UNIVERSIDADE FEDERAL DE VIÇOSA

GLÓRIA RAMOS SOARES

INTERAÇÕES TRI-TRÓFICAS NO DOSSEL: O PAPEL DA FORMIGA *Azteca chartifex* NA DISTRIBUIÇÃO DOS ARTRÓPODES E NO SUCESSO REPRODUTIVO DE *Byrsonima sericea*

VIÇOSA - MINAS GERAIS
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Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Ecologia, para obtenção do título de *Doctor Scientiae.*

Orientador: Sérvio Pontes Ribeiro

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APROVADA: 05 de julho de 2019.

Glória Ramos Soares
Autora

Sérvio Pontes Ribeiro
Orientador

À Nilza Soares,

Minha mamãe,

por quem tenho respeito,

muito amor e eterna admiração

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RESUMO

SOARES, Glória Ramos, D.Sc., Universidade Federal de Viçosa, julho de 2019. **Interações tri-tróficas no dossel: o papel da formiga *Azteca chartifex* na distribuição dos artrópodes e no sucesso reprodutivo de *Byrsonima sericea*.** Orientador: Sérvio Pontes Ribeiro. Coorientador: Ricardo Ildefonso de Campos.

As interações interespecíficas estão entre os processos mais importantes que influenciam os padrões de adaptação e variação de espécies, bem como a organização e estrutura de comunidades. Estas relações são caracterizadas por um sistema de custo benefício, variando em um contínuo entre antagonismo e mutualismo. A interação mutualística formiga-planta têm se mostrado importante na defesa da planta contra herbívoros, tendo como principal resultado a proteção efetiva seguida pelo aumento da aptidão da planta. Sabemos que o aumento da complexidade do habitat pode favorecer as formigas predadoras ao possibilitar a expansão de seus territórios. Porém, apesar de habitats mais complexos aumentarem a chance de encontro entre presas e predadores, estes ambientes também podem fornecer refúgios para as presas e dificultar sua localização. Compreender o papel do mutualismo formiga-planta, mediado pela complexidade estrutural do habitat, permitiria detectarmos os efeitos sobre a distribuição de artrópodes e o sucesso reprodutivo da planta hospedeira. Assim, no primeiro momento investigamos o efeito cascata da presença da formiga *Azteca chartifex* na diversidade das guildas de artrópodes do dossel florestal de uma árvore dominante nos ecótonos florestais, *Byrsonima sericea*. No segundo momento investigamos se a associação entre *A. chartifex* e liana influenciaria a efetividade do mutualismo formiga-planta. Realizamos nosso estudo no Parque Estadual do Rio Doce, Sudeste do Brasil, a partir de populações de *B. sericea* monitoradas em longo prazo. Selecionamos arbitrariamente 68 árvores distribuídas em três populações distintas e que tinham lianas em suas respectivas copas. Metade destes indivíduos era patrulhada por *A. chartifex* e a outra metade não possuíam relação com esta formiga. Nós distribuímos as árvores em dois tratamentos dentro das populações para investigarmos o efeito da presença de *A. chartifex* nos artrópodes do dossel florestal: i) *A. chartifex* presente (n = 32) e ii) *A. chartifex* ausente (n = 36). Para investigarmos o efeito da associação entre *A. chartifex* e liana no dossel, nós realizamos um experimento de remoção das lianas e redistribuímos as mesmas árvores em quatro tratamentos dentro das populações: i) *A. chartifex* e liana presente (n = 16); ii) *A. chartifex* ausente e liana presente (n = 18); iii) *A. chartifex* presente e liana removida (n = 16); e iv) *A. chartifex* ausente e liana removida (n = 18). As amostragens foram realizadas em três distintas fases:

março e agosto de 2016 e março de 2017 (daqui por diante, Fase I, Fase II e Fase III, respectivamente). Na Fase I amostramos os artrópodes e coletamos as folhas para mensurar a herbivoria. Na Fase II realizamos o experimento de remoção das lianas das copas de *B. sericea* e, na Fase III, amostramos novamente os artrópodes e coletamos também folhas para mensurar a herbivoria. Para inventariarmos os artrópodes utilizamos a técnica de batimento e para estimarmos a herbivoria mensuramos os danos foliares em laboratório a partir da seleção das folhas através de um cubo aramado. Paralelo as estas amostragens, mensurarmos também o sucesso reprodutivo de *B. sericea* pela taxa de conversão de flores em frutos. Nossos resultados demonstraram que *A. chartifex* é uma espécie central na estruturação das guildas de artrópodes associadas à *B. sericea*, alterando a densidade populacional, a co-existência e as interações dos outros predadores e dos herbívoros. A presença de *A. chartifex* resultou também em um efeito cascata caracterizado por menores danos foliares em *B. sericea*. Detectamos, ainda, que a presença de liana é mais bem utilizada por *A. chartifex* do que pelos insetos herbívoros, potencializando a eficiência do forrageio desta formiga que refletiu no sucesso reprodutivo de *B. sericea*. Ao utilizar das lianas como caminhos alternativos para forragear, *A. chartifex* reduziu a densidade populacional dos herbívoros e aumentou a taxa de conversão de flores em frutos. De maneira geral, podemos concluir que as interações tri-tróficas discutidas nesta tese são afetadas pela presença de formigas territorialistas e dominantes, bem como pela presença de liana. Assim, compreender como estas interações se desenvolvem, bem como seus custos e benefícios, e qual é a espécie central envolvida foram aspectos primordiais para nosso entendimento acerca da dinâmica de comunidades nos ecótonos florestais. Estes aspectos contribuem para direcionarmos esforços para aquelas espécies estruturalmente importantes, auxiliando futuras práticas de manejo ou conservação do ambiente.

Palavras-chave: Interação formiga-planta. Liana. Dossel. Interações interespecíficas.

ABSTRACT

SOARES, Glória Ramos, D.Sc., Universidade Federal de Viçosa, July, 2019. **Canopy tri-trophic interactions: *Azteca chartifex* ant role in distribution of arthropods and *Byrsonima sericea* reproductive success.** Advisor: Sérvio Pontes Ribeiro. Co-advisor: Ricardo Ildefonso de Campos.

Interspecific interactions are among most important processes that influence patterns of species adaptation and variation, as well as organization and structure of communities. These relationships are characterized by a system of cost-benefit, varying from a continuum between antagonism and mutualism. Ant-plant mutualistic has been shown to be important in plant defense against herbivores, having as main result effective protection followed by increase of plant fitness. We know that increasing habitat complexity may favor predatory ants by allowing expansion of their territories. However, although more complex habitats increase encounters chance between preys and predators, these environments can also provide refuges for prey and make it difficult to locate. Understanding the role of ant-plant mutualism, mediated by habitat structural complexity, would allow us to detect the effects on arthropods distribution and host plant reproductive success. Thus, at first moment we investigated cascading effect of *Azteca chartifex* ant presence on arthropod guilds diversity of forest canopy on a dominant tree in forest ecotones, *Byrsonima sericea*. In second moment we investigated whether association between *A. chartifex* and liana influences ant-plant mutualism effectiveness. We conducted our study in the Rio Doce State Park, Southeastern Brazil, from populations of *B. sericea* monitored in long term. We arbitrarily selected 68 trees distributed in three distinct populations and that had lianas in their respective crowns. Half of these individuals were patrolled by *A. chartifex* and other half had no relation to this ant. We distributed the trees in two treatments within of populations to investigate the effect of *A. chartifex* presence on forest canopy arthropods: i) *A. chartifex* present (n = 32) and ii) *A. chartifex* absent (n = 36). To investigate the effect of association between *A. chartifex* and liana on canopy, we performed liana removal experiment and redistributed same trees in four treatments within of populations: i) *A. chartifex* and liana present (n = 16); ii) *A. chartifex* absent and liana present (n = 18); iii) *A. chartifex* present and liana removed (n = 16); and iv) *A. chartifex* absent and liana removed (n = 18). Samplings were performed in three distinct phases: March 2016, August 2016 and March 2017 (hereafter, Phase I, Phase II and Phase III, respectively). In Phase I we sampled arthropods and collected leaves to measure herbivory. In Phase II we performed liana removal experiment from *B. sericea* crowns and, in Phase III, we again sample arthropods and also collected leaves to measure herbivory. In order to inventory arthropods we used beating samples, and to estimate herbivory we measured foliar damage in laboratory by selecting leaves by wire-framed cube. Parallel to these samplings, we also measured *B. sericea* reproductive success by flower-fruit conversion rate. Our results demonstrated that *A. chartifex* is a central species in structuring of arthropod guilds associated with *B. sericea*, changing population density, coexistence and interactions of other predators and herbivores. *Azteca chartifex* presence also resulted in cascading effect characterized by lower leaf damage on *B. sericea*. We also detected that liana presence is better used by *A. chartifex* than by herbivorous insects, enhancing foraging efficiency of this ant that reflected in reproductive success of *B. sericea*. When using lianas as alternative foraging routes, *A. chartifex* reduced herbivores population density and increased flower-fruit conversion rate. In general, we can conclude that multi-trophic interactions discussed in this thesis were affected by presence of territorialist and dominant ants, as well as by habitat complexity. Thus, understanding how multi-trophic interactions develop, as well as their costs and benefits, and which keystone species is involved were primordial aspects for our understanding about communities dynamics in forest ecotones. These aspects contribute to directing efforts to those structurally important species, helping future management practices or environment conservation.

Keywords: Ant-plant interaction. Liana. Canopy. Interspecific Interactions.

SUMÁRIO

CAPÍTULO 1 - INTRODUÇÃO GERAL

Entender os mecanismos pelo quais as interações tróficas são realizadas e quais organismos estão envolvidos é um dos focos principais da ecologia trófica (Garvey & Whiles 2016). As interações interespecíficas estão entre os componentes mais importantes que influenciam os padrões de adaptação e variação de espécies, bem como a organização e estrutura de comunidades (Rico-Gray *et al.* 2008; Palmer *et al.* 2015). Estas interações se apóiam em um sistema de custo benefício, variando em um contínuo entre antagonismo e mutualismo (Rico-Gray 2001). As interações antagonísticas (como herbivoria, predação e competição) são caracterizadas pela redução da aptidão de um dos indivíduos envolvidos e pelo aumento da aptidão do outro (Rico-Gray 2001). Já as interações mutualísticas são definidas como alguma forma de cooperação que envolve duas ou mais espécies trocando benefícios (Bronstein 2015; New 2017). Um bom exemplo são as interações inseto-planta, que possuem resultados variados e distribuição ampla, abrangendo diferentes ambientes (New 2017).

As plantas realizam uma variedade de interações antagonísticas e mutualísticas com os insetos, ocasionando diversos efeitos. A herbivoria, por exemplo, é uma interação antagônica que reduz significativamente o sucesso reprodutivo das plantas (Hawkes & Sullivan 2001). A pressão ocasionada pelos insetos herbívoros pode ainda reduzir a capacidade competitiva e fotossintética, afetando negativamente o desempenho das plantas (Crawley 1989; Maron & Crone 2006; Anstett *et al.* 2016). Entretanto, os danos ocasionados pelos insetos herbívoros podem ser amenizados por meio de associações mutualísticas entre plantas e formigas, gerando assim benefícios para as espécies relacionadas (Rico-Gray & Oliveira 2007).

A interação mutualística formiga-planta têm se mostrado importante na defesa da planta contra herbívoros, tendo como o principal resultado a proteção efetiva contra inimigos naturais com consequente aumento da aptidão da planta (Rico-Gray & Oliveira 2007; Nascimento & Del-Claro 2010). Outros benefícios comumente relatados nos estudos são o decréscimo da herbivoria foliar e da abundância de herbívoros (Rosumek *et al.* 2009). As formigas são habilidosas em proteger as plantas por serem espacialmente e temporalmente comuns e abundantes, além de possuírem o mecanismo de recrutamento em massa, ocasionando a proteção da planta (Agrawal & Rutter 1998; Rico-Gray & Oliveira 2007). Uma vez que a formiga está em associação ou sobre a planta, alguma forma de recompensa é oferecida, retendo este visitante e mantendo a execução do serviço (Ness *et al.* 2006). Na interação mutualística formiga-planta ocorre trocas de recursos e serviços onde a planta produz recurso alimentar (como néctar, elaiossomos, domácias) ou abrigo para as formigas, e estas defendem a planta contra herbívoros, patógenos e até vegetação invasora (González-Teuber & Heil 2010; Trager *et al.* 2010; Del-Claro *et al.* 2016).

A associação mutualística entre as formigas e plantas é um dos mecanismos que restringe a distribuição dos insetos herbívoros no habitat, especialmente pela predação direta (Fagundes *et al.* 2017). Como o risco de predação é maior em plantas que são protegidas por formigas (Offenberg *et al.* 2004), estes herbívoros evitam territórios de formigas dominantes. Formigas que são dominantes e territorialistas possuem o comportamento de demarcar seus territórios com feromônio e isto pode sinalizar para as presas o risco de predação, ocasionando o afugentamento do herbívoro (Offenberg *et al.* 2004). Dentre estas formigas, destacamos as espécies do gênero *Azteca* spp., que são conhecidas pela sua agressividade e territorialismo (Dejean *et al.* 2009).

Pertencente a família Dolichoderinae, *Azteca* spp. possui comportamento de caça em grupo, recrutando as demais companheiras nas tarefas relacionadas ao forrageio e a defesa de território (Freitas & Oliveira 1992; Morais 1994). A espécie *Azteca chartifex* Forel, 1896 é uma formiga territorialista, dominante e polidômica, pertencente a um grupo estritamente neotropical de formigas arborícolas (Longino 2007). Constrói seus ninhos usando fibras de celulose e processados, protegendo a colônia que pode conter até milhares de indivíduos (Baccaro *et al.* 2015). Esta formiga é facilmente reconhecida devido ao seu cheiro característico quando a pressionamos entre os dedos.

Apesar de formigas territorialistas desestimularem a chegada do herbívoro, este efeito não é igualmente eficaz para todos os tipos de herbívoros, pois a heterogeneidade do habitat também afeta positivamente a distribuição dos artrópodes (Wardhaugh 2014). Em ambientes mais complexos há maior disponibilidade de recurso (Lawton 1983), um importante fator que determinam os padrões de distribuição temporal e espacial entre os insetos arbóreos (Wardhaugh 2014). Além disto, o aumento da complexidade do habitat promove uma gama de condições favoráveis que atraem inimigos naturais e presas (Langellotto & Denno 2004; Dial *et al.* 2006).

A presença de lianas no dossel florestal pode aumentar a complexidade estrutural do habitat, promovendo conectividade entre as copas das árvores, mais locais para nidificação, substratos para acasalamento, espaços livres de inimigos naturais e manutenção da diversidade de formigas arbóreas (Putz & Mooney 1992; Michel *et al.* 2015; Yanoviak 2015; Adams *et al.* 2019). Formigas predadoras, por exemplo, utilizam com eficiência de lianas no forrageio em árvores, alcançando com maior rapidez o recurso alimentar (Clay *et al.* 2010).

Porém, apesar das lianas aumentarem a chance de encontro de presas e predadores, estas plantas também podem fornecer refúgios para as presas e dificultar sua localização (Langellotto & Denno 2004; Šipoš & Kindlmann 2013). Além disto, as lianas ocupam mais de 70% do dossel florestal (Ingwell *et al.* 2010), vêm aumentando em abundância nas florestas tropicais (Schnitzer 2015, 2018) e consequentemente devem exercer uma grande influência sobre a comunidade de herbívoros mastigadores (Odell *et al.* 2019). Assim, entender o papel da associação do mutualismo formiga-planta, mediado pela presença de liana, nos ajudaria a compreender os efeitos sobre a distribuição de artrópodes e o sucesso reprodutivo da planta hospedeira.

1.1 ESTRUTURA DA TESE

Esta tese integra as ideias expostas acima da seguinte maneira:

1) Keystone ant species determine distribution of arthropod guilds in a rainforest canopy

Neste capítulo investigamos o efeito cascata da presença de *Azteca chartifex* na diversidade das guildas de artrópodes do dossel florestal de uma árvore dominante dos ecótonos florestais, *Byrsonima sericea* DC (Malpighiaceae). Nós testamos três hipóteses:

i) *Azteca chartifex* reduz a diversidade dos artrópodes co-existentes, causando um efeito em cascata na redução do nível de herbivoria de *B. sericea* devido ao seu comportamento dominante e de predador generalista (Baccaro *et al.* 2015; Adams 2016) e estes efeitos negativos persistem sobre o tempo;

ii) A presença de *A. chartifex* restringe a ocorrência tanto de competidores quanto de presas, causando diferença na composição e na distribuição de espécies em seu território devido ao seu comportamento de patrulhamento altamente denso (Longino 2007; Baccaro *et al.* 2015). Na perspectiva da co-ocorrência com outra formiga dominante e territorialista, esperamos encontrar uma distribuição em mosaico de territórios ou forrageamento (Majer *et al.* 1994; Blüthgen & Stork 2007; Ribeiro *et al.* 2013) e

iii) *Azteca chartifex* causa diferença na estrutura das redes de interação de artrópodes devido à sua alta atividade de patrulhamento e por ser competitivamente dominante (Dejean *et al.* 2007; Longino 2007).

2) Positive effects of ant predation are mediated by liana on canopy

Neste capítulo investigamos se a associação entre *A. chartifex* e liana sobre o dossel influencia a efetividade do mutualismo formiga-planta. Estudamos um sistema envolvendo *A. chartifex* e interações tri-tróficas em indivíduos de *B. sericea* que tinham suas copas naturalmente ocupadas por lianas. Nós testando as seguintes hipóteses:

i) Copas ocupadas por lianas favorecem a permanência de *A. chartifex*. Nós esperamos que a presença de liana favoreça maior abundância desta formiga, gerando efeito negativo nas densidades populacionais de insetos herbívoros e na taxa de herbivoria. Esta predição é sustentada pelo fato de que liana fornece caminhos alternativos que são acessados por formigas predadoras, facilitando a expansão de sua área de forrageamento (Clay *et al.* 2010).

ii) Haverá um aumento na aptidão de *B. sericea* quando *A. chartifex* estiver associada a lianas. Já sabemos que as árvores hospedeiras e lianas estão em uma competição constante que compromete o desempenho das plantas, seja por obstrução à luz, estresse estrutural, redução do crescimento ou obstrução da condução da seiva (Putz & Mooney 1992; van der Heijden & Phillips 2009; Schnitzer 2018). No entanto, quando as formigas dominantes são favorecidas pela presença de lianas, esperamos que haja um aumento no sucesso reprodutivo das plantas.

iii) Haverá um gradiente de eficiência de proteção das formigas, no qual *A. chartifex* se destaca. Esperamos encontrar de uma a poucas espécies de formigas efetivas e um número maior de espécies menos protetoras. Estudos sugerem que os sistemas multi-tróficos de formigas geralmente abrangem apenas algumas poucas espécies centrais que podem atuar como parceiros mutualistas (Costa *et al.* 2016; Fagundes *et al.* 2017).

1.2 REFERÊNCIAS

Adams, B.J., Schnitzer, S.A. & Yanoviak, S.P. (2019). Connectivity explains local ant community structure in a Neotropical forest canopy: a large-scale experimental approach. *Ecology*, e02673.

Adams, E.S. (2016). Territoriality in ants (Hymenoptera : Formicidae): a review. *Myrmecological News*, 23, 101–118.

Agrawal, A.A. & Rutter, M.T. (1998). Dynamic Anti-Herbivore Defense in Ant-Plants: The Role of Induced Responses. *Oikos*, 83, 227–236.

Anstett, D.N., Nunes, K.A., Baskett, C. & Kotanen, P.M. (2016). Sources of Controversy Surrounding Latitudinal Patterns in Herbivory and Defense. *Trends Ecol. Evol.*, 31, 789–802.

Baccaro, F.B., Feitosa, R.M., Fernandez, F., Fernandes, I.O., Izzo, T.J., Souza, J.L.P., *et al.* (2015). *Guia para os gêneros de formigas do Brasil*. *Ed. INPA*.

Blüthgen, N. & Stork, N.E. (2007). Ant mosaics in a tropical rainforest in Australia and elsewhere: A critical review. *Austral Ecol.*, 32, 93–104.

Bronstein, J.L. (2015). The study of mutualism. In: *Mutualism*. Oxford University Press, Oxford, UK, pp. 3–19.

Clay, N.A., Bauer, M., Solis, M. & Yanoviak, S.P. (2010). Arboreal substrates influence foraging in tropical ants. *Ecol. Entomol.*, 35, 417–423.

Costa, F. V., Mello, M.A.R., Bronstein, J.L., Guerra, T.J., Muylaert, R.L., Leite, A.C., *et al.* (2016). Few ant species play a central role linking different plant resources in a network in rupestrian grasslands. *PLoS One*, 11, 1–17.

Crawley, M.J. (1989). Insect Herbivores and Plant Population Dynamics. *Annu. Rev. Entomol.*, 34, 531–562.

Dejean, A., Corbara, B., Orivel, J. & Leponce, M. (2007). Rainforest Canopy Ants: The Implications of Territoriality and Predatory Behavior. *Funct. Ecosyst. Communities*, 1, 105–120.

Dejean, A., Grangier, J., Leroy, C. & Orivel, J. (2009). Predation and aggressiveness in host plant protection: A generalization using ants from the genus Azteca. *Naturwissenschaften*, 96, 57–63.

Del-Claro, K., Rico-Gray, V., Torezan-Silingardi, H.M., Alves-Silva, E., Fagundes, R., Lange, D., *et al.* (2016). Loss and gains in ant–plant interactions mediated by extrafloral nectar: fidelity, cheats, and lies. *Insectes Soc.*, 63, 207–221.

Dial, R.J., Ellwood, M.D.F., Turner, E.C. & Foster, W.A. (2006). Arthropod Abundance , Canopy Structure , and Microclimate in a Bornean Lowland Tropical Rain Forest Author (s): Roman J . Dial , Martin D . F . Ellwood , Edward C . Turner and William A . Foster Published by : Association for Tropical Biology and Conser. *Biotropica*, 38, 643–652.

Fagundes, R., Dáttilo, W., Ribeiro, S.P., Rico-Gray, V., Jordano, P. & Del-Claro, K. (2017). Differences among ant species in plant protection are related to production of extrafloral nectar and degree of leaf herbivory. *Biol. J. Linn. Soc.*, 1–13.

Freitas, A.V.L. & Oliveira, P.S. (1992). Biology and behavior of Eunica bechina (Lepidoptera: Nymphalidae) with special reference to larval defense against ant predation. *J. Res. Lepid.*, 31, 1–11.

Garvey, J.E. & Whiles, M.R. (2016). Food Webs. In: *Trophic ecology* (ed. Press, C.). Hoboken, New Jersey, pp. 209–241.

González-Teuber, M. & Heil, M. (2010). Pseudomyrmex ants and acacia host plants join efforts to protect their mutualism from microbial threats. *Plant Signal. Behav.*, 5, 890–892.

Hawkes, C. V. & Sullivan, J.J. (2001). The impact of herbivory on plants in different resource conditions: A meta-analysis. *Ecology*, 82, 2045–2058.

van der Heijden, G.M.F. & Phillips, O.L. (2009). Liana infestation impacts tree growth in a lowland tropical moist Forest. *Biogeosciences*, 6, 2217–2226.

Ingwell, L.L., Joseph Wright, S., Becklund, K.K., Hubbell, S.P. & Schnitzer, S.A. (2010). The impact of lianas on 10 years of tree growth and mortality on Barro Colorado Island, Panama. *J. Ecol.*, 98, 879–887.

Langellotto, G.A. & Denno, R.F. (2004). Responses of invertebrate natural enemies to complex-structured habitats: A meta-analytical synthesis. *Oecologia*, 139, 1–10.

Lawton, J.H. (1983). Plant Architecture and the Diversity of Phytophagous Insects. *Annu. Rev. Entomol.*, 28, 23–39.

Longino, J.T. (2007). *A taxonomic review of the genus Azteca*. *Zookeys*.

Majer, J.D., Delabie, J.H.C. & Smith, M.R.B. (1994). Arboreal Ant Community Patterns in Brazilian Cocoa Farms. *Biotropica*, 26, 73.

Maron, J.L. & Crone, E. (2006). Herbivory: Effects on plant abundance, distribution and population growth. *Proc. R. Soc. B Biol. Sci.*, 273, 2575–2584.

Michel, N.L., Robinson, W.D. & Sherry, T.W. (2015). Liana-bird relationships: a review. In: *Ecology of lianas*. Oxford, pp. 362–397.

Morais, H.C. (1994). Coordinated group ambush: A new predatory behavior in Azteca ants

(Dolichoderinae). *Insectes Soc.*, 41, 339–342.

Nascimento, E.A. & Del-Claro, K. (2010). Ant visitation to extrafloral nectaries decreases herbivory and increases fruit set in Chamaecrista debilis (Fabaceae) in a Neotropical savanna. *Flora Morphol. Distrib. Funct. Ecol. Plants*, 205, 754–756.

Ness, J.H., Morris, W.F. & Bronstein, J.L. (2006). Integrating Quality and Quantity of Mutualistic Service to Contrast Ant Species Protecting Ferocactus Wislizeni. *Ecology*, 87, 912–921.

