectários extraflorais são comuns no cerrado (Oliveira & Leitão-Filho 1987; Oliveira & Oliveira-Filho 1991), e constituem bons modelos para o estudo de como interações multitróficas podem moldar a organização de comunidades naturais (Del-Claro 2004).

Justificativa e objetivos

Como pertencentes ao terceiro nível trófico, formigas e aranhas têm o potencial de beneficiar plantas por meio da supressão de herbívoros. No entanto, estes dois grupos são potenciais competidores e predadores mútuos (Sanders & Platner 2007). Assim, quando coocorrem no mesmo substrato vegetal os resultados das interações com plantas dependerão da natureza das interações entre esses predadores, ou seja, se agem de uma maneira aditiva ou antagônica (Schmitz 2007).

Neste contexto, esse estudo teve como objetivo geral determinar o impacto da fauna de aranhas e formigas sobre herbivoria e reprodução de uma espécie de planta com nectários extraflorais, *Qualea multiflora* (Vochysiaceae) (Figura 1). Verificou-se se há diferença nos efeitos desses dois grupos de predadores quando agem em conjunto ou separadamente. Para o cumprimento deste objetivo foram investigadas as seguintes questões específicas:

- 1- Quais espécies de aranhas e formigas visitam *Qualea multiflora* no cerrado?
- 2- Aranhas e formigas que visitam *Q. multiflora* no cerrado exercem algum impacto significativo sobre a riqueza e abundância de herbívoros que visitam essas mesmas plantas?
- 3- A presença de formigas tem influência sobre a riqueza e abundância de espécies de aranhas que utilizam *Q. multiflora* e vice-versa?
- 4- A ação das aranhas e formigas tem algum reflexo sobre a perda de área foliar e/ou reprodução das plantas?

A dissertação está apresentada em capítulo único, redigido em formato de artigo científico.

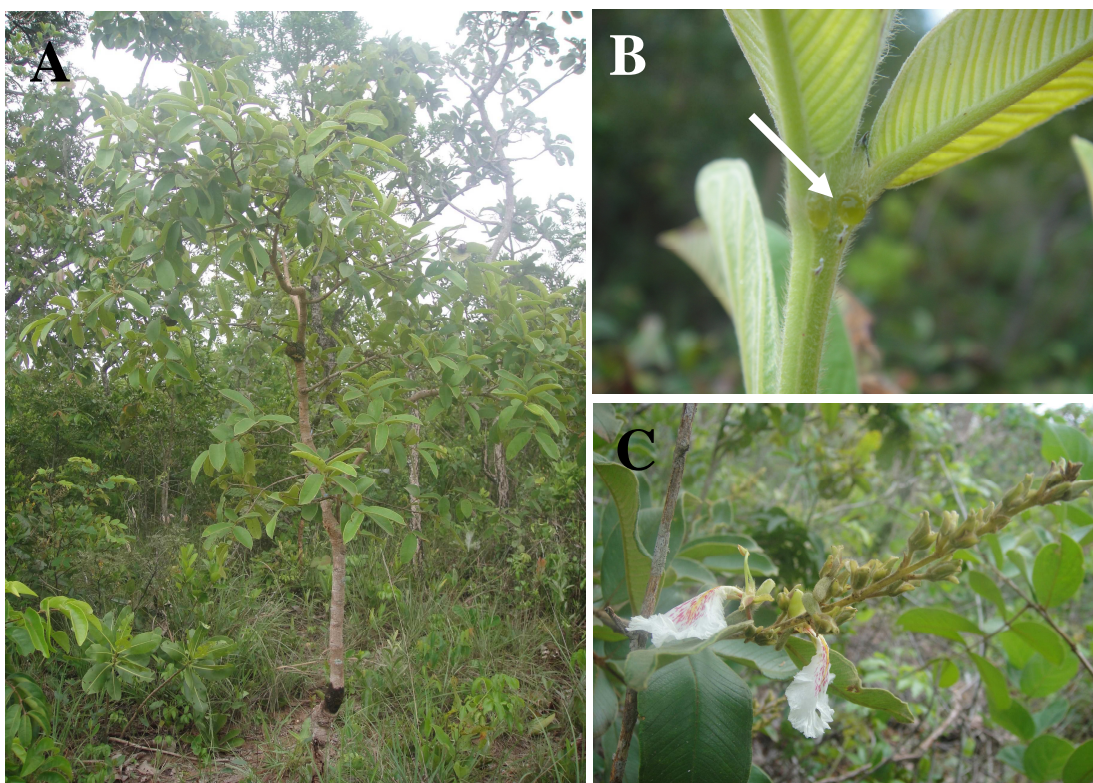


Figura 1. Árvore de *Qualea multiflora* (Vochysiaceae) (A). Nectários extraflorais ativos em *Q. multiflora* (B). Ramo de *Q. multiflora* florido (C).

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2. ARTIGO

Additive effect of two predator guilds on the reduction of herbivory and herbivores in *Qualea multiflora* (Vochysiaceae)

(Manuscrito em fase final de preparação)

**Additive effect of two predator guilds on the reduction of herbivory and herbivores in
Qualea multiflora (Vochysiaceae)**

Larissa Nahas¹, Marcelo O. Gonzaga² & Kleber Del-Claro²

¹ Pós-graduação em Ecologia e Conservação de Recursos Naturais, Universidade Federal de Uberlândia, Uberlândia, MG, Brazil.

² Instituto de Biologia, Universidade Federal de Uberlândia, Uberlândia, MG, Brazil.

Abstract

The study of biotic interactions, such as indirect effects of predators on plants, are important to comprehension of community dynamics. Spiders and ants are among the most important predators of herbivores and may significantly reduce damages to host plants. However, when these predators co-occur in the same vegetation substrate the outcomes of interactions on plants will depend on whether their action will have or not an additive effect. We experimentally evaluated the effects of spiders and ants (jointly and separately) on herbivory and reproduction of an extrafloral nectary-bearing plant, *Qualea multiflora* (Vochysiaceae), in cerrado vegetation. Plants were divided in four experimental groups, depending on the presence or absence of ants and spiders. We compared the effects of each treatment on richness and abundance of herbivores, herbivory (leaf area loss), production of buds, fruits and seeds, length and weight of fruits and relation of fruits per buds and seeds per fruits. The exclusion experiments showed that, the removal of one or both types of predators resulted in a significant increase in abundance of herbivores and herbivory level. Neither ants nor spiders had some impact in the production of buds, flowers or fruits (including fruits vigor: weight, length and number of viable samaras) among plants of different groups. This study highlights the importance of evaluate the effect of the predator fauna as a whole and not only one specific group (generally ants) on herbivory and reproduction of extrafloral nectary-bearing plants.

Key words: ants; spiders; cerrado; tropical savanna; extrafloral nectaries.

