Universidade Federal de Uberlândia

Instituto de Biologia

Programa de Pós-Graduação em Ecologia e Conservação de Recursos Naturais

O impacto da distribuição de ninhos de formiga e de efeitos associativos em interações formiga-planta mediadas por nectários extraflorais

Renan Fernandes Moura

2021

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

Orientador

Profª Dr. Kleber Del Claro

Uberlândia, agosto de 2021

Ficha Catalográfica Online do Sistema de Bibliotecas da UFU
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M929
2021

Moura, Renan Fernandes, 1990-
O impacto da distribuição de ninhos de formiga e de efeitos associativos em interações formiga-planta mediadas por nectários extraflorais [recurso eletrônico] / Renan Fernandes Moura. - 2021.

Orientador: Kleber Del Claro.
Tese (Doutorado) - Universidade Federal de Uberlândia, Pós-graduação em Ecologia e Conservação de Recursos Naturais.
Modo de acesso: Internet.
Disponível em: http://doi.org/10.14393/ufu.te.2021.382
Inclui bibliografia.
Inclui ilustrações.

1. Ecologia. I. Claro, Kleber Del,1965-, (Orient.). II. Universidade Federal de Uberlândia. Pós-graduação em Ecologia e Conservação de Recursos Naturais. III. Título.

CDU: 574

Bibliotecários responsáveis pela estrutura de acordo com o AACR2:

Gizele Cristine Nunes do Couto - CRB6/2091

UNIVERSIDADE FEDERAL DE UBERLÂNDIA
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ATA DE DEFESA - PÓS-GRADUAÇÃO

Programa de Pós-Graduação em:	Ecologia e Conservação de Recursos Naturais				
Defesa de:	Tese, número 72, COPEC				
Data:	trinta de agosto de dois mil e vinte e um	Hora de início:	14:00	Hora de encerramento:	18:03
Matrícula do Discente:	11713ECR006				
Nome do Discente:	Renan Fernandes Moura				
Título do Trabalho:	O impacto da distribuição de ninhos de formiga e de efeitos associativos em interações formiga-planta mediadas por nectários extraflorais				
Área de concentração:	Ecologia				
Linha de pesquisa:	Ecologia comportamental e de interações				
Projeto de Pesquisa de vinculação:	Riqueza e distribuição de interações entre plantas, formigas e herbívoros trofobiontes em vegetação de Cerrado				

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Documento assinado eletronicamente por **Alan Nilo da Costa**, **Professor(a) do Magistério Superior**, em 30/08/2021, às 17:57, conforme horário oficial de Brasília, com fundamento no art. 6º, § 1º, do Decreto nº 8.539, de 8 de outubro de 2015.

Documento assinado eletronicamente por **Jean Carlos Santos**, **Usuário Externo**, em 31/08/2021, às 10:10, conforme horário oficial de Brasília, com fundamento no art. 6º, § 1º, do Decreto nº 8.539, de 8 de outubro de 2015.

Documento assinado eletronicamente por **Diego Vinícius Anjos Silva**, **Usuário Externo**, em 01/09/2021, às 06:52, conforme horário oficial de Brasília, com fundamento no art. 6º, § 1º, do Decreto nº 8.539, de 8 de outubro de 2015.

Documento assinado eletronicamente por **Rodrigo Augusto Santinelo Pereira**, **Usuário Externo**, em 06/09/2021, às 12:11, conforme horário oficial de Brasília, com fundamento no art. 6º, § 1º, do Decreto nº 8.539, de 8 de outubro de 2015.

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Referência: Processo nº 23117.050857/2021-00 SEI nº 2946646

Agradecimentos

Agradeço à minha companheira, Drielly, por todo amor e amizade ao longo de tantos anos juntos.

Agradeço à minha mãe, Fátima, pelo grande apoio e torcida ao longo de todos esses anos em que estive na academia.

Agradeço a meu orientador, Kleber, uma pessoa e profissional excepcional que sempre me incentivou e abriu diversas portas que me permitiram trilhar meu próprio caminho e desenvolver-me ao máximo como profissional.

Agradeço a todo pessoal do nosso laboratório. Não vou citar nomes, mas todos de alguma forma me ajudaram: seja com palavras de apoio, discussões de ideias, críticas em manuscritos, ou com assistência em trabalhos de campo.

Agradeço aos integrantes do Marquis Lab e todas as fantásticas pessoas que conheci da Universidade e do Jardim Botânico do Missouri, especialmente ao Bob Marquis por tantas conversas e discussões importantes; cresci muito profissionalmente ao conhecê-lo.

Por fim, agradeço à UFU e ao Clube Caça e Pesca pela estrutura e à CAPES pelo fundamental apoio financeiro. Serei eternamente grato a todos aqueles que confiam na ciência brasileira.

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Resumo

As interações ecológicas são amplamente distribuídas na natureza e são capazes de afetar a diversificação e manutenção da biodiversidade global. Nesta tese, avaliamos como diversas variáveis ecológicas afetam a intensidade de interações mutualistas entre formigas e plantas com nectários extraflorais (NEFs), como tais interações afetam e são afetadas por interações associativas entre plantas do Cerrado, e, por fim, realizamos uma ampla revisão a fim de quantificar os impactos dos efeitos associativos entre plantas de forma mais ampla. No primeiro capítulo, avaliamos o efeito da distribuição e riqueza de ninhos de formiga, além de potenciais efeitos causados pela presença de plantas vizinhas com NEFs, sobre uma espécie de liana do Cerrado, *Smilax polyantha*. Amostramos ninhos de formigas e plantas vizinhas com NEFs no entorno de cada planta *S. polyantha*, além de medirmos sua herbivoria foliar e a produção de frutos. Observamos que a maior densidade de ninhos de formiga contribuiu para a redução da herbivoria foliar e para o aumento da produção de frutos em *S. polyantha*. Todavia, uma maior riqueza de ninhos de formiga esteve associada a maiores valores de herbivoria foliar, enquanto a diversidade de plantas vizinhas esteve associada a reduções na herbivoria e produção de frutos. Os efeitos da distribuição de ninhos de formiga e de plantas vizinhas foram, portanto, antagônicos. No segundo capítulo, testamos os efeitos da associação entre *S. polyantha* e plantas associadas (suporte) sobre a herbivoria e a produção de frutos de *S. polyantha*. Medimos a herbivoria foliar, assimetria flutuante, e produção de flores e frutos em *S. polyantha* e verificamos a presença de NEFs entre as espécies de plantas suporte. As *S. polyantha* associadas a plantas com NEFs foram mais visitadas por formigas e tiveram menor herbivoria foliar e assimetria flutuante. Plantas com NEFs podem, portanto, beneficiar outras espécies vegetais próximas e, possivelmente, impactar a estruturação de comunidades vegetais. No terceiro capítulo, realizamos uma ampla revisão qualiquantitativa a respeito da resistência associativa (RA) entre plantas. Inicialmente realizamos uma revisão histórica a respeito do uso do termo RA seguida de uma revisão qualitativa. Compilamos dados de estudos publicados em plataformas digitais e utilizamos ferramentas meta-analíticas para investigar os principais mecanismos por trás da RA em associação com uma série de variáveis ecológicas (e.g., traços vegetativos e variáveis espaciais). Por fim, nós discutimos os padrões ecológicos observados e suas implicações em práticas de controle biológico e na estruturação de comunidades. Concluímos que a intensidade e direção das interações ecológicas dependem não apenas das espécies diretamente envolvidas, mas do contexto ecológico do entorno. No atual cenário global, a preservação da diversidade é vegetal fundamental visto que a mesma está associada à manutenção da biodiversidade como um todo.

Palavras-chave: defesa indireta, facilitação, mutualismo, simbiose, susceptibilidade associativa

Abstract

Ecological interactions are widely distributed in nature and can affect the diversification and maintenance of the global biodiversity. In this dissertation, we evaluated how several ecological variables affect the intensity of mutualistic interactions between ants and plants with extrafloral nectaries (EFNs), how such interactions affect and are affected by associative interactions between Cerrado plants, and, at last, we performed a comprehensive review aiming to quantify the impact of associative effects among plants in a broader sense. In the first chapter, we evaluated the effects of ant nest distribution and richness, in addition to the potential effects caused by the presence of neighboring plant species with EFNs, on a liana plant from the Brazilian Cerrado, *Smilax Polyantha*. We sampled ant nests and neighboring plants with EFNs around each *S. polyantha*, and measured its foliar herbivory and fruit production. We observed that higher densities of ant nests contributed to a reduction of foliar herbivory and to increases in fruit production. However, higher ant nest richness was associated with higher foliar herbivory values, while the diversity of neighboring plants was associated with reductions in herbivory and fruit production. The effects of ant nest distribution were, thus, antagonistic. In the second chapter, we tested the associative effects between *S. polyantha* and support plants on the herbivory and fruit production of *S. polyantha*. We measured foliar herbivory, fluctuating asymmetry, and the fruit production of *S. polyantha*, and we verified the presence of EFNs in support plant species. *Smilax polyantha* individuals associated with plants with EFNs were more visited by ants and had lower herbivory and fluctuating asymmetry. Plants with EFNs can, thus, benefit closely distributed plants and possibly impact the structuring of plant communities. In the third chapter, we performed an extensive quali-quantitative review about associative resistance (AR) between plants. We initially performed a historical review regarding the AR term, and then we conducted a quantitative review. We gathered data from studies on online databases and used meta-analytical tools to identify and measure the main mechanisms behind AR and measure them against a series of ecological variables (e.g., plant traits, and spatial variables). At last, we discuss the patterns found and their implications for biological control practices and the structuring of communities. We conclude that the intensity and direction of ecological interactions rely not only on the directly involved species, but on the surrounding ecological context. In the current global scenario, preserving plant biodiversity is essential since it is associated with the maintenance of biodiversity as a whole.

Keywords: associative susceptibility, indirect defense, facilitation, mutualism, symbiosis

Introdução geral

As interações ecológicas são amplamente distribuídas na natureza e são organizadas em cinco grandes classes (mutualismo, comensalismo, competição, predação e parasitismo) responsáveis, em grande medida, pela diversificação e manutenção dos padrões de biodiversidade globais (Hembry e Weber 2020, Bronstein 2021). As interações entre animais e plantas são de particular interesse, visto que virtualmente todas as espécies vegetais interagem de alguma forma com animais, seja por meio de interações mutualísticas como a polinização, ou por interações predatórias como a herbivoria (Pearse et al. 2020). Diversos estudos demonstram que a herbivoria é uma pressão ecológica com força suficiente para afetar o padrão evolutivo das espécies (Marquis e Braker 1994, Marquis e Moura 2021). Em resposta às pressões dos herbívoros, as plantas evoluíram traços defensivos que podem ser genericamente caracterizados como defesas diretas ou indiretas (Price et al. 1980, Dicke e Sabelis 1988).

As defesas diretas não dependem de nenhum tipo de intermediador e podem deter ou inibir a ação de herbívoros por meio de mecanismos físicos e químicos. Os mecanismos físicos incluem, por exemplo, a presença de espinhos e acúleos, além do aumento da dureza de estruturas vegetativas como as folhas. Os mecanismos químicos, por outro lado, são caracterizados pela produção de uma miríade de metabólitos secundários tóxicos que podem ser voláteis ou não. As defesas diretas são primariamente constitutivas, portanto são continuamente expressas ao longo do desenvolvimento da planta (Boege e Marquis 2005). Por outro lado, as defesas indiretas podem ser induzidas (Zangerl e Rutledge 1996) e aumentam o fitness vegetal por meio de mediadores biológicos, geralmente através da atração ou a manipulação do comportamento de inimigos naturais dos herbívoros (Pearse et al. 2020). Embora as defesas indiretas possam envolver um maquinário vegetal químico (por meio de compostos orgânicos voláteis ou nutrientes como néctares e corpúsculos vegetais), elas são caracterizadas, em termos últimos, pela ação predatória dos inimigos naturais sobre os herbívoros. Nesse contexto, os inimigos naturais são chamados de agentes bióticos, razão pela qual as defesas indiretas também são classificadas como “defesas bióticas” (Del-Claro et al. 2016; Moura et al. 2021). Os impactos ecológicos das defesas diretas são amplamente documentados e discutidos na literatura, mas os impactos das defesas indiretas ainda são relativamente pouco estudados, especialmente fora das clássicas interações tritróficas envolvendo plantas, herbívoros e inimigos naturais (e.g., Heil 2014).

As interações entre formigas e plantas são um dos exemplos mais conhecidos de interações indiretas. A importância das formigas como agentes de defesa biótica foi popularizada a partir de meados da década de 1960 por estudos de Daniel Janzen (e.g., Janzen 1966). Em países da América Central, Janzen verificou que algumas espécies do gênero *Pseudomyrmex* nidificam em plantas do gênero *Acacia*, e, além de usarem a planta como domicílio e fonte secundária de recursos alimentares, ele observou que as formigas protegem a planta da ação de herbívoros. Dessa forma, além de se configurar como um sistema envolvendo defesa biótica, a relação entre a acácia e as formigas pode ser considerada um tipo de mutualismo, isto é, uma interação ecológica interespecífica onde ambas as espécies envolvidas se beneficiam por meio da troca de serviços ou recompensas (Bronstein 1994).

A partir das observações iniciais de Janzen, diversos outros pesquisadores voltaram seus olhares ao estudo das interações mutualísticas entre formigas e plantas. Bentley (1977), por exemplo, foi um dos primeiros a estudar experimentalmente as interações entre formigas e plantas com estruturas conhecidas como nectários extraflorais (NEF). Os NEFs são estruturas vegetais que podem ser encontradas em diversas regiões das plantas, como folhas, galhos, estípulas, pecíolos e pedicelos (e.g., Machado et al. 2008, Schoereder et al. 2010, Marazzi et al. 2013) e são distribuídas em mais de 100 famílias de plantas ao redor do planeta (Weber e Keeler 2013). Essa estrutura produz néctares ricos em açúcares (mas com pequenas quantidades de aminoácidos, lipídios e outros compostos orgânicos) capazes de atrair diversas espécies de animais como vespas, aranhas e, principalmente, formigas (Blüthgen et al. 2004, González-Teuber e Heil 2009, Bixenmann et al. 2011, Moura et al. 2021). São especialmente comuns na região Neotropical, onde, por exemplo, compõem mais de 33% das espécies lenhosas e lianas presentes nas florestas tropicais da Ilha de Barro Colorado, Panamá (Schupp e Feener 1991). Na Amazônia, até 53% das espécies lenhosas apresentam NEFs, o que corresponde a cerca de 50% do total de indivíduos (Morellato e Oliveira 1991). Já no Cerrado brasileiro, 25% de todas as espécies lenhosas possuem NEFs, o que representa mais de 30% de todos os indivíduos vegetais (Oliveira e Oliveira-Filho 1991).

Diversos estudos já demonstraram que a visitação de formigas agressivas pode reduzir o dano vegetal por herbivoria e, consequentemente, aumentar o fitness da planta (Cuautle et al. 2005, Baker-Méio e Marquis 2012, Stefani et al. 2015). Em uma meta-análise, Rosumek et al. (2009) concluiu que o fitness vegetal foi reduzido em quase 60% quando as formigas foram removidas das plantas com NEFs, enquanto Trager et al. (2010) demonstrou que a presença de formigas reduziu o dano por herbivoria em aproximadamente 60%, levando a uma produção de frutos cerca de 50% superior. No entanto, o resultado das interações entre formigas e plantas com NEFs é variável e depende de diversos fatores ecológicos (Barton 1986, Chamberlain e Holland 2009, Staab et al. 2017, Calixto et al. 2021). Especificamente, a eficiência da proteção fornecida depende de fatores como a fenologia da planta (Miller 2014), a concentração de nutrientes do néctar (Flores-Flores et al. 2018; Pacelhe et al. 2019) e a agressividade, capacidade de recrutamento e frequência de visitação das formigas (Agrawal 1998, Cuautle et al. 2005, Del-Claro e Marquis 2015, Fagundes et al. 2017).

Capítulo 1

A capacidade de recrutamento e frequência de visitação de formigas são certamente fatores fundamentais para o sucesso da proteção vegetal e são parcialmente regulados pela distribuição espacial dos ninhos das espécies. Apesar disso, a distribuição dos ninhos de formigas foi pouquíssimo apreciada em estudos envolvendo mutualismo entre formigas e plantas (Inouye e Taylor 1979, Wagner 1997). Sabemos, por exemplo, que a presença de recursos alimentares próximos aos ninhos aumenta a probabilidade de uso e o número de formigas explorando o recurso (e.g., Fewell et al. 1992, Belchior et al. 2012, Lanan e Bronstein 2013). Além disso, as plantas com NEFs afetam diretamente a distribuição espacial das formigas, pois se sabe que as formigas tendem a nidificar em locais próximos a essas plantas (Wagner e Nicklen 2010, Lanan e Bronstein 2013). A riqueza de ninhos de formiga também pode afetar as interações formiga-planta, já que as espécies de formigas visitantes dependem, ao menos em parte, da disponibilidade de ninhos. Além disso, uma elevada riqueza de ninhos de formigas pode intensificar a competição entre as espécies de formiga por acesso ao néctar extrafloral. (Blüthgen e Fiedler 2004). Apesar de haver a hipótese de que diferentes espécies de formigas poderiam se especializar na captura de diferentes espécies de herbívoros (veja Nahas et al. 2012), os estudos conduzidos indicam que a ocorrência de múltiplas espécies fornece pouco ou nenhum benefício às plantas (Miller 2007, Del-Claro e Marquis 2015).

No primeiro capítulo desta tese, portanto, examinamos como a abundância e riqueza de ninhos de formiga afeta uma espécie de planta do Cerrado que possui NEFs (*Smilax polyantha* [Smilacaceae]). Para isso, amostramos todos os ninhos de espécies mutualistas dentro de um raio de 12 m de cada planta estudada e, em seguida, medimos a herbivoria foliar e a produção de frutos de cada *S. polyantha*. Todas as plantas vizinhas com NEFs em um raio de 10 metros de cada *S. polyantha* também foram amostradas. Formulamos as hipóteses de que (i) grandes quantidades de ninhos ao redor de *S. polyantha* reduziriam a herbivoria foliar e aumentariam a produção de frutos de cada indivíduo, enquanto que (ii) altas riquezas de ninhos aumentariam a herbivoria foliar e reduziriam a produção de frutos.

Capítulo 2

Quase todos os estudos que investigaram a relação entre formigas e plantas com NEFs estavam interessados na planta hospedeira (e.g., Rosumek et al. 2009, Beaumont et al. 2016, Yamawo e Suzuki 2018), em suas formigas visitantes (Byk e Del-Claro 2011), ou na comunidade de formigas em geral (Dáttilo et al. 2014, Camarota et al. 2015, Lange e Del-Claro 2014, Madureira et al. 2018). Existe um único estudo em que se testou o efeito das defesas bióticas de plantas com NEFs em plantas do entorno (veja Jezorek et al. 2011). No estudo de Jezorek (2011), verificou-se que as plantas no entorno são beneficiadas pelo compartilhamento de formigas atraídas pelas plantas produtoras de néctar extrafloral. Essa relação indireta entre a planta produtora (vizinha) e a planta beneficiada (focal) configura-se como um caso de como resistência associativa (RA). Essa interação ocorre, especificamente, quando uma planta vizinha é capaz de reduzir, direta ou indiretamente, a herbivoria em plantas focais (Barbosa et al. 2009). A RA é, portanto, um tipo específico de facilitação, onde a planta vizinha não é beneficiada nem penalizada e a planta focal é beneficiada através de quaisquer mecanismos capazes de reduzir os danos por herbivoria.

No segundo capítulo, verificamos se a RA pode ocorrer por meio do compartilhamento de defesa biótica entre plantas, usando *S. polyantha* como espécie modelo. Por ser uma espécie de liana, *S. polyantha* pode ser particularmente suscetível à RA, pois necessita do suporte de outras plantas para evitar os herbívoros de solo e para aumentar sua exposição à luz solar (Gianoli e Molina-Montenegro 2005, Gallagher e Leishman 2012). Além disso, as lianas são particularmente sensíveis ao dano por herbivoria porque produzem folhas ricas em nutrientes (Salzer et al. 2006, Cai e Bongers 2007, Zhu e Cao 2010), e, ao mesmo tempo, possuem poucas defesas químicas contra herbívoros (Aide e Zimmerman 1990, Ødegaard 2000, Tang et al. 2012). Em campo, marcamos diversos indivíduos de *S. polyantha* e medimos a herbivoria foliar, assimetria flutuante (medida de estresse ambiental), produção de frutos, variáveis estruturais e verificamos se as plantas vizinhas à *S. polyantha* (nesse caso, plantas suporte) possuíam NEFs. Nossa principal hipótese é a de que indivíduos de *S. polyantha* associados a plantas com NEFs teriam menores valores de herbivoria e assimetria flutuante e maior produção de frutos quando comparados a indivíduos associados a plantas sem NEFs. Considerando o efeito dos NEFs sobre a visitação de formigas (Lange e Del-Claro 2014), também testamos a hipótese de que a diversidade de formigas depende da presença ou ausência de NEFs das plantas vizinhas.

Capítulo 3

Para a formulação do capítulo 2, foi necessário um estudo aprofundado a respeito da resistência associativa (RA). Assim, nos deparamos com uma rica literatura sobre o tema, porém que ainda carece de estudos aprofundados, além de apresentar considerável variação no uso de termos e em sua fundamentação teórica. Por ser um tipo de interação ecológica genérica, a resistência associativa entre duas espécies pode ser alcançada de diversas maneiras. Barbosa et al. (2009) classificam a RA a partir de dois tipos amplos de mecanismos: os bióticos e abióticos. Os mecanismos bióticos são aqueles que envolvem a ação de componentes biológicos como a produção de compostos químicos, ou a atração de inimigos naturais (e.g., formigas) pela planta focal, enquanto os mecanismos abióticos envolvem componentes ambientais, como mudanças na luminosidade e umidade ou nos nutrientes do solo. Apesar de bem estabelecida a ideia da RA, os mecanismos por trás de seu funcionamento são pouquíssimos examinados pela literatura, especialmente os mecanismos abióticos. Passados mais de 10 anos desde a última grande revisão (Barbosa et al. 2009), decidimos, no capítulo 3, promover uma nova revisão a respeito do tema. O capítulo foi dividido em duas seções. Na primeira, nós realizamos uma revisão histórica qualitativa a respeito do tema. Na segunda seção, nós realizamos um apanhado dos artigos científicos publicados acerca do tema e efetuamos diversas meta-análises de modo a medir e avaliar os principais mecanismos reguladores da RA e contrastá-los com distintas variáveis ecológicas.

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Capítulo 1

Ant nest distribution and richness have opposite effects on a Neotropical plant with extrafloral nectaries

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Capítulo submetido ao periódico Ecological Entomology

Abstract

1. Studies assessing the effects of the spatial distribution of ant nests on ant-plant mutualisms are rare, even though they could be decisive to the outcomes of such interactions. Here, we investigated how ant nest abundance and richness affected a Neotropical plant with extrafloral nectaries (EFN), *Smilax polyantha* (Smilacaceae).
2. We used baits to sample all nests of potential mutualistic ants within a 12 m radius of each plant. All neighboring plants with EFN within 10 m of each tagged plant were also sampled. We measured foliar herbivory and fruit production of each *S. polyantha*. We hypothesized that (i) high numbers of ant nests near *S. polyantha* individuals would reduce foliar herbivory and increase fruit production, and that (ii) high ant nest richness would increase foliar herbivory and reduce fruit production.
3. Results showed that plants surrounded by more ant nests had lower foliar herbivory and higher fruit production. However, ant nest richness was associated with higher foliar herbivory. Furthermore, plants producing more leaves and those surrounded by more neighboring plants bearing EFN had reduced herbivory. Despite this, *S. polyantha* had low numbers of ant nests and reduced fruit production when surrounded by high numbers of neighboring plants with EFN.
4. We suggest that the spatial distribution of ant nests and resources (EFN-bearing plants) plays an important role in ant-mediated mutualisms, where both ants and plants are likely competing for each other's services. Thus, incorporating these two variables in ecological models should provide insights into how protective mutualisms are structured.