New, T.R. (2017). Classic Themes: Ants and Other Insects – Lepidoptera. In: *Mutualisms and Insect Conservation*. Springer International Publishing, pp. 119–142.

Odell, E.H., Stork, N.E. & Kitching, R.L. (2019). Lianas as a food resource for herbivorous insects: a comparison with trees. *Biol. Rev.*, brv.12508.

Offenberg, J., Nielsen, M.G., MacIntosh, D.J., Havanon, S. & Aksornkoae, S. (2004). Evidence that insect herbivores are deterred by ant pheromones. *Proc. R. Soc. B Biol. Sci.*, 271, 433–435.

Palmer, T.M., Pringle, E.G., Stier, A. & Holt, R.D. (2015). Mutualism in a community context. In: *Mutualism* (ed. Bronstein, J.L.). Oxford University Press, pp. 159–180.

Putz, F.E. & Mooney, H.A. (1992). *The Biology of Vines*. *Cambridge Univ. Press*. Cambridge University Press, Cambridge.

Ribeiro, S.P., Espirito Santo, N.B., Delabie, J.H.C. & Majer, J.D. (2013). Competition, resources and the ant (Hymenoptera: Formicidae) mosaic: A comparison of upper and lower canopy. *Myrmecological News*, 18, 113–120.

Rico-Gray, V. (2001). Interspecific Interaction. In: *Encyclopedia of Life Sciences*. John Wiley & Sons, Ltd, Chichester, UK, pp. 1–6.

Rico-Gray, V. & Oliveira, P.S. (2007). *The Ecology and Evolution of Ant-Plant Interactions*. University of Chicago Press, Chigago.

Rico-Gray, V., Oliveira, P.S., Parra-Tabla, V., Cuautle, M. & Díaz-Castelazo, C. (2008). Ant–Plant Interactions: Their Seasonal Variation and Effects on Plant Fitness. In: *Coastal Dunes*. Springer, Berlin, Heidelberg, pp. 221–239.

Rosumek, F.B., Silveira, F.A.O., De S. Neves, F., Newton, N.P., Diniz, L., Oki, Y., *et al.* (2009). Ants on plants: a meta-analysis of the role of ants as plant biotic defenses. *Oecologia*, 160, 537–549.

Schnitzer, S.A. (2015). The Contribution of Lianas to Forest Ecology, Diversity, and Dynamics. In: *Biodiversity of Lianas*, Sustainable Development and Biodiversity (ed. Parthasarathy, N.). Springer International Publishing, Cham, pp. 149–160.

Schnitzer, S.A. (2018). Testing ecological theory with lianas. *New Phytol.*, 220, 366–380.

Šipoš, J. & Kindlmann, P. (2013). Effect of the canopy complexity of trees on the rate of predation of insects. *J. Appl. Entomol.*, 137, 445–451.

Trager, M.D., Bhotika, S., Hostetler, J.A., Andrade, G. V., Rodriguez-Cabal, M.A., Mckeon, C.S., *et al.* (2010). Benefits for plants in ant-plant protective mutualisms: A meta-analysis. *PLoS One*, 5.

Wardhaugh, C.W. (2014). The spatial and temporal distributions of arthropods in forest canopies: Uniting disparate patterns with hypotheses for specialisation. *Biol. Rev.*, 89, 1021–1041.

Yanoviak, S.P. (2015). Effects of lianas on canopy arthropod community structure. In: *Ecology of lianas* (eds. Schnitzer, S.A., Bongers, F., Burnham, R.J. & Putz, F.E.). Wiley-Blackwell, Oxford, pp. 345–361.

CHAPTER 2 - KEYSTONE ANT SPECIES DETERMINE DISTRIBUTION OF ARTHROPOD GUILDS IN A RAINFOREST CANOPY

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Abstract

The alternation of large territories by dominant and aggressive ant species is an event commonly seen in tropical canopy. However, canopy studies are still challenging, limiting our understanding of species distribution patterns. We evaluated the cascading effect caused by the ant species *Azteca chartifex* in the forest canopy associated to the dominant tree *Byrsonima sericea* (Malpighiaceae). From a long-term monitored population, we sampled 68 *B. sericea* trees where half of them never had *A. chartifex* patrolling their leaves, and the other half was constantly patrolled for about two decades by this ant species. We investigated the hypothesis that decreased richness and abundance of associated arthropods is due to ant biotic defense that can reduce herbivory. We expect that this dominant ant species causes a mosaic of patrolled territories which affects the distribution of whole arthropod guild. We also investigate whether *A. chartifex* presence affect network of interactions between *B. sericea* and its associated arthropods. We found that *A. chartifex* is a central species influencing the occurrence of other arthropod species, mainly due to its aggressive and dominant behavior. The presence of *A. chartifex* reduced herbivores and other predators abundance as well as leaf herbivory. *Azteca chartifex* territorial behavior affected the pattern of arthropods spatial distribution by moving other predators out of its territory. Both frequency and diversity of interaction were similar regardless of *A. chartifex* presence. Our findings point to *A. chartifex* ability to modify community composition and generate effects along the trophic cascade. Thus, detecting the keystone effects of the interaction networks helps us understand which species actually define canopy arthropod community, and determine spatial distribution and interaction patterns of other associated arthropods.

Key words: ecological networks, top-down effect, trophic cascade, central species, enemy-free space.

2.1 INTRODUCTION

Behind trophic interactions, predation is one of the most important processes driving population dynamics, community structure and promoting the organism diversity in some ecosystems (Romero & Koricheva 2011; Garvey & Whiles 2016). Paine (1966) was the first to experimentally demonstrate how predation maintains community diversity over by regulating inferior competitors and herbivores. Trophic interactions such as predation trigger cascading effects by causing indirect effects along the food web, i.e., effects that alter abundance or biomass at more than one trophic level (Paine 1980; Polis *et al.* 2000). Paine (1969) coined the term 'keystone species' describing the disproportionate importance of species that are capable of modify community composition and generate trophic cascades. Since then, studies have highlighted the influence of keystone species in community structure using species of different trophic levels, such as lianas (Schnitzer 2018), herbivores (Poelman & Kessler 2016), and ants (Vandermeer *et al.* 2010).

Keystone species such as ants stand out for efficient predation ability and are singled out as excellent models to understand community structure (Dejean *et al.* 2018), through cascading effects on lower trophic levels (Sanders & Platner 2007; Moreira *et al.* 2012). Ants are able to reduce the species richness of competitors (such as spiders, ladybugs and other ants) and herbivorous insects (Novotny *et al.* 1999; Rosumek *et al.* 2009; Vandermeer *et al.* 2010; Nahas *et al.* 2012; Lourenço *et al.* 2015) causing lower leaf damage in plants (Rosumek *et al.* 2009; Trager *et al.* 2010). Still, although many arboreal ant species are well known as keystone species, detailed studies on canopy arthropod interactions are relatively low compared to other habitat (Yanoviak & Kaspari 2000; Campos *et al.* 2006; Ribeiro & Basset 2007; Espírito Santo *et al.* 2012; Ribeiro *et al.* 2013).

Dominant arboreal ant species constantly patrol their host, thereby modulating the distribution of other organisms, such as non-dominant ants, herbivores, and other predators (e.g. spiders). This group of aggressive ants are characterized by dominance behavior (inter- and intraspecific confrontations to defend resources and territory) and by having a populous colony (Davidson 1998). These ants are skilled at building large nests for the main colony, which is normally connected by a network of small bivouac nests, sometimes related to polidomy. Such complex housing system facilitates movement along tree branches and allows a broad territory defense. As a consequence, greater arthropods species richness is found in sites not occupied by dominant ants, avoiding confrontation (Ribeiro *et al.* 2013; Lourenço *et al.* 2015). Jeffries and Lawton (1984) defined sites such as these as 'enemy-free space', which are sites associated with less susceptibility to natural enemies and that are preferably selected by herbivorous insects. Another pattern due to territoriality is called 'ant mosaic', where two or more dominant ant colonies do not share any territory (Majer 1972; Leston 1973; Majer *et al.* 1994; Blüthgen & Stork 2007; Ribeiro *et al.* 2013). However, among these ant territories there are mosaic-free spaces, which seems to be an important cause of spatial distribution patterns of other arthropods in the canopies (Ribeiro *et al.* 2013; Lourenço *et al.* 2015).

There are few ant species that really are dominant in ant-plant interaction networks (Del-Claro *et al.* 2018). Dominant ant species are competitively superior in monopolizing resources and in preventing access by other arthropods, in addition to having high recruitment rates and well-established territories (Dáttilo *et al.* 2013, 2014; Costa *et al.* 2016). Among these ant species, *Azteca chartifex* Emery, 1896 (Formicidae: Dolichoderinae) stands out for its territorial and dominant behavior (Longino 2007). Altogether, this is a suitable model for interactions studies on the dominance and structure of tri-trophic interactions among plant, herbivores and predators.

We evaluated the cascading effect of *A. chartifex* presence on arthropod guild of a forest canopy dominates by *Byrsonima sericea* DC (Malpighiaceae) tree. We test three hypotheses: i) *Azteca chartifex* reduces species richness and abundance of coexisting arthropods, causing a cascading effect on *B. sericea* herbivory level due to their dominant behavior and generalist predator (Baccaro *et al.* 2015; Adams 2016) and these negative effects persist over time; ii) *Azteca chartifex* presence restricts occurrence of both competitors and preys, causing a difference in species composition and distribution between sites with or without *A. chartifex* due to its highly dense patrolling behavior (Longino 2007; Baccaro *et al.*

2015). In the perspective of co-occurrence with another dominant and territorialist species ant, we expect to find a mosaic distribution of territories or foraging (Majer *et al.* 1994; Blüthgen & Stork 2007; Ribeiro *et al.* 2013); iii) *Azteca chartifex* causes difference in structure of arthropod interaction networks due to its high patrolling activity and being competitively dominant (Dejean *et al.* 2007; Longino 2007).

2.2 MATERIALS AND METHODS

2.2.1 Study area

The study was conducted in the Rio Doce State Park (PERD in Brazilian acronym) (19°48'-19°29'S and 42°38'-42°28'W), in Minas Gerais State, southeastern Brazil. The climatic regime of region is tropical seasonal (Aw), according to Köeppen's classification (Alvares *et al.* 2013). The climatic seasons are well defined, with dry period between May-September and rainy season between October-April. Average precipitation is around 1,500 mm per year (Alvares *et al.* 2013). PERD covers an area of approximately 36,000 ha of Atlantic Forest, varying from 200 and 500 m above sea level, and is part of largest natural Neotropical lake system. About 11% of the area Park is covered by 42 lakes that have an intimate, though evolutionarily young, history with the forest (Fonseca-Silva *et al.* 2015, 2018). The lake system inside this Park support a very particular ecotonal areas that are characterized by natural transitions of forest-lake, where trees grow branches bent towards water, seeking for light. This results in what has been called 'brought low canopy', which is, strictly speaking, a typical canopy habitat laying resting close to the ground, on ecotone shore or over lakes (Barbosa 2014; Lourenço *et al.* 2019). The PERD is a Long-Term Ecological Research site (international LTER) whose tree-arthropod system have been investigated since 2002 (Campos *et al.* 2006; Coelho & Ribeiro 2006; Ribeiro *et al.* 2008).

2.2.2 Study system

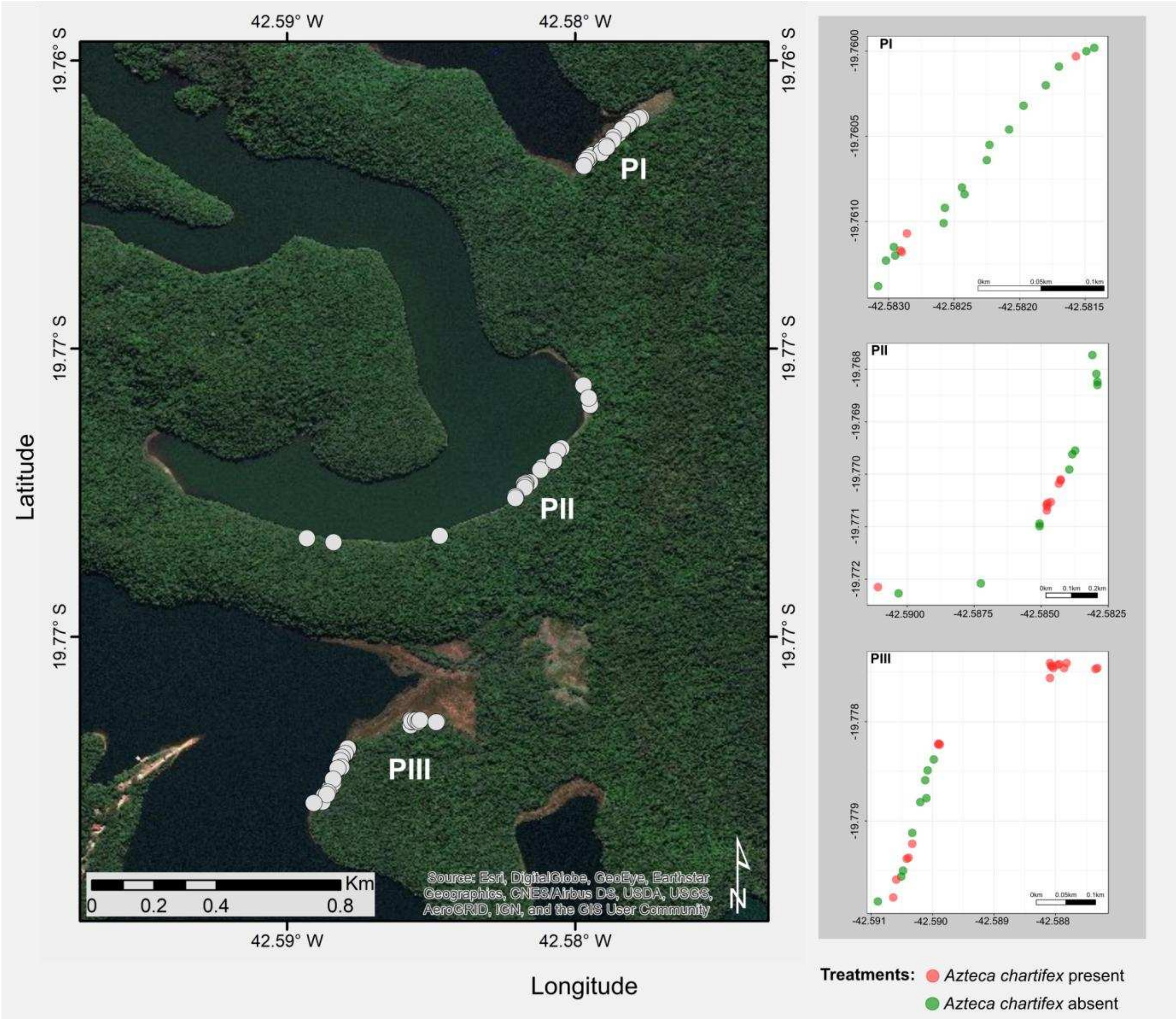
Azteca chartifex is a territorialist, dominant, and polydomic ant belonging to a strictly Neotropical group of arboreal ants (Longino 2007) and builds its nests using cellulose and processed fibers, which protects colony that may contain up to thousands of individuals (Baccaro *et al.* 2015). This ant has a non-obligatory mutual association with *Byrsonima sericea* establishing the main nest pending in its trunk and numerous smaller satellite nests are distributed along of tree branches. For instance, we counted in average 23 satellite nests per tree in a radius of 8 m. *Byrsonima sericea* defines ecotone vegetation, making it a dominant tree species that has long-lived, with sclerophyllous leaves and a complex crown architecture (Barbosa 2014). In these ecotones, *B. sericea* crowns are structured both vertically as also by crowns whose slope over the lakes, positioning at same height of understory stratum. Flowering and fruiting of *B. sericea* occur between second fortnight of October until end of April (Teixeira & Machado 2000). *Byrsonima sericea* tree in PERD have a mean volume of 6,797 leaves/m^3 (550.58 leaves/0.081m^3), mean height of 5.68 m (±0.13 SE), and mean circumference at breast height of 0.0059 m (± 0.0003 SE).

2.2.3 Experimental design

In order to examine whether *A. chartifex* presence influence species richness, abundance and distribution of other arthropod species, in March 2016 we arbitrarily selected 68 individuals of *B. sericea* distributed in two treatments: i) *A. chartifex* present (n = 32): trees colonized by active workers and with nests and ii) *A. chartifex* absent (n = 36): trees that were naturally not colonized by the ant, lasting as such for more than a decade (S.P. Ribeiro, personal observation). We sampled these trees from three independent populations located in ecotone areas and each of populations had following treatments arrangement: population I (PI): *A. chartifex* present (n= 4) and *A. chartifex* absent (n = 16); population II (PII): *A. chartifex* present (n = 9) and *A. chartifex* absent (n = 11); population III (PIII): *A. chartifex* present (n = 19) and *A. chartifex* absent (n = 9) (Figure 1).

In order to examine whether there was a temporal effect of the *A. chartifex* on the other arthropods, in March 2017 we again sample half of the same plants. We raffle and sampled 34 individuals of *B. sericea* (16 trees with *A. chartifex* and 18 without *A. chartifex*) distributed within each population following the treatments arrangement: PI: *A. chartifex* present (n=1) and *A. chartifex* absent (n=9); PII: *A. chartifex* present (n=5) *A. chartifex* absent (n=5), and PIII: *A. chartifex* present (n=10) and *A. chartifex* absent (n=4).

Figure 1: *Byrsonima sericea* populations (PI, PII and PIII) and sampling design distributed among each population located in three distinct forest-lake ecotone in Rio Doce State Park, Brazil. Arrangement of two experimental treatments: i) *Azteca chartifex* present (red circle) and ii) *A. chartifex* absent (green circle).



2.2.4 Arthropods sampling and herbivory estimation

We sampled the arthropods and leaves of *B. sericea* crowns with the aid of an aluminum ladder (max. 5 m high) and with basic climbing security gears. We collected arthropods using beating, performing 10 beats in at least three randomly selected branches (Ribeiro *et al.* 2005; Neves *et al.* 2010). These beats caused arthropods to fall in entomological umbrella, positioned just below the selected branches (Ribeiro *et al.* 2005). This equipment is formed by a funnel (1 x 1 m and 60 cm deep) composed of a white cloth coupled with a plastic bag to collect the samples and adapted for a quantitative sampling.

Arthropods were identified with the aid of revisions and taxonomic keys (Arnett *et al.* 2002; Baccaro *et al.* 2015; Anzaldo 2017), as well as the assistance of taxonomists. Vouchers were deposited in Laboratório de Ecohealth, Ecologia de Insetos de Dossel e Sucessão Natural of Universidade Federal de Ouro Preto, Mina Gerais State, Brazil. Permits for the field studies were issued by state authority Instituto Estadual de Florestas (IEF) and the national authority Sistema de Autorização e Informação em Biodiversidade/Instituto Chico Mendes de Conservação da Biodiversidade (SISBIO/ ICMBio).

We also sampled *A. chartifex* patrolling activity on *B. sericea* branches at time of collection to estimate the effect of this ant on species richness, abundance and distribution of other arthropod species and herbivory. The patrolling activity was measured by counting individuals number of this ant that fell into entomological umbrella through the beating of *B. sericea* branches.

We collected leaves to estimate herbivory level with guidance of a 0.027 m^3 wire-framed cube positioned at three distinct points in crowns (adapted from Shaw et al. 2006, Ribeiro and Basset 2007) (Appendix A, Fig. A1). This methodology guarantees a real random leaf sampling. In order to better represent tree herbivory, we positioned the cube using a ladder and climbing devices and sampled in three different branches inside crowns. We collected all leaves that were inside the cube, resulting in a final volume of 0.081 m^3 per tree. Leaves were scanned and processed using ImageJ software (Rasband 1997). Subsequently, we quantified herbivory level by measuring proportion of foliar damage from sum of leaf area removed from each leaf in relation to total leaf area estimated.

2.2.5 Data analysis

2.2.5.1 *Azteca chartifex* effect on arthropods and herbivores diversity

We quantified for each of 68 *B. sericea* individuals studied: i) species richness, abundance and composition of arthropods (insects and arachnids) ii) herbivory level, and iii) patrolling activity of *A. chartifex*. We used Generalized Linear Models (GLMs) to test effect of *A. chartifex* presence on arthropods diversity using presence/absence and patrolling activity of *A. chartifex* as explanatory variables, and species richness and abundance of other predators and chewing herbivores as response variables. We also tested *A. chartifex* effect on herbivory level using presence/absence and patrolling activity of *A. chartifex* as explanatory variables, and proportion of leaf area removed by herbivores as response variable. In all models we used the sampling years (2016 and 2017) as cofactor (to control the variance attributable to temporal effects) and the interaction between them. Significance of variables in appropriate minimum models was obtained by contrasting more complex models (association of explanatory variables plus interaction) with the simpler ones (only association of explanatory variables). Adequate minimum models were selected when there was no difference in explanatory power when comparing a more complex model with a simpler one ($p > 0.05$). When there were significant differences between model comparisons, the most complex model was maintained (Crawley 2013). We compared the minimum models to a null model and models adequacy were assessed by residual analysis (Zuur *et al.* 2009).

In order to test the differences in species composition of other predators and herbivorous insects between presence/absence of *A. chartifex*, we used Generalized Linear Model for multivariate response data (GLM_{mv}) using the package "mvabund" (Wang *et al.* 2012) with a negative binomial distribution. This package allows a multivariate analysis of abundance based on models (rather than distances). To identify differences in predators and herbivores species composition and distribution among sampling points, we used a nonmetric multidimensional scaling (NMDS) ordinations, with Bray-Curtis distances, for each treatment, using the package "vegan" (Oksanen *et al.* 2016). We examined the stress values, which are mismatch between the dissimilarity matrix and the distance in the two-dimensional plot. We consider the following thresholds: low stress values < 0.05 represent excellent accuracy; < 0.1 is very good; <0.2 is good; and > 0.3 close to arbitrary (Zuur *et al.* 2009).

All analyses were performed in software R(R Core Team 2018).

2.2.5.2 Plant-arthropod interaction networks

We constructed networks of plant-arthropod interactions to evaluate the effect of *A. chartifex* presence on herbivorous insect and other predators**.** These networks were built from the 2016 and 2017 data in the same three populations of the 68 *B. sericea* individuals distributed in the two treatments: i) *A. chartifex* present (n = 32) and ii) *A. chartifex* absent (n = 36). Plant-arthropod networks were separated into two bipartite networks: plant-predator and plant-herbivore. Plant-predator network to interactions among *B. sericea* and predatory arthropods and plant-herbivore network corresponds to interactions among *B. sericea* and herbivorous insects. We classified each interaction event as occurrence of the arthropod in the *B. sericea* individual. We built the networks from weighted matrices, with *B. sericea* individuals as rows and arthropod species as columns, and cells filled with interaction frequency (m) between *B. sericea* individual *i* and arthropods species *j*. The frequency corresponds to arthropods abundance recorded in each *B. sericea* individual obtained by the sum of interactions performed in years in each individuals sampled. We constructed a matrix for each of three *B. sericea* populations in treatments, thus generating six weighted matrices in each network.

We used the frequency (m) and diversity (Shannon *H*) of interactions to evaluate the structure of network-level interactions. Diversity of interactions deals with interactions in each species pair in matrix that occur at different interaction frequencies. We chose these metrics because we consider them appropriate to compare forest canopy arthropod community organization mediated by *Azteca chartifex* presence. We used the "bipartite" package (Dormann *et al.* 2008, 2009; Dormann 2011) in software R (R Core Team 2018) to design networks and calculate the metrics cited. We used GLMs to test differences between treatments, and metrics of each network were the response variables and treatments (presence/absence of *A. chartifex*) from each population studied, explanatory variable. We used the metric of *degree centrality* (*Cd*) to identify central species in the network and understand their contribution to the overall network structure (Jordán *et al.* 2007; Mello *et al.* 2015). Centraly metrics reflect the amount of interactions performed by a species and how these interactions are distributed among species, thereby determining their position on network (i.e., central or peripheral) (Mello *et al.* 2015; Costa *et al.* 2016). We calculated *degree centrality* by interaction frequency performed by each species (predators and herbivores) and determined predators and herbivores central those that had centrality degree above the average of network for each treatment and within each population (Costa *et al.* 2016). We calculated Generalized Linear Models for multivariate response data (GLM_{mv}) using the package “mvabund” (Wang *et al.* 2012) with a binomial distribution to test whether species composition present in core (central species) differ between networks in *A. chartifex* presence/absence. This analysis is suitable for binary data since it allows us to determine the family for the errors distribution, such data as presence or absence of species in networks core (Klunk *et al.* 2018).

All analyses were performed in software R (R Core Team 2018).

2.3 RESULTS

We sampled 5,302 individuals of arthropods distributed in 154 morphospecies in two years of sampling (Appendix A, Table S1). Among the registered morphospecies, we found 115 predator and 39 herbivores species. Predators were mainly represented by spiders (58.3%), followed by ants (31.3%), beetle (9.6%), mantis and pseudoscorpions (1.7%). Herbivores were mainly represented by beetle (84.6%), followed by grasshoppers and crickets (10.2%) and caterpillar (5.1%).