Introduction

Biotic interactions can provide particular insights into community dynamics (Simberloff 2006; Clement *et al.* 2008). Indirect positive effects of predators on plants, for example, may be influenced by interactions among trophic levels and intraguild predation and competition (Fagan 1997; Borer *et al.* 2005). In addition, other factors, such as combination of herbivore and predator metabolic characteristics, predator identities (Borer *et al.* 2005; Byk & Del-Claro 2010a), the quality of the available resources for herbivores (Leibold 1989) and the types of predation-avoidance behaviors employed by herbivores (Schmitz *et al.* 2004; Sendoya *et al.* 2009) may be very important to determine the strength of trophic cascades (Terborg & Estes 2010). In terrestrial ecosystems, strong cascades usually involve invertebrate herbivores presenting a high grazing efficiency allied with an also high vulnerability to predators, such as Lepidoptera larvae (Polis & Strong 1996). Among the most important predators of these herbivores, spiders and ants may significantly reduce damages to host plants (Ruiz *et al.* 2009; Nascimento & Del-Claro 2010).

Several plant species offer feeding resources and/or shelters used by ants and spiders and are benefited by their presence. One of the commonest resource plants offer to ants is extrafloral nectar (EFN), a liquid substance rich in carbohydrates with diluted concentrations of amino acids, lipids, phenols, alkaloids and volatile organic compounds (González-Teuber & Heil 2009). This food source can improve ant fitness increasing colony growth rate and body mass (Byk & Del-Claro 2010b). On the other hand, many authors have demonstrated that ants can benefit EFN-bearing plants because they prey upon the herbivores and/or reduce their activity on foliage (Bentley 1977; Del-Claro *et al.* 1996; Koptur 2005; Rico-Gray & Oliveira 2007).

Experimental studies with ant-exclusion, showed that the absence of ants can increase leaf area loss in plants possessing EFNs (Koptur 1984; Kelly 1986; Costa *et al.* 1992; Oliveira 1997; Korndörfer & Del-Claro 2006), reduction in fruit (Oliveira *et al.* 1999; Nascimento & Del-Claro 2010) and seed production (Vesprini *et al.* 2003), and germination (Sobrinho *et al.* 2002). Plants presenting extrafloral nectaries attract not only ants, but several other arthropods (Koptur 2005). These arthropods include spiders (Ruhren & Handel 1999), wasps (Stapel *et al.* 1997; Cuautle & Rico-Gray 2003), beetles (Pemberton & Vandenberg 1993; Spellman *et al.* 2006) and neuropterans (Limburg & Rosenheim 2001). Spiders may be directly attracted by the presence of EFN, used as a supplementary source of water and energy (Vogelei &

Greissi 1989; Taylor & Foster 1996; Jackson *et al.* 2001), or by the presence of abundant potential prey living in or visiting these plants. As a consequence, these predators may also prey on or repel herbivores, possibly also reducing damages in EFN-plants (Ruhren & Handel 1999; Whitney 2004).

In general, ants and spiders are generalist predators and can compete for preys on the same trophic level (Sanders & Platner 2007). So, when these predators co-occur in the same vegetation substrate the outcomes of interactions on plants will depend on whether the predator action will have or not an additive effect, mainly reducing herbivores numbers and herbivory intensity (Schmitz 2007). In the occurrence of an additive and complementary effect in biotic interactions, the expected result will be the sum of individual effects (Chang 1996). However, if ants and spiders act in an agonistically way, the co-occupation of the same plants may not result in herbivore or herbivory reduction, mainly due to intraguild competition and/or predation (Sokol-Hessner & Schmitz 2002).

The Brazilian tropical savanna (cerrado) is an ecosystem dominated by small trees and shrubs, where EFNs are commonly in more than 28% of families and 32% of individuals (Rico-Gray & Oliveira 2007). Our personal observations in more than 20 years of research in cerrados have already showed that EFNs are commonly visited by ants that benefit from them (Del-Claro & Torezan-Silingardi 2009). Additionally spiders (e.g. Salticidae, Clubionidae, Oxyopidae) are also common in cerrado plants (e.g. Souza 1999) where they found shelter, preys, and exudations like extrafloral nectar to feed on, sometimes simultaneously with ants in the same plants (personal observations). Thus, in the present study we hypothesized that ants and spiders can have a complementary action on the EFN-bearing tree *Qualea multiflora* (Vochysiaceae) in cerrado vegetation, promoting a reduction in herbivory in a more efficient way than when acting exclusively. To test our hypothesis, three questions were addressed: (1) Do ants and spiders that visit *Q. multiflora* in cerrado exert any significant impact on herbivores richness and abundance on these plants? (2) Does ants and spiders' action have any reflex on foliar lost area and/or plant reproduction? (3) Do these possible effects on herbivores diversity, herbivory and plant reproduction differ when ants and spiders act jointly or exclusively?

Methods

Study site and plant model

Field study was conducted between August 2009 and May 2010 in the Cerrado reserve (127 ha) of Clube de Caça e Pesca Itororó (CCPIU) (18°56'21.04"S and 48°16'14.33"O), Uberlândia, Minas Gerais, Brazil. The tropical savanna in this area is as a typical Cerrado (*Stricto sensu* Goodland 1971) characterized by the presence of shrubs and trees in a proportion varying between 10 and 60% in an area of grasses predominance (Eiten 1972). Like other Cerrado areas (Oliveira & Marquis 2002) two seasons are well defined, a dry season between May and September (autumn-winter) and a rainy season, between October and April (spring-summer).

In this study site *Qualea multiflora* is a tree (2-5 m tall), bearing paired EFNs on the stem next to the insertion of the leaves, and on the bud pedicels. This plant species is one of the six most abundant trees in the area (Erdogmus 2010). Arthropods and several ant species are attracted by the extrafloral nectar (Figure 1) effectively benefiting the plant through the reduction of leaf lost area and increasing fruit production (Del-Claro *et al.* 1996). This plant species is deciduous, losing leaves in the end of July and resprouting in August, with flourishing in October (Lorenzi 2000).



Figure 1. The ant, *Ectatomma quadridens* (Ectatomminae) and the spider *Oxyopes macroscelides* (Oxyopidae), feeding on extrafloral nectar of the cerrado tree, *Qualea multiflora* (Vochysiaceae) in cerrado vegetation. Photo: Kleber Del-Claro.

Experiments

In August, we tagged 60 similar individuals of *Q. multiflora* in the same phenological state: 1.5 to 2.5 tall; 4 to 6 stems; without leaves and with the presence of vegetative gems. Each individual was distant at least five meters from other. We compared the plants to

establish groups of trees possessing the most similar individuals in all aspects. Then these plants were raffled off in four treatments, each one with 15 individuals. Thus, treatments had similar groups of trees when compared to each other.