Keywords: Ant colony, biotic defense, Brazilian savanna, facilitation, indirect interaction, symbiosis

Introduction

Mutualisms are common interspecific ecological interactions in which two species receive net benefits (reviewed by Bronstein 1994). A well-known example is the protective mutualisms between ants and plants with extrafloral nectaries (EFNs) (Rico-Gray and Oliveira 2007; Moura et al. 2021). The EFNs are structures found on different plant above-ground parts such as leaves, stems, stipules, and flower buds (e.g., Machado et al. 2008; Schoereder et al. 2010; Marazzi et al. 2013) and are distributed among at least 100 plant families worldwide (Weber and Keeler 2013). They produce a valuable food resource composed mostly of water and sugars (it may contain other organic compounds), which attracts several ant species to the producing plant (Koptur 1994; Blüthgen et al. 2004; González-Teuber and Heil 2009; Bixenmann et al. 2011).

Numerous studies have demonstrated that aggressive ants visiting plants with EFNs can decrease damage caused by herbivores and increase plant fitness (Cuautle et al. 2005; Baker-Méio and Marquis 2012; Stefani et al. 2015). For instance, Rosumek et al. (2009) concluded that plant fitness decreased almost 60% when ants were removed from plants, while Trager et al. (2010) showed that the presence of ants enhanced plant reproductive production by 49% and decreased herbivory by 62%. However, interactions between ants and EFN-bearing plants are highly variable depending on the involved species and the environmental conditions (Barton 1986; Chamberlain and Holland 2009; Staab et al. 2017; Calixto et al. 2021). The efficiency of ant protection depends on several factors such as plant phenology (Miller 2014), nectar concentration (Fagundes et al. 2017; Flores-Flores et al. 2018; Pacelhe et al. 2019), frequency of ant visitation (Cuautle et al. 2005), and ant aggressiveness and recruitment capacity (Agrawal 1998; Del-Claro and Marquis 2015). Despite the numerous studies assessing ant-plant mutualisms, two potentially important aspects were not well-explored: the role of ant nest distribution and ant nest species richness.

The distribution of ant nest distribution and plant resources may naturally affect the outcomes of ant-plant interactions. Some ant species tend to construct nests near plants producing food rewards (Wagner and Nicklen 2010; Lanan and Bronstein 2013), increasing the probability and number of foraging workers exploring the resource (e.g., Fewell et al. 1992; Belchior et al. 2012). Given this, it is expected that ant nests near plants with active EFNs should be able to recruit more individuals to feed on extrafloral nectar (Lanan and Bronstein 2013), increasing the biotic protection of plants. To our knowledge, however, the specific effects of ant nest distribution on ant-plant mutualisms were only considered twice (Inouye and Taylor 1979; Wagner 1997).

Ant nest species richness might also affect ant-plant interactions since the observed visiting ant species partially depend on the availability of nests. Although high ant nest richness may raise the chances of mutualistic ants finding *S. polyantha*, it may also allow the occurrence of many visiting species that do not provide any protection to plants (Miller 2007; Byk and Del-Claro 2010, Fagundes et al. 2017). An increased number of ant nest species should also intensify the interspecific competition for accessing plants with resources (Blüthgen and Fiedler 2004). While multiple ant species could reward plants by capturing different types of herbivores (see Nahas et al. 2012 for an example involving mutualistic ants and spiders), empirical data suggests that they provide little or no benefits to plants (Miller 2007; Del-Claro and Marquis 2015).

In the Brazilian Cerrado, more than 30% of all plant individuals and about 25% of all tree species have EFNs (Oliveira e Oliveira-Filho 1991), making it a suitable environment to study such mutualistic interactions between these plants and ants (Del-Claro and Torezan-Silingardi 2009). In this study, we aimed to quantify the effects of ant nests distribution and richness on foliar herbivory and fruit production of a native plant species bearing EFNs. Using ant nest abundance as a proxy for ant protection (see Lanan and Bronstein 2013), we hypothesized that (i) high numbers of ant nests near EFN-bearing plants would reduce foliar herbivory and increase fruit production. Conversely, we hypothesized that (ii) high ant nest richness would be associated with high foliar herbivory and low fruit production. We expect that since most visiting ant species are not mutualists (Byk and Del-Claro 2010, Fagundes et al. 2017), and heavily-protected plants are usually visited by one or few ant species (e.g., Miller 2007).

Materials and methods

Study site and plant species

We carried out the study at a natural Cerrado reserve (Clube Caça e Pesca Itororó de Uberlândia; 18°59'00.0"S 48°18'00.0"W) in Uberlândia city, Minas Gerais state, southeastern Brazil. The landscape is composed of a typical cerrado vegetation, with a predominant understory of shrubs, grasses, and perennial herbs, with trees ranging from 2–8 m in height. The region has two well-defined seasons: a rainy season occurring from October to April and a dry season from May to September (Velasque and Del-Claro 2016).

For this study, we used as a model the plant *Smilax polyantha* Griseb. (Smilacaceae) (Fig. 1d), a liana that occurs throughout the reserve. This plant has EFNs located at the base of the leaf petioles, which are mainly active when leaves are young (Figs. 1b-c). Ants such as *Ectatomma tuberculatum* (Fig. 1a) are commonly found feeding on the extrafloral nectar. At least 11 ant species from 5 subfamilies are known to visit *S. polyantha*. A single plant produces a considerable volume of extrafloral nectar—about 6.5uL a day, which contains approximately 30 calories (Pires et al. 2017).

Ant nest distribution, species identification, and visiting ants

The fieldwork was conducted three times a week from October 2017 to September 2018, in the morning (7:40-11:30h). We established nine transects of 50 m x 10 m separated from each other by at least 50 m. In the transects, we found and tagged 23 plants (using a piece of string), with a maximum size of 2 m, that presented at least three young leaves with no herbivory. We identified the young leaves by their size (maximum of 7 cm length), texture (young leaves are thin and smooth), and color (they often present a reddish coloration compared to mature leaves green) (Fig. 1c). After all plant identification and markings, we identified all ant nests within a 12 m radius from each plant. To do this, we positioned 12 baits around each plant, distributed on the ground (over a piece of white paper with 8.0 x 5.0 cm) in all four cardinal directions (north, south, east, and west of the plant). Three baits were positioned per cardinal direction: one immediately at the plant base and two others at distances of 5 m and 10 m. Baits were composed of sardine and honey (approximately 15 g). We chose this study design based on the work of Gómez and Espadaler (1998) and Yamamoto and Del-Claro (2008), who showed that many ant species do not often travel more than 10 m from their nests to acquire food resources. In our system, we would expect that *S. polyantha* individuals near ant nests would be frequently visited by ants and, hence, be well-protected against herbivores.

After positioning the baits, we waited 30 minutes to 1 hour until the ants' arrival (this time variation is due to weather conditions; at cooler and rainy periods, ants took more time to leave the nests). After the arrival of the first ants, we observed each bait for at least 30 minutes. We waited until at least one individual of each species returned to its respective nest. When we successfully found the ant nest entrance, we collected at least one ant individual and stuck a numbered stick into the ground, indicating the nest entrance. After identifying all nest entrances, we measured the distance from each ant nest entrance to *S. polyantha*.

We identified each collected ant individual (according to Baccaro et al. 2015, taxonomic key) at the Laboratory of Behavioral Ecology and Interactions (LECI) from the Federal University of Uberlândia, Brazil. We sampled a total of 394 ant nests from 25 species (see supplementary material 1). Preliminary observations, however, showed that most sampled species either do not interact with EFN-bearing plants or they perform as robbers, using the extrafloral nectar but providing no benefits to the plant. Thus, we performed all analyses using a subset of species that would have the highest potential for mutualistic impact on *S. polyantha*. To select the most appropriate ant species, we observed the ant visitation on each tagged *S. polyantha*, once a week, for 10 straight weeks, from April to June 2018. Observations lasted five minutes per plant, always in the morning periods, from 7:40 to 11:30h. After recording and identifying the number of foraging ants we concluded that, at most times, *S. polyantha* is visited by several *Camponotus* species and *Ectatomma tuberculatum* (see supplementary material 2). Ant observations also revealed that many ant genera such as *Pheidole*, *Crematogaster*, *Solenopsis*, *Pseudomyrmex*, and *Cephalotes*, either do not visit *S. polyantha* (see Pires et al. 2017) or have a minor role in protecting these plants from herbivores. That occurs due to their lack of aggressiveness and small size, as other studies suggest as well (e.g., Byk and Del-Claro 2010; Fagundes et al. 2017). This is not surprising since many studies demonstrated that plant protection depends on the identity of the visiting ant species (Palmer et al. 2008, 2010; Sendoya et al. 2009; Byk and Del-Claro 2010; Fagundes et al. 2017; Schuldt et al. 2017). Many *Camponotus* species and *Ectatomma tuberculatum* are considered efficient mutualists (Del-Claro and Marquis 2015; Fagundes et al. 2017) due to their high level of aggressiveness and abundance on plants with EFNs (Lange et al. 2013; Pires et al. 2017). Given this, we considered for this study only the effects of ant nests of species of *Camponotus* and *Ectatomma tuberculatum* (see Fig. S1).

Ant visitation

We visited each of the 23 plants once a week during September and October 2018 in the morning periods (7:40 - 11:30). During this period, we observed each plant for five minutes, recording the identity of all visiting ant species. When we found an unknown species, we collected it for subsequent identification. Taxonomical identifications were based on Baccaro's (2015) taxonomic key.

Plant measurements and neighboring plants

Immediately after mapping nest distribution, we recorded the total number of leaves of each *S. polyantha* and we randomly tagged four young and intact (no signs of herbivory) leaves (approximately one week old; see Fig. 1c) from the studied plants. The total number of leaves was recorded as we believed that variation in leaf number among individuals could influence the observed herbivory values (see Barbosa et al. 2009). After two weeks, we brought all tagged leaves to the laboratory, and we photographed them under a flat piece of translucent glass (Moura et al. 2017). From these pictures, we measured the leaf area and the amount of foliar area loss using the software ImageJ (Rasband 2016). Foliar herbivory was calculated as a proportion by dividing the mean foliar area loss by the estimated mean leaf area. From August to September 2018, we revisited each plant and recorded the number of fruits produced per individual.

In the field study, we also recorded all plant species with EFNs around each tagged *S. polyantha.* We speculated that the additional sources of extrafloral nectar would drive away potential ants that otherwise would visit tagged *S. polyantha* (reviewed by Barbosa et al. 2009, but see Vilela and Del-Claro 2018), thus we also evaluated whether the availability of other plants with EFNs would interfere with the foliar herbivory and fruit production of our focal plant species. Specifically, we recorded the neighboring plants (with at least 1 m height) from the seven most common native species within a radius of 10 m from tagged individuals of *S. polyantha*: *Caryocar brasiliense* (Caryocaraceae)*, Ouratea hexasperma* (Ochnaceae), *O. spectabilis* (Ochnaceae), *Qualea grandiflora* (Vochysiaceae), *Q. multiflora* (Vochysiaceae), *Q. parviflora* (Vochysiaceae), non-tagged *S. polyantha,* and *Stryphnodendron polyphyllum* (Fabaceae).

Statistical analyses

All statistical analyses were conducted using the R software (R Core Team 2018). We performed Generalized Linear Models (GLMs) to test the effects of ant nest abundance, richness and distance, the number of leaves, and the neighboring plants (predictor/independent variables) over *S. polyantha* foliar herbivory and the number of produced fruits (dependent variables). We applied square-root transformations to number of fruits to normalize the data. Several models were performed combining all these independent variables and we used the Akaike Information Criteria and R^2 and p-values to select the best models. In the results, we show all possible significant or nearly significant models ($P < 0.10$).

We verified statistical assumptions visually, using histograms and boxplots, and by performing formal analyses (Zuur et al. 2010). The *plot* function was used to diagnose normality and residuals distribution. Formal analyses included Shapiro-Wilk normality tests and homogeneity tests of variance performed using the *var.test* function from *stats* package (R Core Team 2018). Variables used in GLMs were tested for collinearity using the *ols_coll_diag* function from *olsrr* package (Hebbali 2018). Variance Inflation Factor values higher than 4 indicate moderate collinearity between variables and should be investigated, while values higher than 10 indicate severe collinearity and must be avoided (Hebbali 2018). Despite ant nest abundance and richness having considerably high correlation ($r = 0.60$, $P = 0.002$, D.F. = 21), collinearity analysis revealed low values of Variance Inflation Factor (max value = 2.57), so we proceeded using all variables in our GLM models (see results).

Results

Ant nest distribution

We found 117 nests of mutualistic ant species near 23 *S. polyantha* plants across nine studied transects. The sampled nests comprised five ant species of *Camponotus* and one species of *Ectatomma* (Table 1; see Materials and Methods for further details). All species were directly observed on *S. polyantha*, except *Camponotus renggeri*, which was not recorded on plants probably due to its nocturnal foraging activity (Del-Claro and Oliveira 1999; Anjos et al. 2017).

All sampled nests occurred at distances that varied between 0.3 to 11.7 m (5.9 ± SE 0.3) from tagged plants. The mean percentage of foliar herbivory per plant varied from 0.02% to 17% (3.7% ± SE 0.01) and the number of leaves per plant varied from 24 to 224 (87.4 ± SE 12.9). Regarding the number of neighboring plants with EFNs, we found 12 to 47 individuals (at least 1 m height) around each plant (Table 1).

Ant visitation

Ant nest abundance and richness had overall small effects on ant visitation. Although we found a positive trend between ant nest abundance and the total number of ants found on the plants, the relationship was not significant ($F_{1,21} = 3.80$, $R^2 = 0.15$, $P = 0.065$). We found no link between ant nest richness and the number of visiting ant species per focal plant of *S. polyantha* ($F_{1,21} = 0.14$, $R^2 = 0.007$, $P = 0.71$). There was a positive non-significant trend between the abundance of neighboring plants with EFNs and the number of visiting ant species ($F_{1,20} = 4.13$, $R^2 = 0.17$, $P = 0.056$). We found no association between the abundance of plants with EFNs and ant visitation ($F_{1,20} = 2.43$, $R^2 = 0.11$, $P = 0.135$).

Foliar herbivory models

In Table 2 we kept only significant or closely significant models, and since ant nest distance was not significant in our models (see Table S1 and Fig. S2 for details), we omitted this variable from the models presented below.

According to the performed GLMs, the two most complete models (nest abundance+nest richness+EFN neighbors and nest abundance+nest richness+leaf number+EFN neighbors, see Table 2) best explained the observed foliar herbivory according to the AIC and coefficient of determination (R^2) values. Even though the complete model (nest abundance+nest richness+leaf number+EFN neighbors) had the lowest AIC and the highest R^2 values, the second one (nest abundance+nest richness+EFN neighbors) had similar R^2 values: a difference of only 0.03 between these models (Table 2). While the complete model explained 54% of the variation in foliar herbivory, the second most complete model explained 51% of its variation. All independent variables from the significant models above had negative associations with foliar herbivory, except ant nest richness (Table 2). We also observed that although ant nest abundance and richness had opposite effects on these models, there was a significant positive relationship between these two variables ($F_{1,21} = 12.08$, $R^2 = 0.37$, $P = 0.002$).

Fruit set models

A complete model using the number of fruits (dependent variable) and a set of independent variables (ant nest abundance, ant nest richness, ant nest distance, leaf number, and EFN neighbors) revealed non-significant results ($F_{1,17} = 1.88$, $R^2 = 0.36$, $P = 0.15$). However, we observed certain significant patterns when using independent variables separately. There was a negative association between the number of neighboring plants with EFNs and the number of ant nests around each *S. polyantha* ($F_{1,21} = 6.07$, $R^2 = 0.22$, $P = 0.022$; Fig. 2a). We also observed that the number of fruits produced per focal plant of *S.*

polyantha was positively associated with ant nest abundance ($F_{1,20} = 6.07$, $R^2 = 0.23$, $P = 0.023$; Fig. 2b) and negatively associated with the number of neighboring plants ($F_{1,21} = 4.59$, $R^2 = 0.18$, $P = 0.044$; Fig. 2c). We found no relationship between ant nest richness and fruit production ($F_{1,21} = 1.76$, $R^2 = 0.08$, $P = 0.19$; Fig. 2d).

Discussion

We observed opposite effects of ant nest abundance and nest richness on foliar herbivory in *S. polyantha*, an extrafloral-bearing plant. As stated by our first hypothesis, ant nest abundance was negatively associated with foliar herbivory and positively associated with fruit production. As for our second hypothesis, ant nest richness was positively associated with foliar herbivory, as expected, but we observed no association of it with fruit production. Ant nest abundance and nest richness themselves partially explained the observed patterns of foliar herbivory, but the best models included the number of leaves per plant and the number of neighboring plants. We also observed that the number of neighboring plants was negatively associated with fruit production, suggesting that EFNs-bearing plants may compete for ant services. Lastly, we found no association between the number of visiting ant species of *S. polyantha* and ant nest richness, suggesting that environmental filters might prevent some ant species from exploiting *S. polyantha* resources.

Ant nest abundance may affect *S. polyantha* herbivory and fruit production by increasing ant visitation. Other studies already demonstrated how ants forage and manage recruitment when dealing with valuable resources. For instance, ants can regulate their recruitment capability according to the resource distribution and quality (e.g., Holldobler and Wilson 1990; Robson and Traniello 1998; Belchior et al. 2012; Pacelhe et al. 2019). Thus, ant nests in contact with valuable food resources may spend high numbers of foragers (Holway 1998), reducing herbivory damage and increasing the fruit production of plants with EFNs

(Cuautle et al. 2005; Rosumek et al. 2009; Del-Claro and Marquis 2015; Del-Claro et al. 2016). The observed increase in fruit production is of particular importance since true mutualisms require gains in fitness (Heil 2008).

We found no association between ant nest richness and the number of visiting ant species on *S. polyantha*. This result does not support the idea that plant species-rich environments should benefit EFN-bearing plants (Ribeiro et al. 2018). Environmental filters may prevent the local diversity of ant nests to be translated into the observed visiting ant species of *S. polyantha*. Specifically, we suggest that competition for extrafloral resources among ant species might prevent weak competitors from accessing resources (Blüthgen and Fiedler 2004). This argument is sustained in our study by the fact that the main visitors of *S. polyantha* were *Camponotus* species (supplementary material 2), which are considered a group of aggressive and territorial ants (Fagundes et al. 2017; Lange et al. 2019). Dáttilo et al. (2014) found that most plants bearing EFNs had few dominant ant species, arguing that this could be occurring due to competition effects. Miller (2007) showed that *Crematogaster* and *Liometopum* ants never occurred simultaneously on the same plant and that *Liometopum*, the superior competitor, tends to occur on plants when they are offering better food resources. In fact, multiple aggressive ant species seldom occur, simultaneously, on the same resource for long periods, as dominant ant species can exclude weak competitors from high-quality resources and more productive habitats (Yu and Davidson 1997; Flores-Flores et al. 2018). Even when ant competitors occur on the same plant, they tend to explore distinct parts of it. For instance, a dominant species can occur in a higher canopy, while a subordinate can only explore the lower canopy (Ribeiro et al. 2013). Interspecific competition might be distracting EFN-visiting ants from the presence of herbivores, increasing herbivory; in fact, we observed three cases of aggression between *Camponotus* and *Ectatomma* on *S. polyantha* individuals (personal observation). Although experimental studies are needed to clarify this matter, our study shows that species-rich plots do not necessarily increase the number of EFN-visiting ant species on plants.

We expected that *S. polyantha* individuals with high numbers of neighbors (with EFNs) would have high values of herbivory as the resource offered by these neighbors could drain potential visiting ants of *S. polyantha* (see Vilela and Del-Claro 2018). Many studies found positive relationships between tree diversity and foliar herbivory, as diverse environments may provide a plethora of resources for generalist herbivores (Jactel and Brockerhoff 2007; Joshi et al. 2008; Unsicker et al. 2008, Schuldt et al. 2010). We found, however, a negative association between foliar herbivory and the abundance of neighboring plants (see Barbosa et al. 2009 and Salazar et al. 2013). Since the potential damage caused by herbivorous insects is limited, focal *S. polyantha* plants surrounded by dense vegetation might be benefited by dilution or other associational effects between plants (Barone 2000; Otway et al. 2005; Dyer et al. 2007; Barbosa et al. 2009; Hambäck et al. 2014), resulting in decreased levels of foliar loss per individual. Dilution effects also explain why *S. polyantha* with increased leaf numbers presented low herbivory levels, although we cannot discredit that plants with many leaves may also have high numbers of EFNs, which would increase ant recruitment (e.g., Dáttilo et al. 2014; Lange et al. 2017; Queiroga and Moura 2017). The influence of neighboring plants on fruit production was, however, negative. Even though we cannot assure a causal correlation between these variables, a plausible explanation would be competition (e.g., for water or sunlight) between focal *S. polyantha* and neighboring plants. Our results, nonetheless, suggest that neighboring plants might be draining potential ant nests that would otherwise be serving focal *S. polyantha* (see Fig. 2a). Since extrafloral nectars constitute a relevant complementary food source to ants (Byk and Del-Claro 2011), neighboring plants producing more nutritious nectars than *S. polyantha* should not only attract more ants (see Alves-Silva and Del-Claro 2013; Pacelhe et al. 2019) but also interfere with nesting site selection (Wagner and Nicklen 2010; Lanan and Bronstein 2013).

We did not find a consistent effect of ant nest distance on foliar herbivory as this variable was not explicative in our statistical models. Although the ant nest distance from plants with EFNs is not associated with ant visitation for some ant species (see Mody and Linsenmair 2003), we hypothesize that the distancing considered in this study (up to 12 m from nests) were not enough to interfere with the outcomes of ant-plant interactions. While some researchers recorded that most ant species can travel no more than 10 m carrying food resources (Gómez and Espadaler 1998; Yamamoto and Del-Claro 2008), recent studies showed that some ant species traveled for distances farther than 100 m (e.g., Grüter et al. 2018). Thus, a study considering farther distances between nests and plants might achieve different results. Alternatively, the presence of litter might be acting as a barrier that affects the movement of ants (see Farji-Brener et al. 2004), masking the effects of resource distancing.

Ant-plant mutualisms are usually generalized associations regulated by the effectiveness of shared services and resources between guilds (Bronstein 2021). Despite its considerable context-dependency (e.g., Baker-Méio and Marquis 2012), it is well-established that mutualistic ants can have significant and positive effects on plant fitness and evolution (Rosumek et al. 2009). We showed that the spatial distribution of ant nests and plants is associated with the effectiveness of a protective mutualism and that both ants and plants are likely competing for each other's services. The consequences of those interactions are complex and evoke distinct responses of plant features such as foliar herbivory and fruit production. The effects of nest distribution and ant richness are rarely considered, and we believe these variables could help researchers understand why some studies had shown relative discrepancies concerning these interactions (e.g., Barton 1986; Fagundes et al. 2017).

To clarify how mutualistic ant-plant interactions are formed and sustained, it is necessary to understand how mutualistic ant species interact with each other and how ant nests, in addition to the community of EFNs-bearing plants, are spatially and temporally distributed in natural environments.

Acknowledgements

We thank Robert J. Marquis, Eva Colberg, Miguel Chaves-Fallas, Estefania Fernandez, Jared Chauncey, Diego Anjos, Rodrigo Pereira, and Drielly Queiroga for comments and suggestions on earlier versions of this manuscript. RFM thanks the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), code 001, for funding.

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Tables

Table 1. The number of ant nests and the most abundant neighboring plant species with extrafloral nectaries found near tagged *Smilax polyantha* plants. Ant nests and neighboring plants were recorded within 12 and 10 meters away, respectively, from each tagged plant. Data between parentheses represent the relative abundance (%) of ant nests.

Ant species	Number of nests	Mean nests/*Smilax*
Camponotus crassus	58 (50)	2.70
Camponotus sp.1	25 (21)	1.17
C. blandus	15 (13)	0.91
Ectatomma tuberculatum	13 (11)	0.61
C. melanoticus	4 (3)	0.17
C. renggeri	2 (2)	0.09
Total	117	5.65*

EFN neighbor species	Number of individuals	Mean neighbor/*Smilax*
Qualea multiflora	110 (18)	4.78
Stryphnodendron polyphyllum	104 (17)	4.52
Smilax polyantha	89 (14)	3.87
Q. parviflora	78 (12)	3.39
Ouratea spectabilis	72 (12)	3.13
Caryocar brasiliense	71 (11)	3.09
O. hexasperma	67 (11)	2.91
Q. grandiflora	31 (5)	1.35

Total	622	27.04

*Notice that the number of nests per plant is higher than the expected for a total of 117 sampled nests. That occurred because some nests were near to more than one plant.