As expected, *Azteca chartifex* reduced species richness and abundance of other predators and herbivores, as well as herbivory level, but it did not affect herbivore species richness, patterns that have been repeated in both years (Table 1). Species richness and abundance of other predators were lower in sites where *A. chartifex* was present (Fig. 2a, c) and which had greater patrolling activity of this ant (Fig. 2b, d). A similar pattern was observed for herbivore abundance, which decreased in response to patrolling activity of *A. chartifex* workers (Fig. 2e, f). *Azteca chartifex* presence also resulted in lower herbivory, proportionally to the amount of ant workers foraging per sample (Fig. 2g, h).

Confirming our expectations, *A. chartifex* restricted occurrence of competitors and preys, causing a difference in species composition in response to their presence. There was differences in both predator (Dev=248.6; p=0.001; stress = 0.29) and herbivore (Dev=60.85; p=0.02; stress = 0.23) species composition (Fig. 3). Besides this, we also observed an ant mosaic distribution in the ecotones when other dominant species occurred (Fig. 4). *Azteca chartifex* had a minimum overlap with the next dominant and abundant species, *Crematogaster* sp.1, whose occurrence was in 89% of the trees not occupied by *A. chartifex.* Conversely, subordinate ant species, such as *Cephalotes minutus* and *Camponotus sanctaefidei*, occurred with 63% and 52% of overlap with *A. chartifex* territory, respectively, thus shown to be tolerated by this ant.

Table 1. Results from Generalized Linear Models (GLMs) constructed to test the *Azteca chartifex* effect on herbivores, other predators, and herbivory. Explanatory variables include (1) presence or absence of *Azteca chartifex* (aztc) in *Byrsonima sericea*; (2) patrolling activity of *Azteca chartifex* (patrol_aztc); and (3) two years of sampling (year), 2016 and 2017. Plotting models were, hence, y ~ aztc + year + aztc:year and y ~ patrol_aztc + year + patrol_aztc:year. In order to plot such models, coefficients have been re-estimated keeping only the significant terms in model. For each model, the deviance (Dev.), the residual degrees of freedom (Resid. d.f.), the residual deviance (Resid. Dev), the *F*-Value, and *p*-Value are known.

Model	**Dev.**	**Resid. d.f.**	**Resid. Dev.**	***F*-Value**	***p*-Value**
y = predator species richness (error = quasipoisson)					
aztc	11.85	100	214.04	6.29	0.0137*
year	19.38	99	194.66	10.29	0.0017**
aztc:year	0.07	98	200.20	0.03	0.84
patrol_aztc	7.50	100	218.38	3.97	0.0490*
year	18.11	99	200.27	9.58	0.0025*
patrol_aztc:year	0.04	98	194.61	0.02	0.87
y = predator abundance (error = negative binomial)					
aztc	20.56	100	123.69	-	5.752e-06***
year	13.17	99	110.51	-	0.0002***
aztc: year	0.68	98	110.48	-	0.40
patrol_aztc	13.07	100	122.47	-	0.0003***
year	12.08	99	110.39	-	0.0005***
patrol_aztc:year	0.14	98	110.43	-	0.70
y = herbivore species richness (error = poisson)					
aztc	2.73	100	125.60	-	0.09
year	12.66	99	112.94	-	0.0003***
aztc:year	0.69	98	112.24	-	0.40
patrol_aztc	0.49	100	127.84	-	0.48
year	12.42	99	115.42	-	0.0004***
patrol_aztc:year	0.49	98	114.93	-	0.48
y = herbivore abundance (error = negative binomial)					
aztc	4.01	100	117.95	-	0.0452*
year	5.85	99	112.10	-	0.0155*
aztc:year	0.11	98	112.09	-	0.73
patrol_aztc	3.87	100	117.27	-	0.0490*
year	5.21	99	112.05	-	0.0223*
patrol_aztc:year	0.35	98	112.06	-	0.55
y = herbivory (error = quasibinomial)					
aztc	1.49	100	28.90	5.47	0.0212*
year	4.75	99	24.14	17.48	6.273e-05***
aztc: year	0.03	98	24.11	0.12	0.72
patrol_aztc	4.38	100	26.01	18.69	3.667e-05***
year	5.20	99	20.80	22.20	8.016e-06***
patrol_aztc:year	0.06	98	20.73	0.28	0.59

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, $\alpha < 0.05$

Figure 2: *Azteca chartifex* effects on arthropods community of *Byrsonima sericea* canopy in two sample years. On left panel the effects of presence/absence of *A. chartifex* on (a) predator species richness, (c) predator abundance, (e) herbivore abundance, and (g) herbivory. On right panel the effects of *A. chartifex* patrolling activity on (b) predator species richness, (d) predator abundance, (f) herbivore abundance, and (h) herbivory. Lines represent the first and four quartiles, box represents second and third quartiles and line within the box represents the median. Points outside of boxplot represent atypical data, and different letters above boxplot indicate significant differences (α < 0.05). Shaded area represents 95% confidence interval.

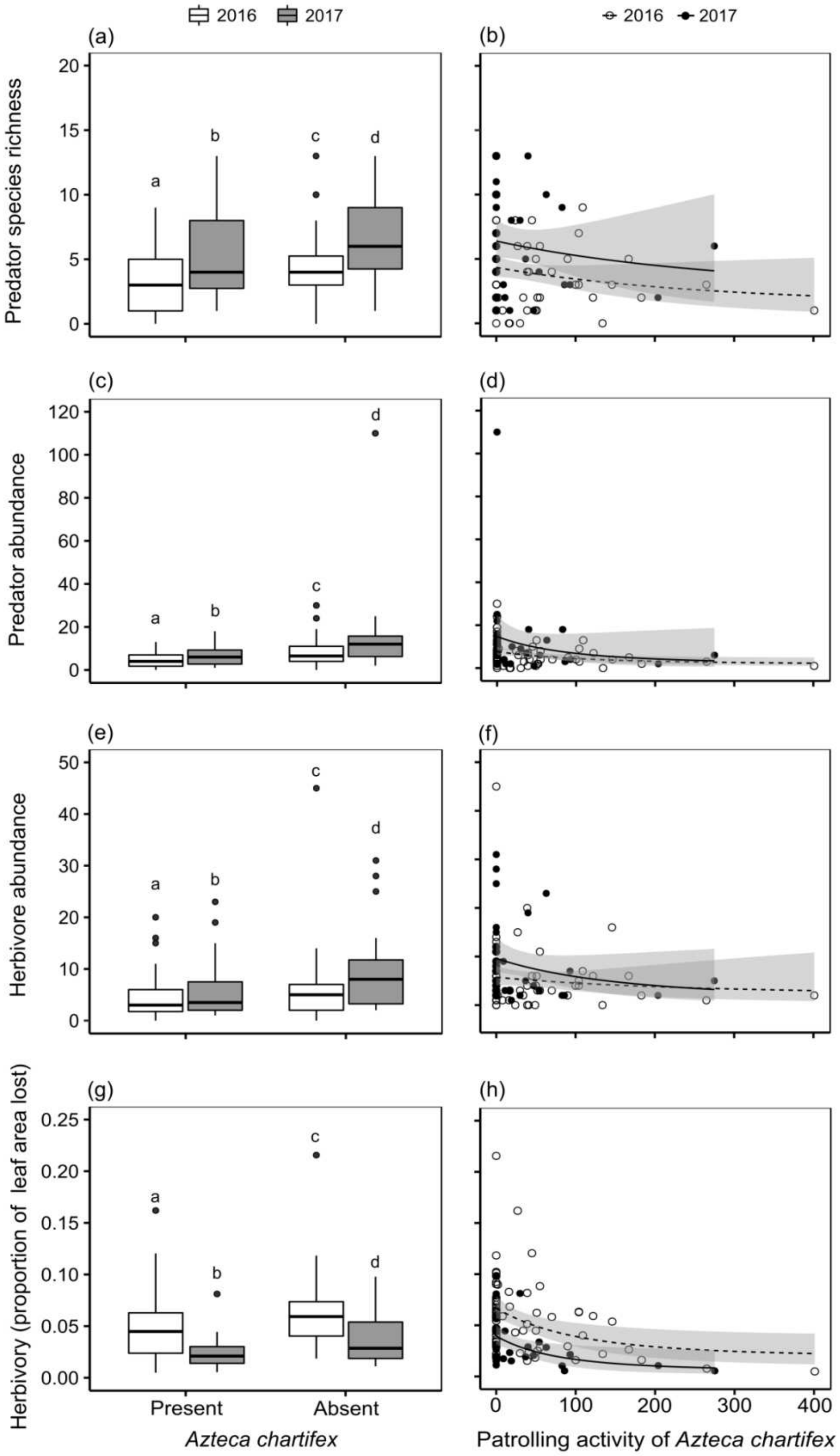


Figure 3: Non-metric multidimensional scaling ordination based on composition of (a) predators and (b) herbivorous insects within treatments. Each point corresponds to species of predator and herbivore encountered in a single tree. Symbols represent the treatments: *Azteca chartifex* present (circle grey) and *Azteca chartifex* absent (circle white). Outlines encompass all of the points for each treatment.

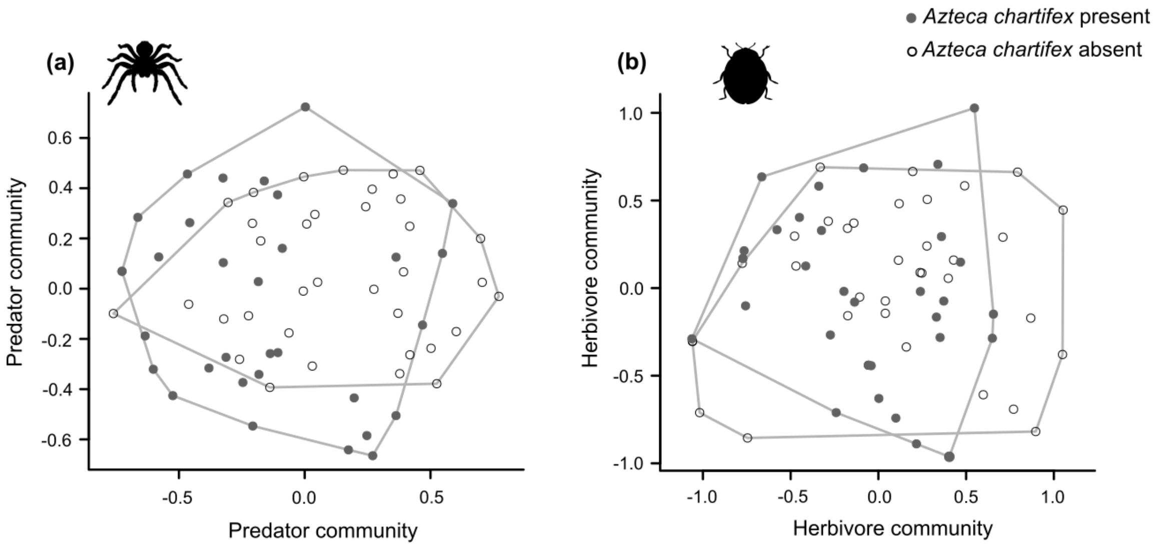
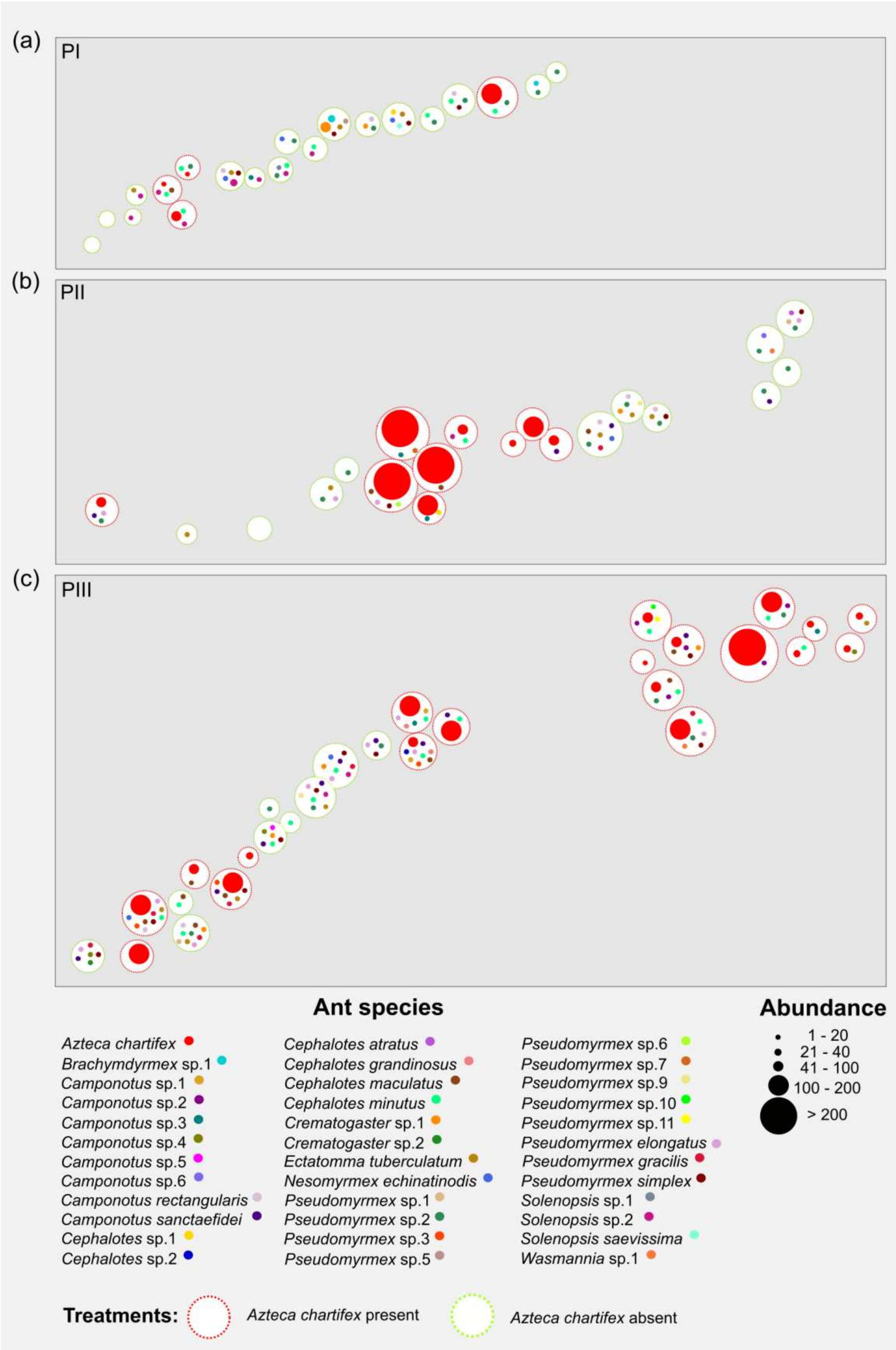


Figure 4: Species richness and absolute abundance of ant species and ant foraging mosaic distribution among three sampled populations. (a) PI: sample with lower patrolling activity of *Azteca chartifex* abundance (n = 184) and higher *Crematogaster* sp.1 abundance (n = 80). (b) PII: higher aggregated patrolling activity of *Azteca chartifex* (n = 1,802). (c) PIII: higher dispersed patrolling activity of *Azteca chartifex* (n = 1,750).



2.3.1 Plant-arthropod interaction networks

We recorded a total of 176 interactions event among 68 individuals of *B. sericea* and 176 morphospecies of arthropods, 133 predators and 43 herbivores (Appendix A, Table S2). Among all interactions, 86.2% corresponded to predators and 13.8% to herbivorous insects. Among predators, ants performed 92.3% of interactions, and 79.4% were exclusively carried out by *A. chartifex*. Then, spiders performed 5.3% of interactions and beetle 2.2%. Among chewing herbivores, beetle performed 88.7% of interactions, followed by caterpillar with 9.2% and grasshoppers and crickets with 2.1%.

Azteca chartifex presence did not modify the structure of plant-predator and plant-herbivore networks and did not determine community structure of forest canopy arthropod in interaction network (Table 2). Both frequency and diversity of interaction were similar regardless of *A. chartifex* presence.

Table 2: Results from Generalized Linear Models (GLMs) constructed to test the effect of *Azteca chartifex* presence on plant-herbivore and plant-predator interaction networks. Response variables include (1) interaction diversity (Shannon *H*) and (2) interaction frequency (m). Plotting models were, y ~ aztc, where, aztc = presence or absence of *Azteca chartifex*. For each model, the deviance (Dev.), the residual degrees of freedom (Resid. d.f.), the residual deviance (Resid. Dev), the *F*-Value, and *p*-Value are known.

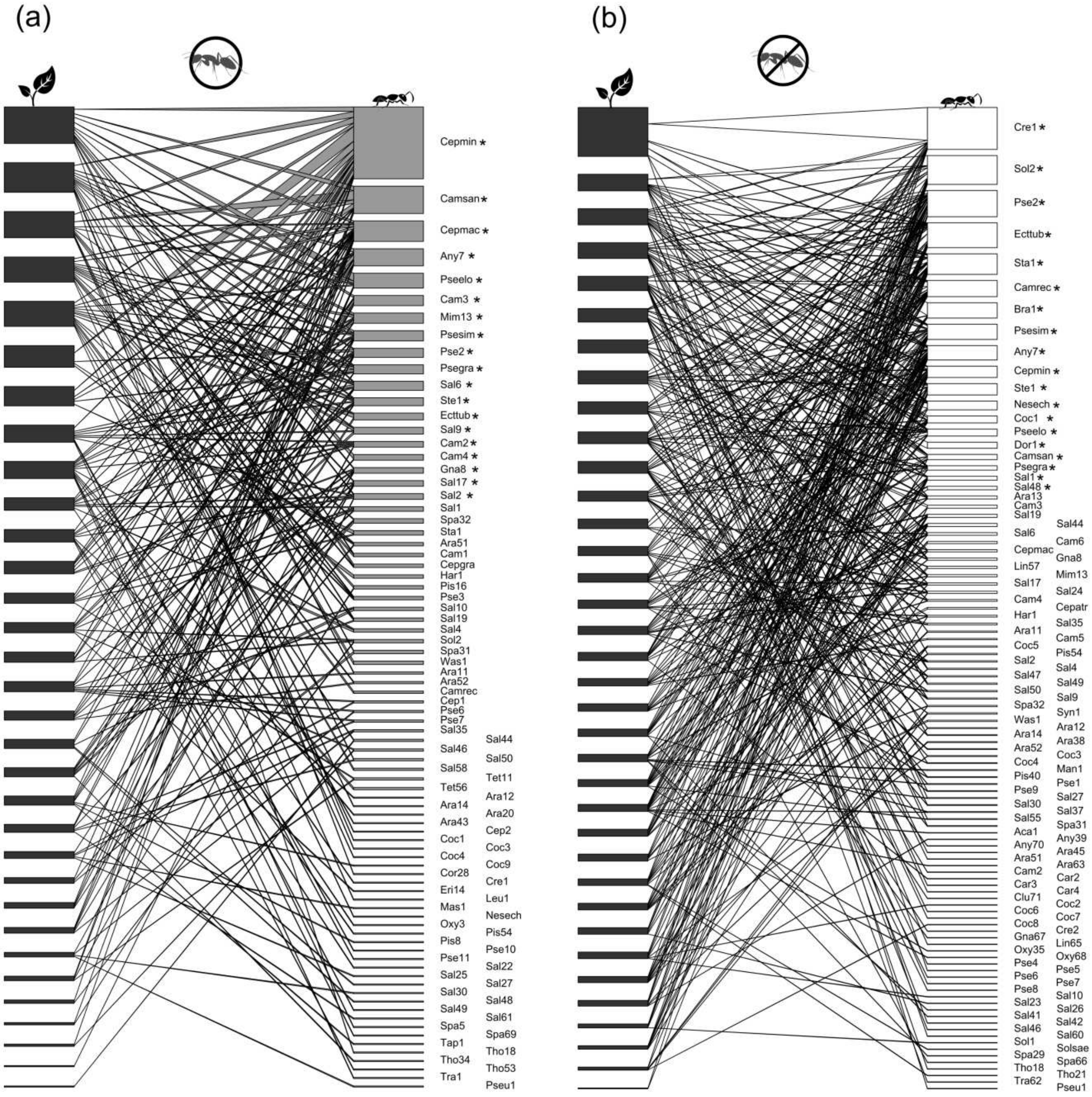
Network type	**Dev.**	**Resid. d.f.**	**Resid. Dev.**	***F*-Value**	***p*-Value**
Plant-predator					
y = Shannon *H* (error gaussian)	0.46	4	2.46	0.75	0.43
y = m (error negative binomial)	3.18	4	6.35	-	0.07
Plant-herbivore					
y = Shannon *H* (error gaussian)	0.23	4	1.14	0.80	0.41
y = m (error negative binomial)	1.51	4	6.26	-	0.21

$^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, $\alpha < 0.05$

We observed that in plant-predator network the central species changed when *A. chartifex* was present (Dev=94.14, *P*=0.03). In presence of *A. chartifex* there were 19 central predator species, and *Cephalotes minutus* was species that most interacted with *B. sericea*, performing 18.7% of interactions (Fig. 5a). In networks without *A. chartifex* (Fig. 5b) we also recorded 19 central predators, in which *Crematogaster* sp.1, *Solenopsis* sp.2 and *Pseudomyrmex* sp.2 acquired territory and performed together a large part of the interactions (11.8%, 8.1% and 7.3%, respectively).

Figure 5: Interaction networks between individuals of *Byrsonima sericea* and predators performed (a) in presence and (b) in absence of *Azteca chartifex*. Each node represents an individual of *B. sericea* (left bars) or a morphospecies of predator (right bars). Lines represent plant-predator interactions. Linkage width indicates the frequency of each interaction. Central species are indicated with asterisk (*). Predator taxon codes are defined in Tables S2 (Appendix A).

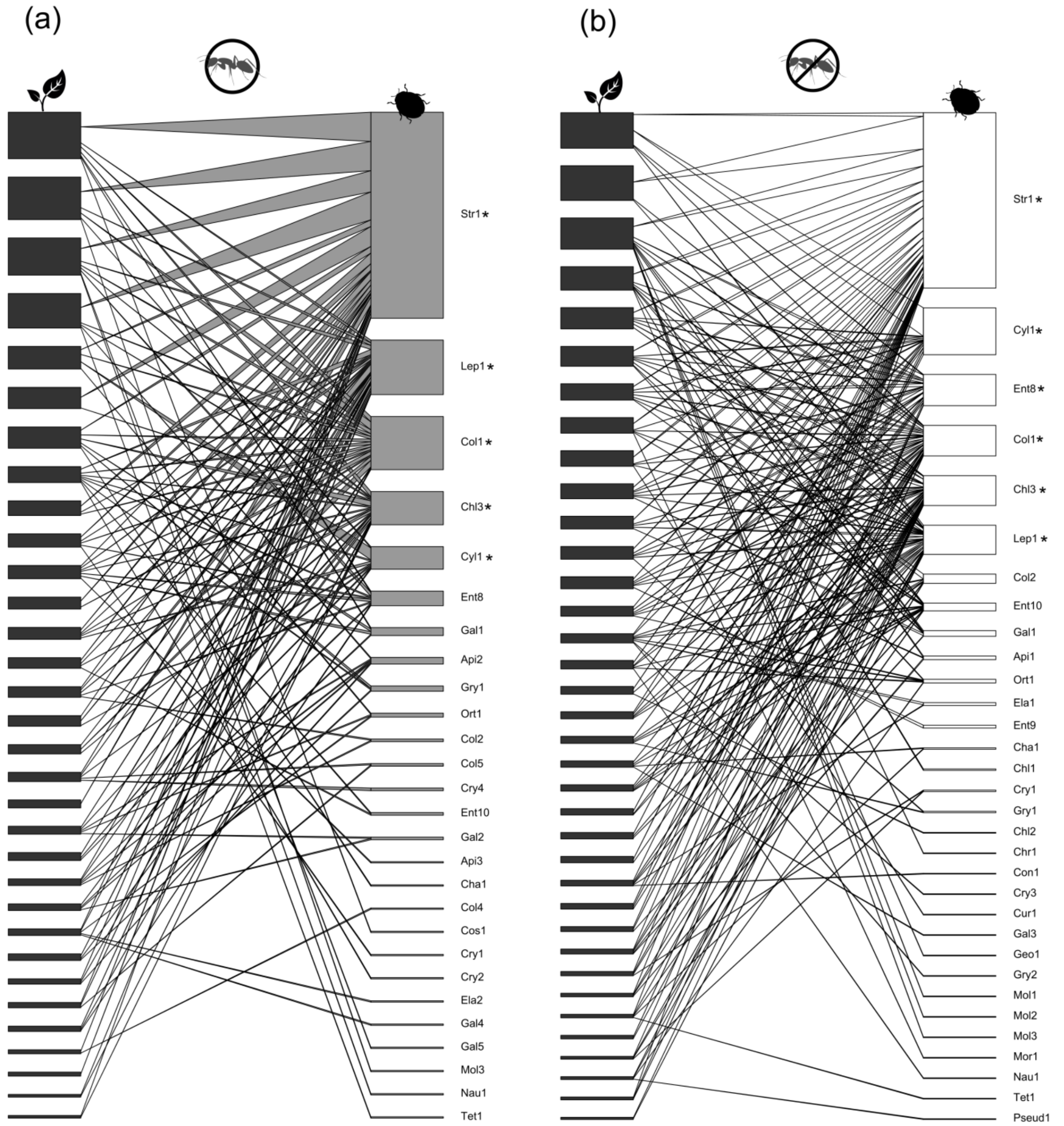
Treatments: *Azteca chartifex* present *Azteca chartifex* absent



Conversely, composition of the central species were similar in the plant-herbivore network, both in presence and absence of *A. chartifex* (Dev=10.81, P=0.23). The occurrence of beetle *Strabala* sp.1 in core reflects similarity between plant-herbivore networks. This species performed about 45% of interactions, regardless *A. chartifex* presence. In plant-herbivore networks we observed five central species in *A. chartifex* presence (Fig.6a) and six in absence (Fig. 6b). The three herbivores that performed the most interactions in *A. chartifex* presence were *Strabala* sp.1, *Colaspis* sp.1 and lepidopteran caterpillars (together they performed 73% of interactions). In *A. chartifex* absence, *Strabala* sp.1, *Cylindrocopturinus* sp.1 and Morphospecies sp. 8 (Curculionidae: Entiminae) together performing 64% of the interactions.