The first group was named “Control” and plants did not receive any manipulation. So, ants and spiders had free access to all plant parts. The second group was named “Exclusion”, and ants and spiders were all removed from the plants. The third treatment was named “Ants”, due the fact that only spiders were removed and the last one, was named “Spiders”, and in this case, only ants were removed (Figure 2). Each tree received one numerical identification mark in the trunk. We performed the spider exclusion (Exclusion/Ants) manually every three days, and specimens were collected and fixed for further identification (Ethanol 70%). This interval was established during a pre-experimental phase, in which we removed spiders from plants and followed the spider recolonization inspecting plants daily during one week. We observed a very low recolonization until the sixtieth day (Figure 3). We also excluded ants manually (Exclusion/Spiders) and immediately before it, in the basis of each plant, 30 cm above the ground level, we covered the trunk with a 5 cm large adhesive paper strap and applied over it a lay of sticky resin (Tanglefoot ®; The Tanglefoot Company, Rapids, Michigan, USA) to avoid ants to climb onto the plants. All structures of other plants and grasses that could be used by ants as bridges to get access to experimental plants were removed. In the groups Control and Ants, to show that the sticky resin did not interfere in results, we also covered the trunk in the same way with a paper strap, however, we applied the resin only at one side of the trunk.



			
60 trees (<i>Qualea multiflora</i>)	Control group (n=15)	✓	✓
	Exclusion group (n=15)	X	X
	Ants group (n=15)	X	✓
	Spiders group (n=15)	✓	X

Figure 2. Schematic illustration of the experimental design. The marker symbol means presence of ants or spiders, and an ex means absence of one or both of them.

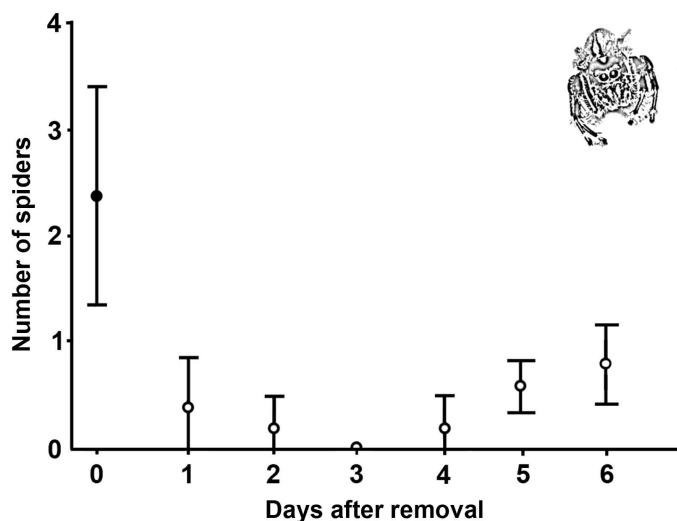


Figure 3. Recolonization of spiders in *Qualea multiflora* (n = 5) during a week. In the day 0 all spiders were removed of the plants.

Evaluation of plant herbivory and reproduction

We inspected all plants of all groups three times per month, each nine/ten days, from the first (August 2009) up to the last month (May 2010) of experiments. In each inspection, always the same researcher recorded the abundance and richness of ants, spiders and herbivores in the plants. Voucher specimens were collected in non experimental plants to identification. We quantified leaf herbivory monthly in the first week of each month. To determine the mean leaf area loss per individual, per month, we recorded this data of 12 leaves per plant, four from the most apical stem, four from a middle stem and four from the most basal stem. It was done without leaf removal. Measurements of herbivory rates on leaves were assessed by placing them on a transparent grid (divided into millimeters). An index of herbivory from each leaf was estimated as the proportion of points in the grid falling within damage and undamaged areas of the leaf blade (e.g. Dirzo & Domínguez 1995; Korndörfer & Del-Claro 2006). We also registered, in the same way, leaf area loss due the action of mould and gall infestation. In the case of galls we counted their number per sampled plant.

Additionally, we also counted the number of floral buds produced by each stem (in October). Fruit and seed production by experimental stems were expressed as the proportion of fruits formed per buds produced, and as the proportion of seeds per fruits produced, respectively (in May). In the last month of experiments (May), we collected all fruits and, in laboratory conditions, they were measured (major length) and, after dried (65°C/48hs), they were weighted. After it fruits were stored in ethanol 70% during one week to re-hydrate and then opened to count the number of viable samaras (seeds).

Statistical analysis

When data presented normality (sometimes obtained through transformation: $\sqrt{x+0.5}$) means of four experimental groups were compared using repeated measures ANOVA (richness and abundance of herbivores; herbivory, mould and gall infestation). To compare the structure of spider community in plants with and without ants, spiders were divided in four guilds according to Heikkinen & MacMahon (2004), considering: trappers (e.g. Araneidae, Theridiidae, Nephilidae, Tetragnatidae); jumpers (e.g. Salticidae and Oxyopidae); ambushers (e.g. Thomisidae) and pursuers (e.g. Anyphaenidae). Means of non-parametric data were compared using Kruskal-Wallis test (buds produced; fruits produced; fruits formed per buds produced; seeds formed per fruits produced; weight and length of fruits; number of viable samaras). We used the statistical software Systat 10.2.

Results

In the multitrophic system composed by *Q. multiflora*, its herbivores, ants and spiders, these predators had a positive impact in the reduction of both leaf area loss and herbivores abundance, when their effects were considered complementary. Seasonality was evident through time. Herbivores and ants were more abundant in the beginning of the rainy season, between October and November, months in what plants were producing new leaves and flowering. Spiders become more abundant one month later, in November to December (Figure 4). The most abundant herbivores in all groups of plants were: Cicadellidae, Aphididae, Coreidae, Coccidae and Chrysomelidae (Appendix 1).

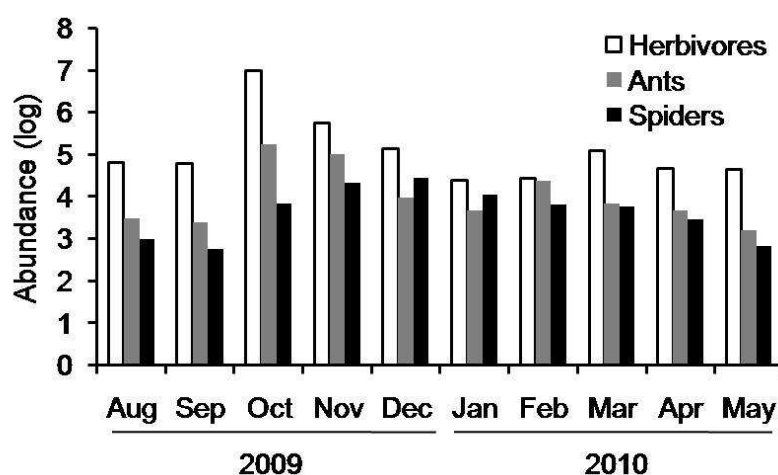


Figure 4. Seasonal variation (August 2009 to May 2010) in the abundance of: herbivores, ants and spiders on *Qualea multiflora* (Vochysiaceae) trees in cerrado vegetation.