Table 2. GLMs results for foliar herbivory regarding several independent variables associated with the extrafloral nectar-producing plant, *Smilax polyantha*. The following variables indicate: Lea = leaf number, Nei = EFN neighbors, Nes = nest abundance, and Ric = nest richness. Ant richness was the only variable positively related to foliar herbivory (see asterisks). Bold values indicate significant models (α = 5%). For simplicity, we removed the ant nest distance variable since it was not significant in any model.

Model β				F	R^2	D.F	P	AIC
Nes								
-0.02				3.71	0.15	21	0.07	-39.84
Nes	+ Lea							
-0.02	-0.04			2.92	0.23	20	0.08	-39.98
Nes	+ Ric							
-0.03	-0.2			6.59	0.39	20	**0.006**	-45.73
Nes	+ Ric	+ Lea						
-0.03	0.19	-0.02		4.47	0.41	19	**0.015**	-44.38
Nes	+ Lea	+ Nei						
-0.03	-0.07	-0.006		3.94	0.40	18	**0.025**	-48.92
Nes	+ Ric	+ Nei						
-0.04	0.26	-0.005		6.15	0.51	18	**0.005**	-46.92
Nes	+ Ric	+ Lea	+ Nei					
-0.04	0.14	-0.06	-0.006	4.9	0.54	17	**0.008**	-52.68

Figure legends

Figure 1. Overview of *Smilax polyantha* (Smilacaceae) and a visiting ant. (A) An *Ectatomma tuberculatum* ant visiting a *S. polyantha* plant, (B) a drop of extrafloral nectar produced by the extrafloral nectary, (C) a nectar-producing young leaf, and (D) an adult specimen of *Smilax polyantha*.

Figure 2. Linear regressions associating the ant nest abundance around *Smilax polyantha* plants and their fruit production with several independent variables. The number of neighboring plants with extrafloral nectaries negatively affected the ant nest abundance around *S. polyantha* (a), which ultimately reduces fruit production (c). Conversely, ant nest abundance increased fruit production in *S. polyantha* (b). Ant nest richness had no effect on fruit production (d) considering $\alpha = 0.05$. We applied square root transformation on fruit production to normalize the data.

Figures

Figure 1

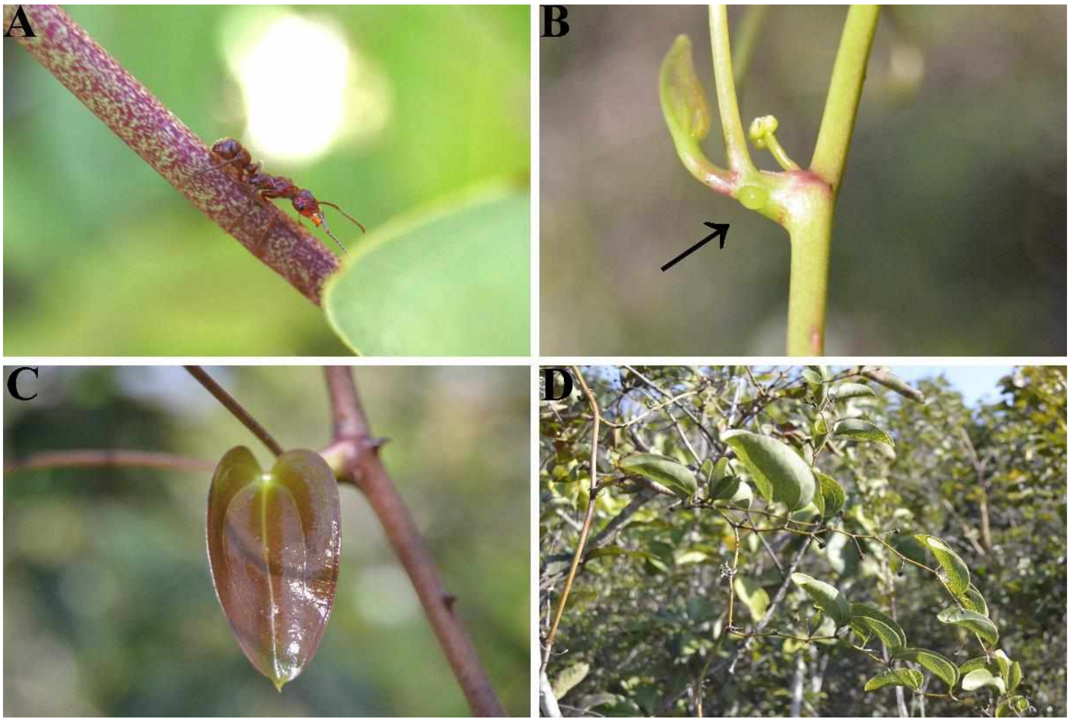
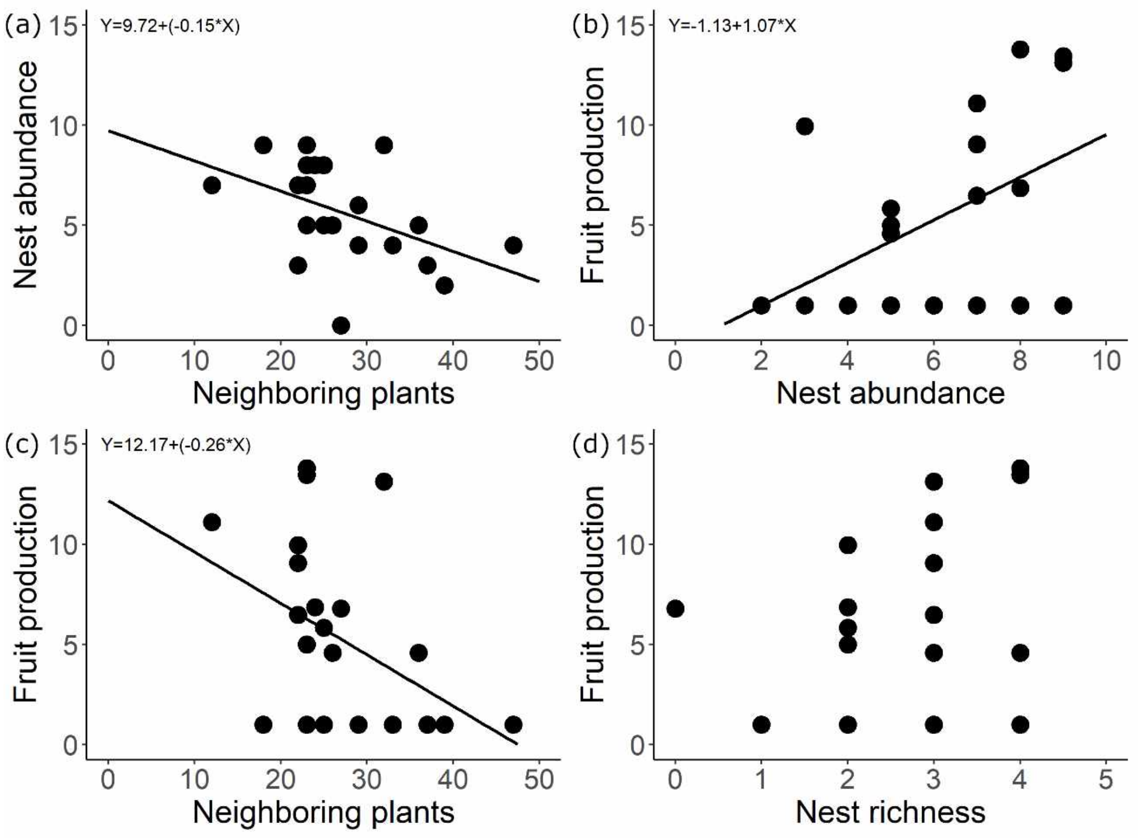


Figure 2


(a)
Y=9.72+(-0.15*X)
Nest abundance
Neighboring plants
0
5
10
15
0
10
20
30
40
50
(b)
Y=-1.13+1.07*X
Fruit production
Nest abundance
0
5
10
15
0
2
4
6
8
10
(c)
Y=12.17+(-0.26*X)
Fruit production
Neighboring plants
0
5
10
15
0
10
20
30
40
50
(d)
Fruit production
Nest richness
0
5
10
15
0
1
2
3
4
5

Capítulo 2

Associational resistance effects mediated by extrafloral nectaries of plants from the Brazilian Cerrado

Renan Fernandes Moura and Kleber Del-Claro

* Referências formatadas de acordo com o periódico Journal of Ecology

Abstract

Associational resistance (AR) is a type of positive interaction in which a plant suffers less damage caused by herbivores due to its association with a protective plant. In this study, we evaluated whether supporting plants with extrafloral nectaries can share their biotic protections with a climbing plant, *Smilax polyantha* (Smilacaceae). We sampled 45 individuals of *S. polyantha,* recorded its respective supporting plant species and whether it had or not extrafloral nectaries. From *S. polyantha* we measured foliar herbivory, fluctuating asymmetry (measure of environmental stress), and flower and fruit production. We also examined the ant visitation and composition of *S. polyantha* and whether they changed according to its type of supporting plant (with or without extrafloral nectaries). We found that supporting plants with EFNs indirectly benefit *S. polyantha* by sharing mutualistic ant species. When supporting plant species had extrafloral nectaries, *S. polyantha* had a higher number of visiting ants and ant richness, lower foliar herbivory, and fluctuating asymmetry values, and a distinct composition of visiting ant species. Despite this, we have not observed differences in fruit production between the two groups of *S. polyantha*. Plants with extrafloral nectaries may benefit other plant species at local scales and potentially affect the structure of plant communities.

Keywords: indirect defense, facilitation, mutualism, nurse effect, simbiosis

Introduction

Interactions among plants are considered one of the main ecological drivers of plant communities (Bronstein 2009, Callaway 1995). Although many of these interactions are considered negative to the involved parties (e.g., competition), there are also facilitation mechanisms involving several species (Brooker et al. 2008). Associational resistance (AR) is a type of positive interaction in which a plant suffers less damage caused by herbivores due to its association with a protective plant (Pfister and Hay 1988, Hambäck et al. 2000, Stiling et al. 2003, Barbosa et al. 2009). Neighboring plants can make the herbivore's search for its host plants difficult (Bell 1990) or may promote host plant protection by providing physical (Gutiérrez and Squeo 2004), chemical or biotic defenses (Barbosa et al. 2009).

Biotic defenses of plants usually involve vegetative structures that increase the abundance of polyphagous predators that control the damage caused by herbivores (Hambäck et al. 2000). Mutualistic interactions between ants and plants with extrafloral nectaries (EFNs) represent an example of biotic defense (see Del-Claro et al. 2016). EFN is a plant structure that secretes sugary substances consumed by arthropods, including several ant species (Koptur 1994, Blüthgen et al. 2004, González-Teuber and Heil 2009). Aggressive ants may prey or remove the arthropod herbivores from plants, reducing the plant damage and increasing fruit production (Cuautle et al. 2005, Rosumek et al. 2009).

Most studies investigating interactions between ants and EFN-bearing plants aimed to test interaction effects on target plants (e.g., Rosumek et al. 2009, Beaumont et al. 2016, Yamawo and Suzuki 2018), the directed involved ants (Byk and Del-Claro 2011) and the ant community, in general (Dáttilo et al. 2014b, Camarota et al. 2015, Lange and Del-Claro 2014, Madureira et al. 2018). However, there is only one study that addressed how these mutualistic plants affect other individual plants in the neighborhood (see Jezorek et al. 2011). From the AR perspective, EFN-bearing plants could induce indirect biotic defense, through the attraction of ants, on support plants, especially when the involved parties are in direct contact.

In this study, we aimed to verify whether the associational resistance occurs on interactions between a focal plant and support plants with and without EFNs, in natural conditions. To achieve this goal, we used as a model *Smilax polyantha* (Smilacaceae), a liana with EFNs that is often observed climbing on other plants in a Brazilian Cerrado. Lianas may be particularly susceptible to associational resistance interactions as they need other plants for physical support and thus receive sufficient amount of sunlight and protection from ground herbivores (Gianoli and Molina-Montenegro 2005, Gallagher and Leishman 2012). In addition, lianas produce nutrient-rich leaves—especially in nitrogen (Salzer et al. 2006, Cai and Bongers 2007, Zhu and Cao 2010), but have low levels of chemical foliar defenses, making them more vulnerable to the attack of herbivores (Aide and Zimmerman 1990, Ødegaard 2000, Tang et al. 2012).

To understand the effects of support plants on of *S. polyantha*, we measured the foliar herbivory, fluctuating asymmetry (FA) – a measure of environmental stress –, fruit production, and physical attributes of *S. polyantha*. We also recorded ant visitation on *S. polyantha* individuals supported by EFN-bearing plants and plants without EFNs. We hypothesized that *S. polyantha* individuals supported by EFN-bearing plants will experience distinct values of foliar herbivory, fruit production, and FA in comparison to individuals supported by plants without EFNs. Since EFNs affect the community of ants (Lange and Del-Claro 2014), we also hypothesized that the visiting ant species of *S. polyantha* will vary according to their supported plants. We predicted that *S. polyantha* individuals supported by plants bearing EFNs will have lower foliar herbivory and FA, increased production of inflorescences and fruits, and higher ant richness and visitation than the group supported by plants without EFNs, as the ant visitation of mutualistic ants is strongly associated with the amount of nectar produced by these plants (Fagundes et al. 2017).

Materials and methods

Study site and plant species

The study was carried from October 2017 to August 2018 at natural Cerrado reserve – Clube Caça e Pesca Itororó de Uberlândia; 18°59'00.0"S 48°18'00.0"W) located at Uberlândia city, Minas Gerais state, south-eastern Brazil. This reserve is a private conservation entity, with more than 400 ha of Cerrado vegetation (Vilela et al. 2014). The predominant vegetation type is a *sensu stricto* cerrado (Brazilian Savanna), with an understory composed of shrubs, grasses, and perennial herbs and most trees ranging from 2–8 m height. The region's climate is divided into a rainy season that lasts from October to April and a dry season that occurs from May to September (see Oliveira and Marquis 2002).

Plant sampling

At the reserve, we established 11 transects of 50 m x 10 m separated from each other by at least 50 m. At all transects, we marked 45 *S. polyantha* individuals that had at least three young leaves with no signs of herbivory that were in direct contact with support plants. We fixed a piece of string around the undamaged young leaves that we identified according to their size, texture, and color. To analyze the potential influence of these interactions, we recorded the support species in which *S. polyantha* was attached to and observed whether they presented EFNs or not. Then, we stablished two *S. polyantha* groups: the first group included *S. polyantha* supported by EFN-bearing plants, and the second group included *S. polyantha* supported by plants without EFN.

Support plants with EFNs included individuals from nine species: *Banisteriopsis malifolia* (Malpighiaceae), *Caryocar brasiliense* (Caryocaraceae), *Eriotheca gracilipes*

(Malvaceae), *Ouratea hexasperma* (Ochnaceae), *O. spectabilis* (Ochnaceae), *Qualea grandiflora* (Vochysiaceae), *Q. multiflora* (Vochysiaceae), *Q. parviflora* (Vochysiaceae), and *Stryphnodendron polyphyllum* (Fabaceae). After six months, we collected three to five leaves of each *S. polyantha* that were physical contact with its support plant. We believe the collected number is sufficient to have an accurate evaluation of its herbivory values since *S. polyantha* does not produce high numbers of leaves ($\bar{x}$ = 87.35 ± SD 62.23). Furthermore, we only collected young leaves from the intersection point between the plants, so we had few leaves available to collect.

Foliar herbivory and fluctuating asymmetry

In the laboratory, we took pictures of all collected leaves under a transparent glass plate with a ruler positioned beside it as a measuring reference (see Ivanov et al. 2015, Alves-Silva and Del-Claro 2016, Moura et al. 2017). All measurements from pictures were performed using the Image J software (Rasband 2016). We calibrated the software to 0.01 mm accuracy (see Cornelissen and Stiling 2005) and then measured the foliar area, the amount of foliar loss (herbivory), and the width of each leaf side starting from the midrib to each of its blade edges (used to calculate the fluctuating asymmetry). Since leaf size varied among all sampled plants, we calculated the mean proportional leaf loss of each plant dividing the mean foliar area loss by the mean leaf area of the collected leaves.

Fluctuating asymmetry (FA) represents small, random variations within a bilateral axis (left-right sides) that deviates from perfect symmetry (Palmer 1994). FA can be caused by several environmental issues such as pollution, luminous stress, and for plants, the foliar damage caused by herbivores (Hódar 2002, Puerta-Piñero et al. 2003, Moura et al. 2017). Currently, FA is being used as a reliable measure of developmental stability, indicating whether a population is under potential environmental stress or not (reviewed by Beasley et al. 2013). After measuring each side of the leaves, we applied the following formula:

$$\frac{\sum\left[\frac{|R_i - L_i|}{(R_i + L_i)/2}\right]}{N}$$

where *R* is the right side and *L* is the left side of the same leaf, and *N* represents the total number of leaves measured per plant. We divided the difference between leaf sizes by the average leaf size $(R + L)/2$ to control for size-scale effects, as FA may be size-dependent (Cornelissen and Stiling 2005, Alves-Silva and Del-Claro 2016, Miljković et al. 2018). Although FA is diffused throughout nature, there are other types of symmetries, such as directional asymmetry (DA) or antisymmetry (AS) (Graham et al. 2010), and they should be evaluated. While FA is induced and enhanced by environmental and biotic/abiotic factors, including foliar damages caused by herbivores (Silva et al. 2016, Moura et al. 2017, Telhado et al. 2017), DA and AS are mainly caused by genetic factors (Graham et al. 2010). In DA, one of the trait sizes is always greater than the other, which means that a histogram may show skewed data distribution when sizes are subtracted. AS depicts a scenario where a given population presents a bimodal distribution, hence, high values of both $R > L$ and $L > R$ measurements are commonly observed and may also be evident in a histogram. On the other hand, a plant population with FA presents random and small variations between its leaf sides that are normally distributed. To analyze the potential presence of these three types of symmetry, we performed histograms to visually inspect our data.

Ant visitation

After sampling foliar herbivory and FA, we visited each of the 45 plants weekly, during September and October 2018 in the morning periods (7:40 - 11:30). During this period, we observed each plant for five minutes and recorded the species identity and total number of visiting ants. When we found an unknown species, we collected it for subsequent identification. Taxonomical identifications were based on Baccaro's (2006) entomological key.

Statistical analysis

Although we were only interested in the effects of EFNs of support plants on our target species, structural differences (e.g., height and canopy size) among support plants (with and without EFNs) could affect *S. polyantha* attributes (e.g., foliar herbivory and fruit production). Thus, we measured the canopy size (length and width), plant height, and stem diameter (15 cm from the ground) of all support plants (with and without EFNs) and then we conducted a Principal Component Analysis (PCA) to create an index that accounted for the total variance explained by these variables combined (Bro and Smilde 2014, Moura et al. 2017). Using the obtained values, we performed a Mann-Whitney test to seek differences between groups using a new variable called "structural complexity" (Alves-Silva and Del-Claro 2014).

We re-measured a leaf subset of 32 plants and performed a correlation test between using the original and the re-measured R and L difference to examine how comparable and related the variables were (Hódar 2002, Moura et al. 2017). This procedure allowed us to check whether our measurements were accurate enough to allow the subsequent statistical procedures without measurement errors (Yezerinac et al. 1992, Cornelissen and Stiling 2005). To rule out DA, we performed a one sample Student's t-test using the R minus L measurements to see whether the obtained values deviated from zero. A significant result indicates the presence of DA in *S. polyantha* leaves. To investigate AS, we subjected the R minus L measurements to a normality test together with the visual examination in a histogram, which might reveal bimodality, an indicative of AS (Alves-Silva and Del-Claro

2016). Once these tests were not statistically significant, FA could be considered the type of asymmetry found in *S. polyantha* leaves.

We used sets of GLMs to test the effects of plants groups and ant recruitment and richness on plant traits. To evaluate the effects of support plants (with and without EFNs) on *S. polyantha*, we performed GLMs on foliar herbivory, FA, the number of inflorescences and fruit production per inflorescence, and the abundance and richness of visiting ants. We performed a GLM between foliar herbivory (independent variable) and FA (dependent variable) to analyze the effect of foliar herbivory on FA. Afterward, we conducted an ANCOVA to evaluate whether the FA values between the two plant groups (partner plant with and without EFNs) differed, using the herbivory values as a covariate (e.g., Moura et al. 2017). On another set of GLMs, we tested whether ant recruitment and ant richness affected foliar herbivory, number of inflorescences and fruit production per inflorescence. Finally, we conducted two binomial logit regressions to assess whether the ant visitation and richness affected the probability of *S. polyantha* in producing fruits.

We analyzed differences in species composition of visiting ants of the two groups of paired plants by performing an analysis of similarities with 999 computed permutations (ANOSIM; see Clarke 1993, Antoniazzi et al. 2019). Then, we used the Bray-Curtis distance transformation to graphically expose the results in a non-metric multidimensional scaling (NMDS). We also performed a similarity percentage breakdown (SIMPER), with 999 computed permutations, between the two plant groups to identify what ant species had greater weight when forming the functional groups (Neves et al. 2013).

All statistical assumptions were verified according to Zuur et al. (2010). Data normality was assessed by using boxplots, histograms, and Lilliefors normality tests. All tests were performed in the R statistical software version 4.0.0 (R Core Team 2018). Variance homogeneity was assessed by using the function “var. test” from the “stats” package. The “InfluencePlot” function from the “car” package (Fox and Weisberg 2018) and the “chisq.out.test” function from the “outliers” package (Dixon 1950) were used to identify, analyze, and remove possible outliers.

Results

All variables combined included in the PCA explained 81.3% of the total variance observed. Since we observed no differences regarding this variable concerning the two groups of support plants ($U_{1,44} = 216$; $P = 0.61$), we assumed that both groups had similar physical attributes and any variation found can be accounted as an effect of EFNs.

Foliar herbivory and fluctuating asymmetry

Our correlation analysis between leaf side (*L* and *R*) measurements revealed a 96% match (n = 32). Therefore, we considered that measurements to be accurate. DA was not significant ($t_{1,32} = 0.73$; $P = 0.47$) and we did not observe any sign of AS during our exploratory analysis. We observed a significant association between *S. polyantha* foliar herbivory and FA ($F_{1,42} = 18.76$; $R^2 = 0.31$; $P < 0.001$).

Associational resistance effects

There was a significant difference between the two plant groups (support plants with and without EFNs) concerning the FA of *S. polyantha* leaves ($F_{1,43} = 6.21$; $R^2 = 0.13$; $P = 0.02$), where *S. polyantha* supported by plants with EFNs had lower values of FA ($\bar{x} = 0.015 \pm 0.006$) in comparison to plants without EFNs ($\bar{x} = 0.029 \pm 0.027$; Fig.2a). We also observed that *S. polyantha* supported by plants with EFNs had lower values of foliar herbivory (leaf loss proportion) in comparison with plants without EFNs ($\bar{x} = 0.014 \pm 0.026$; $\bar{x} = 0.036 \pm 0.04$; $F_{1,43} = 10.83$; $R^2 = 0.20$; $P = 0.002$; Fig.2b). However, the ANCOVA revealed differences between the two plant groups when controlling for the effects of foliar herbivory

($F_{1,42}$ = 5.13; P = 0.028; Fig. 3), meaning that FA was not only caused by the foliar loss experienced by *S. polyantha*. The inflorescence production between the two groups was not significant ($F_{1,43}$ = 3.14; R^2 = 0.07; P = 0.083; Fig. 2c), neither the number of fruits/inflorescence ($F_{1,43}$ = 0.002; R^2 < 0.001; P = 0.96; Fig. 2d). *S. polyantha* supported by plants with EFNs had significant higher ant recruitment ($F_{1,43}$ = 5.34; R^2 = 0.11; P = 0.026; Fig. 2e) and richness ($F_{1,43}$ = 4.18; R^2 = 0.09; P = 0.047; Fig. 2f) than plants without EFNs.