Figure 6: Interaction networks between individuals of *Byrsonima sericea* and herbivores performed (a) in presence and (b) in absence of *Azteca chartifex*. Each node represents an individual of *B. sericea* (left bars) or a morphospecies of chewing herbivore (right bars). The lines represent plant-herbivore interactions. Linkage width indicates the frequency of each interaction. Central species are indicated with asterisk (*). Herbivore taxon codes are defined in Tables S2 (Appendix A).

Treatments: *Azteca chartifex* present *Azteca chartifex* absent



2.4 DISCUSSION

Our findings show that *Azteca chartifex* is a keystone species in structuring the arthropod community associated with *B. sericea*, as its presence changed population densities, coexistence, and interactions between guilds of arthropod species. *Azteca chartifex* reduced abundance of other predators and herbivores, thus generating a cascading effect ending in reduced herbivory levels in *B. sericea* with this ant. After mapping the co-occurrences of species, we observed that *A. chartifex* occurred in an aggregate manner on continuous trees, where other predators tended to avoid. Its presence forced the opportunistic and not dominant predators (e.g. *Crematogaster* spp.) and most of herbivores out of its territory. *Azteca chartifex* seems to alternate its occurrence with another dominant ant, following the expected canopy pattern of ant territories mosaic (Majer *et al.* 1994; Blüthgen & Stork 2007; Dejean *et al.* 2007; Ribeiro *et al.* 2013). Although *A. chartifex* presence did not affect predator and herbivore interaction networks, this ant caused change of central predator species, modifying species composition of other predators in their territory. However, *A. chartifex* did not influence plant-herbivore networks, where herbivorous central insect species remained unaffected by ant presence.

Azteca chartifex proved to be efficient in patrolling and defending its territory, reducing abundance of other predators, herbivores and herbivory. The effect caused by *A. chartifex* was density-dependent, as intensity its patrolling on *B. sericea* foliage. Where there was greater patrolling activity of *A. chartifex*, it was possibly more probability to encounter, pursuit and attack other predators and herbivores. Territorial ants like *A. chartifex* have ostensible and strategic patroll on trees, preventing or discouraging arrival of arthropods (Oliveira & Freitas 2004; Fernandes *et al.* 2005; Rosumek *et al.* 2009; Lourenço *et al.* 2015; Zhang *et al.* 2015). They are still skilled predators, with group hunting tactics (Dejean *et al.* 2007, 2009). These strategies are likely crucial for existence of a mosaic of ant dominant species territories and its effects on remaining arthropods species spatial distribution.

In present study, ants corresponded to 81% of the total arthropod abundance, with *A. chartifex* being the most abundant species (n = 3.781). Our results are in line with canopy studies showing that ants can achieve 94% of the total arthropod abundance of this stratum (Dial *et al.* 2006; Rico-Gray & Oliveira 2007; Dejean *et al.* 2018). The forest canopy has strong segregation among ants species, evidencing that territories are almost exclusively occupied by a few dominant species (Ribeiro *et al.* 2013; Dejean *et al.* 2015; Yusah *et al.* 2018). Structural arrangement of *A. chartifex* nests allowed a strategic spatial distribution, enlarging its territory and improving its foraging from main nest. We identified that this distribution was not arbitrary, evidencing a hierarchical structure among arthropods, emphasizing functional dominance of *A. chartifex* in system. In addition, features such as extremely populous colonies and large nests and/or polydomic nests may be as important as to ensure *A. chartifex* success. These characteristics have been considered essential for several arboreal ant species (Leston 1973; Taylor 1977; Dejean *et al.* 2007, 2018; Ribeiro *et al.* 2013) and confirmed in this study.

Negative association among dominant ants and similar patterns of occupation contributed to occurrence of aggregate populations that we detected in our study. Territorially dominant ants, such as *Azteca* spp. and *Crematogaster* spp., have complementary spatial distribution and suppress density and activities of hierarchically inferior species (Dejean *et al.* 2018). These ants share characteristics that promote ant dominance mosaic, such as individuals of similar size, large colonies and often polydomic nests and a massive recruitment capacity (Yanoviak & Kaspari 2000; Ribeiro *et al.* 2013; Camarota *et al.* 2016; Dejean *et al.* 2018), evidencing that spatial distribution of species is not random.

Although frequency and diversity of interaction were similar between treatments, the other predators interacted differently. We observed that *Cephalotes minutus* (sub-dominant species) performed most interactions in *A. chartifex* territories, being the most tolerated species. Tolerance is probably due to small size of colonies *Cephalotes* spp., which implies a small negative effect on host (Adams 1990). Adams (1990) found a similar result when observing interaction between *Azteca* spp. and *Cephalotes* spp. (subgenre *Zacryptocerus*), demonstrating that this coexistence is opportunistic. *Cephalotes* spp. uses pheromone markings made by *Azteca* spp. to find food resources more easily, increasing its establishment and survival in *Azteca* spp. territory (Adams 1990), phenomena known as 'trophic parasitism' (*sensu* WILSON & HOLLDOBLER 1990a). Results of other studies conducted in tropical forests similar to ours, recorded *Azteca* spp. as most abundant species in forest canopy (Yanoviak & Kaspari 2000; Ribeiro *et al.* 2013; Dejean *et al.* 2018) and *Cephalotes* spp. as a sub-dominant species in their territories (Yanoviak & Kaspari 2000; Ribeiro *et al.* 2013).

Curiously, *C. minutes* did not perform as well without *A. chartifex*, and other ant species in dominant core were responsible by interactions in our absence. Other record predators, such as spiders, also failed to interact with sub-dominant ants. This scenario suggests that there may have been competition by resource between spiders and ants, with spiders susceptible to ant predation, regardless of species (Mody & Linsenmair 2004; Sanders & Platner 2007; Katayama *et al.* 2015; Schuldt & Staab 2015). The probability of ants and spider attacks may be higher because ants found spiders more easily by its patrolling behavior on whole tree, reflecting lower spider abundance recorded in our study and higher ant competitiveness.

Regardless *A. chartifex* presence, networks were dominated by interactions performed by beetle *Strabala* sp.1. Although there was a change of position among central species in networks, *Strabala* sp.1 was the herbivore that had highest interactions frequency in both presence and absence of *A. chartifex*. The beetles of Altiinae subfamily, as *Strabala* sp.1, are known for the remarkable characteristic of ability to jump, like fleas, using the jump to escape from predators or to move in vegetation (Furth 1988). When confronted with *A. chartifex*, *Strabala* sp.1 jumps and lands on another leaf, indicating that ant does not necessarily prey on these beetles, but may scare them off. In addition, connectivity between canopies, favored by presence of lianas, may have facilitated both access and escape, and herbivorous insects dispersion (Campos *et al.* 2006; Madeira *et al.* 2009). Thus, ostensive patrolling of *A. chartifex* is an important action that reduces feeding time *Strabala* sp.1 beetle. These colonies recruit more soldiers and can reduce herbivores residence time in host plant, causing reduction of herbivory (Rocha & Bergallo 1992; Pringle *et al.* 2011; Fagundes *et al.* 2017).

Our findings point to the importance of studies on dynamics of arthropods interaction, highlighting the ability of *A. chartifex* to modify community composition and generate effects along of trophic chain. The benefits of *A. chartifex* to *B. sericea* arose when this ant reduced herbivore numbers and herbivory. In this study, *A. chartifex* efficiently patrolled its territory, made it difficult for arthropods to remain in *B. sericea* and favored herbivory reduction in individuals that hosted it. Decrease in herbivory level may consequently increase the reproductive success of *B. sericea*, facilitating its establishment in ecotones. *Azteca chartifex* also showed to be a keystone species defining canopy arthropod community, and determining spatial distribution and interaction patterns of other associated arthropods. Future studies may help to understand effects of connectivity and crowns architectural complexity on arthropods diversity in plants associated with *A. chartifex*. In more complex environments, herbivores have more places to shelter or hide from predators and more escape routes. Conversely, *A. chartifex* would have greater ease to patrolling in more complex site.

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2.6 References

Adams, E.S. (1990). Interaction Between the Ants Zacryptocerus maculatus and Azteca trigona : Interspecific Parasitization of Information. *Biotropica*, 22, 200–206.

Adams, E.S. (2016). Territoriality in ants (Hymenoptera : Formicidae): a review. *Myrmecological News*, 23, 101–118.

Alvares, C.A., Stape, J.L., Sentelhas, P.C., Gonçalves, J.L. de M. & Sparovek, G. (2013). Köppen's climate classification map for Brazil. *Meteorol. Zeitschrift*, 22, 711–728.

Anzaldo, S.S. (2017). Review of the genera of conoderinae (Coleoptera, Curculionidae) from north America, central America, and the Caribbean. *Zookeys*, 2017, 51–138.

Arnett, R.H., Thomas, M.C., Skelley, P.E. & Frank, J.H. (2002). *American beetles, Volume II: Polyphaga: Scarabaeoidea through Curculionoidea*. CRC Press, Boca Raton.

Baccaro, F.B., Feitosa, R.M., Fernandez, F., Fernandes, I.O., Izzo, T.J., Souza, J.L.P., *et al.* (2015). *Guia para os gêneros de formigas do Brasil*. *Ed. INPA*.

Barbosa, B. de C. (2014). Arquitetura de ramos, alocação de biomassa e herbivoria em duas espécies arbóreas com diferentes histórias de vida em uma Floresta Tropical Semidecidual. Universidade Federal de Minas Gerais.

Blüthgen, N. & Stork, N.E. (2007). Ant mosaics in a tropical rainforest in Australia and elsewhere: A critical review. *Austral Ecol.*, 32, 93–104.

Camarota, F., Powell, S., S. Melo, A., Priest, G., J. Marquis, R. & L. Vasconcelos, H. (2016). Co-occurrence patterns in a diverse arboreal ant community are explained more by competition than habitat requirements. *Ecol. Evol.*, 6, 8907–8918.

Campos, R.I., Vasconcelos, H.L., Ribeiro, S.P., Neves, F.S. & Soares, J.P. (2006). Relationship between tree size and insect assemblages associated with Anadenanthera macrocarpa. *Ecography (Cop.).*, 29, 442–450.

Coelho, I.R. & Ribeiro, S.P. (2006). Environment heterogeneity and seasonal effects in ground-dwelling ant (Hymenoptera: Formicidae) assemblages in the Parque Estadual do Rio Doce, MG, Brazil. *Neotrop. Entomol.*, 35, 19–29.

Costa, F. V., Mello, M.A.R., Bronstein, J.L., Guerra, T.J., Muylaert, R.L., Leite, A.C., *et al.* (2016). Few ant species play a central role linking different plant resources in a network in rupestrian grasslands. *PLoS One*, 11, 1–17.

Crawley, M.J. (2013). *The R Book*. 2nd edn. Wiley, United Kingdom.

Dáttilo, W., Díaz-Castelazo, C. & Rico-Gray, V. (2014). Ant dominance hierarchy determines the nested pattern in ant-plant networks. *Biol. J. Linn. Soc.*, 113, 405–414.

Dáttilo, W., Guimarães, P.R. & Izzo, T.J. (2013). Spatial structure of ant-plant mutualistic networks. *Oikos*, 122, 1643–1648.

Davidson, D.W. (1998). Resource discovery versus resource domination in ants: A functional mechanism for breaking the trade-off. *Ecol. Entomol.*, 23, 484–490.

Dejean, A., Corbara, B., Orivel, J. & Leponce, M. (2007). Rainforest Canopy Ants: The Implications of Territoriality and Predatory Behavior. *Funct. Ecosyst. Communities*, 1, 105–120.

Dejean, A., Grangier, J., Leroy, C. & Orivel, J. (2009). Predation and aggressiveness in host plant protection: A generalization using ants from the genus Azteca. *Naturwissenschaften*, 96, 57–63.

Dejean, A., Orivel, J., Leponce, M., Compin, A., Delabie, J.H.C., Azémar, F., *et al.* (2018). Ant–plant relationships in the canopy of an Amazonian rainforest: the presence of an ant mosaic. *Biol. J. Linn. Soc.*, 1–11.

Dejean, A., Ryder, S., Bolton, B., Compin, A., Leponce, M., Azémar, F., *et al.* (2015). How territoriality and host-tree taxa determine the structure of ant mosaics. *Sci. Nat.*, 102, 1–9.

Del-Claro, K., Lange, D., Torezan-Silingardi, H.M., Anjos, D.V., Calixto, E.S., Dáttilo, W., *et al.* (2018). The Complex Ant–Plant Relationship Within Tropical Ecological Networks. In: *Ecological Networks in the Tropics* (eds. Dáttilo, W. & Rico-Gray, V.). Springer International Publishing, Cham, pp. 59–71.

Dial, R.J., Ellwood, M.D.F., Turner, E.C. & Foster, W.A. (2006). Arthropod Abundance , Canopy Structure , and Microclimate in a Bornean Lowland Tropical Rain Forest Author (s): Roman J . Dial , Martin D . F . Ellwood , Edward C . Turner and William A . Foster Published by : Association for Tropical Biology and Conser. *Biotropica*, 38, 643–652.

Dormann, C.F. (2011). How to be a specialist? Quantifying specialisation in pollination networks. *Netw. Biol.*, 1, 1–20.

Dormann, C.F., Frund, J., Bluthgen, N. & Gruber, B. (2009). Indices, Graphs and Null Models: Analyzing Bipartite Ecological Networks. *Open Ecol. J.*, 2, 7–24.

Dormann, C.F., Gruber, B. & Fründ, J. (2008). Introducing the bipartite Package: Analysing Ecological Networks. *R News*, 8, 8–11.

Espírito Santo, N.B., Ribeiro, S.P. & Santos Lopes, J.F. (2012). Evidence of competition between two canopy ant species: Is aggressive behavior innate or shaped by a competitive environment? *Psyche (Stuttg).*, 2012.

Fagundes, R., Dáttilo, W., Ribeiro, S.P., Rico-Gray, V., Jordano, P. & Del-Claro, K. (2017). Differences among ant species in plant protection are related to production of extrafloral nectar and degree of leaf herbivory. *Biol. J. Linn. Soc.*, 1–13.

Fernandes, G.W., Fagundes, M., Greco, M.K.B., Barbeitos, M.S. & Santos, J.C. (2005). Ants and their effects on an insect herbivore community associated with the inflorescences of Byrsonima crassifolia (Linnaeus) H.B.K. (Malpighiaceae). *Rev. Bras. Entomol.*, 49, 264–269.

Fonseca-Silva, F.M., de Araujo Carvalho, M. & Ribeiro, S.P. (2015). Caracterização da matéria orgânica particulada dos últimos 10 mil anos a partir de um testemunho do parque estadual Do Rio Doce, Mg, Brasil: Implicações paleoambientais. *Rev. Bras. Paleontol.*, 18, 161–170.

Fonseca-Silva, F.M., Carvalho, M. de A. & Ribeiro, S.P. (2018). Palynological evidence of vegetation change during the last 10,000 years in the mid-valley of the Rio Doce, Brazil. *Acta Bot. Brasilica*, 33, 29–38.

Furth, D.G. (1988). The jumping apparatus of flea beetles (Alticinae) - The metafemoral spring. In: *Biology of Chrysomelidae* (eds. Jolivet, P., Petitpierre, E. & Hsiao, T.H.). Dordrecht, pp. 285–297.

Garvey, J.E. & Whiles, M.R. (2016). Predation. In: *Trophic ecology*. CRC Press, Hoboken, New Jersey, pp. 81–100.

Holldobler, B. & Wilson, E.O. (1990). *The ants*. Harvard University Press, Cambridge.

Jeffries, M.J. & Lawton, J.H. (1984). Enemy free space and the structure of ecological communities. *Biol. J. Linn. Soc.*, 23, 269–286.

Jordán, F., Benedek, Z. & Podani, J. (2007). Quantifying positional importance in food webs: A comparison of centrality indices. *Ecol. Modell.*, 205, 270–275.

Katayama, M., Kishimoto-Yamada, K., Tanaka, H.O., Endo, T., Hashimoto, Y., Yamane, S., *et al.* (2015). Negative correlation between ant and spider abundances in the canopy of a bornean tropical rain forest. *Biotropica*, 47, 363–368.

Klunk, C.L., Giehl, E.L.H., Lopes, B.C., Marcineiro, F.R. & Rosumek, F.B. (2018). Simple does not mean poor: grasslands and forests harbor similar ant species richness and distinct composition in highlands of southern Brazil. *Biota Neotrop.*, 18.

Leston, D. (1973). The Ant Mosaic - Tropical Tree Crops and the Limiting of Pests and Diseases. *Pest Artic. News Summ.*, 19, 311–341.

Longino, J.T. (2007). *A taxonomic review of the genus Azteca*. *Zookeys*.

Lourenço, G.M., Campos, R.B.F. & Ribeiro, S.P. (2015). Spatial distribution of insect guilds in a tropical montane rainforest: effects of canopy structure and numerically dominant ants. *Arthropod. Plant. Interact.*, 9, 163–174.

Lourenço, G.M., Soares, G.R., Santos, T.P., Dáttilo, W., Freitas, A.V.L. & Ribeiro, S.P. (2019). Equal but different: Natural ecotones are dissimilar to anthropic edges. *PLoS One*, 14, e0213008.

Madeira, B.G., Espírito-Santo, M.M., Neto, S.D., Nunes, Y.R.F., Arturo Sánchez Azofeifa, G., Wilson Fernandes, G., *et al.* (2009). Changes in tree and liana communities along a successional gradient in a tropical dry forest in south-eastern Brazil. *Plant Ecol.*, 201, 291–304.

Majer, J.D. (1972). The ant mosaic in Ghana cocoa farms. *Bull. Entomol. Res.*, 62, 151.

Majer, J.D., Delabie, J.H.C. & Smith, M.R.B. (1994). Arboreal Ant Community Patterns in Brazilian Cocoa Farms. *Biotropica*, 26, 73.

Mello, M.A.R., Rodrigues, F.A., Costa, L. da F., Kissling, W.D., Şekercioğlu, Ç.H., Marquitti, F.M.D., *et al.* (2015). Keystone species in seed dispersal networks are mainly determined by dietary specialization. *Oikos*, 124, 1031–1039.

Mody, K. & Linsenmair, K.E. (2004). Plant-attracted ants affect arthropod community structure but not necessarily herbivory. *Ecol. Entomol.*, 29, 217–225.

Moreira, X., Mooney, K.A., Zas, R. & Sampedro, L. (2012). Bottom-up effects of host-plant species diversity and top-down effects of ants interactively increase plant performance. *Proc. R. Soc. B Biol. Sci.*, 279, 4464–4472.

Nahas, L., Gonzaga, M.O. & Del-Claro, K. (2012). Emergent Impacts of Ant and Spider Interactions: Herbivory Reduction in a Tropical Savanna Tree. *Biotropica*, 44, 498–505.

Neves, F.S., Araújo, L.S., Espírito-Santo, M.M., Fagundes, M., Fernandes, G.W., Sanchez-Azofeifa, G.A., *et al.* (2010). Canopy herbivory and insect herbivore diversity in a dry forest-savanna transition in Brazil. *Biotropica*, 42, 112–118.

Novotny, V., Basset, Y., Auga, J., Boen, W., Dal, C., Drozd, P., *et al.* (1999). Predation risk for herbivorous insects on tropical vegetation: A search for enemy-free space and time. *Austral Ecol.*, 24, 477–483.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., *et al.* (2016). Vegan: Community Ecology Package. R Package Version. 2.0-10, 0–291.

Oliveira, P.S. & Freitas, A.V.L. (2004). Ant-plant-herbivore interactions in the neotropical cerrado savanna. *Naturwissenschaften*, 91, 557–570.

Paine, R.T. (1966). Food web complexity and species diversity. *Am. Nat.*, 100, 65–75.

Paine, R.T. (1969). A note on trophic complexity and community stability. *Am. Nat.*, 103, 91–93.

Paine, R.T. (1980). Food Webs: Linkage, Interaction Strength and Community Infrastructure. *J. Anim. Ecol.*, 49, 666.

Poelman, E.H. & Kessler, A. (2016). Keystone Herbivores and the Evolution of Plant Defenses. *Trends Plant Sci.*, 21, 477–485.

Polis, G.A., Sears, A.L.W., Huxel, G.R., Strong, D.R. & Maron, J. (2000). When a trophic cascade is a trophic cascade? *Trends Ecol. Evol.*, 15, 473–475.

Pringle, E.G., Dirzo, R. & Gordon, D.M. (2011). Indirect benefits of symbiotic coccoids for an ant-defended myrmecophytic tree. *Ecology*, 92, 37–46.

R Core Team, R. (2018). R: A Language and Environment for Statistical Computing.

Rasband, W. (1997). Image J.

Ribeiro, S.P. & Basset, Y. (2007). Gall-forming and free-feeding herbivory along vertical gradients in a lowland tropical rainforest: The importance of leaf sclerophylly. *Ecography (Cop.).*, 30, 663–672.

Ribeiro, S.P., Borges, P.A.V., Gaspar, C., Melo, C., Serrano, A.R.M., Amaral, J., *et al.* (2005). Canopy insect herbivores in the Azorean Laurisilva forests: Key host plant species in a highly generalist insect community. *Ecography (Cop.).*, 28, 315–330.

Ribeiro, S.P., Espirito Santo, N.B., Delabie, J.H.C. & Majer, J.D. (2013). Competition, resources and the ant (Hymenoptera: Formicidae) mosaic: A comparison of upper and lower canopy. *Myrmecological News*, 18, 113–120.

Ribeiro, S.P., Soares, J.P., Campos, R.I. de C. & Martins, R.P. (2008). Insect herbivores species associated to pioneer tree species: contrasting within forest and ecotone canopy habitats. *Zoociências*, 10, 237–248.

Rico-Gray, V. & Oliveira, P.S. (2007). *The Ecology and Evolution of Ant-Plant Interactions*. University of Chicago Press, Chigago.

Rocha, C.F.D. & Bergallo, H.G. (1992). Bigger ant colonies reduce herbivory and herbivore residence time on leaves of an ant-plant: Azteca muelleri vs. Coelomera ruficornis on Cecropia pachystachya. *Oecologia*, 91, 249–252.

Romero, G.Q. & Koricheva, J. (2011). Contrasting cascade effects of carnivores on plant fitness: A meta-analysis. *J. Anim. Ecol.*, 80, 696–704.

Rosumek, F.B., Silveira, F.A.O., De S. Neves, F., Newton, N.P., Diniz, L., Oki, Y., *et al.* (2009). Ants on plants: a meta-analysis of the role of ants as plant biotic defenses. *Oecologia*, 160, 537–549.

Sanders, D. & Platner, C. (2007). Intraguild interactions between spiders and ants and top-down control in a grassland food web. *Oecologia*, 150, 611–624.

Schnitzer, S.A. (2018). Testing ecological theory with lianas. *New Phytol.*, 220, 366–380.

Schuldt, A. & Staab, M. (2015). Tree species richness strengthens relationships between ants and the functional composition of spider assemblages in a highly diverse forest. *Biotropica*, 47, 339–346.

Shaw, D.C., Ernest, K.A., Rinker, H.B. & Lowman, M.D. (2006). Stand-level herbivory in an old-growth conifer forest canopy. *West. North Am. Nat.*, 66, 473–481.

Taylor, B. (1977). The ant mosaic on cocoa and other tree crops in Western Nigeria. *Ecol. Entomol.*, 2, 245–255.

Teixeira, L.A.G. & Machado, I.C. (2000). Sistema de polinização e reprodução de Byrsonima sericea DC (Malpighiaceae). *Acta Bot. Brasilica*, 14, 347–357.

Trager, M.D., Bhotika, S., Hostetler, J.A., Andrade, G. V., Rodriguez-Cabal, M.A., Mckeon, C.S., *et al.* (2010). Benefits for plants in ant-plant protective mutualisms: A meta-analysis. *PLoS One*, 5.