A total of 21 ant species, belonging to 10 genera and five subfamilies were sampled foraging on EFNs of experimental shrubs (Appendix 2). The most frequent genera feeding on EFNs were, respectively: *Camponotus*, *Cephalotes*, *Ectatomma* and *Brachymyrmex*. Richness and abundance of ants were not different (Repeated measures Anova - $F=1.044$, $p=0.316$ and $F=1.404$, $p=0.246$, respectively, Figure 5) in the presence or absence of spiders. In order, the most abundant ants were *Camponotus crassus*, followed by *Brachymyrmex* sp, *Cephalotes pusillus* and *Ectatomma edentatum*. The few differences among experimental groups were related mainly to small ants that commonly nest in dead stems like *Azteca* and *Brachymyrmex*, thus being more abundant in some plants than in others, or simple by chance like the case of *E. edentatum* (Figure 6).

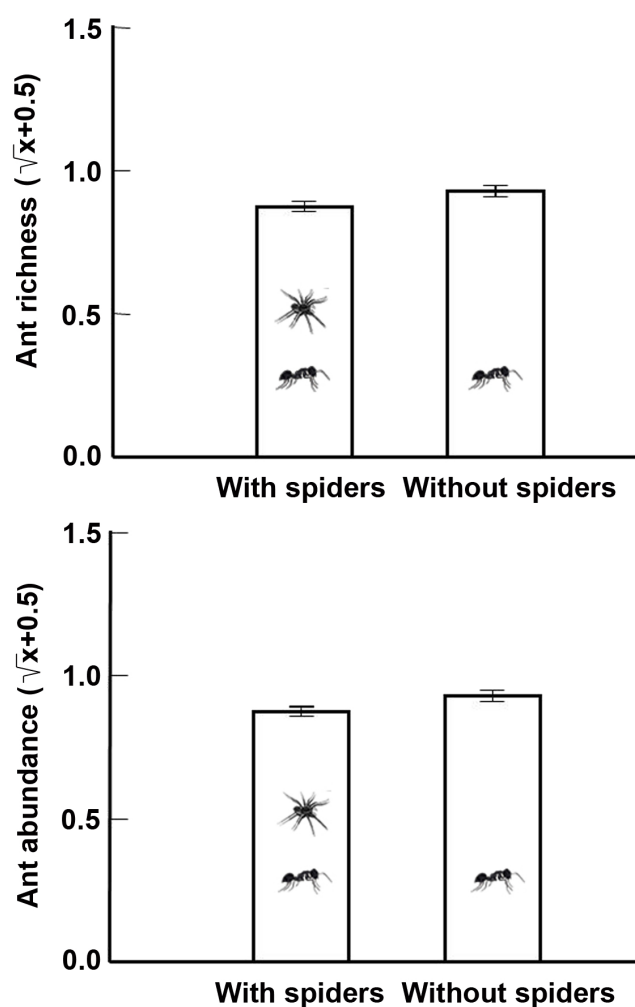


Figure 5. Richness and abundance of ants on *Qualea multiflora* (Vochysiaceae) trees in the cerrado vegetation, with ($n=15$) and without ($n=15$) the presence of spiders. The values are means \pm 1EP. There was not statistical significant difference between samples (Repeated Measures Anova, $p < 0.05$).

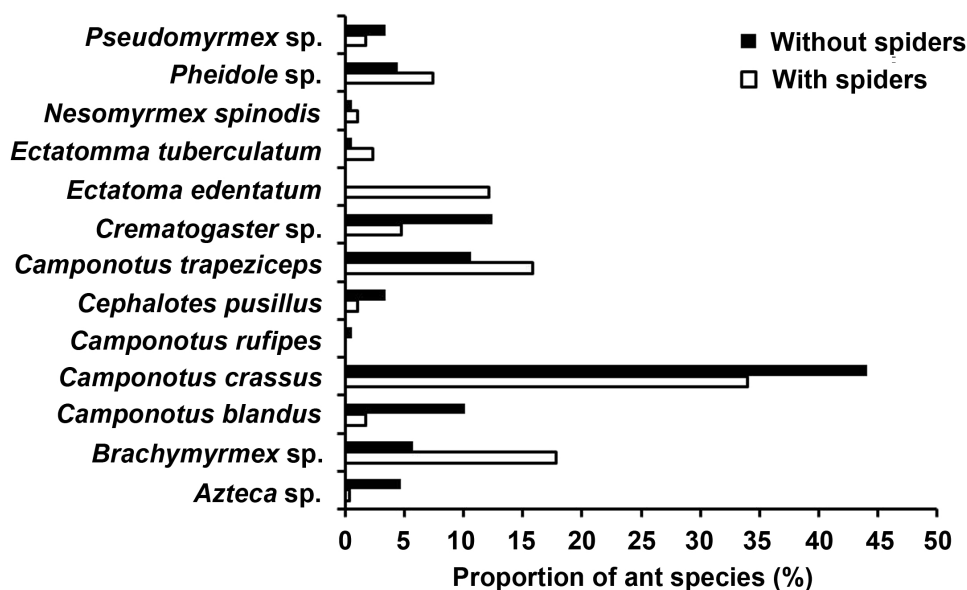


Figure 6. Proportion (= (total of individuals / total of all ant individuals) X 100) of ant species on *Qualea multiflora* (Vochysiaceae) trees, with and without spiders, in the cerrado vegetation.

Spiders were very diverse in *Q. multiflora* trees, a total of 43 species, belonging to 30 genera and 10 families were sampled (Appendix 3). Some species of Anyphaenidae (*Arachosia* sp.), Salticidae (Salticidae sp1.), Thomisidae (*Misumenops* sp.) and Oxyopidae (*Oxyopes macroscelides*) (Appendix 3), were observed feeding in EFNs mainly in october and november, when they were more active. Richness and abundance of spiders were lower (Repeated measures Anova - $F=12.129$, $p=0.002$ and $F=9.788$, $p=0.004$, respectively, Figure 7) in plants visited by ants than in plants without ants. All spiders family were present in all treatments and control, however, they were about two times more abundant in plants without ants ('group spiders'). The most common guilds were 'trappers', followed by "jumpers", "ambushers" and "pursuers", respectively (Figure 8).