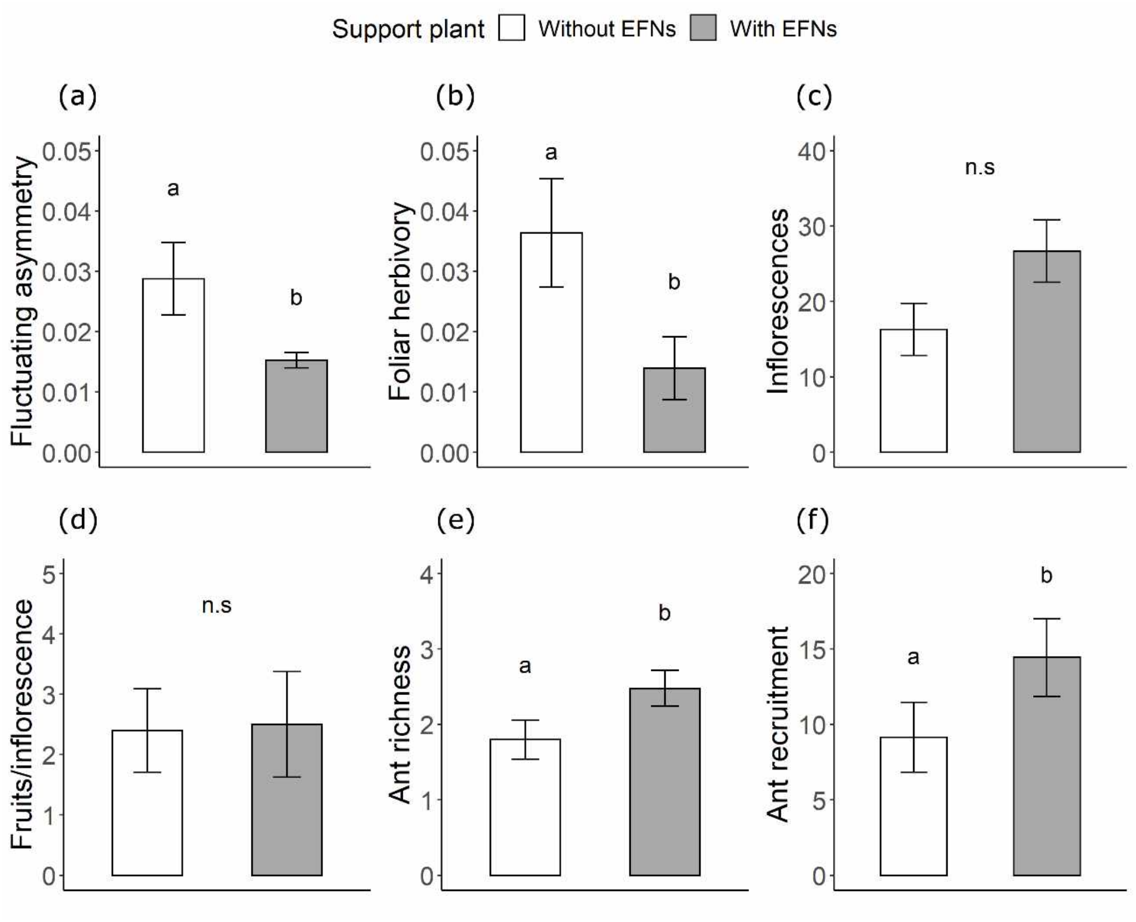


Figure 2. GLM analyses results among several variables between two groups of *Smilax polyantha* and its support plants. *S. polyantha* plants supported by plants with extrafloral nectaries (NEFs) had decreased fluctuating asymmetry (a) and foliar herbivory (b) and increased ant richness (e) and recruitment (f). There were no differences regarding the number of produced fruits/inflorescence (d) and the absolute number of inflorescences (c). Letters "a"

and “b” denote significant differences between treatments while “n.s” indicate non-significant comparisons, both according to $\alpha = 5\%$. Notice that most y-axis exhibit distinct scales.

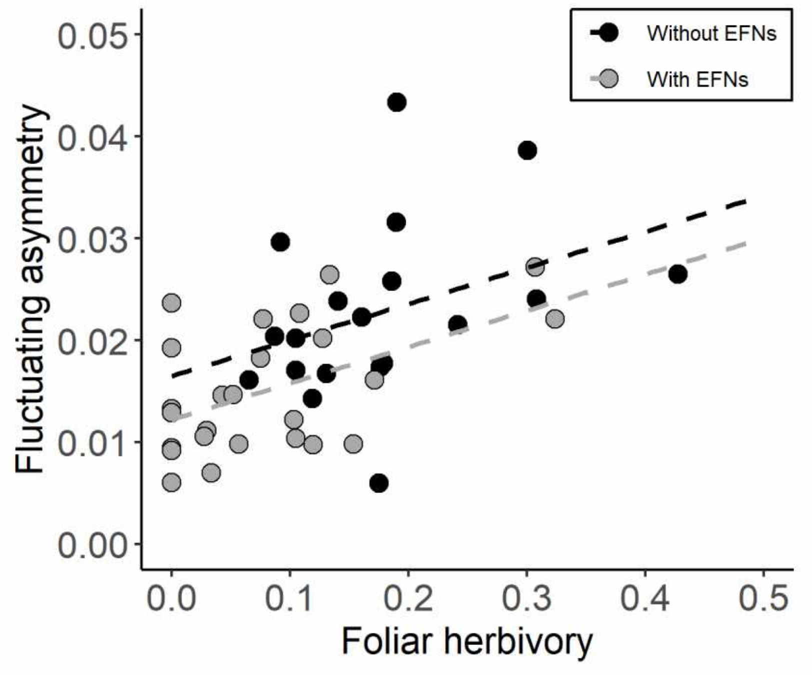


Figure 3. Graph showing ANCOVA results between two groups of *Smilax polyantha* plants (supported by plants with and without extrafloral nectaries – EFNs). *S. polyantha* supported by plants without EFNs (black) had higher fluctuating asymmetry than *S. polyantha* supported by other plants bearing EFNs (gray), even after controlling for the foliar herbivory factor.

Ant visitation

We observed a total of 15 ant species visiting *S. polyantha* individuals (supplementary material). Ant recruitment positively affected fruit production (fruits/inflorescence) ($F_{1,43}$ = 5.04; $R^2 = 0.11$; P = 0.030; Fig. 4a), but we found no association between ant richness and fruit production ($F_{1,43} = 2.83$; $P = 0.09$; Fig. 4b). There was no effect of ant recruitment on the number of inflorescences ($F_{1,43} = 2.31$; $P = 0.14$; Fig. 4c), but we observed a positive relationship between ant richness and the number of inflorescences ($F_{1,43} = 5.45$; $R^2 = 0.11$; $P = 0.024$; Fig. 4d). Foliar herbivory was not affected neither by ant recruitment ($F_{1,43} = 0.76$; $P = 0.39$; Fig. 4e) and ant richness ($F_{1,43} = 1.16$; $P = 0.29$; Fig. 4f). The probability of fruit production in *S. polyantha* was positively associated by both ant recruitment ($\chi^2 = 1.88$; $P = 0.021$; Fig. 5a) and ant richness of visiting ants ($\chi^2 = 1.99$; $P = 0.029$; Fig. 5b). For each additional visiting ant individual, the probability of fruit production increased by 8.4% (odds ratio = 1.084), while each additional ant species increased the probability of fruit production by 84% (odds ratio = 1.84). The ANOSIM showed significant differences regarding the species composition between the two plant groups ($R = 0.16$, $P = 0.002$; Fig. 6). The SIMPER analysis revealed that the species that strongly influenced the formation of groups within the plant groups were *Crematogaster* sp. ($P = 0.031$) and *Pseudomyrmex gracilis* ($P = 0.051$), where these two species were more common among *S. polyantha* individuals supported by plants without EFNs.

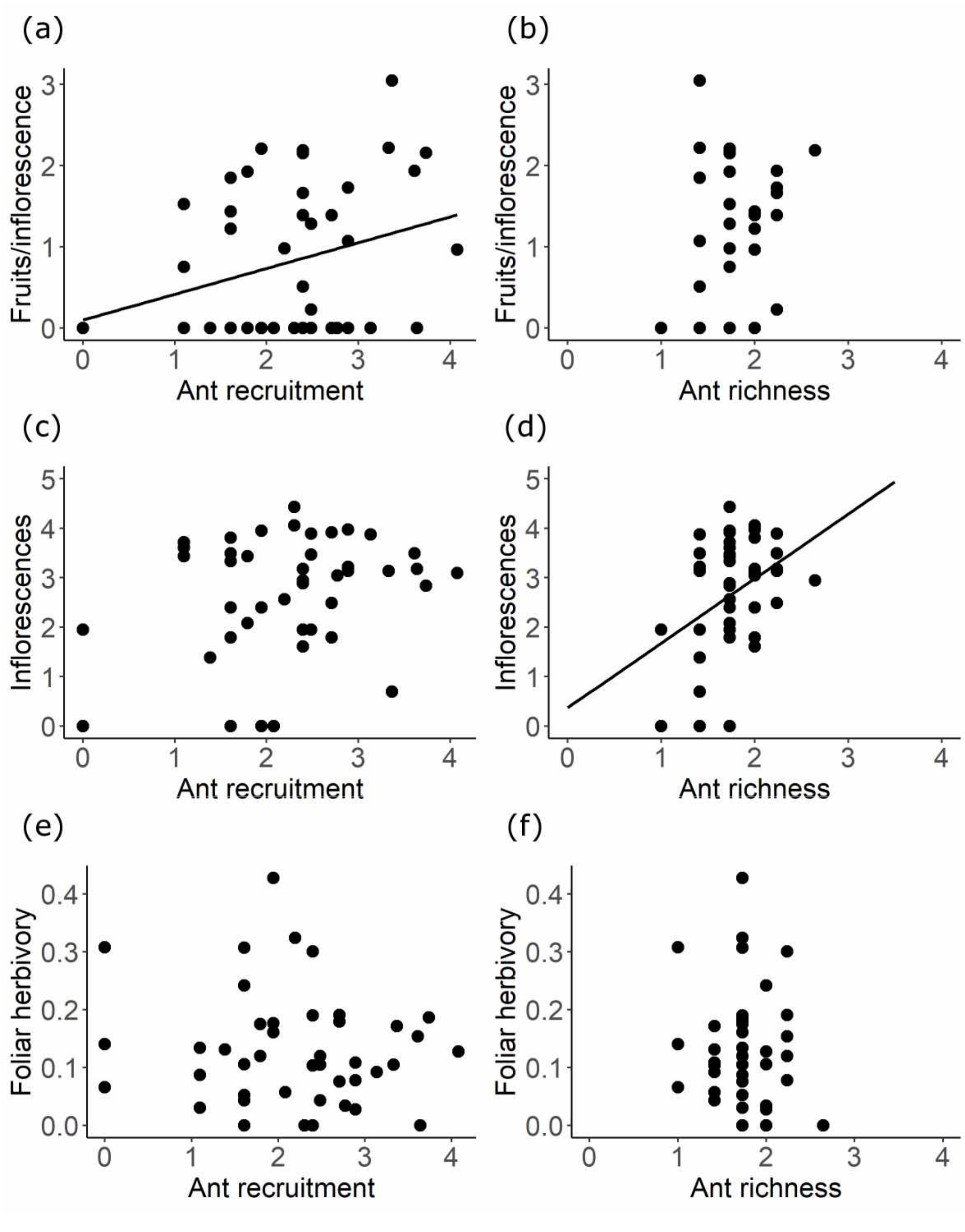


Figure 4. The effect of ant recruitment and species richness on the number of produced fruits per inflorescence (a, b), inflorescence number (c, d), and foliar herbivory (e, f) in *Smilax polyantha*. The number of fruits produced was positively affected by ant recruitment (a), while the number of inflorescences produced was positively affected by ant

richness. All the other comparisons were not statistically significant accordingly to α = 0.05. We used squared root transformations in ant recruitment and richness to normalize the data.

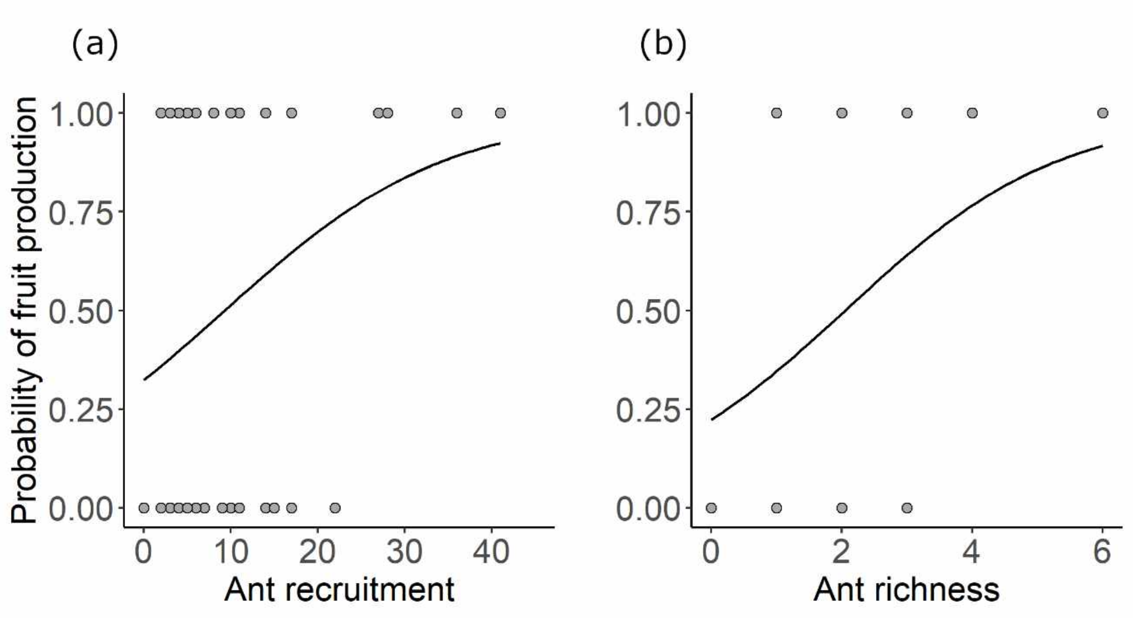


Figure 5. Logistic regression depicting positive effects of ant recruitment and richness on the probability of *Smilax polyantha* in producing or not fruits. Each additional visiting ant individual increased the probability of fruit production by 8.4% (a), while each additional visiting ant species increased the probability of production by 84% (b).

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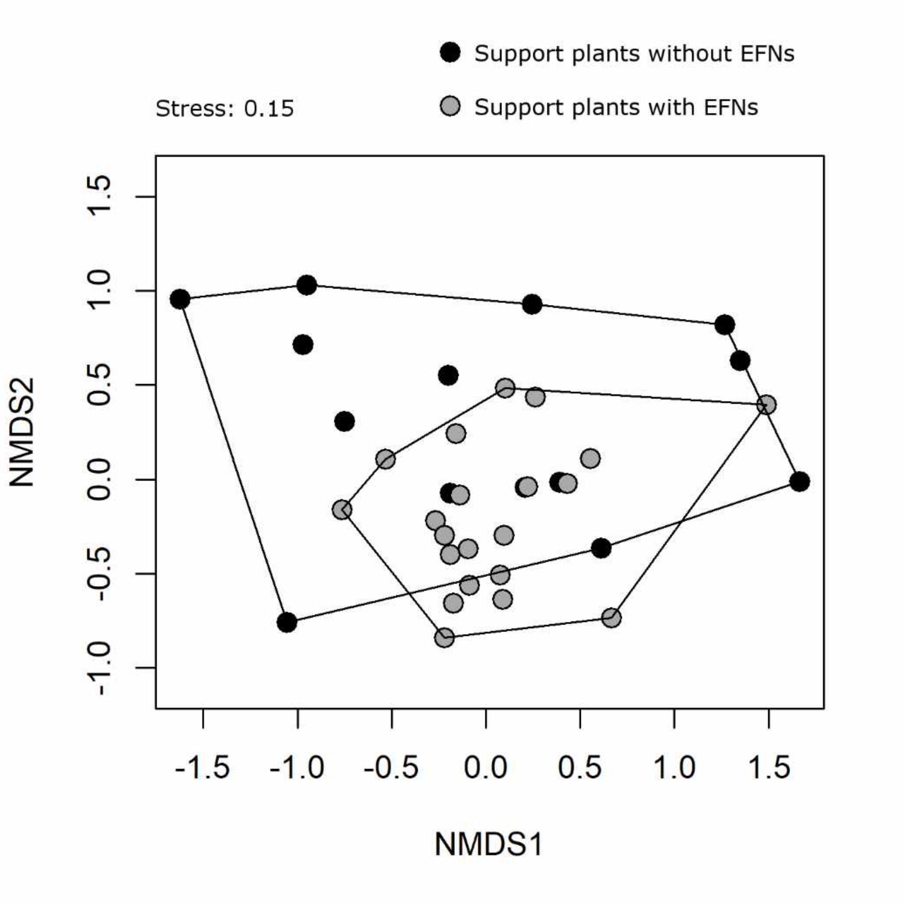

Figure 6. Ant species composition present in two groups of plants. Each dot represents a pair of plants: An individual of *Smilax polyantha* and its associated plant (that may have or not extrafloral nectaries – EFNs). When *S. polyantha* plants were supported by EFN-bearing plants, they experienced distinct richness and composition of visiting ants, when compared to *S. polyantha* supported by plants without EFNs, forming two separate groups (see analysis of similarities—ANOSIM—in results).

Discussion

Our results strengthen the predictions that associated plants with EFNs indirectly benefit *S. polyantha* by boosting the attraction of mutualistic ant species that might be visiting both plants. When supported by other EFN-bearing plants, *S. polyantha* exhibited a higher number of visiting ants and ant richness, had lower foliar herbivory and fluctuating asymmetry (measure of environmental stress) values, and a distinct composition of visiting ant species when compared to *S. polyantha* supported by plants without EFNs. Although we did not observe differences between the two plant groups regarding the number of inflorescences and fruit production, we demonstrated that the recruitment and richness of visiting ants had positive effects on *S. polyantha* production (inflorescences and fruits per inflorescence). To our best knowledge, this is the first study demonstrating that a neighboring (support) plant can influence both the ant richness and composition of visiting ants in another plant individual.

Specifically, we observed that *S. polyantha* supported by other EFN-bearing plants had increased ant richness, and this variable was positively related to the inflorescence production and the probability of fruit production. There is a debate in the literature on how the ant community is associated with EFN-bearing plants and how ant richness affects these mutualisms (see Lange et al. 2013, Camarota et al. 2015, Belchior et al. 2016, Ribeiro et al. 2018). Although we do not know studies that observed how the community of visiting ants affects EFN-bearing plants, some researchers concluded that plants visited by more than one ant species often experience low protection (Miller 2007, Palmer et al. 2008, Del-Claro and Marquis 2015). This occurs because most ant species are opportunistic and do not provide benefits for EFN-bearing plants (see Del-Claro et al. 2016). Few or single ant species are observed in well-protected plants because effective mutualistic ants are aggressive; hence, they do not only exclude herbivores but other competing ant species to seize resources (Palmer et al. 2008, Dáttilo et al. 2014a, Clark and Singer 2018). However, even though aggressive ant species are presumed to offer better protection (Miller 2007), there are also cases where extremely aggressive ants can cause harm to the visited plants by driving off potential pollinators (Ness 2006, Hanna et al. 2015, Melati and Leal 2018) or damaging vegetative parts (Palmer et al. 2008; Villamil et al. 2018).

These examples demonstrate how ant-plant mutualisms are complex and context-dependent (Baker-Méio and Marquis 2012). In our study system, ant richness prompted by an associated plant caused a positive impact in *S. polyantha*, although, how exactly it benefits EFN-bearing plants is still an open question. We hypothesize that different ant species may be specialized in preying different types of herbivores since they vary in behavioral traits, size, and recruitment capacity (see Del-Claro and Marquis 2015). Also, ants have distinct activity periods, so EFN-bearing plants visited by more ant species may be benefited by a turnover of ant species along the day (see Díaz-Castelazo et al. 2004, Anjos et al. 2017).

There were some inconsistencies regarding the effects of ants and associated plants since we did not observe the ant richness effect on *S. polyantha* foliar herbivory. Furthermore, fruit production was not different between the two plant groups, although ant recruitment was positively associated with the number of fruits produced. Thus, we conclude that the mechanisms benefiting *S. polyantha* supported by other EFN-bearing plants might not be related to the absolute ant recruitment nor richness, since we have noticed no effects of ant recruitment nor richness on foliar herbivory. We, however, discarded the structural differences between the associated plant groups, as we observed no variation in structural complexity, a trait that should affect factors such as ant visiting and foliar herbivory. According to the observed difference in FA between the two plant groups, after controlling for foliar herbivory effects, we concluded that associated EFN-bearing plants might be benefiting *S. polyantha* in another way than by just attracting ants. Although we cannot offer a response for this outcome, we hypothesize that support plants with EFNs might reduce the *S. polyantha* investment EFNs or extrafloral nectar (volume or composition; see Calixto et al. 2021), which could decrease the leaf development instability (i.e., FA). Investment reduction was already observed in plants protected by neighboring plants (Coverdale et al. 2018, 2019), and it is known that the production of extrafloral nectar can be regulated by external factors (Calixto et al. 2021).

The composition of ants might partially explain how associated plants with EFNs might have benefited *Smilax polyantha*. It is known that most ant species in the Brazilian Cerrado are not involved in mutualistic interactions with EFN-bearing plants, and we observed a subtle, but significant, difference in ant composition regarding the two plant groups. *S. polyantha* supported by plants without EFN-bearing plants were visited by more ants such as *Crematogaster* sp. and *Pseudomyrmex gracilis*. Although *Crematogaster* sp. exhibits considerable aggressiveness and recruitment, its reduced size mitigates its ability in attacking herbivores efficiently (Del-Claro and Marquis 2015). Conversely, *P. gracilis* is greater than *Crematogaster* sp., but its individuals are not aggressive, so its presence on EFN-bearing plants does not indicate any effective protection (Fagundes et al. 2017). Even though studies showed that the composition of ant species differs between plants with and without EFNs (Camarota et al. 2015), no studies demonstrated that associated or close-ranged support plants can impact the ant composition and richness of focal plants.

That said, we assume that the benefits, such as increased fruit and inflorescence production, were possible as the mutualistic ants might have a stronger effect than the exploiter ants on our models. We cannot discredit, however, that the positive effect of ant recruitment on fruit production was caused by mutualistic ants during the flowering period, as some ants can prey or drive-off flower herbivores, increasing the plant’s performance and fitness (Leal et al. 2006). There are also rare cases where ants perform pollination themselves (Del-Claro et al. 2019). These two scenarios would explain our results, but since we did not directly observe the behavior of ants during the flowering period of *S. polyantha*, we cannot offer a decisive explanation.

Taken together, our results suggest that EFN-bearing plants do not only affect the parties directly involved—the EFN-bearing plants and their ant partners—but, at least in fine scales, they may benefit the vegetal community, overall. Of course, this will only happen if the competition effects between these plants do not surpass the associational benefits, and, if that is the case, associational resistance can promote the coexistence of less competitive plants (Coverdale et al. 2018). The benefits should be even greater for lianas since they have nitrogen-rich leaves (Salzer et al. 2006, Cai and Bongers 2007, Zhu and Cao 2010) and few defenses against herbivores (Aide and Zimmerman 1990, Ødegaard 2000, Tang et al. 2012). A promising next step would be to evaluate whether EFN-bearing lianas reduce their defense investment when supported by other EFN-bearing plants and what are its effects on the associated plants. Defense investments can be evaluated not only by measuring their nectar production (volume, compounds concentration and identity) but also by verifying physical defenses such as leaf toughness and spine production (see Coverdale et al. 2018, 2019). Additionally, evaluating distinct populations of associated plants can clarify how abiotic factors and the ant community interact and affect the outcomes of the associated plant relationships.