Vandermeer, J., Perfecto, I. & Philpott, S. (2010). Ecological Complexity and Pest Control in Organic Coffee Production : Uncovering an Autonomous Ecosystem Service, 60, 527–537.

Wang, Y., Naumann, U., Wright, S.T. & Warton, D.I. (2012). Mvabund- an R package for model-based analysis of multivariate abundance data. *Methods Ecol. Evol.*, 3, 471–474.

Yanoviak, S.P. & Kaspari, M. (2000). Community structure and the habitat templet: ants in the tropical forest canopy and litter. *Oikos*, 89, 259–266.

Yusah, K.M., Foster, W.A., Reynolds, G. & Fayle, T.M. (2018). Ant mosaics in Bornean primary rain forest high canopy depend on spatial scale, time of day, and sampling method. *PeerJ*, 6, e4231.

Zhang, S., Zhang, Y. & Ma, K. (2015). The equal effectiveness of different defensive strategies. *Sci. Rep.*, 5, 1–9.

Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. (2009). *Mixed effects models and extensions in ecology with R*. Statistics for Biology and Health. Springer New York, New York, NY.

APPENDIX A – FIGURES AND TABLES

Figure A1. Scheme of wire-framed cube used for leaves selection. (a) Cube in volume of 0.027 m^3 and (b) model of arrangement of cubes inside crown.

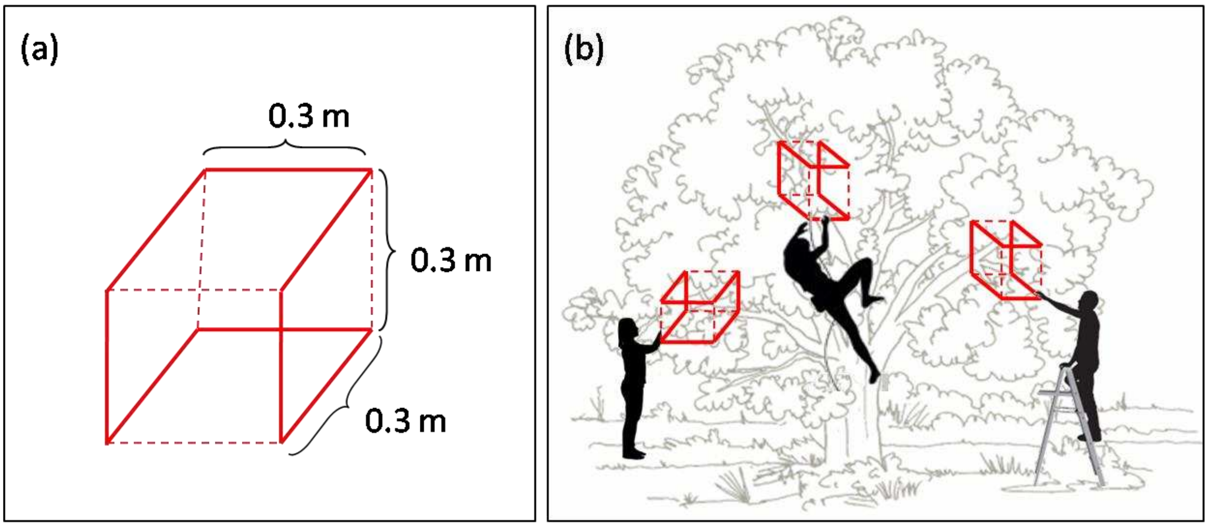

Table A1. Arthropod taxa abundance recorded in *Byrsonima sericea* during the years 2016 and 2017. P = Predator; H = Herbivore

Taxon	Trophic position	Abundance
ARANEAE		
Anyphaenidae		
Morphospecies sp.39	P	1
Morphospecies sp.7	P	33
Araneidae		
Acacesia sp.1	P	1
Eriophora sp.14	P	1
Morphospecies sp.11	P	5
Morphospecies sp.12	P	2
Morphospecies sp.13	P	4
Morphospecies sp.14	P	3
Morphospecies sp.20	P	1
Morphospecies sp.38	P	2
Morphospecies sp.43	P	1
Morphospecies sp.45	P	1
Morphospecies sp.51	P	2
Morphospecies sp.52	P	4
Clubionidae		
Morphospecies sp.71	P	1
Corinnidae		
Morphospecies sp.28	P	1
Gnaphosidae		
Morphospecies sp.67	P	1
Morphospecies sp.8	P	8
Linyphiidae		
Morphospecies sp.57	P	4
Morphospecies sp.65	P	1
Mimetidae		
Morphospecies sp.13	P	7
Oxyopidae		
Morphospecies sp.3	P	1
Tapinillus sp.1	P	1
Pisauridae		
Morphospecies sp.16	P	3
Morphospecies sp.40	P	2
Morphospecies sp.54	P	4
Salticidae		
Morphospecies sp.1	P	8
Morphospecies sp.2	P	7
Morphospecies sp.4	P	6
Morphospecies sp.6	P	14
Morphospecies sp.9	P	7

Taxon	Trophic position	Abundance
Morphospecies sp.10	P	1
Morphospecies sp.17	P	9
Morphospecies sp.19	P	10
Morphospecies sp.22	P	1
Morphospecies sp.23	P	1
Morphospecies sp.24	P	4
Morphospecies sp.25	P	1
Morphospecies sp.26	P	1
Morphospecies sp.27	P	3
Morphospecies sp.30	P	3
Morphospecies sp.35	P	5
Morphospecies sp.37	P	2
Morphospecies sp.41	P	1
Morphospecies sp.42	P	1
Morphospecies sp.44	P	8
Morphospecies sp.47	P	1
Morphospecies sp.49	P	4
Morphospecies sp.50	P	3
Morphospecies sp.55	P	2
Morphospecies sp.58	P	2
Morphospecies sp.61	P	1
Synemosina sp.1	P	3
Sparassidae		
Morphospecies sp.5	P	1
Morphospecies sp.29	P	1
Morphospecies sp.31	P	2
Morphospecies sp.32	P	6
Morphospecies sp.66	P	1
Morphospecies sp.69	P	1
Tetragnathidae		
Leucauge sp1	P	1
Morphospecies sp.11	P	2
Morphospecies sp.56	P	2
Thomisidae		
Morphospecies sp.18	P	2
Morphospecies sp.21	P	1
Morphospecies sp.34	P	1
Morphospecies sp.53	P	1
Trachelidae		
Trachelas sp.1	P	1
COLEOPTERA		
Morphospecies sp.2	H	7
Morphospecies sp.4	H	1
Morphospecies sp.5	H	2

Taxon	Trophic position	Abundance
Brentidae		
Apioninae		
Morphospecies sp.1	H	4
Morphospecies sp.2	H	3
Morphospecies sp.3	H	1
Carabidae		
Morphospecies sp.3	P	1
Morphospecies sp.4	P	1
Harpalinae		
Morphospecies sp.1	P	2
Stenolophina sp.1	P	26
Chrysomelidae		
Morphospecies sp.1	H	1
Alticinae		
Strabala sp.1	H	264
Chlamisinae		
Chlamisus sp.2	H	1
Chlamisus sp.3	H	54
Morphospecies sp.1	H	2
Eumolpinae		
Colapsis sp.1	H	53
Galerucinae		
Morphospecies sp.1	H	13
Morphospecies sp.2	H	2
Morphospecies sp.3	H	1
Morphospecies sp.4	H	1
Morphospecies sp.5	H	1
Coccinellidae		
Morphospecies sp.1	P	16
Morphospecies sp.2	P	1
Morphospecies sp.3	P	3
Morphospecies sp.4	P	1
Morphospecies sp.5	P	1
Morphospecies sp.8	P	1
Curculionidae		
Conoderinae		
Cylindrocopturinus sp.1	H	80
Cossoninae		
Morphospecies sp.1	H	1
Curculioninae		
Morphospecies sp.1	H	1
Cryptorhynchinae		
Morphospecies sp.1	H	2
Morphospecies sp.3	H	1
Morphospecies sp.4	H	2

Taxon	Trophic position	Abundance
Entiminae		
Morphospecies sp.8	H	51
Morphospecies sp.9	H	4
Naupactus sp.1	H	1
Morphospecies sp.10	H	9
Molytinae		
Chalcodermus sp.1	H	3
Morphospecies sp.1	H	1
Morphospecies sp.2	H	1
Morphospecies sp.3	H	2
Elateridae		
Morphospecies sp.1	H	3
Morphospecies sp.2	H	1
Staphylinidae		
Morphospecies sp.1	P	46
HYMENOPTERA		
Formicidae		
Dolichoderinae		
Azteca chartifex	P	3781
Ectatomminae		
Ectatomma tuberculatum	P	35
Formicinae		
Camponotus sp.1	P	3
Camponotus sp.2	P	5
Camponotus sp.3	P	11
Camponotus sp.4	P	4
Camponotus sp.5	P	3
Camponotus sp.6	P	4
Camponotus rectangularis	P	28
Camponotus sanctaefidei	P	25
Brachymyrmex sp.1	P	32
Myrmicinae		
Cephalotes sp.1	P	1
Cephalotes sp.2	P	1
Cephalotes atratus	P	4
Cephalotes grandinosus	P	2
Cephalotes maculatus	P	15
Cephalotes minutus	P	72
Crematogaster sp.1	P	91
Crematogaster sp.2	P	1
Nesomyrmex echinatinodis	P	18
Solenopsis sp.1	P	1
Solenopsis sp.2	P	46
Solenopsis saevissima	P	1
Wasmannia sp.1	P	6

Taxon	Trophic position	Abundance
Pseudomyrmecinae		
Pseudomyrmex sp.1	P	4
Pseudomyrmex sp.2	P	55
Pseudomyrmex sp.3	P	3
Pseudomyrmex sp.5	P	1
Pseudomyrmex sp.6	P	1
Pseudomyrmex sp.7	P	1
Pseudomyrmex sp.9	P	2
Pseudomyrmex sp.10	P	1
Pseudomyrmex sp.11	P	1
Pseudomyrmex elongatus	P	23
Pseudomyrmex gracilis	P	10
Pseudomyrmex simplex	P	31
LEPIDOPTERA		
Morphospecies sp.1	H	61
Geometridae		
Morphospecies sp.1	H	1
MANTODEA		
Morphospecies sp.1	P	2
ORTHOPTERA		
Gryllidae		
Morphospecies sp.1	H	4
Morphospecies sp.2	H	1
Morphospecies sp.1	H	8
Tettigoniidae		
Morphospecies sp.1	H	2

Table A2. Data from arthropods and their interactions recorded in *Byrsonima sericea* during the years 2016 and 2017.
Species code = morphospecies code in the interaction network; P = Predator; H = Herbivore.

Taxon	Species code	Trophic position	Interaction frequency
ARANEAE			
Anyphaenidae			
Morphospecies sp7	Any7	P	48
Morphospecies sp39	Any39	P	1
Morphospecies sp.70	Any70	P	1
Araneidae			
Acacesia sp.1	Aca1	P	1
Eriophora sp.14	Eri14	P	1
Morphospecies sp.11	Ara11	P	5
Morphospecies sp.12	Ara12	P	3
Morphospecies sp.13	Ara13	P	7
Morphospecies sp.14	Ara14	P	3
Morphospecies sp.20	Ara20	P	1
Morphospecies sp.38	Ara38	P	2
Morphospecies sp.43	Ara43	P	1
Morphospecies sp.45	Ara45	P	1
Morphospecies sp.51	Ara51	P	4
Morphospecies sp.52	Ara52	P	4
Morphospecies sp.63	Ara63	P	1
Clubionidae			
Morphospecies sp.71	Clu71	P	1
Corinnidae			
Morphospecies sp.28	Cor28	P	1
Gnaphosidae			
Morphospecies sp.8	Gna8	P	10
Morphospecies sp.67	Gna67	P	1
Tetragnathidae			
Leucauge sp.1	Leu1	P	1
Linyphiidae			
Morphospecies sp.57	Lin57	P	5
Morphospecies sp.65	Lin65	P	1
Mimetidae			
Morphospecies sp.13	Mim13	P	14
Oxyopidae			
Tapinillus sp.1	Tap1	P	1
Morphospecies sp.3	Oxy3	P	1
Morphospecies sp.35	Oxy35	P	1
Morphospecies sp.68	Oxy68	P	1
Pisauridae			
Morphospecies sp.8	Pis8	P	1
Morphospecies sp.16	Pis16	P	3

Taxon	Species code	Trophic position	Interaction frequency
Morphospecies sp.40	Pis40	P	2
Morphospecies sp.54	Pis54	P	4
Salticidae			
Morphospecies sp.1	Sal1	P	13
Morphospecies sp.2	Sal2	P	8
Morphospecies sp.6	Sal6	P	14
Morphospecies sp.4	Sal4	P	6
Morphospecies sp.9	Sal9	P	9
Morphospecies sp.10	Sal10	P	4
Morphospecies sp.17	Sal17	P	10
Morphospecies sp.19	Sal19	P	10
Morphospecies sp.22	Sal22	P	1
Morphospecies sp.23	Sal23	P	1
Morphospecies sp.24	Sal24	P	5
Morphospecies sp.25	Sal25	P	1
Morphospecies sp.26	Sal26	P	1
Morphospecies sp.27	Sal27	P	3
Morphospecies sp.30	Sal30	P	3
Morphospecies sp.35	Sal35	P	6
Morphospecies sp.37	Sal37	P	2
Morphospecies sp.41	Sal41	P	1
Morphospecies sp.42	Sal42	P	1
Morphospecies sp.44	Sal44	P	9
Morphospecies sp.46	Sal46	P	3
Morphospecies sp.47	Sal47	P	3
Morphospecies sp.48	Sal48	P	9
Morphospecies sp.49	Sal49	P	4
Morphospecies sp.50	Sal50	P	5
Morphospecies sp.55	Sal55	P	2
Morphospecies sp.58	Sal58	P	2
Morphospecies sp.60	Sal60	P	1
Morphospecies sp.61	Sal61	P	1
Synemosina sp.1	Syn1	P	3
Sparassidae			
Morphospecies sp.5	Spa5	P	1
Morphospecies sp.29	Spa29	P	1
Morphospecies sp.31	Spa31	P	5
Morphospecies sp.32	Spa32	P	7
Morphospecies sp.66	Spa66	P	1
Morphospecies sp.69	Spa69	P	1
Tetragnathidae			
Morphospecies sp.11	Tet11	P	2
Morphospecies sp.56	Tet56	P	2

Taxon	Species code	Trophic position	Interaction frequency
Thomisidae			
Morphospecies sp.18	Tho18	P	2
Morphospecies sp.21	Tho21	P	1
Morphospecies sp.34	Tho34	P	1
Morphospecies sp.53	Tho53	P	1
Trachelidae			
Trachelas sp.1	Tra1	P	1
Morphospecies sp.62	Tra62	P	1
COLEOPTERA			
Morphospecies sp.2	Col2	H	15
Morphospecies sp.4	Col4	H	1
Morphospecies sp.5	Col5	H	2
Brentidae			
Apioninae			
Morphospecies sp.1	Api1	H	5
Morphospecies sp.2	Api2	H	5
Morphospecies sp.3	Api3	H	1
Carabidae			
Morphospecies sp.2	Car2	P	1
Morphospecies sp.3	Car3	P	1
Morphospecies sp.4	Car4	P	1
Stenolophina sp.1	Ste1	P	33
Harpalinae			
Morphospecies sp.1	Har1	P	7
Chrysomelidae			
Morphospecies sp.1	Chr1	H	1
Alticinae			
Strabala sp.1	Par1	H	402
Chlamisinae			
Morphospecies sp.1	Chl1	H	2
Chlamisus sp.2	Chl2	H	1
Chlamisus sp.3	Chl3	H	67
Eumolpinae			
Colapsis sp.1	Col1	H	99
Galerucinae			
Morphospecies sp.1	Gal1	H	14
Morphospecies sp.2	Gal2	H	2
Morphospecies sp.3	Gal3	H	1
Morphospecies sp.4	Gal4	H	1
Morphospecies sp.5	Gal5	H	1
Coccinellidae			
Morphospecies sp.1	Coc1	P	17
Morphospecies sp.2	Coc2	P	1
Morphospecies sp.3	Coc3	P	3

Taxon	Species code	Trophic position	Interaction frequency
Morphospecies sp.4	Coc4	P	3
Morphospecies sp.5	Coc5	P	3
Morphospecies sp.6	Coc6	P	1
Morphospecies sp.7	Coc7	P	1
Morphospecies sp.8	Coc8	P	1
Morphospecies sp.9	Coc9	P	1
Curculionidae			
Cossoninae			
Morphospecies sp.1	Cos1	H	1
Conoderinae			
Cylindrocopturinus sp.1	Mic1	H	83
Cryptorhynchinae			
Morphospecies sp.1	Cry1	H	3
Morphospecies sp.2	Cry2	H	1
Morphospecies sp.3	Cry3	H	1
Morphospecies sp.4	Cry4	H	2
Curculioninae			
Morphospecies sp.1	Cur1	H	1
Entiminae			
Morphospecies sp.8	Ent8	H	55
Morphospecies sp.9	Ent9	H	4
Morphospecies sp.10	Ent10	H	13
Naupactus sp.1	Nau1	H	2
Molytinae			
Chalcodermus sp.1	Cha1	H	3
Morphospecies sp.1	Mol1	H	1
Morphospecies sp.2	Mol2	H	1
Morphospecies sp.3	Mol3	H	2
Elateridae			
Morphospecies sp.1	Ela1	H	4
Morphospecies sp.2	Ela2	H	1
Mordellidae			
Morphospecies sp.1	Mor1	H	1
Staphylinidae			
Morphospecies sp.1	Sta1	P	51
HYMENOPTERA			
Formicidae			
Dolichoderinae			
Azteca chartifex	Aztcha	P	4461
Dorymyrmex sp.1	Dor1	P	14
Formicinae			
Brachymyrmex sp.1	Bra1	P	35
Camponotus sp.1	Cam1	P	3
Camponotus sp.2	Cam2	P	6

Taxon	Species code	Trophic position	Interaction frequency
Camponotus sp.3	Cam3	P	16
Camponotus sp.4	Cam4	P	9
Camponotus sp.5	Cam5	P	3
Camponotus sp.6	Cam6	P	5
Camponotus rectangularis	Camrec	P	39
Camponotus sanctaefidei	Camsan	P	36
Myrmicinae			
Cephalotes sp.1	Cep1	P	2
Cephalotes sp.2	Cep2	P	1
Cephalotes atratus	Cepatr	P	4
Cephalotes grandinosus	Cepgra	P	3
Cephalotes maculatus	Cepmac	P	23
Cephalotes minutus	Cepmin	P	89
Crematogaster sp.1	Cre1	P	97
Crematogaster sp.2	Cre2	P	1
Solenopsis sp.1	Sol1	P	1
Solenopsis sp.2	Sol2	P	69
Solenopsis saevissima	Solsae	P	1
Wasmannia sp.1	Was1	P	6
Nesomyrmex echinatinodis	Nesech	P	21
Ectatomminae			
Ectatomma tuberculatum	Ecttub	P	63
Pseudomyrmecinae			
Pseudomyrmex sp.1	Pse1	P	2
Pseudomyrmex sp.2	Pse2	P	68
Pseudomyrmex sp.3	Pse3	P	3
Pseudomyrmex sp.4	Pse4	P	1
Pseudomyrmex sp.5	Pse5	P	1
Pseudomyrmex sp.6	Pse6	P	3
Pseudomyrmex sp.7	Pse7	P	3
Pseudomyrmex sp.8	Pse8	P	1
Pseudomyrmex sp.9	Pse9	P	2
Pseudomyrmex sp.10	Pse10	P	1
Pseudomyrmex sp.11	Pse11	P	1
Pseudomyrmex elongatus	Pseelo	P	29
Pseudomyrmex gracilis	Psegra	P	18
Pseudomyrmex simplex	Psesim	P	44
LEPIDOPTERA			
Morphospecies sp.1	Lep1	H	82
Geometridae			
Morphospecies sp.1	Geo1	H	1
MANTODEA			
Morphospecies sp.1	Man1	P	2

Taxon	Species code	Trophic position	Interaction frequency
NEUROPTERA			
Mantispidae			
Morphospecies sp.1	Mas1	P	1
ORTHOPTERA			
Morphospecies sp.1	Ort1	H	8
Tettigoniidae			
Morphospecies sp.1	Tet1	H	2
Conocephalinae			
Morphospecies sp.1	Con1	H	1
Pseudophyllinae			
Morphospecies sp.1	Pse1	H	1
Gryllidae			
Morphospecies sp.1	Gry1	H	6
Morphospecies sp.2	Gry2	H	1
PSEUDOSCORPIONES			
Pseudoscorpiones sp.1	Pse1	P	2

CHAPTER 3 - POSITIVE EFFECTS OF ANT PREDATION ARE MEDIATED BY LIANA ON CANOPY

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Abstract

Understanding ant protection to plants, associated with lianas, is essential to reveal how these two ecological components contribute to mutualism effectiveness. By conducting a field experiment of liana removal, we investigated how interaction between ant *Azteca chartifex* and liana influenced the effectiveness of ant protection for a canopy host tree. We found that *A. chartifex* better explored lianas structure, using it resource to maximize foraging activity thus reducing species richness, herbivores abundance, herbivory, and increasing fruit set. This result reflected in the protection mutualism efficiency, suppressing negative effect of having lianas on host plant crown. Also, *A. chartifex* outstand among any other ant species, being the only species that effectively protected the plant. Our findings suggest that ant-plant mutualism must be investigated such a multi-trophic approach to elucidate its role in structuring invertebrate community and its relationship with plant reproductive success.

Key words: Ant–plant mutualisms; herbivory; liana; mutualism effectiveness; plant protection mutualisms; reproductive success.

3.1 INTRODUCTION

Mutualistic protection relationships between ants and plants involve at least three species: ant, protected species (e.g., plant), and herbivore species (e.g., herbivorous insects). In this interaction there are resources and services exchanges, in which plant offer food sources (as nectar) or shelter for ants, and these protect the plant against herbivores, pathogens and even invasive vegetation (González-Teuber & Heil 2010; Trager *et al.* 2010; Del-Claro *et al.* 2016). Ants are likely candidates to evolve as cheap plant induced defense, due to its spatially and temporally predictability and to recruitment mechanism, which allows rapid increase of individuals on plant if attacked (Agrawal & Rutter 1998). Among the benefits of this association, decrease foliar herbivory and reduced herbivore abundance are outcomes commonly observed (Rosumek *et al.* 2009; Trager *et al.* 2010). However, protection mutualism effectiveness may differ depending on partner species and outcome efficiency relies on the extend in which the quality and quantity of the service provided varies (Ness *et al.* 2006). In addition, to detect ant protection effect on plants, we should account with benefits of fitness concomitantly with processes related to herbivores exclusion (Trager *et al.* 2010). The outcome efficiency raised from mutualistic relationship depends on combination of interaction quality (e.g., plant fruit set) and quantity (e.g., number of enemies excluded) (Ness *et al.* 2006; Schupp *et al.* 2017). In this context, the term 'plant protection mutualism effectiveness' is defined as the resulted effect of ant-plant interaction that can be untangled in quantitative and qualitative components (Schupp *et al.* 2017).

The intrinsic complexity of a multi-trophic system often forces us to investigate the role of few interacting species, neglecting other species effects (generally the higher trophic levels) (Bronstein 2015), as well as habitat structural complexity, especially tree crown connectivity. Tree crown connectivity may influence the outcome of ant-plant mutualism, as it is a good predictor of arthropod diversity (Adams *et al.* 2019). Canopy size increases habitat structural complexity, leading to a greater availability and diversity of niches and refuges, and promoting the coexistence among populations of predators and prey (Lawton 1983; Šipoš & Kindlmann 2013; Adams *et al.* 2019). Lianas are the main responsible for forest canopy connectivity (Odell *et al.* 2019) and are used by ants as food resource via extra-floral nectar (Bluthgen & Fiedler 2002). Additionally, arboreal ants use lianas as alternative paths that also expand their foraging area and patrolling (Clay *et al.* 2010), especially ant species that require abundant resources to maintain a large colony (e.g., *Azteca* spp) (Holldobler & Wilson 1990a). For herbivorous insects, lianas can act as enemy free spaces, since they can hide and use lianas as escape routes from predators (Jeffries & Lawton 1984; Šipoš & Kindlmann 2013). Thus, lianas are important components in determining the distribution of ants, herbivorous insects, and thus influencing the whole host plant community (Odegaard 2000; Adams *et al.* 2017).

Several studies have addressed the deleterious effect of lianas on host trees (Putz 1984; van der Heijden & Phillips 2009; Ingwell *et al.* 2010; Schnitzer & Carson 2010), however their positive effects are poorly understood (Estrada-Villegas & Schnitzer 2018; Odell *et al.* 2019). It is known that lianas maintain animal diversity by increasing the environment structural complexity, representing persistent source of connectivity among crowns, favoring species diversity (Odegaard 2000; Parthasarathy 2015; Yanoviak 2015; Adams *et al.* 2017; Schnitzer 2018). Despite the current knowledge on liana ecology, little is known about the synergistic effect of lianas and its host plants on the associated arthropod community (Schnitzer 2018; Odell *et al.* 2019).