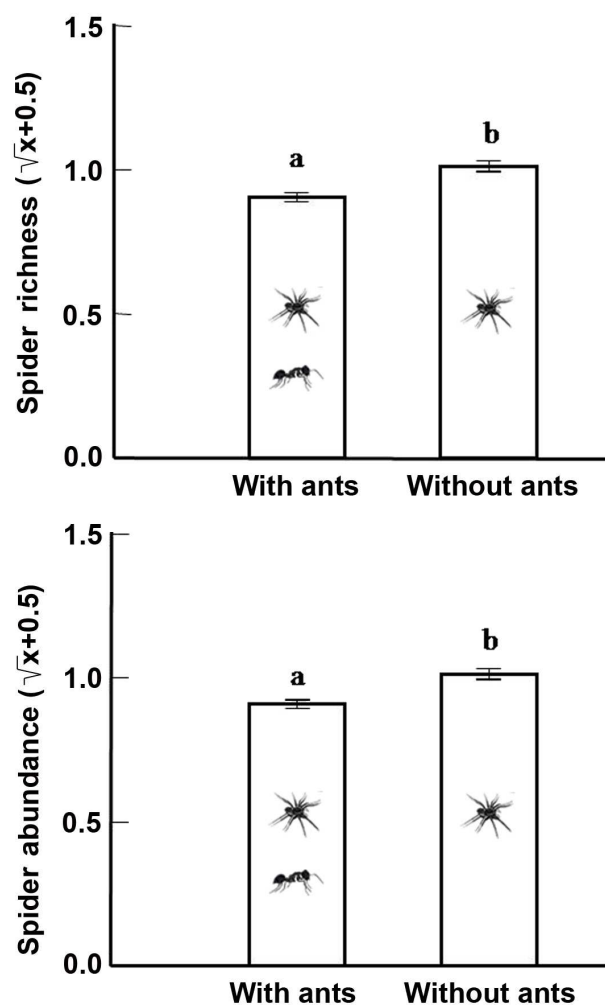


Figure 7. Richness and abundance of spiders on *Qualea multiflora* (Vochysiaceae) trees with (n=15) and without (n=15) ants. The values are means \pm 1EP. Different letters indicate statistical significant difference between samples (Repeated Measures Anova, $p < 0.05$).

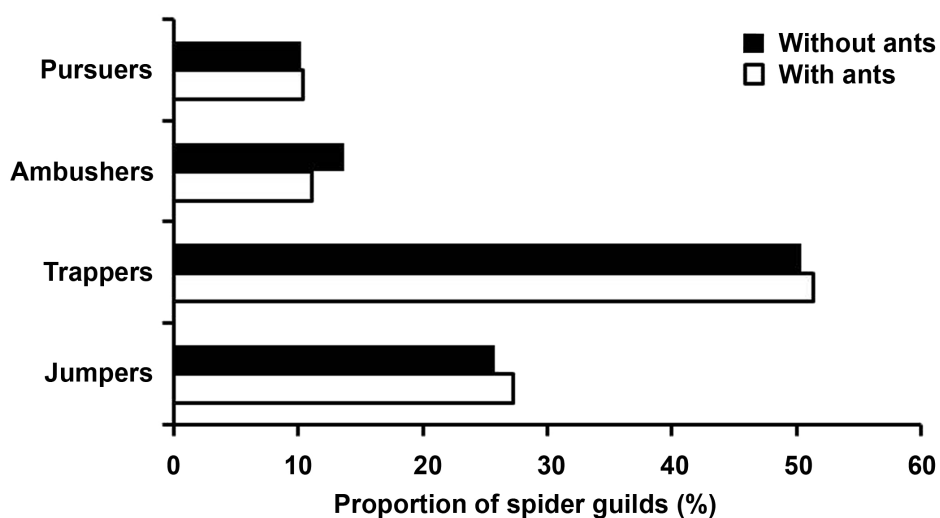


Figure 8. Proportion (= (total of individuals / total of all spider individuals) X 100) of spider guilds on *Qualea multiflora* (Vochysiaceae) trees, with and without ants, in the cerrado vegetation.

The exclusion experiments showed that, the removal of one or both types of predators resulted in a significant increase in abundance of herbivores and herbivory level (percentage of leaf area loss) in *Q. multiflora* in this cerrado savanna area. Richness and abundance of herbivores were significant lower (repeated measures Anova - $F=3.782$, $p=0.015$ and $F=4,271$, $p=0.009$, respectively) in plants of control group, thus possessing ants and spiders simultaneously. Other treatments didn't differ among them (Figure 9). The same occurred in relation to herbivory, thus spiders and ants acting together (control group) resulted in 1.5 times less leaf area loss than other groups (repeated measures Anova - $F=12.447$, $p=0.0001$; Figure 10).

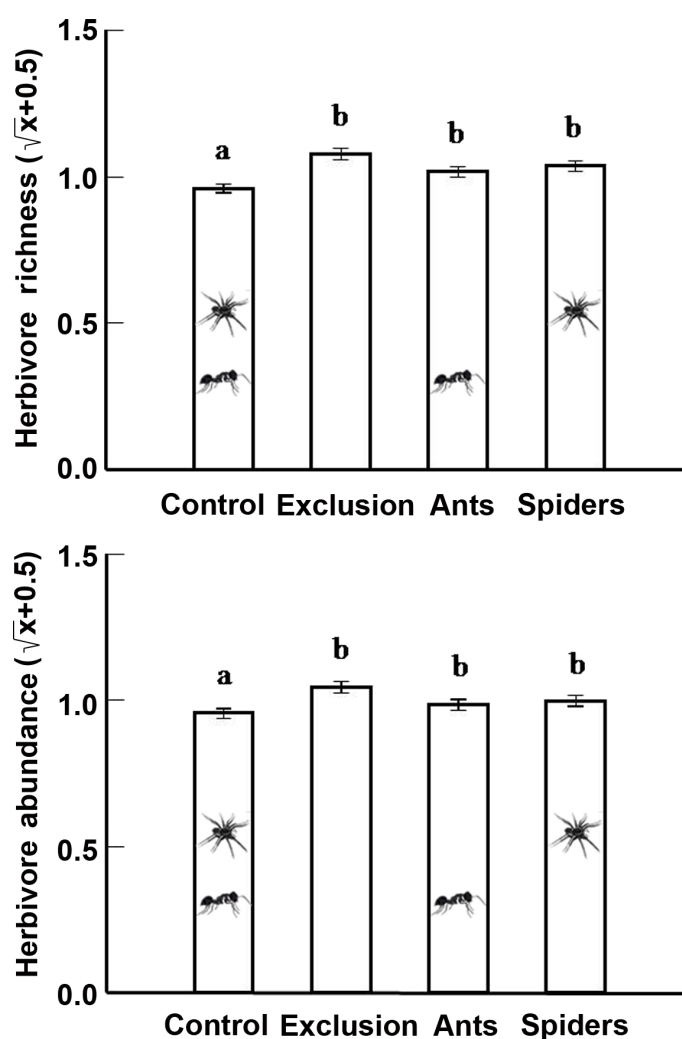


Figure 9. Richness and abundance of herbivores on *Qualea multiflora* (Vochysiaceae) trees with spiders and ants (Control Group $n=15$); without spiders and ants (Exclusion Group $n=14$), with ants and without spiders (Ant Group $n=15$) and with spiders and without ants (Spider Group $n=15$). Values are means $\pm 1EP$. Different letters indicate significant statistical difference between samples (Repeated Measures Anova, $p < 0.05$).