Acknowledgements

We thank Eduardo Calixto, Robert Marquis, Eva Colberg, Miguel Chaves-Fallas, Estefania Fernandez, Jared Chauncey, Diego Anjos, Rodrigo Pereira, and Drielly Queiroga for interesting discussions and suggestions on previous versions of this manuscript.

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Capítulo 3

The associational resistance effects among plants: a review

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Abstract

Associational resistance (AR) is a specific case of facilitation where a neighboring plant provides benefits to focal plants by reducing their herbivore pressure. Associational effects have great application in agroecological practices and also considerable impacts on the structuring of natural communities. Despite the great number of studies depicting AR, there is still misinterpretations about its terminology and little information on the mechanisms behind these interactions. This chapter is divided into two parts. In part I we provide a qualitative review on the historical aspects of the AR term. In Part II we used quantitative and meta-analytical tools to identify and measure the main mechanisms of AR against a series of ecological variables (e.g., plant traits and spatial variables). Lastly, we discuss the patters found and their implications for biological control practices and the structuring of natural ecological communities.

Keywords: associative effects, facilitation, pest control, plant diversity, natural enemy hypothesis

Introduction

Many studies have shown that the identity of neighboring plant species can either directly or indirectly affect the fitness of focal plants. Early studies focused on antagonistic interactions between plant neighbors, particularly competition or apparent competition (Bronstein 1994, Callaway 1995, Bertness and Leonard 1997, Kunstler et al. 2016, Holt and Bonsall 2017). However, a growing number of studies since the 1970s show that neighbor identity and diversity can also contribute to the maintenance of plant diversity in natural and manipulated environments (i.e., cropping systems), across spatial scales (Letourneau et al. 2011, Mathis and Bronstein 2020, Sato 2018).

Associational resistance (AR) is a type of positive interaction among plants, wherein the presence of intra- or interspecific neighbors benefits focal individuals by reducing susceptibility to herbivores (Tahvanainen and Root 1972, Wahl and Hay 1995). AR effects mitigate the impact of herbivores by reducing their abundance, attack intensity, or simply their probability of finding focal plants, through direct (e.g., production of repellent compounds by neighbors) or indirect (e.g., attraction of predatory arthropods by induced biotic defenses) mechanisms (Hambäck et al. 2000, Barbosa et al. 2009, Plath et al. 2012). AR has received significant attention especially after a meta-analysis published by Barbosa et al. (2009) showing that positive associational effects are more frequently documented than negative ones. However, many conceptual and technical aspects of AR still require attention due to its broad conceptualization as a neighbor-mediated reduction in herbivore impacts. In particular, AR overlaps with several other ecological concepts—e.g., facilitation, nursing effects, background matching—and it is most likely to be caused by many different biotic and abiotic scale-dependent mechanisms acting simultaneously (see Agrawal et al. 2006, Bronstein 2009, Underwood et al. 2014, Mathis and Bronstein 2020). To summarize, AR can be caused by any type of direct or indirect interaction provided by neighboring plants, or even by changes in microclimate conditions caused by specific traits of neighboring plants, that result in reduced herbivore pressure.

Due to this great complexity and breadth, it is imperative to understand how different mechanisms of AR interact with other important ecological factors in herbivore susceptibility, such as scale-dependent interactions and functional trait diversity. For instance, attracting natural enemies of herbivores is one mechanism by which neighboring plants can benefit focal plants. It is expected, nonetheless, for factors such as the spatial arrangement of focal and neighboring plants to be relevant when considering AR mechanisms. For example, the attraction of natural enemies by neighboring plants can be studied at both local and geographical scales. At local scales, AR mechanisms rely on specific plant traits; taking natural enemies as an example, we could argue that neighboring plants can produce food resources that attract them to the system. Conversely, herbivory damage can be reduced due to a heterogeneous distribution of resources that depends on the arrangement and distribution of plants rather than specific plant traits.

Due to a lack of data, past reviews and meta-analyses could not provide strong quantitative information on the mechanisms of AR (see Agrawal 2006, Barbosa et al. 2009, Letourneau et al. 2011, Underwood et al. 2014). However, with a growing number of AR studies, more and better data can be gathered to provide a synthesis. Our main goal in this review is to identify and quantify, using meta-analytical tools, the main mechanisms of associational resistance This paper is divided into two sections. In the first, we summarize and discuss the historical and conceptual aspects of AR. In the second section, we review the AR literature and use statistical and meta-analytical tools to evaluate and compare the effects of the main mechanisms driving AR, as well as the role of plant traits and distinct spatial scales in AR.

Part I

Historical and conceptual aspects of AR

The core idea of AR is usually attributed to Tahvanainen and Root (1972) and Root (1973). In an agroecological study, Tahvanainen and Root (1972) observed that vulnerable crops received protection against herbivores when they were intercropped with another plant species. They argued that, in addition to the natural individual resistance of plants, complex communities exhibit a special type of protection known as “associational resistance”, which is regulated by a combination of biotic and abiotic factors. This resistance is lost when complexity is reduced (e.g., monocultures), leaving plants more vulnerable to specialist herbivores. In a long term study, Root (1973) expanded the AR concept (without mentioning the term) by formally proposing two alternative mechanisms—the natural enemy hypothesis and the resource concentration hypothesis —to explain the benefits provided by intercropping practices. The “enemies” hypothesis states that neighboring plants attract predatory arthropods (e.g., carnivorous mites) that then control herbivore populations occurring on focal plants. In contrast, the “resource concentration” hypothesis asserts that complex communities should suffer fewer impacts of specialist herbivores because the resources provided by certain plant species are not evenly distributed, reducing the ability of such herbivores to find their correct hosts (see Hambäck et al. 2014).

Despite the use of AR since the 1970s and its increasing development, there has been no consensus regarding its application. For example, Atsatt and O’Dowd (1976) and McNaughton (1978) applied the term “defense guilds” when referring to associated plants that use any mechanism to resist to herbivores, while Bach (1979) opted to test the “resource concentration” and the “enemies” hypotheses independently—even Root (1973) did not apply the AR concept in his study. One of the possible reasons for this is that the connection between Roots' hypotheses and AR were not clear at that time, and some studies considered them to be three alternative hypotheses explaining plant-herbivore interactions (Letourneau 1986, 1995). Eventually, however, studies by Risch (1981) and Stamps and Linit (1997) suggested that the hypotheses proposed by Root (1973) represent some of the mechanisms that drive AR. This view stimulated future studies that investigated Root's hypotheses in light of AR. Despite this, the number of studies that have tested AR mechanisms is still limited almost 50 years following Root's study.

It is challenging to study AR mechanisms since they potentially involve many different plant-plant interactions that result in reduced herbivory. A simple way to cut through this confusion is to sort the mechanisms according to whether the key factors are abiotic or biotic (see Barbosa et al. 2009, Fig. 1a). Abiotic mechanisms depict physical changes stimulated by neighboring plants, including factors such as temperature, soil type, and light incidence (e.g., Piiroinen et al. 2014, Kim 2017). For instance, Bach (1984) observed that the neighboring plants increase leaf shading of *Cayaponia americana*, a condition that is not conducive to its herbivorous fly (*Acalymma innubum*). Biotic mechanisms require the interaction of biological components and are more frequently investigated. The "enemies" and "resource concentration" hypotheses proposed by Root (1973) are classic examples, but others have been suggested. Neighboring plants, for example, may promote AR by simply offering shading, refuge or camouflage to focal plants (Rausher 1981, Baraza et al. 2006, Danet et al 2017, Kim 2017). Coverdale et al. (2018, 2019) showed that neighboring plants may provide a physical defense to nearby plants growing under spiny *Acacia* bushes and that they were less grazed by large mammals than those growing far away from neighbors. Neighbors may also provide indirect defenses, as in the case of extrafloral-nectary producing plants. These plants usually attract ants that attack their herbivores, but one study has shown that these ants can also benefit nearby plants without extrafloral nectaries (Jezorek et al.

2011). Neighboring plants may also exhibit chemical defenses that benefit nearby focal plants. In crop systems, researchers often observe that plants with high chemical activity, such as volatile organic compounds (VOCs), may reduce the damage and abundance of pest herbivores by acting as a repellent (Kost and Heil 2006, Barman et al. 2016, Zhang et al. 2017, Camacho-Coronel et al. 2021). For instance, Karban et al. (2000) noticed that tobacco plants can use airborne cues produced by neighboring damaged sagebush to increase the production of polyphenol oxidase, an enzyme that produces reactive oxygen compounds and organic free radicals that are toxic for certain herbivore insects (Duffey and Stout 1996, Constabel and Barbehenn 2008). VOCs can also protect focal plants by masking scents used by herbivores to detect appropriate hosts, functioning as a camouflage strategy (Hambäck and Beckerman 2003).

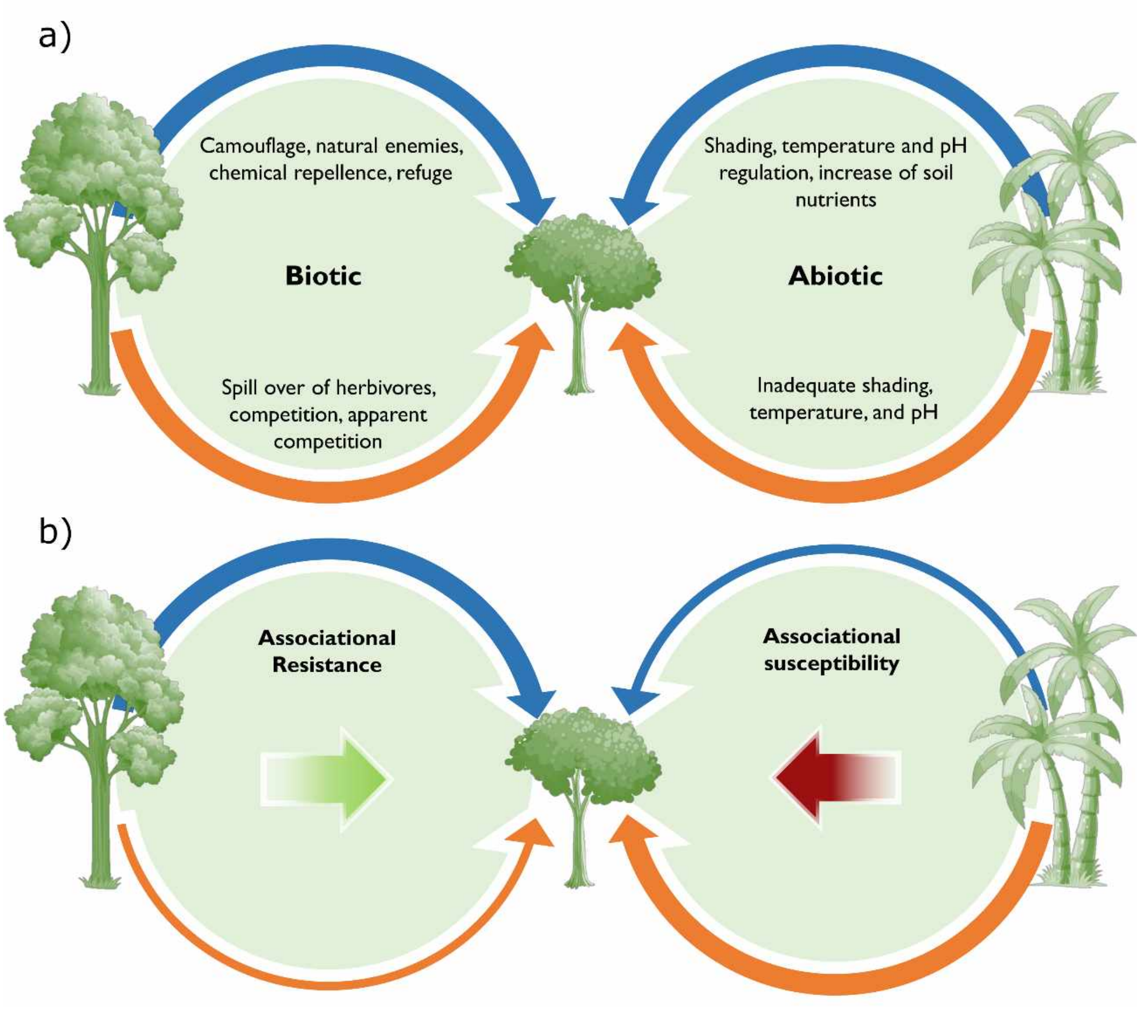

Figure 1. Representation of biotic and abiotic mechanisms (a) and the interaction strength (b) of associational resistance and associational susceptibility. Arrows depict the effects of neighboring plants on focal plants. Blue arrows depict positive interactions while orange arrows depict negative interactions. The width of arrows indicates the interaction's strength, meaning that associational resistance (green arrow) or susceptibility (red arrow) are characterized by the net result of combining positive and negative interactions.

Despite these clear examples of associational resistance, a rising body of studies has shown mixed evidence for AR. Although many studies report positive effects, others demonstrate neutral, or even negative effects when interacting with neighbors (reviewed by Agrawal et al. 2006); the latter case is known as associational susceptibility (AS). Letourneau (1995) was one of the earliest studies to use this term, coined after a growing body of studies showed negative effects of some intercropping practices on herbivore susceptibility. From this point onwards, several researchers focused on understanding the interaction mechanisms and factors that lead to AR or AS.

Thresholds between AR and AS

The threshold between AR and AS is of particular interest for predicting the dynamics of plant communities, although it cannot be easily determined (Castagneyrol et al. 2017). As in any other interaction outcome, associational effects will depend on the net result of multiple and opposite interacting factors. For instance, if focal and neighboring plants strongly compete for resources (i.e, sunlight), AR outcomes will only occur if the neighboring plant can provide enough benefits that overcome competition losses (Fig. 1b). But what plant or herbivore traits dictate the threshold between AR and AS? Agrawal (2004) and Agrawal et al. (2006) argued that the quality of neighbors and the specificity of herbivores determines outcomes: the strength of associational resistance should increase as the host quality (e.g., leaf nutrition) of plant neighbors decreases. However, there is still controversy when it comes to the role of the quality of neighbor plants in AR or AS. Some studies show, for instance, that highly palatable neighboring plants can benefit focal plants as they can attract herbivores that would otherwise be feeding on focal plants (Jiao et al. 2019). The effects of relative palatability may depend on the scale at which herbivores forage, determining whether palatable neighbors "concentrate" herbivores on themselves, or export them to nearby focal plants (Bergvall et al. 2006, Champagne et al. 2016, Huang et al. 2016)

Many different plant traits can be used to define the quality of plants as herbivores' host. Leaf traits, for instance, are well-known for affecting the preference of leaf herbivores, and although distinct herbivore species exhibit distinct nutritional needs and specificity, young and unsclerotized leaves are usually more consumed (Pérez-Herguindeguy et al. 2003). Leaves can be palatable or unpalatable (see Barbosa et al. 2009) according to properties such as carbon/nitrogen ratio (C/N), toughness, chemical properties, etc. Nitrogen-rich leaves, for example, are frequently attacked by insect herbivores, since nitrogen is a limited resource in most natural environments. The use of high-quality neighbors to control for pests in crops is a common practice called "attract and reward": the idea is to provide a trap crop to attract herbivores that would otherwise attack focal plants of economic interest. However, this strategy might provide the opposite result, as neighboring plants can spill over herbivores and contaminate nearby focal plants, leading to AS instead (reviewed by Shelton and Badenes-Perez 2006).

A recent meta-analysis found that the phylogenetic distance between focal and neighboring plants can also affect herbivore pressure in systems containing generalist herbivores: herbivore pressure reduces as the phylogenetic distance between potential hosts increases, leading to AR (Castagneyrol et al. 2014). However, measures of phylogenetic distance may often be a proxy for certain plant traits that directly affect the susceptibility of plants to herbivore attach. Although it is expected that phylogenetically close species exhibit more similar morphophysiological traits than distant species (Pearse and Hipp 2009), in many cases such relationships are weak and cannot be used to predict ecological interactions (Uriarte et al. 2010, Kunstler et al. 2012). Many studies have shown that plants with similar traits can share herbivores (reviewed by Pearse et al. 2013). Plant traits are, thus, a better predictor of interaction strength than phylogenetic signal. In conclusion, models that incorporate trait quality and similarity might provide useful information on associational effects.

The study designs of AR

Most studies apply classic experimental designs inspired in the past works of Root and Tahvanainen (1972). These designs commonly make use of two species (one focal and one neighbor), in which they measure the pest effects in two treatments: monocultures (only the focal plants) and mixed crops (focal plants plus the neighboring plant species). In this design, researchers grow the same number of focal plants in monoculture and mixed treatments while simply adding the neighboring plants in mixed treatments, so the absolute number of plants in mixed crops is at least twice the monocrop (but it can be higher depending on the focal-neighbor ratio applied). This difference does not allow one to disentangle the AR effects from density and relative proportion effects, which, per se, is enough to impact herbivores. Underwood et al. (2014) recommends surface plot designs that combine several focal-neighbor proportions and densities, although we believe this design might be too intricate and not very practical for most studies interested in AR. Sato et al. (2018) provides a simple 2x2 design that consists of plots with high-low and low-high proportions of focal-neighboring plants that are also replicated to control for the presence of herbivores. This design enables the researcher to control for both the proportion and the herbivore effects, although the density effects of each plant species cannot be assessed.

Due to their agricultural roots, most AR studies still focus on agricultural systems, with the goal of ameliorating the effects of pests on commercial crops. However, early studies such as Hambäck et al. (2000) performed the first AR studies in natural systems. They observed that the presence of neighboring plants reduced the impact of herbivores on a focal plant by attracting predators of herbivores, especially ladybugs. This study showed the potential applications of AR for conservation and community ecology studies. Nonetheless, it is challenging to disentangle confounding effects and to prepare experiments in natural communities, especially in diverse and rich environments. Hence, most studies conducted in natural communities struggle to demonstrate the mechanisms behind AR effects.

Although study designs involving AR are relatively consistent, there is a considerable variation regarding how to measure the effect of neighboring plants on herbivores, which results in confusion and replication problems. Some studies, for example, measure as response variables the abundance of arthropod herbivores (adults, eggs, or everything together), while others may measure leaf, fruit, or seed damage. Furthermore, studies are often performed at different scales and systems (natural or crops), an issue identified by Underwood et al. (2014). Distinct scales consider plant distribution and density differently, which affects relations among plant, herbivores, and predators. Given that AR is a result of simultaneous and multi-directional ecological factors, future studies should focus on identifying and measuring multiple mechanisms underlying associative interactions.

Part II

Study objectives and hypotheses

We selected studies performed in agricultural environments where AR effects were tested between monoculture and polyculture (mixed crops) treatments. We used statistical procedures, including meta-analyses, to test and compare the effects of the main mechanisms (i.e., natural enemies, chemical repellency, refuge). In comparison to studying complex ecological systems, studying relatively simple systems (monoculture x polyculture) has some advantages as they can provide finer information on the influence of neighboring plants. Furthermore, complex systems can have a high number of confounding factors since they are ruled by a great number of ecological variables. In cases where it was not possible to find enough studies addressing the same mechanisms, we enumerate available studies and describe their results. Finally, we tested how plot size and trait quality and similarity between focal and neighboring plants affect AR.

Meta-analyses

We used the Web of Science database as a primary source for searching published papers. Using the advanced search tool, we applied several combinations of the following keywords (including plural variations of each term): associational resistance, refuge, neighbor, plant, crop, herbivore, chemical, volatile, VOC, intercrop, pest, repel, mixed crop, multiple cropping, intercrop, polyculture, cover crop, trap crop, push-pull, thorn, spine, graze, browse, and nurse. We individually inspected more than 700 studies to see whether they depicted associational effects (AR and AS) or not. In addition to the studies obtained by this filtering, we sought out additional studies cited within review and meta-analysis papers that escaped our filtering. After gathering all studies, we sorted them into abiotic and biotic groups, and according to the AR mechanisms observed (e.g., “enemies” hypothesis).

Using the R environment, we performed a meta-analysis for each AR mechanism that reached a minimum number of 10 experiments. Each examined experiment had to contain two treatments: one considering the effects of neighboring plants on focal plants (experimental) and another one with only focal plants (control). Here, we included multiple experiments per paper, but when we found experiments involving time series events, we included only those with highest difference between the control and experimental group (adapted from Rosumek et al. 2009). We only selected studies presenting the number of used samples, means, and a measure of variability (standard deviation or standard error of the mean). We extracted these measures from texts, tables or graphs. When data were available in graphs, we digitalized the figure and extracted its values using the ImageJ software (Rasband 2019). Specifically, we used the known values of the Y-axis as a ruler to calibrate our measuring—with 0.01 mm of accuracy—and determine the observed mean and deviation of each group. We calculated the tests statistics using Hedges' g, a corrected version of Hedges' d instead of raw means to control for possible large variations among studies. This method standardizes the data and provides results that are easy to interpret (see Barbosa et al. 2009, Rosumek et al. 2009). Due to the high variability within and among observed studies, we chose to perform all analyses using random effects (Borenstein et al. 2010), which assumes that the sampled studies do not come from the same population. We also evaluated the heterogeneity of each model by using the I^2 index (Higgins et al. 2003).

Meta-analyses are subject to "publication bias" or the "file drawer problem", which assumes that most studies that find non-significant or negative results relationships are not published. Since we only worked with published papers, the number of studies with non-significant and negative results (AS) included in our analyses is likely to be biased. To overcome this problem, we used Rosenthal's fail-safe number test. The fail-safe number calculates the number of negative results that would be necessary to turn a given positive result into a non-significant one (Rosumek et al. 2009). If negative bias is not concerning, the observed fail-safe number should be higher than 5k +10, where k is the number of studies in the analysis. Furthermore, we used the funnel plot as a visual approach to identify publication bias according to sample sizes, by plotting the mean results of each study on the X-axis and the standard error on the Y-axis. When there is no significant bias, it is expected a high number of studies with high variability of results and standard errors (bottom) studies than in large studies (top), so the figure shape reminds an inverted funnel (Hoffman 2015).

Testing the effects of natural enemies on herbivores

The "enemies" hypothesis was the AR mechanism tested in most of our selected studies (see Results). Thus, we evaluated its relationship with AR by performing a meta regression using the natural enemies' increase (abundance, density and frequency of predators and parasitoids), from monocrops to mixed crops, as a predictive variable against herbivores' effect size (abundance, density, or frequency). Our goal here was to test whether increases in natural enemies caused by neighboring plants can reduce the incidence of herbivores. Given this, we only selected studies in which mixed crops had greater numbers of natural enemies when compared to monocrops. If natural enemies can in fact reduce the availability of herbivores from crop treatments, we would expect that greater positive differences in natural enemies will be associated with greater negative differences in herbivore numbers between treatments. Here, we also evaluated whether the number of herbivores depends on plant treatments (monocrops vs. mixed crops) themselves rather than by the natural enemy mechanism.

Testing the effects of plant trait quality

Here we tested how traits related to the relative host quality of focal and neighboring plants (Agrawal 2004, Agrawal et al. 2006, and Castagneyrol et al. 2014) affect the strength of associational resistance in mixtures relative to monocrops. We further tested how the quality of neighboring plants specifically affects herbivores. To do so, we collected data on leaf traits from the Traits Database (https://www.try-db.org/TryWeb/Home.php), which contains compilations of thousands of plant traits available for more than 10.000 species, extracted from peer-review papers and environmental reports. Plants traits sampled included leaf toughness (N/mm), leaf nitrogen (mg/g), leaf carbon/nitrogen ratio (g/cm^3), woodiness (woody/non-woody), growth form (tree/herb), palatability (low/high), plant height (m) and specific leaf area (SLA; mm^2/mg). After collecting data on plant traits, we used meta-regressions to test the effects of neighboring traits on the effect size of herbivores and natural enemies.

Testing the effects of plot size, plant proportion, and plant spacing

Spatial scale is expected to affect the strength of AR (Underwood et al. 2010, Sato 2018). Given this, we extracted data on plot area (m), plant proportion (relative proportion neighboring plants in comparison to focal plants), and plant spacing (distance between plant rows, in cm). When the same study reported distinct plot sizes and plant spacing, we used the lowest reported values. We then performed meta-regressions associating each spatial data point with the number of herbivores and natural enemies found in monocrops and mixed crops. We also performed t tests to evaluate whether equal or distinct proportions (binomial categorical variable) of focal and neighboring plants were associated with the abundance of natural enemies.