Lianas and arboreal ants are important components that share the same forest stratum: the canopy (Yanoviak 2015). Dominant ants can use lianas to constantly patrol their hosts, modulating the distribution of other organisms, such as non-dominant ants, herbivorous insects, and other predators such as spiders. Several studies have shown greater invertebrate species richness in spaces free of ants, as result of confrontation avoidance (Ribeiro *et al.* 2013; Lourenço *et al.* 2015). In addition, dominant ants have a populous colony and display aggressive behavior characterized by inter- and intraspecific confrontations to defend resources and territory (e.g., host plant) (Dejean *et al.* 2007). These ants are skilled at building large nests associated with spaced smaller ones (polidomy), which facilitates their movement over trees and improves territory defense. Among these ant species, *Azteca chartifex* (Formicidae: Dolichoderinae) stands out for its territorialist and dominant behavior (Longino 2007). Altogether, a suitable model to study the context-dependency of ant-plant mutualism effectiveness requires a system that involves a dominant ant species, a host plant naturally occupied by lianas and all associated herbivores and predators.

Considering that habitat complexity improves resource availability, we expect to find higher prevalence of prey and predators in habitats with liana. As long as lianas are a good predictor of canopy structure (Odell *et al.* 2019), we might test whether prey or predators will use them either to hide or to increase foraging efficiency. Unveiling the role of ants on plant fitness in a context of contrasting tree crown complexity would help to understand how forest canopy contribute to mediate plants reproductive success and the diversity of invertebrate arboreal community. Hence, we asked whether does association between *A. chartifex* and liana influences ant-plant mutualism effectiveness. We studied a system involving *A. chartifex* and tri-trophic interactions of *Byrsonima sericea* DC (Malpighiaceae), a dominant forest–lakes ecotone canopy species, naturally occupied by lianas. In a field experiment, we tested whether liana presence on tree crown favor *A. chartifex* prevalence. Thus, we expect that host plant with liana will lead to greater abundance of ants, generating negative effects on herbivorous insects and herbivory. In this scenario, the association between *A. chartifex* and liana on *B. sericea* will lead to decrease in species richness and abundance of herbivorous insects species and, consequently, lower herbivory level. This prediction is based on the fact that liana improve canopy structural complexity and provides alternative paths that are accessed by predatory ants, facilitating the expansion of their foraging area (Clay *et al.* 2010). Secondly, we tested whether there is be an increase in *B. sericea* fitness when *A. chartifex* is associated with lianas. We already know that host trees and lianas are in an constant competition that compromises host plants performance, either by light obstruction, structural stress, growth reduction or obstruction the conduction of sap (Putz & Mooney 1992; van der Heijden & Phillips 2009; Schnitzer 2018). Nevertheless, when dominant ants are favored by liana presence, we might expect that an increase in plant reproductive success (here, flower-fruit conversion). Finally, we tested whether there is a gradient of ant protective efficiency, in which *A. chartifex* standouts. We expected to find one to a few effective ant species and a larger number of less protective species. Lines of evidence suggest that multi-trophic ant-plant systems generally encompass only a few central species that may act as mutualistic partners (Costa *et al.* 2016; Fagundes *et al.* 2017).

3.2 MATERIALS AND METHODS

3.2.1 Study area

The study was conducted in the Rio Doce State Park (PERD in Brazilian acronym) (19°48'-19°29'S and 42°38'-42°28'W), in Minas Gerais State, southeastern Brazil. The climatic regime of the region is tropical seasonal (Aw), according to Köeppen´s classification (Alvares *et al.* 2013). Climatic seasons are well defined, with the dry period between May-September and rainy season between October-April. Average precipitation is around 1,500 mm per year (Alvares *et al.* 2013). PERD covers an area of approximately 36,000 ha of Atlantic Forest varying from 200 and 500 m above sea level and is part of the largest natural Neotropical lake system. About 11% of area Park is covered by 42 lakes that have an intimate, though evolutionarily young, history with forest (Fonseca-Silva et al. 2015, 2018).

The lake system inside this Park produces a very particular ecotone areas that are characterized by natural transitions of forest-lake, where trees grow branches bent towards water, seeking for light. This results in what has been called 'brought low canopy', which is, strictly speaking, a typical canopy habitat laying resting close to ground, on ecotone shore or over lakes (Barbosa 2014; Lourenço *et al.* 2019). PERD is a Long-Term Ecological Research site (international LTER) whose tree-arthropod system have been investigated since 2002 (Campos *et al.* 2006b, a; Coelho & Ribeiro 2006; Ribeiro *et al.* 2008). Our group has proved that ecotones between forest and natural lakes in Atlantic rainforest keep typical upper canopy traits, due to a series of existence of whole crowns bent towards open air above water (Barbosa 2014). Such habitats are occupied by typical canopy insects (Lourenço *et al.* 2019) and fully taken by *Azteca chartifex* (Campos *et al.* 2006a). Studies such as these have a frequent limitation of access to establishment of a suitable experiment because it is a typical upper canopy interaction system. Canopy devices as cranes provide limited access to a certain canopy space, but too limited to allow actual replicates (Basset *et al.* 2012; Ribeiro *et al.* 2013). Also, climbing is time consuming and limited by safety criteria. Thus, due a brought low canopy on ecotone of PERD, access constrains are little and overcome with a short ladder and light climbing gears and procedures, allowing us to produce a vast comprehensive and actually replicated experiment.

3.2.2 Study system

Azteca chartifex Emery, 1896 (Dolichoderinae) is a territorialist, dominant, and polydomic ant belonging to a strictly Neotropical distributed group of arboreal ants (Longino 2007). *Azteca chartifex* nests are structurally based on cellulose and processed fibers, and may contain up to thousands individuals (Baccaro *et al.* 2015). *Azteca chartifex* has a non-obligatory mutual association with *B. sericea* establishing the main nest pending in its trunk and numerous smaller satellite nests are distributed along of the tree branches. For instance, we counted in average 23 satellite nests per tree in a radius of 8 m. *Byrsonima sericea* defines the vegetation of ecotone, making it a dominant tree species that has long-lived, with sclerophyllous leaves and a complex crown architecture (Barbosa 2014). In these ecotones, *B. sericea* crowns are structured both vertically as also by crowns whose slope over the lakes, positioning at the same height of understory stratum. Flowering and fruiting of *B. sericea* occur between the second fortnight of October until the end of April (Teixeira & Machado 2000). *Byrsonima sericea* tree in PERD have a mean volume of 6,797 leaves/m^3 (550.58 leaves/0.081m^3), mean height of 5.68 m (±0.13 SE), and mean circumference at breast height of 0.0059 m (± 0.0003 SE). All *B. sericea* individuals that occur in ecotone areas of PERD host lianas in their crowns (about 10 species of lianas), which spread over the forest canopy of ecotone. An average of 75% of *B. sericea* crown area (± 30% SE) is occupied by lianas and these are used by *A. chartifex* as routes of foraging, maximizing their patrolling.

3.2.3 Experimental design

We arbitrarily selected 68 *B. sericea* individuals, distributed into three populations, located in three distinct forest-lake ecotone areas (Fig. 1). All studied individuals had liana in their crowns, of which 32 were colonized by *A. chartifex*. We considered *A. chartifex* presence in plants when they had active worker ants and nests, and *A. chartifex* absence in plants that were naturally not colonized by this ant. Our field experimental design was carried out in three phases: in March 2016, August 2016 and March 2017 (hereafter, Phase I, Phase II and Phase III, respectively). In Phase I, we divided all marked trees into two treatments to detect the *A. chartifex* effect on arthropod guild: i) *A. chartifex* present and liana present (n = 32) and ii) *A. chartifex* absent and liana present (n = 36) (Fig. 2a,b). Each of the three populations were distributed within the above treatments (for details, see Appendix A). In Phase II, we raffled half of the same *B. sericea* individuals (n = 34) and manually removed the lianas from the crowns. The remaining individuals were not manipulated. We cut lianas near the forest floor and at 2 m from ground level using machetes, tree pruner, and pruning shears, with a ladder or climbing if necessary. Liana removal from crowns aimed to reduce the availability of hanging dead lianas that can be used as support for new lianas shoots. After liana cutting, we visited all areas bi-monthly for the next 16 months to monitor the *B. sericea* individuals and cut resprouting liana shoots on individuals with liana removal. In Phase III, we redistributed the same trees in four treatments to detect the effect of the association between *A. chartifex* and liana on community: i) *A. chartifex* present and liana present (n = 16); ii) *A. chartifex* absent and liana present (n = 18); iii) *A. chartifex* present and liana removed (n = 16); and iv) *A. chartifex* absent and liana removed (n = 18) (Fig. 2). Each of the three populations were distributed within the above treatments (for details, see Appendix A).

Figure 1: Map of three *Byrsonima sericea* populations (PI, PII and PIII) located in three distinct forest-lake ecotone in Rio Doce State Park, Brazil.

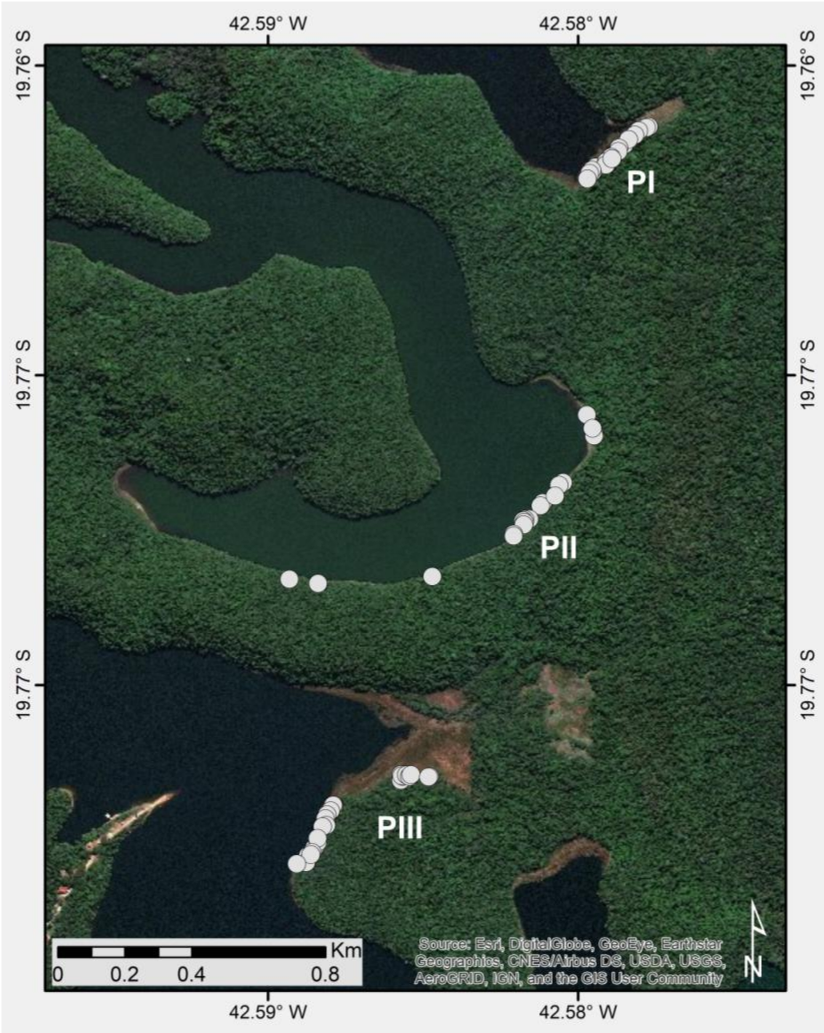


Figure 2: Schematic illustration of the field experiment design and treatments: (a) *Azteca chartifex* present and liana present; (b) *A. chartifex* absent and liana present; (c) *A. chartifex* present and liana removed; and (d) *A. chartifex* absent and liana removed.

3.2.4 Insects sampling and herbivory estimation

In March 2016, we sampled the insects (ants and herbivores) and leaves (for herbivory) in crowns of *B. sericea* individuals in forest-lake ecotone areas with the aid of an aluminum ladder (max. 5 m high) and with basic climbing security gears. We collected the insects using beating samples, performing 10 beats on at least three randomly selected branches (Ribeiro *et al.* 2005; Neves *et al.* 2010). These beats caused insects to fall on entomological umbrella, positioned just below selected branches (Ribeiro *et al.* 2005). This equipment is formed by a funnel (1 x 1 m and 60 cm deep) composed of a white cloth coupled with a plastic bag to collect the samples and adapted for a quantitative sampling. Insects were identified with the aid of revisions and taxonomic keys (Arnett *et al.* 2002; Baccaro *et al.*

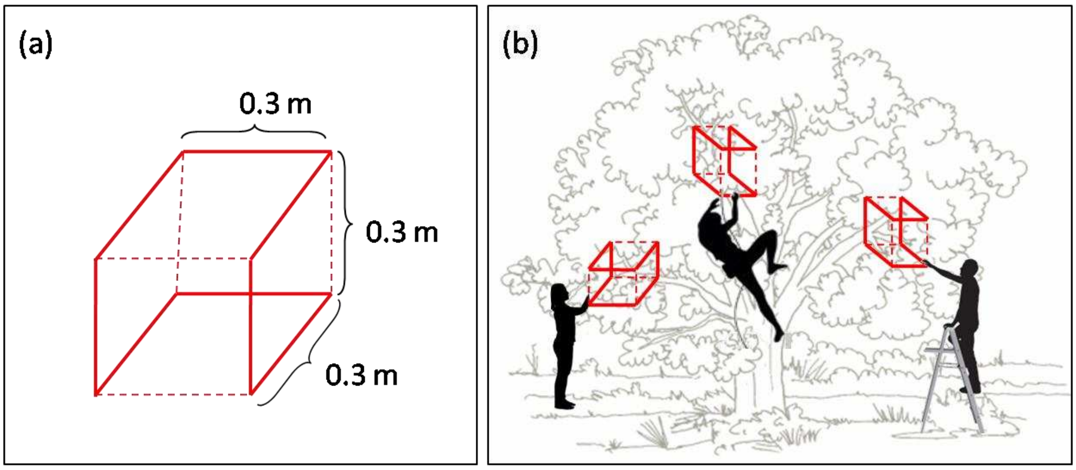
2015; Anzaldo 2017), as well as the assistance of taxonomists. Vouchers were deposited at the in the Laboratório de Ecohealth, Ecologia de Insetos de Dossel e Sucessão Natural of the Universidade Federal de Ouro Preto, Ouro Preto Towns, Minas Gerais State, Brazil. Permits for the field studies were issued by state authority Instituto Estadual de Florestas (IEF) and national authority Sistema de Autorização e Informação em Biodiversidade/ Instituto Chico Mendes de Conservação da Biodiversidade (SISBIO/ ICMBio).

We also sampled *A. chartifex* patrolling activity on *B. sericea* branches at time of collection to estimate the effect of this ant on species richness and abundance of herbivores, herbivory and fruit set. The patrolling activity was measured by counting individuals number of this ant that fell into entomological umbrella through beating of B. sericea branches.

We collected leaves to estimate herbivory level with guidance of a 0.027 m^3 wire-framed cube positioned at three distinct points in crowns (adapted from Shaw *et al.* (2006) and Ribeiro & Basset (2007)) (Fig. 3). This methodology aims to guarantee a real random leaf sampling. In order to better represent tree herbivory, we positioned the cube using a ladder and climbing devices and sampled in three different branches inside crowns. We collected all leaves that were inside cube, resulting in a final volume of 0.081 m^3 per tree. These leaves were scanned and processed using ImageJ software (Rasband 1997). Subsequently, we quantified herbivory level by measuring the percentage of foliar damage from sum of leaf area removed from each leaf in relation to total leaf area.

In order to examine the consistency of *A. chartifex* presence and lianas removal treatment, we repeated the samplings (both insects and leaves) in March 2017.

Figure 3: Scheme of wire-framed cube used for leaves selection. (a) Cube in volume of 0.027 m^3 and (b) model of arrangement of cubes inside crown.



3.2.5 *Byrsonima sericea* fitness estimate

We used fitness measurements to detect the total effect of mutualism on *B. sericea* individuals. We estimated flower-fruit conversion produced per tree produced in each growth unit. A growth unit is defined as terminal cluster of branches in which leaves are originated (Bell *et al.* 1999). To obtain flower-fruit conversion we counted inflorescences and infructescences in their respective reproductive seasons. We counted inflorescences in January/2017 and December/2017 and counted infructescences in February/2017 and February/2018. With aid of a binocular, two independent samplers (one climbing and one in the ground) simultaneously counted inflorescences or infructescences that were within eyes reach and all growth units presented in tree. Thus, we estimate total number of inflorescences or infructescences per tree by rule of three. Finally, flower-fruit conversion was assessed as ratio of infructescences number per number of initial inflorescences produced per tree, in each year of sampling.

3.2.6 Data analysis

We used Generalized Linear Mixed Model (GLMMs) (Bates *et al.* 2015) to test synergistic effect of *Azteca chartifex* and liana on herbivores abundance and species richness, herbivory level, and flower-fruit conversion level (defined as response variables). In these models, we fitted treatments presence/absence of *A. chartifex* and liana, and *A. chartifex* patrolling activity as fixed effects. We treated the year of sampling as random effect in order to control variance into intercepts (1| year). Appropriate families were selected based on data distribution. Significance of variables in appropriate minimum models was obtained by contrasting more complex models (association of explanatory variables plus interaction) with the simpler ones (only association of explanatory variables). Adequate minimum models were selected when there was no difference in explanatory power when comparing a more complex model with a simpler one ($p > 0.05$). When there were significant differences between model comparisons, more complex model was maintained (Crawley 2013). We compared minimum models to a null model and models adequacy were assessed by residual analysis (Zuur *et al.* 2009).

To evaluate the protection effectiveness of each ant species in *B. sericea*, we used the landscape analysis of effectiveness (Schupp *et al.* 2010, 2017; Rodríguez-Rodríguez *et al.* 2013). We combined two variables of protection into an index of ‘plant protection effectiveness’ (PPE). This index ultimately defines the position of each ant on overall PPE landscape characteristic of *B. sericea*. We estimated the plant protection effectiveness for each ant species using the formula:

$$PEE = QTC \times QLC$$

The quantitative component (QTC) was estimated by relative abundance of ant specie per tree. The qualitative component (QLC) was assessed by flower-fruit conversion level, as both represent the final outcome of ant-plant interaction. Each ant species was classified according to the values of PEE. For each ant species, we computed a measure of total protection service that integrates quality and quantity components of service offered. We considered highly-effective protectors those species that had high values of PPE (high quantitative and qualitative values); inefficient protectors those species that had low PPE values (low quantitative and qualitative values); and lowly-effective protectors those species that had intermediate PPE values (low quantitative values and high qualitative values or high quantitative values and low qualitative values).

All analyses were performed in software R (R Core Team 2018).

3.3 Results

In two years of sampling we recorded a total of 6,021 arthropods distributed in 82 morphospecies (39 species of predatory ants and 43 herbivorous insects) (Table 1). Confirming our expectations, liana presence on *Byrsonima sericea* increased *Azteca chartifex* patrolling activity and the efficiency of its foraging, resulting in lower herbivore species richness and abundance, as well as lower herbivory levels (Table 1). Liana presence did not affect herbivore richness, but *Azteca chartifex* presence discourages herbivores arrival and cause reduced herbivore species richness in 20% (*A. chartifex* present: mean ± SE 2.40 ± 1.54, *A. chartifex* absent: 3.01 ± 1.75) (Fig. 4). The association between *A. chartifex* and liana leaded contrasting results concerning insect abundance. While *A. chartifex* presence decrease herbivorous insect abundance in 33.4% (*A. chartifex* present: 5.14 ± 5.27, *A. chartifex* absent: 7.72 ± 8.62), liana presence increased herbivorous abundance in 19.3% (liana present: 8.53 ± 7.99, liana removed: 6.88 ± 7.88). Still, the effect of *A. chartifex* on herbivore abundance was so remarkable that prevented a significant interaction of terms (Fig. 5a). This association also caused lower herbivores abundance as *A. chartifex* patrolling activity increased in crowns with liana (Fig. 5b). The reason for this relies on *A. chartifex* obtaining a greater advantage in crowns with liana, which caused an increase in its patrolling activity of 36.7% (liana present: 31.41 ± 59.52, liana removed: 19.88 ± 32.48). With a decreasing in herbivore species richness and abundance, herbivory level also decreased as the patrolling activity of *A. chartifex* increased (Fig. 6).

Table 1. Summary of mixed effects model. Coefficient estimates and standard errors are shown for the fixed effects. Explanatory variables include (1) *Azteca chartifex* in the *Byrsonima sericea* (aztc): presence or absence; (2) liana removal experiment (exp): present or removed; and (3) patrolling activity of *Azteca chartifex* (patrol_aztc). Plotting models were, hence, y ~ exp + (1|year), y ~ aztc * exp + (1|year), and y ~ patrol_aztc * exp + (1|year). In order to plot such models, coefficients have been re-estimated keeping only the significant terms in the model. For each model, the deviance ($\chi 2$), the degrees of freedom (df), and p-Value are given.

Model	χ^2	**df**	***p*-Value**
y = *Azteca chartifex* patrolling activity (error = poisson)			
exp	91.488	1	< 2.2e-16 ***
y = herbivore species richness (error = poisson)			
aztc:exp	0.1893	1	0.663
aztc	4.6158	1	0.032 *
exp	3.1068	1	0.078
patrol_aztc:exp	0.0713	1	0.789
patrol_aztc	0.3998	1	0.527
exp	3.232	1	0.072
y = herbivore abundance (error = poisson)			
aztc:exp	0.6226	1	0.430
aztc	35.212	1	2.958e-09 ***
exp	5.0608	1	0.024 *
patrol_aztc:exp	2.8628	1	0.090
patrol_aztc	23.65	1	1.156e-06 ***
exp	6.4802	1	0.019 *
y = herbivory (error = binomial)			
aztc:exp	0.4122	1	0.521
aztc	1.5509	1	0.213
exp	0.1044	1	0.747
patrol_aztc:exp	0.635	1	0.425
patrol_aztc	6.768	1	0.009**
exp	0.0763	1	0.782
y = fruit set (error = binomial)			
aztc:exp	3.0432	1	0.081
aztc	5.6474	1	0.017 *
exp	0.2182	1	0.640
patrol_aztc:exp	1.3573	1	0.244
patrol_aztc	1.0175	1	0.313
exp	0.1656	1	0.684

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, $\alpha < 0.05$

Figure 4: Negative effect of *Azteca chartifex* presence on herbivores species richness in two sample years. Vertical lines represent the first and four quartiles, the box represents the second and third quartiles and the line within the box represents the median. Points outside the boxplot represent atypical data, and different letters above boxplot indicate significant differences (α < 0.05).

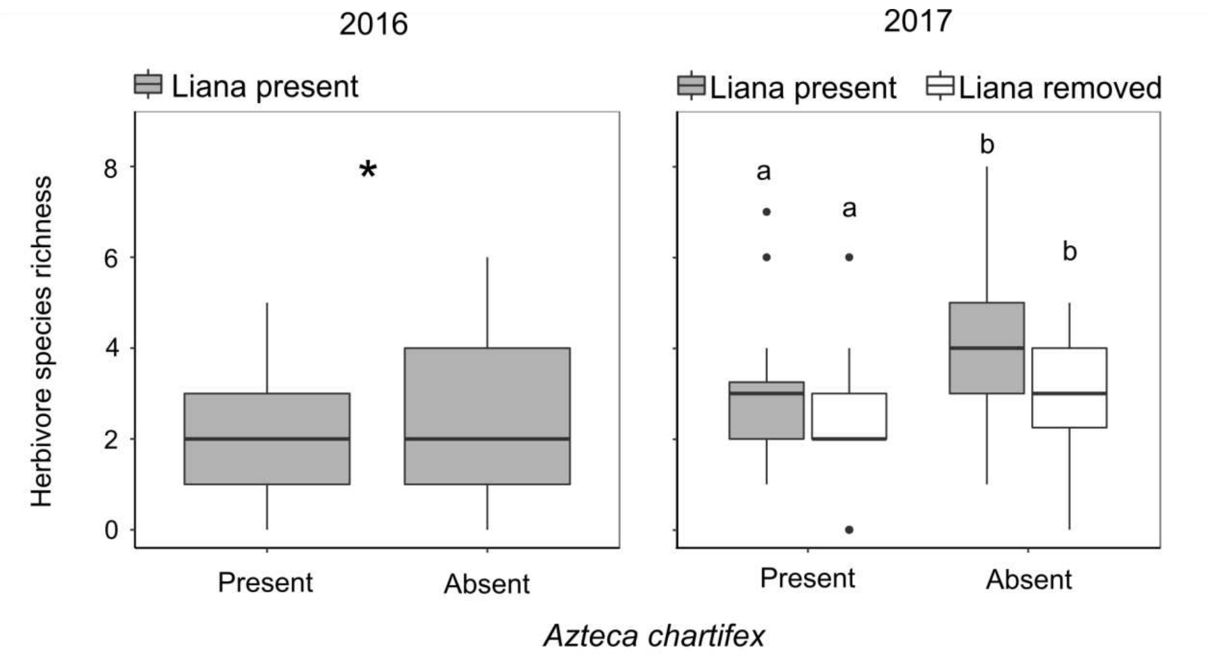


Figure 5: Treatments effect on herbivores abundance in two sample years. (a) *Azteca chartifex* presence reduced herbivores abundance by contrasting liana presence, with advantaged herbivores increase. Vertical lines represent the first and four quartiles, the box represents the second and third quartiles and the line within the box represents the median. The points outside of the boxplot represent atypical data, and different letters above boxplot indicate significant differences (α < 0.05). (b) Negative effect of *A. chartifex* becomes more evident as its patrolling activity increases, reducing herbivores abundance even when liana is present. The shaded area represents the 95% confidence interval.