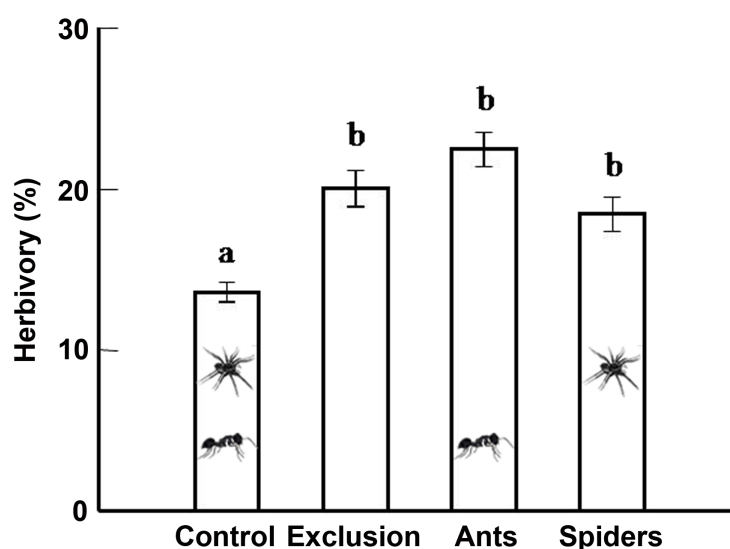


Figure 10. Percentage of herbivory in *Qualea multiflora* (Vochysiaceae) trees of four distinct treatments (Control Group – plants with free access to ants and spiders; Exclusion Group – plants without ants and spiders; Ant Group – plants with free access to ants and without spiders; Spider Group – plants with free access to spiders and without ants). Values are means \pm 1EP. Different letters indicate significant difference between samples (Repeated Measures Anova, $p < 0.05$).

Neither ants nor spiders had some impact in the production of buds, flowers, fruits or seeds (including fruits vigor: weight, length and number of potentially viable samaras) between plants of different groups (Table 1). Also leaf area loss due the action of mould and galls was not significant to any treatment (Table 2).

We rarely observed ants preying on herbivores. Spiders were sometimes observed with prey, which were identified to lowest possible taxonomic level (Table 3).

Table 1. Results of the different treatments (Control group – plants with free access to ants and spiders; Exclusion Group – plants without ants and spiders; Ant Group – plants with free access to ants and without spiders; Spider Group – plants with free access to spiders and without ants) on the buds and fruits production; in the relation between fruits formed per produced buds (fruits per buds) and seeds per fruits, weight and length of the fruits, and number of potentially viable samaras in *Qualea multiflora* trees in cerrado vegetation. Data are means \pm SE. H and P refer to Kruskal-Wallis Test.

	Control Group	Exclusion Group	Ants Group	Spiders Group	H	P
No of buds produced	40.800 \pm 13.941	60.000 \pm 6.904	38.000 \pm 6.094	46.167 \pm 12.180	3.236	0.357
No of fruits produced	1.400 \pm 0.678	2.833 \pm 0.477	1.714 \pm 0.714	1.167 \pm 0.401	4.204	0.240
Fruits per buds	0.019 \pm 0.012	0.047 \pm 0.005	0.000 \pm 0.013	0.028 \pm 0.051	3.266	0.352
Seeds per fruits	1.500 \pm 1.500	1.819 \pm 0.547	0.917 \pm 0.917	2.533 \pm 0.827	2.044	0.563
Weight of the fruits (g)	1.884 \pm 0.237	1.445 \pm 0.122	1.556 \pm 0.170	1.677 \pm 0.232	2.972	0.396
Length of the fruits (cm)	3.450 \pm 0.116	3.038 \pm 0.091	3.259 \pm 0.109	3.228 \pm 0.273	7.197	0.066
No of potentially viable samaras	4.500 \pm 4.500	6.800 \pm 1.855	5.500 \pm 5.500	4.000 \pm 0.577	0.988	0.804

Table 2. Results of the different treatments (Control group – plants with free access to ants and spiders; Exclusion Group – plants without ants and spiders; Ant Group – plants with free access to ants and without spiders; Spider Group – plants with free access to spiders and without ants) on percentage of mould and number of galls in *Qualea multiflora* trees in cerrado vegetation. Data are means \pm SE. F and P refer to Repeated Measures Anova Test.

	Control Group	Exclusion Group	Ant Group	Spider Group	F	P
% Mould	14.118 \pm 0.736	14.680 \pm 0.832	14.047 \pm 0.706	14.811 \pm 0.785	0.213	0.887
No of galls	28.627 \pm 3.912	35.514 \pm 5.145	26.914 \pm 3.971	40.200 \pm 4.665	0.559	0.644

Table 3. List of preys captured (number of events) by spiders in *Qualea multiflora* (Vochysiaceae) trees, in cerrado vegetation.

Preys	Spider Families				
	Araneidae	Oxyopidae	Salticidae	Theridiidae	Thomisidae
	n	n	n	n	n
Araneae			2		
Coleoptera (total)			3	1	
Chrysomelidae			1		
Other Coleoptera			2	1	
Diptera	1		1	2	
Hemiptera (total)		1	4	1	1
Cicadellidae		1	3		
Coreidae			1		1
Pentatomidae				1	
Hymenoptera (total)	5	2		9	17
Apidae		1			
Formicidae(total)	3			8	16
<i>Azteca sp.</i>				1	
<i>Camponotus sp.</i>	1			1	6
<i>Cephalotes pusilus</i>				4	6
<i>Pseudomyrmex sp.</i>	1			1	1
Other ants	1			1	3
Other Hymenoptera	2	1		1	1
Total	6	3	10	13	18

Discussion

Predators, ants and spiders, had an additive and complementary effect on the reduction of leaf area loss caused by herbivores action in *Q. multiflora* trees in cerrado vegetation. The mutual action of these predators also reduced abundance and diversity of herbivores on plants. So, our three main hypothesis that ants and spiders that visit *Q. multiflora* in cerrado: 1- exert any significant impact on herbivores richness and abundance on individual plants; 2- that have any reflex on foliar lost area; and 3- that the effects on herbivores diversity and herbivory, differ when ants and spiders act jointly or exclusively; were corroborated by our data. Only the hypothesis that ants and spiders could have any influence on plant reproduction was refused. Working in this same study site, Del-Claro *et al.* (1996) showed that ants had a significant impact on reduction of herbivory and that these predators had a positive impact on fruit production, increasing it in almost 40%. However, Del-Claro *et al.* (1996) didn't excluded spiders on plants as we did here, thus possibly they also showed the additive effect of two distinct group of predators on this EFN bearing plant in cerrado vegetation. We suggested that the same thinking can be extended to the major part

of studies that evaluated the impact of ant visitors on herbivory reduction in EFN bearing plants in cerrado vegetation (e.g. Costa *et al.* 1992; Oliveira 1997; Nascimento & Del-Claro 2010; see also Del-Claro & Torezan-Silingardi 2009).