Results

We found 401 studies depicting associational effects. From this total, “natural enemies” was the mechanism of associational resistance most frequently tested (43 studies), followed by chemically repellent plants (28), plant palatability (27) and refuge effects (20). A few studies described abiotic mechanisms (10), physical defenses (6), camouflage (2), phylogenetic effects (2), and indirect defenses (1). However, most studies do not clearly describe or demonstrate AR mechanisms (157 studies; see the complete list in the supplementary material and note that some studies may match more than one category of mechanism).

After identifying the main AR mechanisms, we proceeded with the meta-analyses investigating the effect of natural enemies, chemical repellency, and refuge mechanisms. For natural enemies, we used data on abundance, frequency, and presence of predators and parasitoids (see Fig. S1 for details on statistical procedures). We also extracted data on parasitism levels by parasitoids. Data on chemical repellence and refuge included abundance, frequency, and presence of herbivores (adults, larvae and eggs). Furthermore, we classified chemical studies in two types: plant and extract. Most studies performed experiments using neighboring plants themselves ($n = 34$), but some experiments tested the effects of either parts of neighboring plants (e.g., leaves, stems) or their chemical extracts on focal plants ($n =18$).

Effects of the natural enemy hypothesis and parasitism levels

Overall, the number of natural enemies (predators and parasitoids) was greater in mixed crops than in monocrops in studies that tested for associational resistance ($g = 0.54$, 95% CI 0.29 to 0.79, $n = 101$, = $p < 0.001$; Fig. 2). The heterogeneity test was significant ($I^2 = 58\%$; tau = 0.81, $p < 0.01$). When we tested these groups separately, the results remained significant for both predators and parasitoids, but the positive effect of mixed crops tended to be higher on parasitoids (predators: $g = 0.41$, 95% CI 0.11 to 0.71, $n = 75$; parasitoids: $g = 0.90$, 95% CI 0.39 to 1.40, $n = 26$), even though the difference between predators and parasitoids was not significant ($Q = 2.68$, $p = 0.10$). The heterogeneity test was significant for both groups (predators: $I^2 = 57\%$; tau = 0.80, $p < 0.01$; parasitoids: $I^2 = 63\%$; tau = 0.94, $p < 0.01$). Parasitism levels were also higher in mixed crops than monocrops ($g = 0.51$, 95% CI

0.08 to 0.95, n = 23, p = 0.022). The heterogeneity test for parasitism level was also significant (I^2 = 58%; tau = 0.49, p < 0.01).

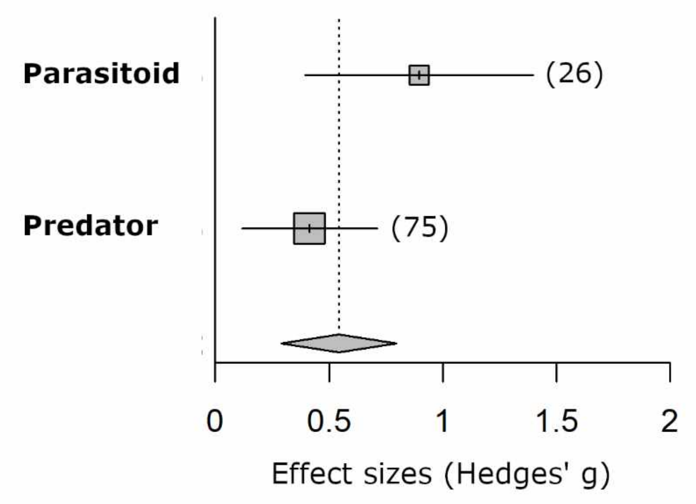

Figure 2. Associational resistance between mixed crops increased the number of parasitoids and herbivore predators relative to monocrops. Squares represent the weighted mean of each group; a larger weight—based on sample size and variance—is given to the group with larger squares. Error bars indicate 95% CI. All results are significant. Numbers in parentheses represent the total number of studies involving each group. The center of the diamond (indicated by the dotted line) shows the pooled effect of plants on parasitoids and predators, while its edges represent 95% CI.

In studies that found associational resistance due to natural enemies, meta regressions showed that an increase in natural enemy abundance (pooled effect of predators and parasitoids) corresponds with a slight reduction in the number of herbivores (Q_m = 10.18, p = 0.0014, R^2 = 0.08, n = 97). However, when we evaluated the effects of natural enemies separately, we found a stronger relationship between predator and herbivore abundance (Q_m = 25.03, p < 0.001, R^2 = 0.36, n = 81; Fig. 3a), and no correlation between parasitoids and herbivores (Q_m = 0.25, p = 0.62, n = 16; Fig. 3b). Furthermore, the impact of plant groups (mixed crops vs monocrops) on herbivores was not significant, suggesting that plant diversity cannot explain, by itself, the reduced numbers of herbivores (g = - 0.20, 95% CI - 0.44 to 0.03, n = 97, p = 0.089).

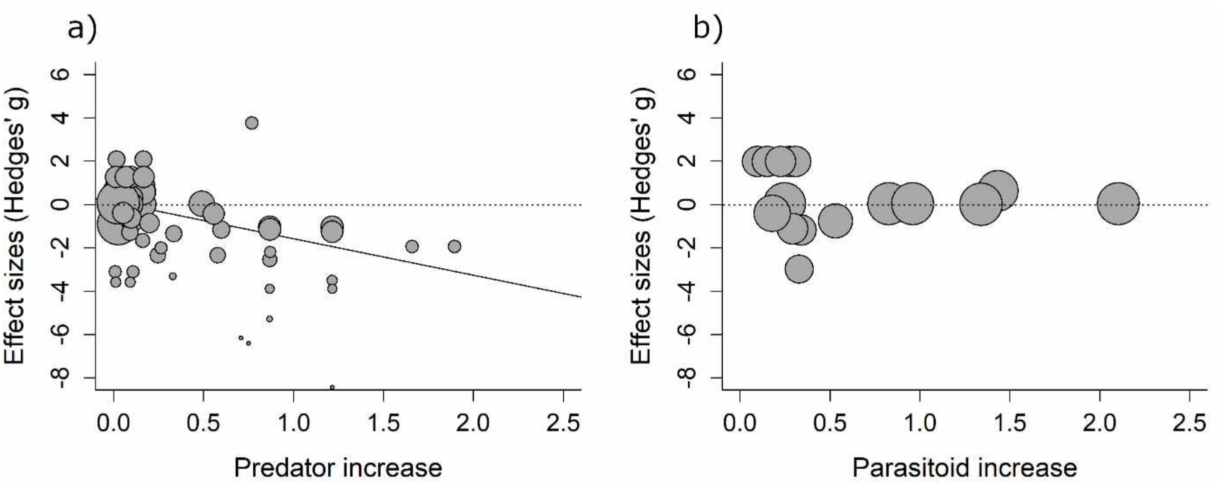

Figure 3. Meta-regressions showing how increases of natural enemies in mixed crops (relative to enemies found in monocrops) affected herbivores. Increases in predator numbers corresponded linearly with reductions in herbivore abundance in mixed crops (a), but parasitoid increases did not (b). All predictive variables were log-transformed for the analysis. Larger circles represent studies with larger weight in the model due to greater sample sizes and lower variance.

Effects of chemical repellence/masking and refuge hypotheses

Chemical and refuge effects reduced the number of herbivores on mixed crops in comparison to monocrops (chemical-repellent plants: g = -1.73, 95% CI -2.20 to -1.26, n = 52; refuge plants: g = -2.01, 95% CI -3.41 to -0.74, n = 11; Fig. 4). There was no difference in the direction or strength of associational effects between these two AR mechanisms (Q = 0.23; p = 0.63). Heterogeneity was high and significant for both groups (chemical-repellent plants: $I^2 = 86\%$; tau = 2.26, $p < 0.01$; refuge plants: $I^2 = 89\%$; tau = 4.14, $p < 0.01$). Subgroup analysis involving only chemical-repellent plants showed that the effect of using live plants was higher than using parts or extracts of plants (extract: g = -0.51, 95% CI -0.93 to -0.09, n = 18; real plant: g = -2.83, 95% CI -3.58 to -2.09, n = 34; Fig. 5), and the difference between these two groups was significant (Q = 28.29, $p < 0.001$). Heterogeneity tests were significant for both groups (extract: $I^2 = 64\%$; tau = 0.44, $p < 0.01$; real plant: $I^2 = 88\%$; tau = 3.92, $p < 0.01$).

Figure 4. Strength of associational resistance due to chemically-defensive plants and plant refuges found in mixed crops and control monocrops. Squares represent the weighted mean of each group; a larger weight—based on sample size and variance—is given to the group with larger squares. Error bars indicate 95% CI. All results are significant, but the difference between groups is not significant (see results for details). Numbers in parenthesis represent the total number of studies involving each group.

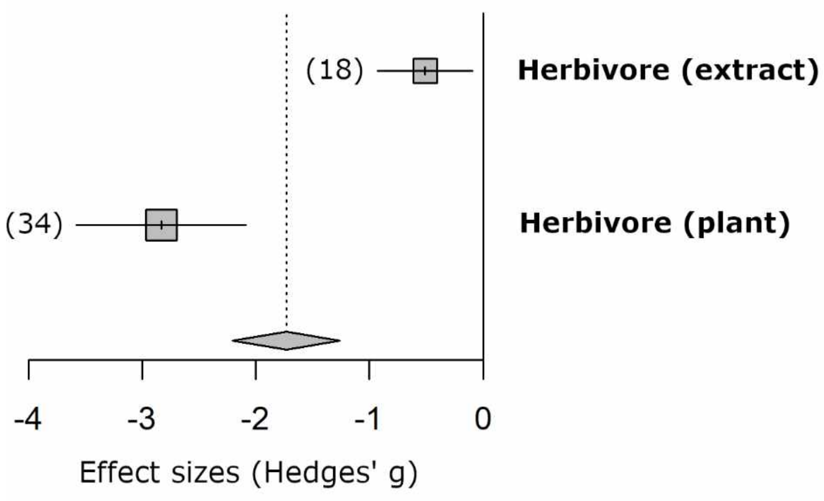

Figure 5. Strength of associational resistance (reduction in herbivore abundance) in studies comparing chemical-repellent mixed crops and control monocrops. Herbivore (extract) indicates studies using treatments with plant parts or extracts, while herbivore (plant) indicates studies using treatments with live chemical-repellent crops. Squares represent the weighted mean of each group; a larger weight—based on sample size and variance—is given to the group with larger squares. Error bars indicate 95% CI. All results are significant. Numbers in parentheses represent the total number of studies involving each group. The center of the diamond (indicated by the dotted line) shows the pooled effect of plant extracts and real plants on herbivores, while its edges represent 95% CI.

Effects of plant trait quality

Plant traits had limited effects on herbivores, where the only significant neighboring plant trait was C/N ratio. Higher C/N values were associated with increased numbers of herbivores on focal plants found in mixed crops ($Q_m = 10.21$, $p = 0.0014$, $n = 27$; Fig. 6), suggesting that low quality neighbors may trigger AS effects.

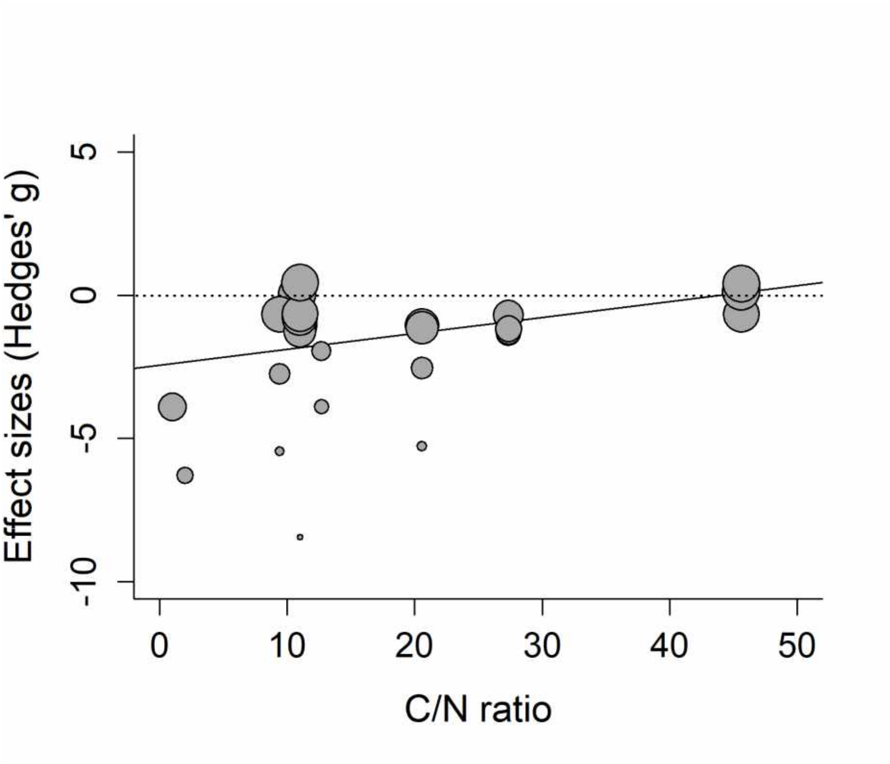

Figure 6. Meta-regression showing how C/N ratio of neighboring plants affects the abundance of herbivores found on focal plants. Larger circles represent studies with larger weight in the model.

Effects of plot size, plant proportion, and plant distancing

Increases in plot size negatively affected the overall number of natural enemies attracted by neighboring plants, in general ($Q_m = 13.51$, $p = 0.0002$, $n = 97$). Separately the effect was significant for predators ($Q_m = 9.25$, $p = 0.0024$, $n = 71$; Fig 7a), but it was not for parasitoids ($Q_m = 2.31$, $p = 0.13$, $n = 26$; Fig 7b).

There was no effect of minimum plant spacing (row distance) on the attraction of natural enemies (pooled) ($Q_m = 0.36$, $p = 0.55$, $n = 81$) or predators only ($Q_m = 0.13$, $p = 0.72$, $n = 65$; Fig 7c), but there was a negative effect on the attraction of parasitoids ($Q_m = 5.16$, $p = 0.023$, $n = 16$; Fig 7d).

There was no effect of focal/neighboring plant proportion on the attraction of natural enemies ($Q_m = 0.73$, $p = 0.39$, $n = 94$) as well as predators specifically ($Q_m = 1.66$, $p = 0.19$, $n = 72$; Fig. 7e). Nonetheless, we found a positive association between neighboring/focal plant proportion and the attraction of parasitoids ($Q_m = 9.84$, $p = 0.0017$, $n = 22$; Fig. 7e). We also found that, within mixed crops, equal proportions of focal and neighboring plants tend to attract more predators ($t_{1,73} = 3.45$, $p = 0.001$), but that was not significant for parasitoids alone ($t_{1,24} = 1.44$, $p = 0.16$) and all natural enemies pooled ($t_{1,99} = 1.86$, $p = 0.065$).

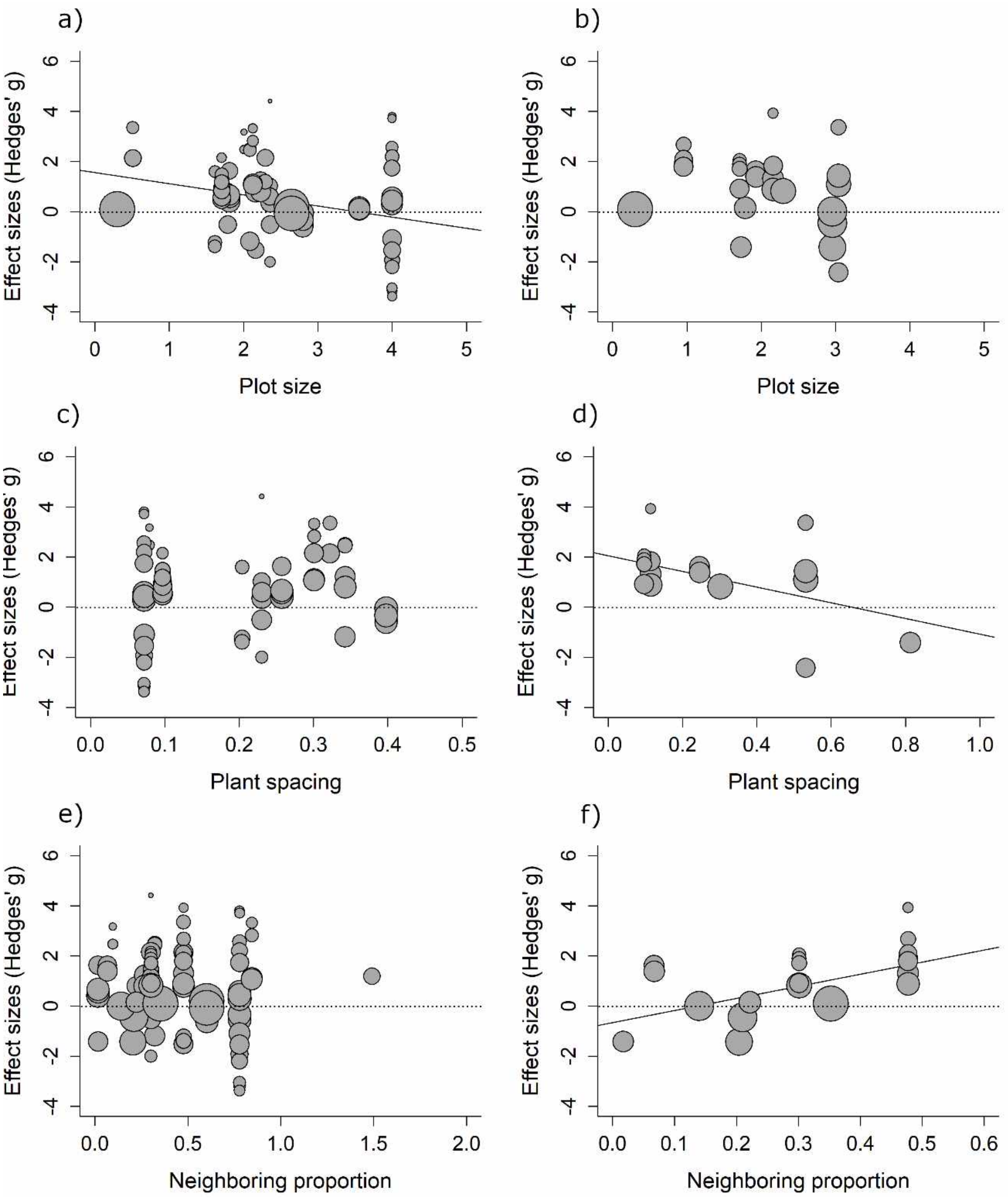

Figure 7. Meta-regressions showing how plot size (m), plant spacing (cm) and neighboring/focal plant proportion affected the attraction of predators (a, c and e) and parasitoids (b, d, and f). Increases in plot size linearly reduced the number of predators found in focal plants in mixed crop treatments (a); this effect was not observed for parasitoids (b). Increases in plant spacing did not affect predators (c), but had a negative effect on the attraction of parasitoids (d). Increases in neighboring proportion relative to focal plants had no

effect on predators, but increased the attraction of parasitoids (f). All predictor variables were log-transformed for the analysis. Larger circles represent studies with larger weight in the model.

Discussion

The main identified AR mechanism was the natural enemies (found in 43 studies), followed by the production of chemical repellents, and refuge. All these mechanisms were associated with reduced numbers of herbivores. C/N ratio of neighboring plants was correlated with increased numbers of herbivores on focal plants, suggesting that herbivores can choose host plants based on the quality of neighboring plants. Plot size was negatively associated with the number of predators, but there was no association with parasitoids. Increased proportions of neighboring plants were associated with an increased abundance of parasitoids, while plant row distance was negatively associated with the abundance of parasitoids. These results provide evidence of the importance of spatial variables in AR studies.

We observed that neighboring plants increased the availability of natural enemies (predators and parasitoids), and that increases in predators were associated with reduced numbers of herbivores. Natural enemies were already known to increase with landscape complexity (e.g., Langellotto and Denno 2004, Chaplin-Kramer et al. 2011, Letourneau et al. 2011), but, unlike similar meta-analyses and review studies, we specifically showed that focal plants can experience increases in natural enemy availability due to associational effects with neighboring plants (Fig. 2). Those effects are also shaped by scale and spatial variables such as plant spacing and the relative proportion of neighboring and focal plants (Fig. 7). Neighboring plants attracted a variety of natural enemies—including ladybugs, spiders, ants, and parasitoid wasps and flies. The attraction of natural enemies, however, can be attributed to many sorts of plant attributes. For instance, natural enemies can use neighboring plants as shelters, nesting sites, or even as food resources (e.g., pollen, nectar), and after visiting or stablishing on those plants, these predators, especially generalists, can conveniently feed on herbivores from focal plants. Increases in landscape complexity also benefits natural enemies by reducing the level of cannibalism (Langellotto and Denno 2006).

Spatial variables also had considerable effects on natural enemies' abundance. Plot size had a negative effect on predators, while plant spacing had a negative effect on parasitoids. Large plots can reduce the ability of predators to move within the vegetation (see Bommarco and Banks 2002, Champagne et al. 2016), while large plant spacing can reduce the likelihood of a plant's visual and chemical cues being detected by parasitoids. Interestingly, higher proportions of neighbors were associated with higher numbers of parasitoids, but not predators. Studying ecological systems at distinct scales conveys opportunities and challenges for those who seek to understand the extent to which neighboring plants can affect focal plants in individual and population levels (Underwood et al. 2014, Sato 2018).

Although natural enemies tend to be more common in conserved and complex environments (reviewed by Chaplin-Kramer et al. 2011, Wan et al. 2020), they do not necessarily provide better control of herbivores (Cohen and Crowder 2017). This might explain why we only observed controlling effects of predators (not parasitoids) on herbivores. Although parasitism rates were higher in mixed crops, our results suggest that parasitoids have limited effects on herbivore numbers, overall. The reason for this result is not clear, but we suggest that the higher prey and plant host specificity of parasitoids might limit their biological control potential (Vattala et al. 2006). Furthermore, plant diversity itself can enhance the vegetal heterogeneity and may ultimately reduce the ability of parasitoids to track herbivores within the vegetation (Bommarco and Banks 2002, Chaplin-Kramer et al. 2011).

Complex systems emit a wide array of visual and chemical cues that may disrupt the ability of natural enemies to find their prey and this may be particularly harmful to parasitoids due to their higher specificity. In fact, generalist predators are usually better biological agents than specialists in diversified environments due to an increased availability of alternative prey (Letourneau 1990). our synthesis suggests that predators are overall better

It is a real challenge to demonstrate causal links between an increase in natural enemies and a resultant decline in herbivore numbers (see Chaplin-Kramer et al. 2011, Letourneau et al. 2011). Herbivore decreases could be correlated with other factors associated with increased plant diversity (Barbosa et al. 2009). In fact, negative associations between natural enemies and herbivores is not even certain, as some studies concluded that diverse herbivore communities enhance the abundance of natural enemies (Dyer and Letourneau 2003, Pearson and Dyer 2006). Regardless, considering the data on natural enemies' experiments, we found two key results that support a causal link between natural enemies increase and herbivore decrease. First, we found a negative correlation between natural enemy diversity and herbivore diversity, and second, and more importantly, we observed that increases in plant diversity (monocrops vs. mixed crops) could not explain, by themselves, the reduction of herbivores on focal plants. Taken together, these results support a top down control of predators via interspecific associational effects.

Other AR mechanisms, including chemical compounds and refuge plants, also decreased the number of herbivores. However, using real plants on mixed plant treatments reduced herbivores even more than using plant extracts or parts of plants to simulate neighboring plants, implying that other mechanisms besides chemical compounds (e.g., refuge) might be benefiting the focal plants. It is important to note that the potential chemical effects of neighboring plants are likely to be diverse, so the chemical mechanism leading to AR can in fact be broke down more refined mechanisms. In fact, some studies fitting the chemical mechanism category can also be considered in other categories such as the natural enemy category since some plants use VOCs to attract natural enemies of herbivores (Zhang et al. 2017). Nevertheless, most studies used in this synthesis consider volatiles produced by plants as repellents or having masking properties. Many neighboring plants selected in these kinds of experiments are known for producing chemicals with strong odors (e.g., garlic), which would drive away potential herbivores. Conversely, plants with masking chemicals can produce volatiles that prevent herbivores from finding host plants, functioning as a form of camouflage (Schröder and Hilker 2008). Such masking effects are certainly the mechanisms of some studies investigating the resource concentration hypothesis and should especially affect specialists and chemically-orienting herbivores (see Marquis and Moura 2021).