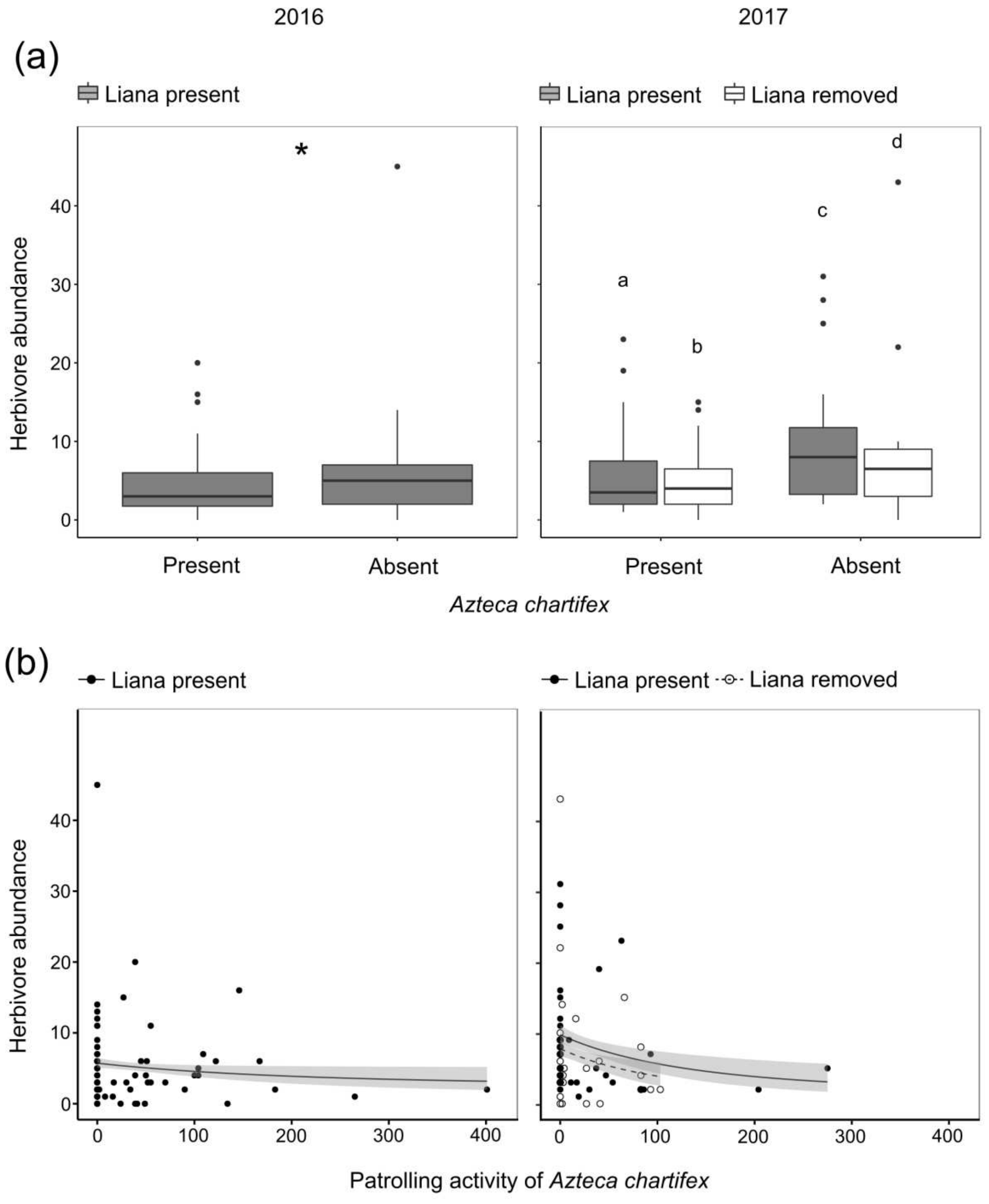
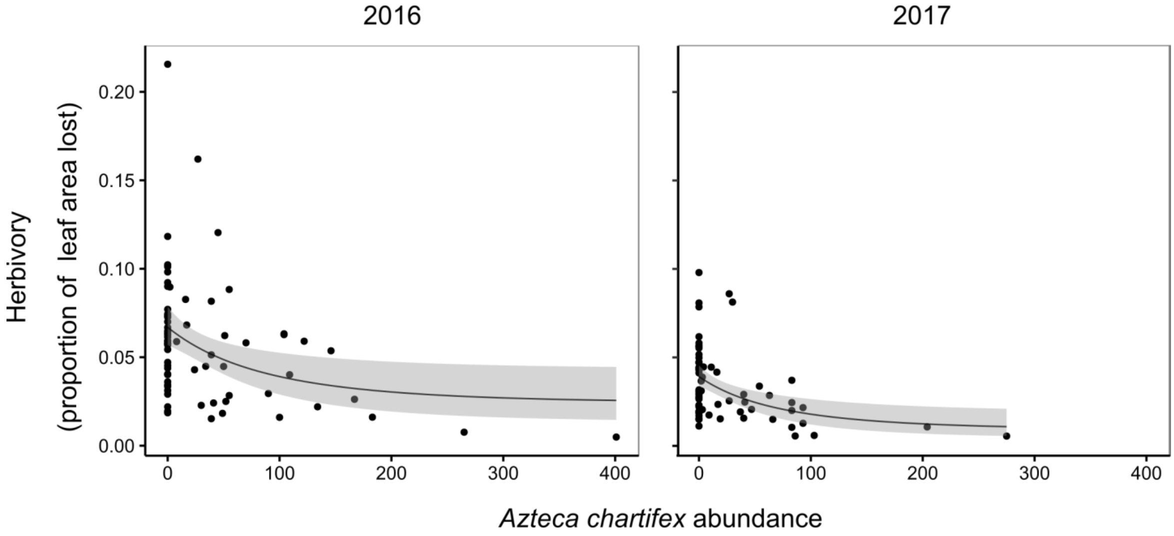


Figure 6: Negative effects of *Azteca chartifex* abundance on the herbivory level in the two years of sampling. The shaded area represents the 95% confidence interval.



Azteca chartifex gain advantage by liana presence by increasing its foraging area, reflecting lower species richness and abundance of herbivores and lower herbivory levels, also leading to higher flower-fruit conversion levels (Table 1). *Azteca chartifex* presence increased in 21% flower-fruit conversion level (*A. chartifex* present 0.85 ± 0.24, *A. chartifex* absent: 0.67 ± 0.33), corroborating our predictions (Fig. 7).

As expected, the protection effectiveness landscape showed that *A. chartifex* stand out among other ants, establishing greater value of 'plant protection effectiveness' index, as it contributes in both qualitative and quantitative components of *B. sericea* protection (Fig. 8). Most species of ants (93%) do not display an effective *B. sericea* protection and only *Dorymyrmex* sp.1 exhibited some level of protection efficiency (Fig. 8).

Figure 7: Positive effect of *Azteca chartifex* presence on flower-fruit conversion level in two sample years. Vertical lines represent the first and four quartiles, box represents second and third quartiles and line within box represents median. Points outside of boxplot represent atypical data, and different letters above boxplot indicate significant differences (α < 0.05).

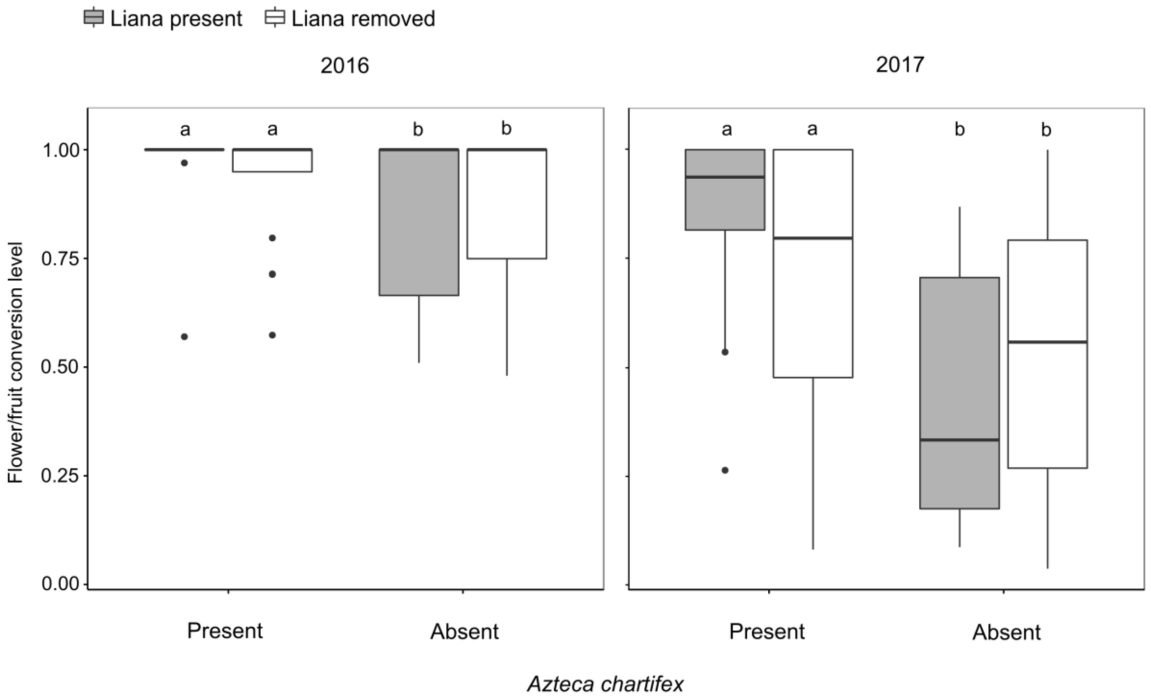
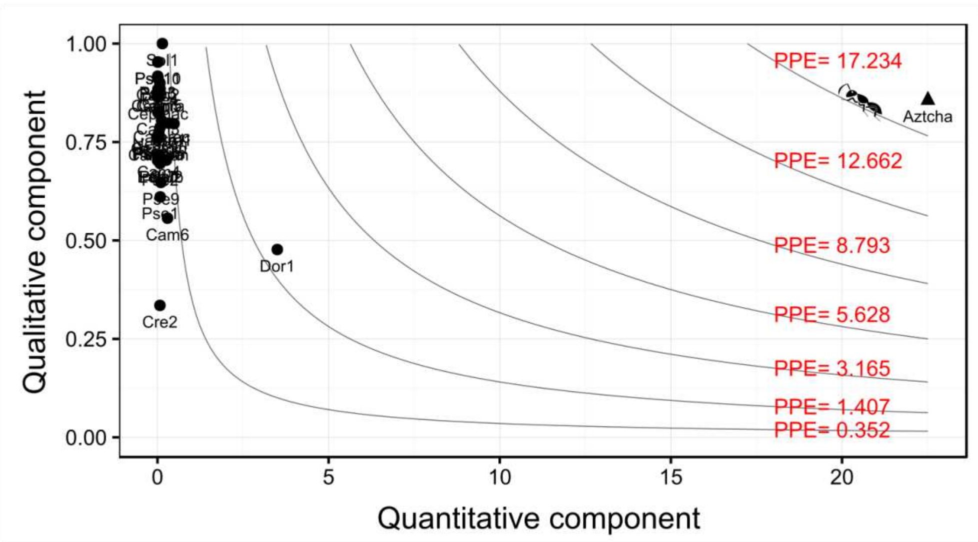


Figure 8: Plant protection effectiveness (PPE) landscape of all ant species recorded on *Byrsonima sericea*. *Azteca chartifex* was the species that most contributed to an effective protection, reaching highest proportional increase in fruit production due to its tending (PPE). Qualitative component is flower-fruit conversion level and quantitative component is ant relative abundance. Symbols represent positions of ant species on landscape. Circles and triangle represent low-effective and high-effective protector ant species, respectively. Isoclines represent all combinations of quantity and quality components with same value of PPE. Ant taxon codes can be found in Table S2 (Appendix B).



3.4 DISCUSSION

Our findings revealed *Azteca chartifex* as a central species driving distribution and diversity of invertebrate arboreal community, mediated by liana presence on canopy, and with positive consequences to *Byrsonima sericea* reproductive success. We have found that liana presence promoted both increase in patrolling activity of *A. chartifex* and herbivorous insects abundance. However, *A. chartifex* better exploited its territory and used these alternative paths to gain space, in detriment of herbivores. With reduction of herbivorous species richness and abundance, there was also a reduction in herbivory level and an increase in flower-fruit conversion level where *A. chartifex* foraged. Additionally, we have found that *A. chartifex* was the only ant species that effectively protected *B. sericea*, contributing qualitatively and quantitatively for plant-protection mutualism effectiveness.

Ants naturally display patrolling behavior, exploiting their habitat in search of food resource and at same time they protect their territory (Holldobler & Wilson 1990b) and lianas are good options to facilitate this behavior. We observed that lianas presence provided alternative paths for *A. chartifex* foraging or patrolling, extending its territory and increasing its local abundance. With an increasing number of ants patrolling trees, is likely that there is also a greater amount of volatile compounds being released into environment, causing negative effects on herbivores and herbivory. *Azteca chartifex* uses volatile compounds produced in pygidial gland as clues that act as alarm-defense pheromones (Holldobler & Wilson 1990a; Do Nascimento *et al.* 1998). In this mechanism, ants mark their territories through a trail of pheromones while foraging through branches and leaves, signaling to co-occurring species their presence in that territory (Offenberg *et al.* 2004; Gonthier 2012). The effect resulted from *A. chartifex* patrolling activity, associated with the release of volatile compounds, probably resulted in lesser herbivore species richness that were discouraged to forage in ants territories. In addition, *A. chartifex* hunts in groups and recruits workers via alarm pheromone when discovering a prey, eliminating it quickly in a short time (Holldobler & Wilson 1990b; Dejean *et al.* 2009).

Arthropods prefer more complex habitats (Jeffries & Lawton 1984; Dial *et al.* 2006), but our results suggest that herbivore preference was negatively affected by increase of *A. chartifex* patrolling activity, which reflected in lower herbivory levels. *Azteca chartifex* presence discourages herbivores foraging in sites where this ant occurs and probably growth rate of herbivores is also negatively affected by predator avoidance behavior. Reason for this is that threat of predation alone has same effect as lethal predation by reducing prey foraging rates in response to stress (Werner & Peacor 2003). This behavior determines an important nonlethal or nonconsumed effect caused by predator presence that characterizes predator-prey dynamics (Bolker *et al.* 2003; Werner & Peacor 2003; Peckarsky *et al.* 2008). In addition predators presence, plant selection by specialist herbivores is determined by other factors such as plant quality and resource availability (D. Coley *et al.* 2006; Carrasco *et al.* 2015). In fact, we observed that three from five plants with the highest herbivory levels in 2016 were same as in 2017 (outliers in Fig. 6). *Byrsonima sericea* individuals sampled in our study have high nutrient content, especially nitrogen concentration in leaves (Pinto et al., unpublished data), and this may have been one of clues used by herbivores to choose a host plant, in spite of *A. chartifex* presence. Nonetheless, it is necessary to explore more factors (e.g., olfactory and chemosensory signals used by herbivorous) to improve our understanding about the mechanisms responsible for host plant choice.

One of strategies used by plants that affects herbivores choice is attraction of predator ants, used as indirect defense and that generally promotes positive effects to plant (e.g., increase reproductive success) (Rico-Gray & Oliveira 2007; Rosumek *et al.* 2009; Trager *et al.* 2010; Romero & Koricheva 2011). Our findings are similar to these studies mentioned before, revealing that *A. chatifex* presence promoted improvement in *B. sericea* fruit set via trophic cascade. This effect is probably a result of reduction both herbivores and herbivory, since leaf damages are short term responses and directly reflected by herbivores density (Schmitz *et al.* 2000). When suffering lower leaf damage, *B. sericea* should have more resources to invest in reproduction since plants reduce investment in direct defenses when herbivorous pressure is reduced (Huntzinger *et al.* 2004).

Although generally ant-plant interactions are mediated by rewards offered by plants, such as nectars (Rico-Gray & Oliveira 2007), we did not detect any apparent food resource offered by *B. sericea* to reward *A. chatifex* patrolling. The protective response caused by *A. chatifex* presence might be derived by its own foraging behavior on the plant. As a predatory ant, *A. chatifex* recognizes herbivorous insect as food source and will predate them independent of any stimulus. Nevertheless, *B. sericea* is the most frequent species in the ecotone-lake forest, being widely distributed and crown-dominant, dropping its branches on the ground and spreading its crowns. The arrangement of *B. sericea* branches on soil can affect amount of solar radiation that reaches the surface of the nest, influencing nest site choice. Being a thermophilic organism, ants have no active characteristic to regulate nest temperature (e.g., as wings to vent or water evaporation), and nesting in inappropriate places would put the whole colony at risk (Holldobler & Wilson 1990b; Jones & Oldroyd 2007). A suitable condition for nests placement is an attribute considered by ants and *B. sericea* seems to meet these requirements. Thus, maintaining the host plant vigor, *A. chatifex* also guarantees breeding success of its own colony. In addition, mutualism associations can improve the performance of interacting species, increasing competitive dominance of the partners (Palmer *et al.* 2015).

Azteca chartifex had a greater value of plant protection effectiveness that others ants, generating a scenario of extremely low functional equivalence. This observed difference in our findings was mainly attributed to their high relative abundance, characteristic highly related to mutualism effectiveness (Fagundes *et al.* 2017). Usually, plant protection by ants is more effective if the ant is dominant, aggressive and display high recruitment rates upon resource (Del-Claro & Marquis 2015). Other attribute that result in greater effectiveness in protection mutualism is the ability to remove or discourage the arrival of herbivorous insects (Fagundes *et al.* 2017). Thus, in our study the most abundant ant species was also the most efficient and *A. chartifex* met all of those characteristics and proved to be main specie in protection mutualism, increasing the *B. sericea* reproductive success. In spite of workers small size, *A. chartifex* is effective in herbivores removal, being considered a keystone species that compose the core of interactions networks among several ant partners and *B. sericea*.

Our findings provide evidence that arboreal herbivorous populations regulation is in function of association between dominant and territorialist ant and habitat structure, culminating in a mutualistic relationship that benefits host plant. Ant-plant mutualism must be investigated in distinct ecological levels, as a multi-trophic approach might help to elucidate its role in structuring invertebrate community. Habitat aspects should also be considered in interaction studies, making it possible to understand the connectivity effect and architectural complexity on canopy arthropods diversity associated with territorialist and dominant ants. The constant *A. chartifex* patrolling, associated with liana presence, increased its patrolling activity and might have enhance its ability to quickly respond under foliar damage caused by herbivores. It is likely that this defense mechanism prevented further leaf damage and significant impacts on *B. sericea* fitness. Considering that ant-plant mutualism outcomes are context dependent (varies according to biotic and abiotic components), the best mutualistic partner may also vary. Thus, future studies should investigate whether the degree of ant protection is temporally and spatially consistent, allowing us to understand how ant protection varies over time and space.

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3.6 References

Adams, B.J., Schnitzer, S.A. & Yanoviak, S.P. (2017). Trees as islands: canopy ant species richness increases with the size of liana-free trees in a Neotropical forest. *Ecography (Cop.).*, 40, 1067–1075.

Adams, B.J., Schnitzer, S.A. & Yanoviak, S.P. (2019). Connectivity explains local ant community structure in a Neotropical forest canopy: a large-scale experimental approach. *Ecology*, 1–7.

Agrawal, A.A. & Rutter, M.T. (1998). Dynamic Anti-Herbivore Defense in Ant-Plants: The Role of Induced Responses. *Oikos*, 83, 227–236.

Alvares, C.A., Stape, J.L., Sentelhas, P.C., Gonçalves, J.L. de M. & Sparovek, G. (2013). Köppen's climate classification map for Brazil. *Meteorol. Zeitschrift*, 22, 711–728.

Anzaldo, S.S. (2017). Review of the genera of conoderinae (Coleoptera, Curculionidae) from north America, central America, and the Caribbean. *Zookeys*, 2017, 51–138.

Arnett, R.H., Thomas, M.C., Skelley, P.E. & Frank, J.H. (2002). *American beetles, Volume II: Polyphaga: Scarabaeoidea through Curculionoidea*. CRC Press, Boca Raton.

Baccaro, F.B., Feitosa, R.M., Fernandez, F., Fernandes, I.O., Izzo, T.J., Souza, J.L.P., *et al.* (2015). *Guia para os gêneros de formigas do Brasil. Ed. INPA*.

Barbosa, B. de C. (2014). Arquitetura de ramos, alocação de biomassa e herbivoria em duas espécies arbóreas com diferentes histórias de vida em uma Floresta Tropical Semidecidual. Universidade Federal de Minas Gerais.

Basset, Y., Cizek, L., Cuénoud, P., Didham, R.K., Guilhaumon, F., Missa, O., *et al.* (2012). Arthropod diversity in a tropical forest. *Science (80-.).*, 338, 1481–1484.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.*, 67.

Bell, A.D., Bell, A. & Dines, T.D. (1999). Branch construction and bud defence status at the canopy surface of a West African rainforest. *Biol. J. Linn. Soc.*, 66, 481–499.

Bluthgen, N. & Fiedler, K. (2002). Interactions between weaver ants Oecophylla smaragdina, homopterans, trees and lianas in an Australian rain forest canopy. *J. Anim. Ecol.*, 71, 793–801.

Bolker, B., Holyoak, M., Krivan, V., Rowe, L. & Schmitz, O. (2003). Connecting theoretical and empirical studies of trait-medated interactions. *Ecology*, 84, 1101–1114.

Bronstein, J.L. (2015). The study of mutualism. In: *Mutualism*. Oxford University Press, Oxford, UK, pp. 3–19.

Campos, R.I., Soares, J., Martins, R.P. & Ribeiro, S.P. (2006a). Effect of habitat structure on ant assemblages (Hymenoptera : Formicidae) associated to two pioneer tree species. *Sociobiology*, 47, 721–727.

Campos, R.I., Vasconcelos, H.L., Ribeiro, S.P., Neves, F.S. & Soares, J.P. (2006b). Relationship between tree size and insect assemblages associated with Anadenanthera macrocarpa. *Ecography (Cop.).*, 29, 442–450.

Carrasco, D., Larsson, M.C. & Anderson, P. (2015). Insect host plant selection in complex environments. *Curr. Opin. Insect Sci.*, 8, 1–7.

Clay, N.A., Bauer, M., Solis, M. & Yanoviak, S.P. (2010). Arboreal substrates influence foraging in tropical ants. *Ecol. Entomol.*, 35, 417–423.

Coelho, I.R. & Ribeiro, S.P. (2006). Environment heterogeneity and seasonal effects in ground-dwelling ant (Hymenoptera: Formicidae) assemblages in the Parque Estadual do Rio Doce, MG, Brazil. *Neotrop. Entomol.*, 35, 19–29.

Costa, F. V., Mello, M.A.R., Bronstein, J.L., Guerra, T.J., Muylaert, R.L., Leite, A.C., *et al.* (2016). Few ant species play a central role linking different plant resources in a network in rupestrian grasslands. *PLoS One*, 11, 1–17.

Crawley, M.J. (2013). *The R Book*. 2nd edn. Wiley, United Kingdom.

D. Coley, P., L. Bateman, M. & A. Kursar, T. (2006). The effects of plant quality on caterpillar growth and defense against natural enemies. *Oikos*, 115, 219–228.

Dejean, A., Corbara, B., Orivel, J. & Leponce, M. (2007). Rainforest Canopy Ants: The Implications of Territoriality and Predatory Behavior. *Funct. Ecosyst. Communities*, 1, 105–120.

Dejean, A., Grangier, J., Leroy, C. & Orivel, J. (2009). Predation and aggressiveness in host plant protection: A generalization using ants from the genus Azteca. *Naturwissenschaften*, 96, 57–63.

Del-Claro, K. & Marquis, R.J. (2015). Ant Species Identity has a Greater Effect than Fire on the Outcome of an Ant Protection System in Brazilian Cerrado. *Biotropica*, 47, 459–467.

Del-Claro, K., Rico-Gray, V., Torezan-Silingardi, H.M., Alves-Silva, E., Fagundes, R., Lange, D., *et al.* (2016). Loss and gains in ant–plant interactions mediated by extrafloral nectar: fidelity, cheats, and lies. *Insectes Soc.*, 63, 207–221.