In the tropical savanna, ant-plant-herbivores relationships can present temporal variation in the outcomes of interactions (e.g. Del-Claro & Oliveira 2000; Moreira & Del-Claro 2005; see also Rico-Gray & Oliveira 2007). This can explain the lack of benefit observed to plant reproduction structures here, on the contrary of Del-Claro *et al.* (1996). In 1996, a beetle named *Macroductylus pumilio* (Melolontinae) was extremely abundant on *Q. multiflora* plants, feeding on petals and reproductive structures of plants. Generally the effects of predators removal are more strong and easily observed in leaf area loss than on the reproductive success of plants. It occurs possibly because leaf herbivory is a more immediate outcome of an increase in herbivores abundance on plants, while effects on fitness can be perceived only in the next reproductive season (Schmitz *et al.* 2000). Not all studies detect a benefit of the presence of EFNs for plants (e.g. O'Dowd & Catchpole 1983; Rashbrook *et al.* 1992; Mody & Linsenmair 2004; see also Bronstein 1998 and references therein). Absence of protection occurs for several reasons, but is mainly due to seasonal variation in interaction strength, and variability in behavior among different ant species (e.g. Del-Claro & Oliveira 2000; Mody & Linsenmair, 2004). Clarification of the nature of these contingencies is critical for understanding how these interactions have evolved and are maintained (see Bronstein 2009). Different ant species can provide different benefits to host plants, as seen for both ant-plant-hemipteran (Del-Claro & Oliveira 2000; Oliveira & Del-Claro 2005) and systems with EFN-bearing plants (Miller 2007; Palmer *et al.* 2008). Perhaps, the predominance of ineffective ants like the Cephalotini *Cephalotes pusillus*, one of the more common ants on plants (Nahas & Del-Claro 2011), may be an additional answer to the lack of protection against herbivory in plants visited exclusively by ants. Although common in EFN-bearing plants in the Neotropics, sometimes nesting inside dead trunks or stems of live trees (Powell 2008), *C. pusillus* are ineffective against herbivores (Sendoya *et al.* 2009), collecting nectar and pollen without offering protection to the plant. As such, they act as a system parasite (Byk & Del-Claro 2010a).

Until the studies of Ruhren & Handel (1999) and Whitney (2004) there was few suggestions in the literature that supported the idea that spiders could have a positive impact on the reduction of herbivory and/or in the increase of plant fitness in nature. A recent meta-analysis of the role of ants as plant biotic defenses (Rosumek *et al.* 2009) showed that on

average, ant exclusion increases the number of herbivores on plants by almost 50%, in turn, doubling the amount of tissue lost to herbivores. *Qualea multiflora* trees visited only by ants or spiders didn't differ from plants where both groups of predators were excluded in terms of leaf area loss or herbivores abundance and diversity. Thus, spiders attracted by extrafloral nectar represent an important partner to plants, complementing the services provide by ants, and in this case vice-versa is also true. More recently, we have noted a significant increase in the number of studies that show direct benefits to plants from visiting or resident spiders (Romero & Vasconcellos-Neto 2004; Romero *et al.* 2006; Romero *et al.* 2008; Morais-Filho & Romero 2010).

According to Miller (2007), for plants that secrete extrafloral nectar, visitation by multiple ant species that vary in anti-herbivore abilities may result in reduced benefits, relative to an exclusive association with one high quality mutualist (see also Mody & Linsenmair 2004). Our results contradict this hypothesis. We showed that more predator species (ants and spiders), with diversified strategies for acquiring prey (here, herbivores) resulted in lower herbivory compared to systems with fewer or no predator species (e.g. Terborgh & Estes 2010). The complementarity among different ant and spiders species seems to be the key for the reduction of herbivory level and herbivores abundance and diversity in *Q. multiflora*.

Complementarity in hunting strategies is, indeed, the main mechanism suggested to explain the importance of additive effect of distinct predators. When hiding and/or attempting to escape of active predators like ants and spiders, preys may be more suitable to, for example, sit-and-wait predators, like other spider species and mantids (Sih *et al.* 1998). However, may occur intra-guild effects, mainly competition between predators, that may impeded the additive effect of predators against preys in some systems (e.g. Ferguson & Stiling 1996; Finke & Denno 2003). Cuautle & Rico-Gray (2003) showed that separately, ants and wasps had similar effect in the reduction of herbivory in the EFN bearing plant *Turnera ulmifolia* (Turneraceae), and no effect when acting together. Here, we observed a negative effect of ants presence on spider richness and abundance, but the contrary didn't occur. It may be a result of the social character of ants, being more efficient to disturb other species, for example through recruiting, than spiders (Moya-Laraño & Wise 2007). We didn't observe any spider predation by ants, so probably they are chased and jump off the plants (e.g. Halaj *et al.* 1997). However, we observed spiders preying on ants, mainly the ineffective *Cephalotes pusillus*. We have also to consider that in environments with high prey diversity, like in the

present system, it can weakness the negative effects of intra-guild predation and competition (Snyder *et al.* 2008).

We suggest that one possible mechanism that favored predators to reduce herbivores richness and abundance may be the increase of risk effect to predation, may be forced pursued herbivores to leave host plants. Predators may have a positive effect on plants same when they are not capable of preying the herbivores (Schmitz 1998; Hlivko & Rypstra 2003). Few direct observation of herbivores predation in our field work is consistent with other studies (Halaj *et al.* 1997; Gaume *et al.* 1998; Sagers *et al.* 2000; Cuautle & Rico-Gray 2003). Thus, just predators presence may contribute to reduce herbivores damage also in *Q. multiflora* system. The present study shows the importance of ecologists to increase efforts to analyze plant-arthropod interactions in a multithrophic and multispecific way, in function to obtain more realistic understanding of the role of each species in the trophic web.