We found that the sampled plant traits had limited effects on herbivores. Rather, C/N ratio of neighboring plants was positively correlated with the abundance herbivores of focal plants. This suggests that low quality neighbors might spill-off herbivores onto focal plants, leading to AS effects. This outcome is precisely the opposite expected by previous models (see Agrawal 2004, Agrawal et al. 2006). Studies investigating the effects of plant diversity on herbivores and natural enemies are usually performed in natural communities. On one hand, studies in natural communities can potentially provide answers more closely related with real conditions. On the other hand, natural communities are rather complex, and results across studies can be conflicting due to a plethora of confounding factors, including high variation in the scale at which the experiment is conducted to inconsistent variable definitions and measurements (Langellotto and Denno 2004, Chaplin-Kramer et al. 2011). Since our meta-analyses only included relatively well-controlled experiments with mixed and control crops, a lower number of confounding effects is expected. We argue that our results considering small-sampled analyses (e.g., refuge effects) should be relatively consistent, and that causal links between variables such as predator and herbivore abundance should more reliable.

Our review shows that AR effects can be caused by many different factors, so it is important to take a step forward and discuss the mechanisms behind the plant diversity consequences on animals. Our study is the first synthesis evaluating the mechanistic effects of AR while combining the influence of plant traits and spatial variables. Future studies should be aware of the distinguished influences of predators and parasitoids in biological control practices and the considerable effects of scale.

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Conclusão geral

Nesta tese avaliamos diversos aspectos a respeito de interações mutualístas entre formigas e plantas com nectários extraflorais, alguns possíveis desdobramentos dessas interações em termos de interações associativas entre plantas do Cerrado, e, por fim, realizamos uma ampla revisão qualiquantitativa a fim de estudar os efeitos associativos de forma mais ampla.

No Capítulo 1, observamos que maiores abundâncias de ninhos estiveram relacionadas a uma menor herbivoria foliar e maior produção de frutos, enquanto maiores riquezas de ninhos estiveram associadas a aumentos em herbivoria. Todavia, não houve relação entre a riqueza de ninhos e a produção de frutos. Além disso, observamos que indivíduos de *Smilax polyantha* tiveram menos ninhos próximos de si quando estiveram em contato com um elevado número de plantas vizinhas com NEFs. Conclui-se, portanto, que a distribuição espacial dos ninhos de formiga é fundamental nas relações entre formigas e plantas com NEFs, onde ambas as plantas e formigas parecem competir pelos serviços um do outro. A inclusão da abundância e riqueza de ninhos de formiga em modelos ecológicos pode fornecer novas pistas a respeito de como as relações entre formigas e plantas são estruturadas.

Já no Capítulo 2, observamos que as plantas suporte com nectários extraflorais beneficiaram indiretamente a trepadeira *Smilax polyantha* por meio do compartilhamento de defesas bióticas efetuadas por formigas mutualistas. As espécies de plantas suporte com nectários extraflorais alteraram a composição e diversidade de formigas visitantes de *S. polyantha*, o que consequentemente contribuiu para a redução da herbivoria foliar e assimetria flutuante da mesma. Apesar disso, não observamos diferenças na produção de frutos entre os dois grupos de *S. polyantha* estudados (*S. polyantha* associada à espécies de plantas suporte com ou sem nectários extraflorais). Concluímos que interações mutualistas formadas a partir de defesas bióticas podem também beneficiar plantas vizinhas por meio da redução de danos por herbivoria. Estudos futuros devem investigar a amplitude de tais efeitos associativos por meio de potenciais impactos na estruturação de comunidades vegetais.

Por fim, no Capítulo 3, concluímos que a resistência associativa pode atuar por uma série de mecanismos distintos, sendo o compartilhamento de defesas bióticas pelas plantas vizinhas o principal mecanismo identificado na literatura. Além de constatarmos que o aumento da diversidade de plantas vizinhas favorece a atração de inimigos naturais, demonstramos que os predadores podem controlar a pressão da herbivoria em plantas focais. Os efeitos de escala e a proporção relativa entre plantas focais e vizinhas apresentaram consideráveis efeitos na atração de predadores naturais. Ademais, observamos que as plantas vizinhas controlam os herbívoros em plantas focais por meio da produção de compostos químicos e pela atuação como barreira física (refúgio). Surpreendentemente, os traços vegetais amostrados tiveram efeitos limitados sobre os herbívoros, apenas a qualidade da folha de plantas vizinhas (razão entre carbono e nitrogênio) teve efeito significativo sobre os herbívoros.

Sugerimos, por fim, que as interações positivas entre plantas apresentam grande potencial para a estruturação de comunidades. Mecanismos fundamentais de resistência vegetal, como as defesas bióticas, dependem não somente da relação direta entre a planta produtora de recurso e a formiga mutualista, mas também da estrutura vegetal local e regional como um todo. Em um planeta ameaçado por constantes impactos antrópicos, é fundamental não apenas a conservação da diversidade vegetal, mas a conservação das interações ecológicas. Como demonstrado nesta tese, o aumento da diversidade vegetal está associado ao aumento da diversidade de inimigos naturais (predadores e parasitóides) e ao controle de insetos herbívoros. Portanto, além de potenciais benefícios econômicos, a conservação da diversidade vegetal pode aumentar a resiliência da comunidades naturais por meio do aumento da diversidade das faunas local e regional.

Apêndice

Capítulo 1

Lista de espécies de formigas amostradas (Supplementary material 1)

transect	plant	nest	ant species
1	1	36	Camponotus crassus
1	1	37	Ectatomma tuberculatum
1	1	38	Pseudomyrmex sp.
1	1	39	Pheidole sp.
1	1	33	Camponotus crassus
1	1	29	Pheidole sp.
1	1	31	Camponotus crassus
1	1	32	Pheidole sp.
1	1	30	Ectatomma opaciventre
1	1	34	Pheidole sp.
1	1	35	Camponotus crassus
1	1	44	Camponotus crassus
1	1	45	Pheidole sp.
1	1	43	Pheidole sp.
1	1	40	Pheidole sp.
1	1	41	Camponotus crassus
1	1	42	Pheidole sp.
1	1	46	Camponotus crassus
1	1	47	Pheidole sp.
1	2	48	Linepithema sp.
1	2	50	Ectatomma edentatum
1	2	58	Pheidole sp.
1	2	49	Camponotus sp.
1	2	51	Ectatomma edentatum
1	2	53	Pheidole sp.
1	2	52	Camponotus sp.
1	2	55	Pheidole sp.
1	2	57	Neoponera sp.
1	2	56	Pheidole sp.
1	2	64	Camponotus sp.
1	2	59	Pheidole sp.
1	2	61	Camponotus crassus
1	2	60	Pheidole sp.
1	2	62	Linepithema sp.
1	2	63	Ectatomma tuberculatum
1	3	65	Pheidole sp.
1	3	66	Ectatomma edentatum
1	3	67	Pheidole sp.
1	3	72	Crematogaster sp.
1	3	68	Ectatomma opaciventre

1	3	71	Camponotus crassus
1	3	70	Pheidole sp.
1	3	69	Ectatomma edentatum
1	3	84	Linepithema sp.
1	3	83	Camponotus crassus
1	3	82	Linepithema sp.
1	3	42	Pheidole sp.
1	3	46	Camponotus crassus
1	3	47	Pheidole sp.
1	3	53	Pheidole sp.
1	3	52	Camponotus sp.
2	1	1	Pheidole sp.
2	1	15	Pheidole sp.
2	1	6	Camponotus sp.
2	1	11	Camponotus crassus
2	1	19	Neoponera sp.
2	1	13	Camponotus crassus
2	1	20	Camponotus crassus
2	1	12	Camponotus crassus
2	1	16	Dorymyrmex sp.
2	1	3	Ectatomma edentatum
2	1	8	Pheidole sp.
2	1	7	Pheidole sp.
2	1	17	Pheidole sp.
2	1	14	Camponotus crassus
2	1	18	Ectatomma tuberculatum
2	2	5	Camponotus sp.
2	2	23	Cephalotes pusillus
2	2	22	Camponotus crassus
2	2	21	Camponotus crassus
2	2	4	Camponotus crassus
2	2	24	Ectatomma tuberculatum
2	2	25	Camponotus crassus
2	2	7	Pheidole sp.
2	2	8	Pheidole sp.
2	2	3	Ectatomma edentatum
2	2	27	Camponotus sp.
2	2	28	Camponotus sp.
2	2	9	Camponotus sp.
3	1	74	Pheidole sp.
3	1	81	Camponotus crassus
3	1	75	Linepithema sp.
3	1	80	Ectatomma opaciventre
3	1	79	Ectatomma tuberculatum
3	1	76	Pheidole sp.
3	1	78	Pheidole sp.

3	1	77	Camponotus crassus
3	1	73	Pheidole sp.
3	1	92	Linepithema sp.
3	1	93	Camponotus crassus
3	1	97	Camponotus crassus
3	1	96	Pseudomyrmex sp.
3	1	88	Pheidole sp.
3	1	94	Camponotus crassus
3	1	91	Camponotus sp.
3	1	90	Pheidole sp.
3	1	89	Ectatomma opaciventre
3	1	87	Pheidole sp.
3	1	86	Ectatomma opaciventre
3	1	98	Solenopsis sp.
3	2	103	Ectatomma opaciventre
3	2	101	Linepithema sp.
3	2	102	Pheidole sp.
3	2	108	Solenopsis sp.
3	2	111	Camponotus crassus
3	2	104	Ectatomma opaciventre
3	2	106	Solenopsis sp.
3	2	99	Pheidole sp.
3	2	100	Neoponera sp.
3	2	105	Linepithema sp.
3	2	109	Crematogaster sp.
3	2	110	Camponotus crassus
3	2	114	Pheidole sp.
3	2	116	Camponotus crassus
3	2	115	Pheidole sp.
3	2	120	Ectatomma opaciventre
3	2	112	Camponotus renggeri
3	2	121	Camponotus crassus
3	2	113	Pheidole sp.
3	2	122	Ectatomma opaciventre
3	3	118	Pheidole sp.
3	3	119	Pheidole sp.
3	3	117	Pheidole sp.
3	3	125	Camponotus crassus
3	3	126	Crematogaster sp.
3	3	106	Solenopsis sp.
3	3	87	Pheidole sp.
3	3	86	Ectatomma opaciventre
3	3	104	Ectatomma opaciventre
3	3	111	Camponotus crassus
3	3	123	Pheidole sp.
3	3	124	Crematogaster sp.

3	3	131	Ectatomma opaciventre
3	3	127	Atta sp.
3	3	132	Ectatomma tuberculatum
3	3	128	Camponotus crassus
3	3	129	Pheidole sp.
3	3	130	Camponotus crassus
4	1	136	Ectatomma edentatum
4	1	135	Camponotus crassus
4	1	139	Camponotus crassus
4	1	138	Ectatomma edentatum
4	1	137	Camponotus crassus
4	1	141	Pheidole sp.
4	1	142	Trachymyrmex sp.
4	1	133	Gnamptogenys sp.
4	1	134	Ectatomma edentatum
4	1	140	Pheidole sp.
4	1	150	Cephalotes pusillus
4	1	144	Camponotus crassus
4	1	145	Ectatomma edentatum
4	1	146	Pheidole sp.
4	1	147	Ectatomma opaciventre
4	1	148	Camponotus crassus
4	1	149	Pseudomyrmex sp.
4	1	143	Pheidole sp.
4	1	151	Camponotus crassus
4	2	152	Pheidole sp.
4	2	158	Ectatomma permagnum
4	2	154	Ectatomma permagnum
4	2	156	Pheidole sp.
4	2	155	Pheidole sp.
4	2	153	Ectatomma opaciventre
4	2	159	Pheidole sp.
4	2	157	Ectatomma opaciventre
4	2	160	Neoponera sp.
4	2	161	Crematogaster sp.
4	2	140	Pheidole sp.
4	2	133	Gnamptogenys sp.
4	2	134	Ectatomma edentatum
4	2	162	Pheidole sp.
4	2	166	Ectatomma edentatum
4	2	165	Pseudomyrmex sp.
4	2	164	Pheidole sp.
4	2	163	Crematogaster sp.
5	1	168	Crematogaster sp.
5	1	170	Camponotus blandus
5	1	169	Ectatomma brunneum

5	1	167	Solenopsis sp.
5	1	171	Camponotus sp.
5	1	182	Camponotus blandus
5	1	181	Pheidole sp.
5	1	183	Cephalotes pusillus
5	1	184	Camponotus blandus
5	1	186	Ectatomma opaciventre
5	1	172	Pheidole sp.
5	1	173	Camponotus blandus
5	1	185	Ectatomma opaciventre
5	1	177	Camponotus blandus
5	1	178	Pheidole sp.
5	1	179	Ectatomma sp.
5	1	180	Camponotus sp.
5	1	197	Solenopsis sp.
5	1	199	Camponotus blandus
5	1	196	Atta sp.
5	1	175	Pheidole sp.
5	1	174	Camponotus blandus
5	2	192	Pheidole sp.
5	2	188	Camponotus crassus
5	2	200	Camponotus blandus
5	2	193	Ectatomma brunneum
5	2	187	Ectatomma brunneum
5	2	189	Solenopsis sp.
5	2	198	Camponotus melanoticus
5	2	190	Ectatomma opaciventre
5	2	191	Pheidole sp.
5	2	194	Ectatomma opaciventre
5	2	195	Camponotus crassus
5	2	196	Atta sp.
5	2	202	Ectatomma brunneum
5	2	203	Pheidole sp.
5	2	204	Camponotus crassus
5	2	201	Crematogaster sp.
5	2	205	Camponotus blandus
5	2	206	Camponotus sp.
5	2	207	Pheidole sp.
5	2	208	Ectatomma brunneum
5	2	209	Camponotus crassus
5	2	210	Pheidole sp.
5	2	211	Camponotus crassus
5	3	217	Camponotus crassus
5	3	216	Cephalotes pusillus
5	3	218	Ectatomma brunneum
5	3	215	Pheidole sp.

5	3	222	Camponotus blandus
5	3	219	Ectatomma brunneum
5	3	201	Crematogaster sp.
5	3	203	Pheidole sp.
5	3	214	Neoponera sp.
5	3	204	Camponotus crassus
5	3	220	Ectatomma edentatum
5	3	221	Ectatomma tuberculatum
5	3	212	Camponotus crassus
5	3	213	Atta sp.
5	3	187	Ectatomma brunneum
5	3	188	Camponotus crassus
5	3	202	Ectatomma brunneum
5	3	200	Camponotus blandus
5	3	193	Ectatomma brunneum
6	1	167	Solenopsis sp.
6	1	168	Crematogaster sp.
6	1	169	Ectatomma brunneum
6	1	170	Camponotus blandus
6	1	172	Pheidole sp.
6	1	173	Camponotus blandus
6	1	174	Camponotus blandus
6	1	175	Pheidole sp.
6	1	225	Atta sp.
6	1	224	Ectatomma brunneum
6	1	223	Neoponera sp.
6	1	226	Pheidole sp.
6	1	231	Ectatomma opaciventre
6	1	227	Odontomachus sp.
6	1	177	Camponotus blandus
6	1	185	Ectatomma opaciventre
6	1	178	Pheidole sp.
6	1	179	Ectatomma sp.
6	1	180	Camponotus sp.
6	2	246	Neoponera sp.
6	2	247	Solenopsis sp.
6	2	245	Neoponera sp.
6	2	257	Camponotus blandus
6	2	184	Camponotus blandus
6	2	183	Cephalotes pusillus
6	2	186	Ectatomma opaciventre
6	2	249	Pheidole sp.
6	2	250	Crematogaster sp.
6	2	256	Neoponera sp.
6	2	251	Neoponera sp.
6	2	258	Pheidole sp.

6	2	260	Pheidole sp.
6	2	266	Camponotus melanoticus
6	2	259	Neoponera sp.
6	2	227	Odontomachus sp.
6	2	248	Odontomachus sp.
6	2	262	Crematogaster sp.
6	2	261	Pheidole sp.
6	2	263	Ectatomma brunneum
6	2	264	Neoponera sp.
6	3	228	Camponotus blandus
6	3	229	Dorymyrmex sp.
6	3	232	Camponotus crassus
6	3	233	Cephalotes pusillus
6	3	237	Cephalotes pusillus
6	3	238	Pheidole sp.
6	3	239	Ectatomma edentatum
6	3	241	Camponotus sp.
6	3	240	Pheidole sp.
6	3	244	Solenopsis sp.
6	3	230	Neoponera sp.
6	3	235	Pheidole sp.
6	3	242	Camponotus sp.
6	3	243	Camponotus crassus
6	3	236	Pheidole sp.
6	3	255	Neoponera sp.
6	3	265	ant_escaped
6	3	253	Ectatomma tuberculatum
6	3	254	Camponotus crassus
6	3	252	Neoponera sp.
7	1	274	Odontomachus sp.
7	1	273	Ectatomma edentatum
7	1	275	Camponotus melanoticus
7	1	276	Camponotus sp.
7	1	277	Ectatomma brunneum
7	1	271	Camponotus crassus
7	1	272	Ectatomma brunneum
7	1	283	Linepithema sp.
7	1	287	Ectatomma edentatum
7	1	270	Neoponera sp.
7	1	268	Ectatomma brunneum
7	1	267	Pheidole sp.
7	1	269	Camponotus blandus
7	1	284	Pheidole sp.
7	1	285	Camponotus crassus
7	1	288	Camponotus sp.
7	1	278	Pheidole sp.

7	1	280	Ectatomma brunneum
7	1	282	Camponotus sp.
7	1	281	Pheidole sp.
7	1	279	Camponotus sp.
7	2	291	Pheidole sp.
7	2	292	Camponotus sp.
7	2	294	Camponotus melanoticus
7	2	293	Camponotus crassus
7	2	286	Camponotus crassus
7	2	297	Camponotus crassus
7	2	289	Pheidole sp.
7	2	290	Ectatomma brunneum
7	2	296	Camponotus crassus
7	2	295	Pheidole sp.
7	2	299	Camponotus crassus
7	2	298	Atta sp.
7	2	301	Odontomachus sp.
7	2	307	Camponotus blandus
7	2	300	Ectatomma brunneum
7	2	302	Ectatomma edentatum
7	2	303	Gnamptogenys sp.
7	2	305	Dorymyrmex sp.
7	2	304	Pheidole sp.
7	2	308	Cephalotes pusillus
8	1	309	Pheidole sp.
8	1	312	Neoponera sp.
8	1	310	Pheidole sp.
8	1	311	Ectatomma edentatum
8	1	317	Ectatomma brunneum
8	1	313	Trachymyrmex sp.
8	1	318	Camponotus crassus
8	1	319	Pheidole sp.
8	1	320	Camponotus sp.
8	1	314	Ectatomma edentatum
8	1	315	Cephalotes pusillus
8	1	316	Pheidole sp.
8	1	327	Pheidole sp.
8	1	332	Linepithema sp.
8	1	328	Ectatomma tuberculatum
8	1	326	Pheidole sp.
8	1	325	Neoponera sp.
8	1	324	Ectatomma edentatum
8	1	321	Ectatomma brunneum
8	1	322	Pheidole sp.
8	1	323	Pheidole sp.
8	1	329	Pseudomyrmex sp.

8	1	330	Cephalotes pusillus
8	2	324	Ectatomma edentatum
8	2	325	Neoponera sp.
8	2	327	Pheidole sp.
8	2	332	Linepithema sp.
8	2	328	Ectatomma tuberculatum
8	2	326	Pheidole sp.
8	2	310	Pheidole sp.
8	2	311	Ectatomma edentatum
8	2	309	Pheidole sp.
8	2	312	Neoponera sp.
8	2	334	Ectatomma tuberculatum
8	2	335	Pheidole sp.
8	2	336	Ectatomma opaciventre
8	2	341	Pseudomyrmex sp.
8	2	338	Camponotus sp.
8	2	337	Camponotus sp.
8	2	339	Pheidole sp.
8	3	347	Linepithema sp.
8	3	348	Ectatomma brunneum
8	3	351	Camponotus sp.
8	3	354	Ectatomma opaciventre
8	3	343	Ectatomma brunneum
8	3	352	Ectatomma opaciventre
8	3	344	Ectatomma edentatum
8	3	346	Ectatomma brunneum
8	3	349	Neoponera sp.
8	3	350	Cephalotes pusillus
8	3	342	Linepithema sp.
8	3	345	Ectatomma brunneum
8	3	355	Solenopsis sp.
8	3	356	Camponotus sp.
8	3	357	Ectatomma edentatum
8	3	360	Linepithema sp.
8	3	359	Linepithema sp.
8	3	361	Ectatomma opaciventre
10	1	362	Atta sp.
10	1	366	Atta sp.
10	1	367	Camponotus blandus
10	1	364	Crematogaster sp.
10	1	365	Dorymyrmex sp.
10	1	369	Camponotus crassus
10	1	368	Pheidole sp.
10	1	370	Pheidole sp.
10	1	363	Linepithema sp.
10	1	377	Pheidole sp.

10	1	376	Linepithema sp.
10	1	378	Ectatomma edentatum
10	1	379	Ectatomma tuberculatum
10	1	380	Camponotus renggeri
10	1	372	Neoponera sp.
10	1	373	Pheidole sp.
10	1	371	Camponotus crassus
10	1	375	Gnamptogenys sp.
10	1	374	Solenopsis sp.
10	2	381	Nomamyrmex sp.
10	2	383	Ectatomma opaciventre
10	2	384	Pheidole sp.
10	2	385	Neoponera sp.
10	2	386	Ectatomma tuberculatum
10	2	382	Ectatomma opaciventre
10	2	387	Ectatomma tuberculatum
10	2	388	Nylanderia
10	2	389	Crematogaster sp.
10	2	390	Pheidole sp.
10	2	391	Pheidole sp.
10	2	392	Pheidole sp.
10	2	393	Camponotus crassus
10	2	394	Camponotus sp.