Dial, R.J., Ellwood, M.D.F., Turner, E.C. & Foster, W.A. (2006). Arthropod Abundance , Canopy Structure , and Microclimate in a Bornean Lowland Tropical Rain Forest Author (s): Roman J . Dial , Martin D . F . Ellwood , Edward C . Turner and William A . Foster Published by : Association for Tropical Biology and Conser. *Biotropica*, 38, 643–652.

Estrada-Villegas, S. & Schnitzer, S.A. (2018). A comprehensive synthesis of liana removal experiments in tropical forests. *Biotropica*, 50, 729–739.

Fagundes, R., Dáttilo, W., Ribeiro, S.P., Rico-Gray, V., Jordano, P. & Del-Claro, K. (2017). Differences among ant species in plant protection are related to production of extrafloral nectar and degree of leaf herbivory. *Biol. J. Linn. Soc.*, 1–13.

Gonthier, D.J. (2012). Do herbivores eavesdrop on ant chemical communication to avoid predation? *PLoS One*, 7.

González-Teuber, M. & Heil, M. (2010). Pseudomyrmex ants and acacia host plants join efforts to protect their mutualism from microbial threats. *Plant Signal. Behav.*, 5, 890–892.

van der Heijden, G.M.F. & Phillips, O.L. (2009). Liana infestation impacts tree growth in a lowland tropical moist Forest. *Biogeosciences*, 6, 2217–2226.

Holldobler, B. & Wilson, E.O. (1990a). Communication. In: *The ants*. Harvard University Press, Cambridge, pp. 469–611.

Holldobler, B. & Wilson, E.O. (1990b). *The ants*. Harvard University Press, Cambridge.

Huntzinger, M., Karban, R., Young, T.P. & Palmer, T.M. (2004). Relaxation of induced indirect defenses of acacias following exclusion of mammalian herbivores. *Ecology*, 85, 609–614.

Ingwell, L.L., Joseph Wright, S., Becklund, K.K., Hubbell, S.P. & Schnitzer, S.A. (2010). The impact of lianas on 10 years of tree growth and mortality on Barro Colorado Island, Panama. *J. Ecol.*, 98, 879–887.

Jeffries, M.J. & Lawton, J.H. (1984). Enemy free space and the structure of ecological communities. *Biol. J. Linn. Soc.*, 23, 269–286.

Jones, J.C. & Oldroyd, B.P. (2007). Nest Thermoregulation in Social Insects. In: *Advances in Insect Physiology* (ed. Simpson, S.J.). Elsevier, pp. 153–191.

Lawton, J.H. (1983). Plant Architecture and the Diversity of Phytophagous Insects. *Annu. Rev. Entomol.*, 28, 23–39.

Longino, J.T. (2007). *A taxonomic review of the genus Azteca*. *Zookeys*.

Lourenço, G.M., Campos, R.B.F. & Ribeiro, S.P. (2015). Spatial distribution of insect guilds in a tropical montane rainforest: effects of canopy structure and numerically dominant ants. *Arthropod. Plant. Interact.*, 9, 163–174.

Lourenço, G.M., Soares, G.R., Santos, T.P., Dáttilo, W., Freitas, A.V.L. & Ribeiro, S.P. (2019). Equal but different: Natural ecotones are dissimilar to anthropic edges. *PLoS One*, 14, e0213008.

Do Nascimento, R.R., Billen, J., Sant'Ana, A.E.G., Morgan, E.D. & Harada, A.Y. (1998). Pygidial gland of Azteca NR. bicolor and Azteca charifex: Morphology and chemical identification of volatile components. *J. Chem. Ecol.*, 24, 1629–1637.

Ness, J.H., Morris, W.F. & Bronstein, J.L. (2006). Integrating Quality and Quantity of Mutualistic Service to Contrast Ant Species Protecting Ferocactus Wislizeni. *Ecology*, 87, 912–921.

Neves, F.S., Araújo, L.S., Espírito-Santo, M.M., Fagundes, M., Fernandes, G.W., Sanchez-Azofeifa, G.A., *et al.* (2010). Canopy herbivory and insect herbivore diversity in a dry forest-savanna transition in Brazil. *Biotropica*, 42, 112–118.

Odegaard, F. (2000). The relative importance of trees versus lianas as hosts for phytophagous beetles (Coleoptera) in tropical forests. *J. Biogeogr.*, 27, 283–296.

Odell, E.H., Stork, N.E. & Kitching, R.L. (2019). Lianas as a food resource for herbivorous insects: a comparison with trees. *Biol. Rev.*, brv.12508.

Offenberg, J., Nielsen, M.G., MacIntosh, D.J., Havanon, S. & Aksornkoae, S. (2004). Evidence that insect herbivores are deterred by ant pheromones. *Proc. R. Soc. B Biol. Sci.*, 271, 433–435.

Palmer, T.M., Pringle, E.G., Stier, A. & Holt, R.D. (2015). Mutualism in a community context. In: *Mutualism* (ed. Bronstein, J.L.). Oxford University Press, pp. 159–180.

Parthasarathy, N. (2015). *Biodiversity of Lianas*. Sustainable Development and Biodiversity. Springer International Publishing, Cham.

Peckarsky, B.L., Abrams, P.A., Bolnick, D.I., Dill, L.M., Grabowski, J.H., Luttbeg, B., *et al.* (2008). Revisiting the classics: Considering nonconsumptive effects in textbook examples of predator-prey Interactions. *Ecology*, 89, 2416–2425.

Putz, F.E. (1984). The Natural History of Lianas on Barro Colorado Island , Panama. *Ecoloy*, 65, 1713–1724.

Putz, F.E. & Mooney, H.A. (1992). *The Biology of Vines*. *Cambridge Univ. Press*. Cambridge University Press, Cambridge.

R Core Team, R. (2018). R: A Language and Environment for Statistical Computing.

Rasband, W. (1997). Image J.

Ribeiro, S.P. & Basset, Y. (2007). Gall-forming and free-feeding herbivory along vertical gradients in a lowland tropical rainforest: The importance of leaf sclerophylly. *Ecography (Cop.)*., 30, 663–672.

Ribeiro, S.P., Borges, P.A.V., Gaspar, C., Melo, C., Serrano, A.R.M., Amaral, J., *et al.* (2005). Canopy insect herbivores in the Azorean Laurisilva forests: Key host plant species in a highly generalist insect community. *Ecography (Cop.).*, 28, 315–330.

Ribeiro, S.P., Espirito Santo, N.B., Delabie, J.H.C. & Majer, J.D. (2013). Competition, resources and the ant (Hymenoptera: Formicidae) mosaic: A comparison of upper and lower canopy. *Myrmecological News*, 18, 113–120.

Ribeiro, S.P., Soares, J.P., Campos, R.I. de C. & Martins, R.P. (2008). Insect herbivores species associated to pioneer tree species: contrasting within forest and ecotone canopy habitats. *Zoociências*, 10, 237–248.

Rico-Gray, V. & Oliveira, P.S. (2007). *The Ecology and Evolution of Ant-Plant Interactions*. University of Chicago Press, Chigago.

Rodríguez-Rodríguez, M.C., Jordano, P. & Valido, A. (2013). Quantity and quality components of effectiveness in insular pollinator assemblages. *Oecologia*, 173, 179–190.

Romero, G.Q. & Koricheva, J. (2011). Contrasting cascade effects of carnivores on plant fitness: A meta-analysis. *J. Anim. Ecol.*, 80, 696–704.

Rosumek, F.B., Silveira, F.A.O., De S. Neves, F., Newton, N.P., Diniz, L., Oki, Y., *et al.* (2009). Ants on plants: a meta-analysis of the role of ants as plant biotic defenses. *Oecologia*, 160, 537–549.

Schmitz, O.J., Hambäck, P.A. & Beckerman, A.P. (2000). Trophic Cascades in Terrestrial Systems: A Review of the Effects of Carnivore Removals on Plants. *Am. Nat.*, 155, 141–153.

Schnitzer, S.A. (2018). Testing ecological theory with lianas. *New Phytol.*, 220, 366–380.

Schnitzer, S.A. & Carson, W.P. (2010). Lianas suppress tree regeneration and diversity in treefall gaps. *Ecol. Lett.*, 13, 849–857.

Schupp, E.W., Jordano, P. & Gómez, J.M. (2010). Seed dispersal effectiveness revisited: A conceptual review. *New Phytol.*, 188, 333–353.

Schupp, E.W., Jordano, P. & Gómez, J.M. (2017). A general framework for effectiveness concepts in mutualisms. *Ecol. Lett.*, 20, 577–590.

Shaw, D.C., Ernest, K.A., Rinker, H.B. & Lowman, M.D. (2006). Stand-level herbivory in an old-growth conifer forest canopy. *West. North Am. Nat.*, 66, 473–481.

Šipoš, J. & Kindlmann, P. (2013). Effect of the canopy complexity of trees on the rate of predation of insects. *J. Appl. Entomol.*, 137, 445–451.

Teixeira, L.A.G. & Machado, I.C. (2000). Sistema de polinização e reprodução de Byrsonima sericea DC (Malpighiaceae). *Acta Bot. Brasilica*, 14, 347–357.

Trager, M.D., Bhotika, S., Hostetler, J.A., Andrade, G. V., Rodriguez-Cabal, M.A., Mckeon, C.S., *et al.* (2010). Benefits for plants in ant-plant protective mutualisms: A meta-analysis. *PLoS One*, 5.

Werner, E.E. & Peacor, S.D. (2003). A Review of Trait-Mediated Indirect Interactions in Ecological Communities. *Ecology*, 84, 1083–1100.

Yanoviak, S.P. (2015). Effects of lianas on canopy arthropod community structure. In: *Ecology of lianas* (eds. Schnitzer, S.A., Bongers, F., Burnham, R.J. & Putz, F.E.). Wiley-Blackwell, Oxford, pp. 345–361.

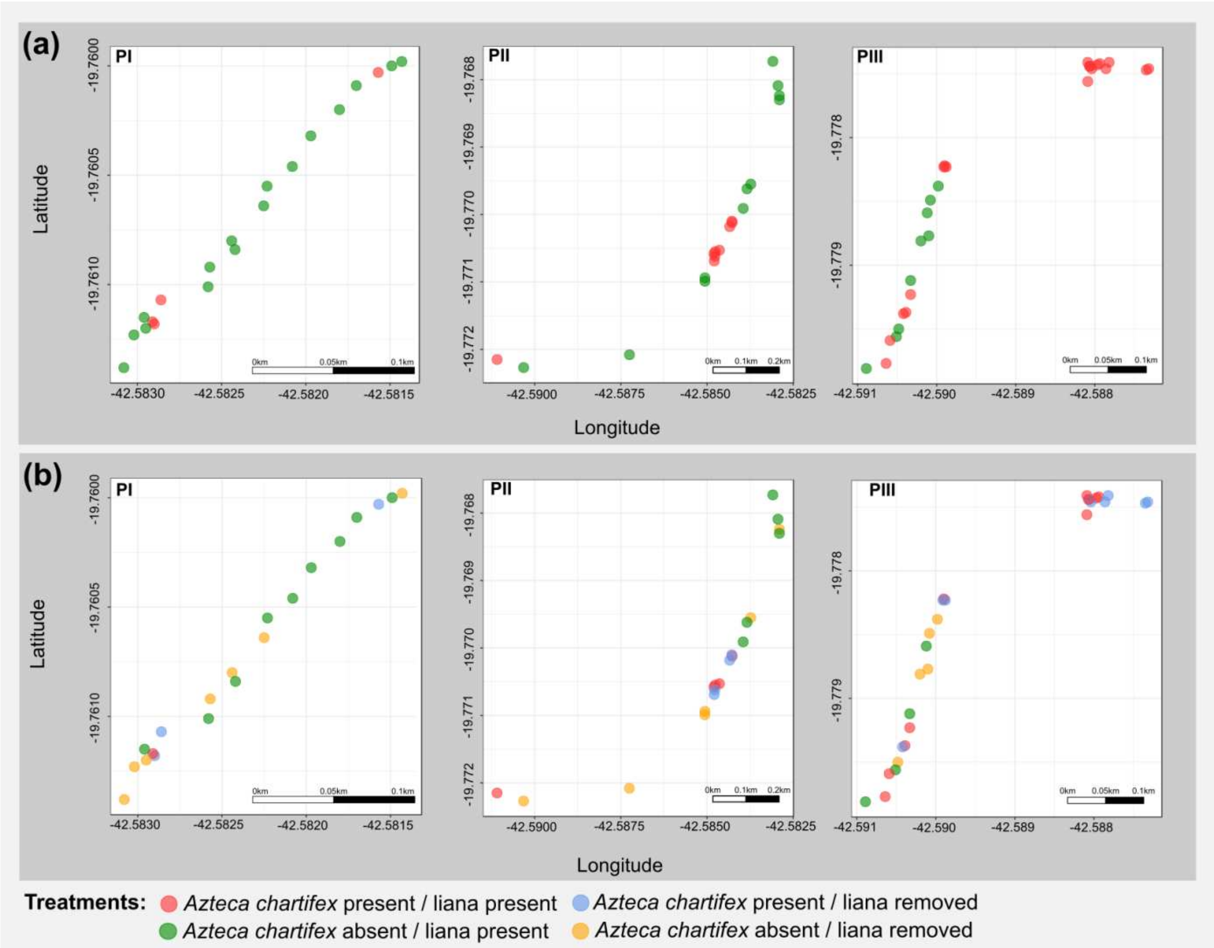
Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. (2009). *Mixed effects models and extensions in ecology with R*. Statistics for Biology and Health. Springer New York, New York, NY.

APPENDIX A – DETAILING ON EXPERIMENTAL DESIGN

In Phase I, we divided all marked trees into two treatments to detect the *A. chartifex* effect on forest community: i) *A. chartifex* present and liana present (n = 32) and ii) *A. chartifex* absent and liana present (n = 36). Each of three populations had the following treatments arrangement: population I (PI): *A. chartifex* present and liana present (n= 4) and *A. chartifex* absent and liana present (n = 16); population II (PII): *A. chartifex* present and liana present (n = 9) and *A. chartifex* absent and liana present (n = 11); population III (PIII): *A. chartifex* present and liana present (n = 19) and *A. chartifex* absent and liana present (n = 9) (Fig. 1a).

In Phase III, we redistributed the same trees in four treatments to detect the effect of the association between *A. chartifex* and liana in the community: i) *A. chartifex* present and liana present (n = 16); ii) *A. chartifex* absent and liana present (n = 18); iii) *A. chartifex* present and liana removed (n = 16); and iv) *A. chartifex* absent and liana removed (n = 18). Now, each of the three populations had the following treatments arrangement: PI: *A. chartifex* present and liana present (n = 1), *A. chartifex* absent and liana present (n = 9), *A. chartifex* present and liana removed (n = 3), and *A. chartifex* absent and liana removed (n = 7); PII: *A. chartifex* present and liana present (n = 5), *A. chartifex* absent and liana present (n = 5), *A. chartifex* present and liana removed (n = 4), and *A. chartifex* absent and liana removed (n = 6); PIII: *A. chartifex* present and liana present (n = 10), *A. chartifex* absent and liana present (n = 4), *A. chartifex* present and liana removed (n = 9), and *A. chartifex* absent and liana removed (n = 5) (Fig. 1b).

Figure 1: Sampling design performed in Phase I and Phase III sampling distributed among populations (PI, PII and PIII). (a) Phase I: arrangement of two experimental treatments: i) *Azteca chartifex* present and liana present (red circle) and ii) *A. chartifex* absent and liana present (green circle) and (b) Phase III: arrangement of four experimental treatments: i) *A. chartifex* present and liana present (red circle); ii) *A. chartifex* absent and liana present (green circle); iii) *A. chartifex* present and liana removed (blue circle) and iv) *A. chartifex* absent and liana removed (orange circle).



APPENDIX B – TABLES

Table S1: Arthropod taxa abundance recorded in *Byrsonima sericea* during the years 2016 and 2017. P = Predator; H = Herbivore

Taxon	Trophic position	Abundance
COLEOPTERA		
Morphospecies sp.2	H	15
Morphospecies sp.4	H	1
Morphospecies sp.5	H	2
Brentidae		
Apioninae		
Morphospecies sp.1	H	5
Morphospecies sp.2	H	5
Morphospecies sp.3	H	1
Chrysomelidae		
Morphospecies sp.1	H	1
Alticinae		
Strabala sp.1	H	402
Chlamisinae		
Morphospecies sp.1	H	2
Chlamisus sp.2	H	1
Chlamisus sp.3	H	67
Eumolpinae		
Colapsis sp.1	H	83
Galerucinae		
Morphospecies sp.1	H	14
Morphospecies sp.2	H	2
Morphospecies sp.3	H	1
Morphospecies sp.4	H	1
Morphospecies sp.5	H	1
Curculionidae		
Cossoninae		
Morphospecies sp.1	H	1
Conoderinae		
Cylindrocopturinus sp.1	H	83
Cryptorhynchinae		
Morphospecies sp.1	H	3
Morphospecies sp.2	H	1
Morphospecies sp.3	H	1
Morphospecies sp.4	H	2
Curculioninae		
Morphospecies sp.1	H	1
Entiminae		
Morphospecies sp.8	H	55
Morphospecies sp.9	H	4
Morphospecies sp.10	H	13

Taxon	Trophic position	Abundance
Naupactus sp.1	H	2
Molytinae		
Chalcodermus sp.1	H	3
Morphospecies sp.1	H	1
Morphospecies sp.2	H	1
Morphospecies sp.3	H	2
Elateridae		
Morphospecies sp.1	H	4
Morphospecies sp.2	H	1
Mordellidae		
Morphospecies sp.1	H	1
HYMENOPTERA		
Formicidae		
Dolichoderina*e*		
Azteca chartifex	P	4.412
Dorymyrmex sp.1	P	14
Formicinae		
Brachymyrmex sp.1	P	35
Camponotus sp.1	P	3
Camponotus sp.2	P	6
Camponotus sp.3	P	16
Camponotus sp.4	P	9
Camponotus sp.5	P	3
Camponotus sp.6	P	5
Camponotus rectangularis	P	39
Camponotus sanctaefidei	P	36
Mirmicinae		
Cephalotes sp.1	P	2
Cephalotes sp.2	P	1
Cephalotes atratus	P	4
Cephalotes grandinosus	P	3
Cephalotes maculatus	P	23
Cephalotes minutus	P	89
Crematogaster sp.1	P	97
*Crematogaste*r sp.2	P	1
Solenopsis sp.1	P	1
Solenopsis sp.2	P	69
Solenopsis saevissima	P	1
Wasmannia sp.1	P	6
Nesomyrmex echinatinodis	P	21
Ectatomminae		
Ectatomma tuberculatum	P	63
Pseudomyrmecinae		
Pseudomyrmex sp.1	P	2
Pseudomyrmex sp.2	P	68

Taxon	Trophic position	Abundance
Pseudomyrmex sp.3	P	3
Pseudomyrmex sp.4	P	1
Pseudomyrmex sp.5	P	1
Pseudomyrmex sp.6	P	3
Pseudomyrmex sp.7	P	3
Pseudomyrmex sp.8	P	1
Pseudomyrmex sp.9	P	2
Pseudomyrmex sp.10	P	1
Pseudomyrmex sp.11	P	1
Pseudomyrmex elongatus	P	29
Pseudomyrmex gracilis	P	18
Pseudomyrmex simplex	P	44
LEPIDOPTERA		
Morphospecies sp.1	P	82
Geometridae		
Morphospecies sp.1	P	1
ORTHOPTERA		
Morphospecies sp.1	P	8
Tettigoniidae		
Morphospecies sp.1	P	2
Conocephalinae		
Morphospecies sp.1	P	1
Pseudophyllinae		
Morphospecies sp.1		1
Gryllidae		
Morphospecies sp.1	P	6
Morphospecies sp.2	P	1

Table S2: Ant taxon codes used in mutualism efficiency analysis recorded on *Byrsonima sericea*.

Taxon	Code
HYMENOPTERA	
Formicidae	
Dolichoderinae	
Azteca chartifex	Aztcha
Dorymyrmex sp.1	Dor1
Formicinae	
Brachymyrmex sp.1	Bra1
Camponotus sp.1	Cam1
Camponotus sp.2	Cam2
Camponotus sp.3	Cam3
Camponotus sp.4	Cam4
Camponotus sp.5	Cam5
Camponotus sp.6	Cam6
Camponotus rectangularis	Camrec
Camponotus sanctaefidei	Camsan
Mirmicinae	
Cephalotes sp.1	Cep1
Cephalotes sp.2	Cep2
Cephalotes atratus	Cepatr
Cephalotes grandinosus	Cepgra
Cephalotes maculatus	Cepmac
Cephalotes minutus	Cepmin
Crematogaster sp.1	Cre1
Crematogaster sp.2	Cre2
Solenopsis sp.1	Sol1
Solenopsis sp.2	Sol2
Solenopsis saevissima	Solsae
Wasmannia sp.1	Was1
Nesomyrmex echinatinodis	Nesech
Ectatomminae	
Ectatomma tuberculatum	Ecttub
Pseudomyrmecinae	
Pseudomyrmex sp.1	Pse1
Pseudomyrmex sp.2	Pse2
Pseudomyrmex sp.3	Pse3
Pseudomyrmex sp.4	Pse4
Pseudomyrmex sp.5	Pse5
Pseudomyrmex sp.6	Pse6
Pseudomyrmex sp.7	Pse7
Pseudomyrmex sp.8	Pse8
Pseudomyrmex sp.9	Pse9
Pseudomyrmex sp.10	Pse10

Taxon	Code
Pseudomyrmex sp.11	Pse11
Pseudomyrmex elongatus	Pseelo
Pseudomyrmex gracilis	Psegra
Pseudomyrmex simplex	Psesim

CAPÍTULO 4 - CONCLUSÃO GERAL

No presente estudo investigamos como a associação entre *Azteca chartifex* e a complexidade do habitat afeta os padrões de co-existência dos artrópodes e o sucesso reprodutivo de *Byrsonima sericea* no dossel florestal. No primeiro capítulo avaliamos o efeito cascata da presença de *A. chartifex* na diversidade das guildas de artrópodes do dossel florestal de *B. sericea*. Nossos resultados revelaram que *A. chartifex* é uma espécie central na estruturação das guildas de artrópodes associadas a *B. sericea.* Esta formiga alterou a densidade populacional, a co-existência e as interações tanto dos outros predadores quanto dos herbívoros, resultando em um efeito cascata de menores danos foliares em *B. sericea*. O território ocupado por *A. chartifex* foi caracterizado por menores riqueza e abundância dos artrópodes associados. Isto configurou uma distribuição agregada destas espécies nos espaços livre deste inimigo natural, apesar de *A. chartifex* não ter alterado a estrutura das redes de interação. Assim, demonstramos a dinâmica de interação entre artrópode-planta, destacando a capacidade de uma espécie territorialista e dominante de modificar a comunidade e gerar efeitos ao longo da cadeia trófica.

Diante destes resultados, ficamos curiosos em saber se componentes dos habitats, como lianas, afetam o comportamento de *A. chartifex*. Assim, no segundo capítulo investigamos se a associação entre *A. chartifex* e a presença de liana influenciariam a efetividade do mutualismo entre esta formiga e *B. sericea*. Nossos resultados apontaram que a presença de liana é mais bem utilizada por *A. chartifex* do que pelos insetos herbívoros. A atividade de patrulhamento de *A. chartifex* aumentou em árvores com lianas, revelando a eficiência do forrageio desta formiga ao refletir no sucesso reprodutivo de *B. sericea*. Ao utilizar das lianas como caminhos alternativos para forragear, *A. chartifex* reduziu a densidade populacional dos herbívoros e aumentou a taxa de conversão de flores em frutos. Além disto, *A. chartifex* foi a única espécie que protegeu efetivamente *B. sericea*, promovendo evidências de estes efeitos são em função de uma relação de mutualismo. A associação entre uma formiga territorialista e dominante e lianas culminou em benéficos mútuos para *B. sericea* e *A. chartifex*, garantindo a dominância competitiva destas espécies.

De maneira geral, podemos concluir que as interações tróficas discutidas nestes dois capítulos são afetadas pela presença de formigas territorialistas e dominantes, bem como pela presença de lianas que favoreceram habitats estruturalmente mais complexos. As interações interespecíficas, como predação e mutualismo, geram custos para os envolvidos que podem ser compensados pelo aumento do sucesso reprodutivo, garantido a perpetuação das espécies no ambiente. Observamos que o efeito negativo que as lianas causam nas árvores pode ser compensado quando há a presença de formigas territorialistas como *A. chartifex*. *Azteca chartifex* utilizou das lianas para aumentar sua atividade de patrulhamento, afugentando os herbívoros, ocasionando a redução dos danos foliares e aumentando a produção de frutos. Ao garantir que *B. sericea* se mantenha vigorosa nos ecótonos florestais, *A. chartifex* também é beneficiada pelo sucesso reprodutivo de sua própria colônia. Assim, compreender como as interações multi-tróficas se desenvolvem, quais os custos e benefícios e a espécie central envolvida foram aspectos primordiais para nosso entendimento acerca da dinâmica de comunidades nos ecótonos florestais. Estes aspectos contribuem para direcionarmos esforços para aquelas espécies estruturalmente importantes, auxiliando futuras práticas de manejo ou conservação do ambiente.