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Appendix 1. Herbivores observed foraging in *Qualea multiflora* (total abundance and proportion in each group) on the period from august 2009 to May 2010, in CCPIU cerrado reserve, Uberlandia, MG.

Family	Control Group		Exclusion Group		Ant Group		Spider Group	
	n	%	n	%	n	%	n	%
Acrididae	8	2	11	1.51	5	0.82	9	1.44
Alydidae	2	0.5	3	0.41	1	0.16	8	1.28
Aphydidae	95	23.75	55	7.55	184	30.06	37	5.92
Cerambycidae	0	0	0	0	0	0	2	0.32
Chrysomelidae	41	10.25	71	9.75	42	6.86	60	9.6
Cicadellidae	152	38	366	50.27	218	35.62	299	47.84
Coccidae	50	12.5	19	2.61	33	5.39	18	2.88
Coreidae	14	3.5	149	20.47	66	10.78	160	25.6
Curculionidae	10	2.5	3	0.41	17	2.78	4	0.64
Flatidae	10	2.5	3	0.41	9	1.47	3	0.48
Gryllidae	1	0.25	1	0.14	2	0.33	0	0
Lepidoptera larvae	4	1	16	2.2	14	2.29	8	1.28
Nogodinidae	0	0	4	0.55	2	0.33	2	0.32
Ortheziidae	5	1.25	12	1.65	8	1.31	4	0.64
Pentatomidae	1	0.25	3	0.41	3	0.49	1	0.16
Proscopiidae	6	1.5	3	0.41	2	0.33	5	0.8
Scutelleridae	0	0	1	0.14	1	0.16	0	0
Tettigoniidae	1	0.25	8	1.1	5	0.82	5	0.8
Total	400	100	728	100	612	100	625	100

Appendix 2. Ant species observed foraging in *Qualea multiflora* (Vochysiaceae) on the period from August 2009 to May 2010, in CCPIU cerrado reserve, Uberlandia, Brazil.

Subfamily	Species
Dolichoderinae	<i>Azteca</i> sp.1
Ectatomminae	<i>Ectatomma edentatum</i> (Roger 1863) <i>Ectatomma tuberculatum</i> (Olivier 1792)
Formicinae	<i>Brachymyrmex</i> sp.1 <i>Brachymyrmex</i> sp.2 <i>Camponotus blandus</i> (Fr. Smith 1858) <i>Camponotus crassus</i> (Mayr 1887) <i>Camponotus rufipes</i> (Fabricius 1775) <i>Camponotus trapeziceps</i> (Forel 1908) <i>Camponotus</i> sp.
Myrmicinae	<i>Cephalotes pusillus</i> (Klug 1824) <i>Crematogaster erecta</i> (Mayr 1866) <i>Crematogaster</i> sp.1 <i>Crematogaster</i> sp.2 <i>Nesomyrmex spininodis</i> (Mayr 1887) <i>Pheidole</i> sp.1 <i>Pheidole</i> sp.2 <i>Pheidole</i> sp.3 <i>Wasmannia auropunctata</i> (Roger 1863)
Pseudomyrmecinae	<i>Pseudomyrmex aff. flavidulus</i> (Fr. Smith 1858) <i>Pseudomyrmex</i> sp.1

Appendix 3. Spider species collected in *Qualea multiflora* (Vochysiaceae) trees in CCPIU cerrado reserve from April 2009 to May 2010.

Family	Species
Anyphaenidae	<i>Arachosia</i> sp. <i>Teudis subrubus</i> (Petrunkevitch 1911)
Araneidae	<i>Acacesia hamata</i> (Hentz 1847) <i>Alpaida nonoai</i> (Levi 1988) <i>Alpaida truncata</i> (Keyserling 1865) <i>Alpaida albocinta</i> (Mello-Leitão 1945) <i>Alpaida</i> sp.1 <i>Araneus</i> sp.1 <i>Araneus</i> sp.2 <i>Argiope argentata</i> (Fabricius 1775) <i>Bertrana striolata</i> (Keyserling 1884) <i>Gasteracantha cancriformis</i> (Linnaeus 1758) <i>Hypognatha</i> sp. <i>Verrucosa</i> sp.1 <i>Wagneriana</i> sp.
Mimetidae	Mimetidae sp.
Miturgidae	<i>Cheiracanthium inclusum</i> (Hentz 1847)
Oxyopidae	<i>Oxyopes macroscelides</i> (Mello-Leitão 1929) <i>Hamataliwa</i> sp.1 <i>Schaenioscelis</i> sp.
Salticidae	<i>Chira thysbe</i> (Simon 1902) <i>Thiodina</i> sp.1 Freyinae sp.1 Salticidae sp.1 Salticidae sp.2
Senoculidae	Senoculidae sp.
Tetragnathidae	<i>Leucauge</i> sp.
Theridiidae	<i>Cryptachaea hirta</i> (Taczanowski 1873) <i>Anelosimus studiosus</i> (Hentz 1850) <i>Anelosimus</i> sp.1 <i>Argyrodes</i> sp. <i>Cryso pulcherrima</i> (Mello-Leitão 1917) <i>Cryso</i> sp. <i>Latrodectus geometricus</i> (Koch 1841) <i>Theridion</i> sp.1 <i>Thymoites</i> sp.
Thomisidae	<i>Aphantochilus rogersi</i> (Cambridge 1870) <i>Deltoclita</i> sp. <i>Misumenops</i> sp. <i>Onoculus</i> sp. <i>Strophius</i> sp. <i>Tmarus</i> sp.1 <i>Tmarus</i> sp.2

3. CONCLUSÃO

1. Há uma diversa e abundante fauna de predadores (formigas e aranhas) e herbívoros que forrageia em *Qualea multiflora*.
2. Há variação sazonal na abundância tanto de predadores quanto de herbívoros ao longo do ano. Formigas e herbívoros em geral são mais abundantes no início da estação chuvosa, e aranhas se tornam mais abundantes cerca de um mês depois.
3. A presença de formigas tem influência sobre a riqueza e abundância de espécies de aranhas em *Qualea multiflora*. Houve uma maior riqueza e abundância de espécies de aranhas em plantas sem formigas. No entanto, o inverso não ocorreu. A presença de aranhas não interferiu significativamente nem na riqueza e nem na abundância de espécies de formigas.
4. Formigas e aranhas exercem impacto sobre herbívoros em *Qualea multiflora* quando agem em conjunto. Em plantas nas quais ambos os tipos de predadores forragearam houve menor riqueza e abundância de herbívoros, e menor proporção de área foliar perdida por herbivoria, comparado a plantas nas quais só havia formigas ou só aranhas, ou nenhum desses predadores.
5. A presença de formigas e/ou aranhas não foi relacionada com nenhuma variável utilizada para medir o sucesso reprodutivo de *Qualea multiflora*.