Espécies de formigas observadas visitando *Smilax polyantha* (Supplementary material 2)

		Week1		Week2		Week3		Week4		Week5		Week6		Week7		Week8		Week9		Week10	
transect	plant	ants	species	ants	species	ants	species	ants	species	ants	species	ants	species	ants	species	ants	species	ants	species	ants	species
1	1	0		1	Camponotus crassus	3	Camponotus crassus	3	Camponotus crassus	2	Camponotus crassus	1	Camponotus crassus	1	Camponotus crassus	3	Camponotus crassus	2	Camponotus crassus	1	Camponotus crassus
1	2	1	Ectatomma tuberculatum	1	Ectatomma tuberculatum	0		0		0		0		0		2	Camponotus crassus	3	Camponotus crassus	1	Ectatomma tuberculatum
1	3	0		0		0		0		0		0		0		0		0		0	
2	1	3	Camponotus sp	1	Camponotus sp	0		1	Camponotus crassus	0		0		0		0		1	Camponotus sp1	0	
2	2	3	Camponotus crassussus	1	Camponotus crassus	0		0		0		0		0		0		0		0	
3	1	1	Camponotus crassussus	3	Camponotus crassus	2	Camponotus crassus	2	Camponotus crassus	1	Pseudomyrmex sp	1	Pseudomyrmex gracilis	0		0		0		1	Camponotus crassus
3	2	0		1	Camponotus crassus	0		0		0		0		1	Ectatomma tuberculatum	0		0		2	1Ectatomma tuberculatum,1Pseudomyrmex gracilis
3	3	0		2	Camponotus crassus	0		3	Camponotus crassus	2	Camponotus crassus	1	Camponotus crassus	3	Camponotus crassus	3	Camponotus crassus	6	Camponotus crassus	2	Camponotus crassus
4	1	0		1	Camponotus crassus	2	Camponotus crassus	4	1Camponotus crassus,3Crematogaster sp	3	Camponotus crassus	1	Camponotus crassus	3	1Camponotus crassus,2Crematogaster sp	3	Camponotus sp1	0		2	Camponotus crassus
4	2	0		0		2	1Camponotus crassus,1Pseudomyrmex gracilis	0		0		0		0		0		0		0	
5	1	0		0		1	Ectatomma tuberculatum	0		0		0		0		0		1	Camponotus blandus	0	
5	2	2	Camponotus crassus	4	Camponotus crassus	3	Camponotus crassus	5	Camponotus crassus	3	Camponotus crassus	0		1	Camponotus crassus	2	Camponotus crassus	5	Camponotus crassus	2	Camponotus crassus
5	3	3	Camponotus crassus	5	Camponotus crassus	4	Camponotus crassus	6	Camponotus crassus	4	Camponotus crassus	5	Camponotus crassus	2	Camponotus crassus	5	4Camponotus crassus,1Camponotus sp1	4	Camponotus crassus	3	Camponotus crassus
6	1	1	Camponotus melanoticus	3	2Camponotus blandus,1Cephalotes pusilus	1	Camponotus crassus	0		3	1Camponotus blandus,2Camponotus crassus	0		0		3	Camponotus blandus	2	Camponotus blandus	1	Cephalotes pusilus
6	2	10	Crematogaster sp	5	2Camponotus crassus,3Crematogaster sp	44	2Camponotus blandus,40Crematogaster sp,1Cephalotes pusilus,1Pseudomyrmex gracilis	1	Camponotus blandus	22	1Camponotus blandus,21Crematogaster sp	18	1Camponotus crassus,17Crematogaster sp	9	Crematogaster sp	29	Crematogaster sp	27	26Crematogaster sp,1Camponotus crassus	5	Crematogaster sp
6	3	0		0		0		0		0		0		0		0		0		0	
7	1	1	Camponotus crassus	2	Cephalotes pusilus	1	Camponotus crassus	0		0		2	Cephalotes pusilus	4	Cephalotes pusilus	3	2Camponotus crassus,1Cephalotes pusilus	1	Camponotus crassus	0	
7	2	3	Camponotus crassus	6	Camponotus crassus	5	Camponotus crassus	5	Camponotus crassus	4	Camponotus crassus	2	Pseudomyrmex gracilis,Camponotus crassus	2	Pseudomyrmex gracilis,Camponotus crassus	3	1Camponotus mus,2Camponotus crassus	5	4Camponotus crassus,1Cephalotes pusilus	1	Camponotus crassus
8	1	2	Cephalotes pusillus	3	1Camponotus crassus,2Crematogaster sp	3	Crematogaster sp	3	1Camponotus crassus,2Crematogaster sp	1	Camponotus crassus	0		0		17	Crematogaster sp	3	1Camponotus crassus,2Crematogaster sp	0	
8	2	4	Crematogaster sp	3	Crematogaster sp	15	Crematogaster sp	10	Crematogaster sp	0		24	Crematogaster sp	4	Crematogaster sp	0		0		0	
8	3	2	Pseudomyrmex gracilis	1	Pseudomyrmex gracilis	0		0		0		0		0		0		1	Camponotus crassus	0	
10	1	0		4	Camponotus crassus	2	Camponotus crassus	0		4	Camponotus crassus	5	Camponotus crassus	4	Camponotus crassus	6	Camponotus crassus	1	Camponotus crassus	2	Camponotus crassus
10	2	1	Camponotus crassus	0		1	Camponotus crassus	0		0		0		1	Camponotus crassus	2	Ectatomma tuberculatum	0		0	
pp	1	0		0		0		1	Camponotus crassus	2	Camponotus crassus	0		0		2	Camponotus crassus	5	Camponotus crassus	0	
pp	2	1	Camponotus crassus	1	Camponotus sp2	0		1	Pseudomyrmex gracilis	1	Camponotus crassus	0		0		0		0		0	
pp	3	1	Ectatomma tuberculatum	2	Ectatomma tuberculatum,Camponotus leydigi	1	Ectatomma tuberculatum	3	1Ectatomma tuberculatum,2Camponotus blandus	3	Ectatomma tuberculatum	0		1	Ectatomma tuberculatum	0		0		0	
pp	4	1	Ectatomma tuberculatum	2	Ectatomma tuberculatum,Camponotus leydigi	0		1	Ectatomma tuberculatum	1	Ectatomma tuberculatum	2	Ectatomma tuberculatum	2	Ectatomma tuberculatum	1	Ectatomma tuberculatum	0		0	

pp	4.2	0		0		2	Camponotus crassus	2	Camponotus crassus	2	Camponotus crassus	0		1	Camponotus crassus	0		0		0	
pp	5	2	Ectatomma tuberculatum,Pseudomyrmex gracilis	1	Ectatomma tuberculatum	1	Camponotus crassus	2	1Camponotus crassus,1Camponotus sp2	0		0		0	142	0		2	Camponotus sp1	2	Camponotus mus,Camponotus sp1
pp	6	0		0		3	Camponotus crassus	1	Camponotus crassus	1	Camponotus crassus	1	Ectatomma tuberculatum	0	0	0		0		0	
pp	7	1	Pseudomyrmex gracilis	0		0		7	Camponotus crassus	0		0		1	Pseudomyrmex gracilis	0		0		0	
pp	8	1	Camponotus crassus	0		3	Camponotus crassus	2	1Camponotus crassus,1Ectatomma tuberculatum	1	Ectatomma tuberculatum	0		0		1	Ectatomma tuberculatum	1	Camponotus blandus	0	
pp	9	2	Camponotus crassus	3	Camponotus crassus	0		3	Camponotus crassus	0		2	Camponotus crassus	0		0		1	Camponotus crassus	0	
pp	10	1	Camponotus crassus	8	6Crematogaster sp,1Camponotus crassus,1Camponotus senex	3	Camponotus crassus	0		0		0		0		0		0		0	
pp	11	2	Camponotus crassus	2	Ectatomma tuberculatum,Camponotus crassus	1	Camponotus sp3	1	Camponotus crassus	0		1	Ectatomma tuberculatum	1	Ectatomma tuberculatum	0		2	Camponotus crassus	1	Camponotus blandus
ad	ad1	1	Camponotus crassus	0		0		1	Pseudomyrmex gracilis	0		0		0		0		0		1	Crematogaster sp
ad	ad2	1	Camponotus crassus	1	Camponotus crassus	0		1	Camponotus crassus	0		0		0		0		0		0	
ad	ad3	0		2	Camponotus crassus	0		3	Camponotus crassus	2	Camponotus crassus	0		3	2Ectatomma tuberculatum,1Camponotus crassus	0		0		0	
ad	ad4	0		1	Pseudomyrmex gracilis	1	Camponotus crassus	0		1	Camponotus crassus	1	Pseudomyrmex sp	0		0		0		0	
ad	ad6	2	Camponotus crassus	3	Camponotus crassus,Crematogaster sp,Cephalotes pusilus	0		2	Ectatomma tuberculatum,Cephalotes pusilus	2	Camponotus crassus	2	Camponotus crassus,Cephalotes pusilus	1	Cephalotes pusilus	3	Camponotus crassus,Camponotus sp1,Ectatomma tuberculatum	2	Camponotus crassus,Ectatomma tuberculatum	1	Ectatomma tuberculatum
ad	ad7	1	Camponotus blandus	7	3Camponotus blandus,4Camponotus crassus	8	7Camponotus crassus,1Camponotus blandusus	7	6Camponotus crassus,1Camponotus blandus	6	4Camponotus crassus,2Camponotus blandus	7	2Camponotus blandus,Camponotus crassus	7	4Camponotus blandus,2Camponotus crassus,1Cephalotes pusilus	5	4Camponotus blandus,1Cephalotes pusilus	9	7Camponotus blandus,2Camponotus crassus	1	Camponotus blandus
ad	t9	3	2Camponotus crassus,1Pseudomyrmex gracilis	5	4Camponotus crassus,1Cephalotes pusilus	4	Camponotus crassus	2	Camponotus crassus	4	1Camponotus crassus,3Cephalotes pusilus	2	Cephalotes pusilus	5	Cephalotes pusilus	4	Camponotus crassus	6	5Camponotus crassus,1Cephalotes pusilus	2	Camponotus crassus
ad	t9	1	Camponotus crassus	0		0		2	Camponotus crassus	2	Camponotus crassus,Pseudomyrmex gracilis	2	Camponotus crassus	2	1Pseudomyrmex gracilis,1Camponotus crassus	5	Camponotus crassus	0		1	Ectatomma tuberculatum
ad	t9	0		0		0		1	Camponotus sp2	0		3	2Camponotus blandus,1Ectatomma tuberculatum	0		0		0		0	
ad	ad10	1	Pseudomyrmex gracilis	2	Camponotus crassus	2	Camponotus crassus	1	Camponotus crassus	4	3Camponotus crassus,Camponotus sp1	3	Camponotus crassus	2	Camponotus crassus	2	Camponotus crassus	0		0	

Figura S1

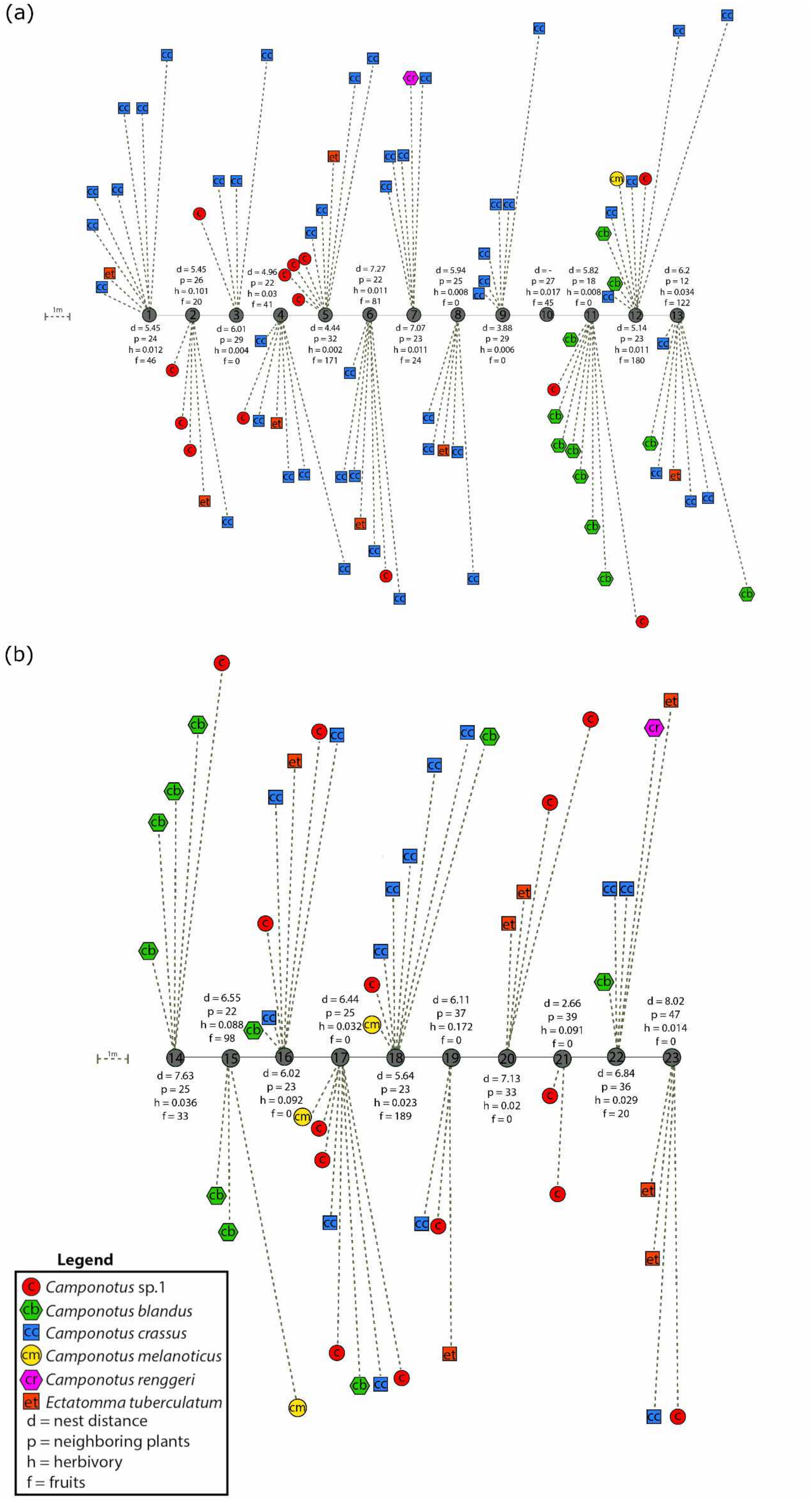
(a)
1m
1
d = 5.45
p = 24
h = 0.012
f = 46
2
d = 5.45
p = 26
h = 0.101
f = 20
3
d = 6.01
p = 29
h = 0.004
f = 0
4
d = 4.96
p = 22
h = 0.03
f = 41
5
d = 4.44
p = 32
h = 0.002
f = 171
6
d = 7.27
p = 22
h = 0.011
f = 81
7
d = 7.07
p = 23
h = 0.011
f = 24
8
d = 5.94
p = 25
h = 0.008
f = 0
9
d = 3.88
p = 29
h = 0.006
f = 0
10
d = -
p = 27
h = 0.017
f = 45
11
d = 5.82
p = 18
h = 0.008
f = 0
12
d = 5.14
p = 23
h = 0.011
f = 180
13
d = 6.2
p = 12
h = 0.034
f = 122
(b)
1m
14
d = 7.63
p = 25
h = 0.036
f = 33
15
d = 6.55
p = 22
h = 0.088
f = 98
16
d = 6.02
p = 23
h = 0.092
f = 0
17
d = 6.44
p = 25
h = 0.032
f = 0
18
d = 5.64
p = 23
h = 0.023
f = 189
19
d = 6.11
p = 37
h = 0.172
f = 0
20
d = 7.13
p = 33
h = 0.02
f = 0
21
d = 2.66
p = 39
h = 0.091
f = 0
22
d = 6.84
p = 36
h = 0.029
f = 20
23
d = 8.02
p = 47
h = 0.014
f = 0
c
cb
cc
cm
cr
et
Legend
c *Camponotus* sp.1
cb *Camponotus blandus*
cc *Camponotus crassus*
cm *Camponotus melanoticus*
cr *Camponotus renggeri*
et *Ectatomma tuberculatum*
d = nest distance
p = neighboring plants
h = herbivory
f = fruits

Figure S1. The distribution of *Smilax polyantha* plants and ant nests, including their relative distances from each studied plant (see results for further details). The top figure (a) shows plants and ant nests studied in the first five established transects, while the bottom figure (b) shows plants and ant nests found within the last four transects. Each numbered circle (1 to 13 and 14 to 23) corresponds to one plant. The six most frequent ant species were chosen to compose these figures, which are: *Camponotus* sp.1, *C. blandus*, *C. crassus*, *C. melanoticus*, *C. renggeri*, and *Ectatomma tuberculatum*. For each nest of a certain species found within the transect of a reference plant, there is a corresponding symbol, which is described in the figure's legend. The exact geographical positions of plants and ant nests are not illustrated in this diagram, but the distance from each ant nest to the plant is represented in scale by dotted lines. Beside each represented plant's circle, the values of the average distance between all ant nests recorded in a transect and the reference plant (d), the absolute number of all neighboring plans (p), the foliar herbivory percentage (h), and the number of fruits (f) are shown.

Figura S2

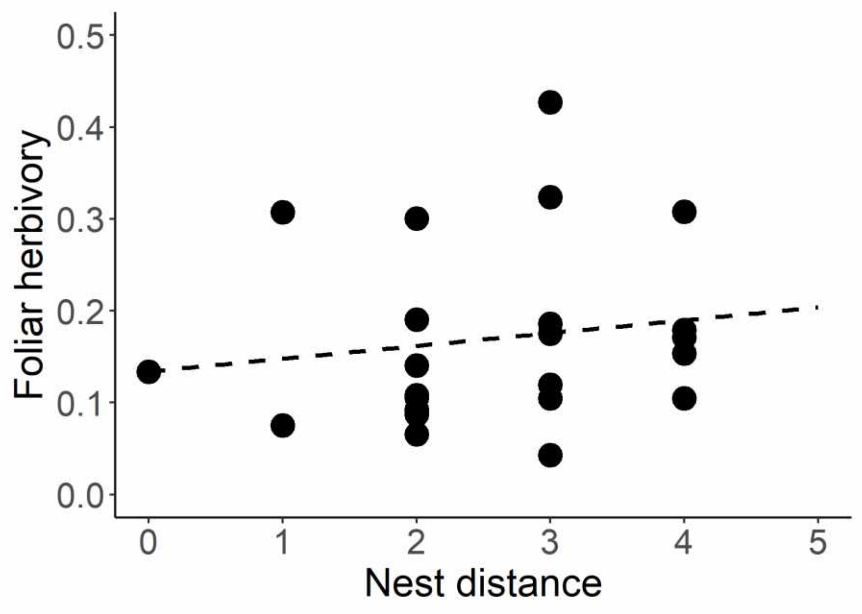

Figure S2. Linear regression between the mean distance of ant nests (m) and foliar herbivory of *Smilax polyantha* ($F_{1,21} = 0.002$, $R^2 < 0.001$, $p = 0.97$).

Capítulo 2

Espécies de formigas observadas visitando *S. polyantha* (Supplementary material)

	c.cras	camposp	camposp1	camposp2	camposp3	c.blandus	c.melanot	c.senex	campo_mus	c.leidy	e.tube	pseudo_p	cephalo	cremat	pseudo_ama
t1_p3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
t2_p1	1	4	1	0	0	0	0	0	0	0	0	0	0	0	0
t2_p2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
t3_p2	1	0	0	0	0	0	0	0	0	0	2	1	0	0	0
t3_p3	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0
t5_p1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
t5_p2	27	0	0	0	0	0	0	0	0	0	0	0	0	0	0
t5_p3	40	0	1	0	0	0	0	0	0	0	0	0	0	0	0
t6_p1	3	0	0	0	0	8	1	0	0	0	0	0	2	0	0
t6_p2	7	0	0	0	0	4	0	0	0	0	0	1	1	160	0
t6_p3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
t7_p1	5	0	0	0	0	0	0	0	0	0	0	0	9	0	0
t8_p1	4	0	0	0	0	0	0	0	0	0	0	0	2	26	0
t8_p2	0	0	0	0	0	0	0	0	0	0	0	0	0	60	0
t10_p2	3	0	0	0	0	0	0	0	0	0	2	0	0	0	0
4	0	0	0	0	0	0	0	0	0	1	9	0	0	0	0
6	5	0	0	0	0	0	0	0	0	0	1	0	0	0	0
10	5	0	0	0	0	0	0	1	0	0	0	0	0	6	0
2ad	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
t9_p3	0	0	0	1	0	2	0	0	0	0	1	0	0	0	0
t1_p1	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0
t1_p2	4	0	0	0	0	0	0	0	0	0	3	0	0	0	0
t3_p1	9	0	0	0	0	0	0	0	0	0	0	1	0	0	1
t4_p1	14	0	1	0	0	0	0	0	0	0	0	0	0	5	0
t4_p2	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
t7_p2	32	0	0	0	0	0	0	0	1	0	0	2	1	0	0
t8_p3	1	0	0	0	0	0	0	0	0	0	0	3	0	0	0
t10_p1	28	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	2	0	0	1	0	0	0	0	0	0	0	1	0	0	0
3	0	0	0	0	0	2	0	0	0	1	8	0	0	0	0
4.2	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	2	0	3	1	0	0	0	0	1	0	2	1	0	0	0
7	7	0	0	0	0	0	0	0	0	0	0	2	0	0	0
8	5	0	0	0	0	1	0	0	0	0	0	3	0	0	0
9	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	6	0	0	0	1	1	0	0	0	0	3	0	0	0	0
1ad	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0
3ad	8	0	0	0	0	0	0	0	0	0	2	0	0	0	0
4ad	2	0	0	0	0	0	0	0	0	0	0	1	0	0	1
6ad	8	0	1	0	0	0	0	0	0	0	4	0	4	1	0

7ad	30	0	0	0	0	26	0	0	0	0	0	0	2	0	0
t9_p1	24	0	0	0	0	0	0	0	0	0	0	1	12	0	0
t9_p2	12	0	0	0	0	0	0	0	0	0	1	2	0	0	0
10ad	15	0	1	0	0	0	0	0	0	0	0	1	0	0	0

Capítulo 3

Figura S1

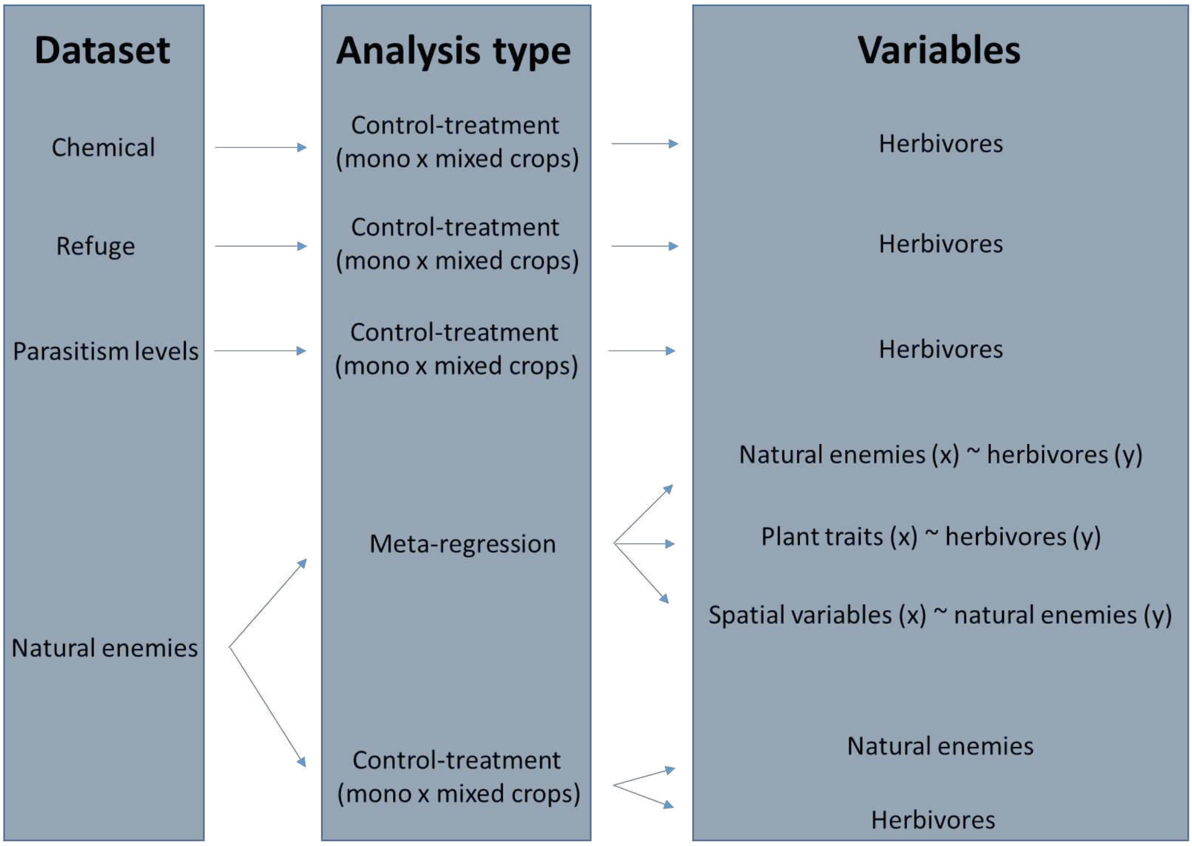

Figure S1. Chart showing the organization of performed meta-analyses

Lista de artigos amostrados a respeito do tema resistência associativa (Supplementary material)

Abdala-Roberts L, Gonzalez-Moreno A, Mooney KA, et al (2016a) Effects of tree species diversity and genotypic diversity on leafminers and parasitoids in a tropical forest plantation. Agric For Entomol 18:43–51. https://doi.org/10.1111/afe.12132

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