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INTERAÇÕES PLANTA-MEMBRACÍDEO-FORMIGA EM REMANESCENTES DE MATA ATLÂNTICA EM SANTA CATARINA, BRASIL

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"Interações planta-membracídeo-formiga em remanescentes de Mata Atlântica em Santa Catarina, Brasil"

Por

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Tese julgada e aprovada em sua forma final pelos membros titulares da Banca Examinadora (16/PPGECO/2016) do Programa de Pós-Graduação em Ecologia - UFSC.

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Resumo

Nas comunidades naturais, interações antagonísticas (e.g. herbivoria e parasitismo) e mutualísticas (e.g. dispersão de sementes e polinização) são comuns e podem servir de base para que se entendam as relações entre as espécies no ecossistema. Organismos altamente numerosos como os insetos, que vivem em diferentes tipos de habitats, podem ocupar vários nichos na comunidade e consequentemente, estabelecer uma grande quantidade de interações com outras espécies. A estrutura dessas interações pode ser representada por redes ecológicas complexas entre as espécies. Devido à elevada biodiversidade existente na Mata Atlântica brasileira, o sistema planta-membracídeo-formiga representa um bom modelo para se estudar interações. Nesse sistema, os insetos fitófagos (membracídeos) se alimentam de seiva elaborada de plantas (antagonismo) e exsudam uma secreção adocicada (*honeydew*), estabelecendo associações com formigas, que podem protegê-los de inimigos naturais e parasitas (mutualismo). Assim, esta tese teve como objetivo principal conhecer a topologia das interações tritróficas entre plantas, membracídeos e formigas em Mata Atlântica no Sul do Brasil. Portanto, buscou-se investigar como os seguintes fatores: (1) poder de recrutamento das formigas, (2) comportamento social dos membracídeos, (3) fenologia das plantas e (4) grau de antropização existente nas áreas de estudo, podem alterar a arquitetura das interações planta-membracídeo-formiga nesse bioma. Três unidades de conservação de Mata Atlântica, com diferentes graus de perturbação antrópica, foram selecionadas para o estudo no Estado de Santa Catarina. As observações de campo e coleta de exemplares ocorreram durante o período quente dos anos de 2013 e 2014. Para descrever a topologia das interações estudadas, foram utilizadas as métricas estruturais de redes ecológicas de conectância, aninhamento, modularidade, especialização da comunidade e de espécies. Os resultados apontaram que os mutualismos entre formigas e membracídeos são interações assimétricas, nas quais as espécies de formigas que tem maior poder de recrutamento monopolizam o *honeydew* produzido pelos membracídeos. As formigas dos gêneros *Brachymyrmex*, *Camponotus*, *Crematogaster* e *Wasmannia* estabeleceram interações com o maior número de espécies de membracídeos. O comportamento social de formar agregados favoreceu que as espécies mais abundantes, como os membracídeos do gênero *Bolbonota*, interagissem com o maior número de espécies de formigas. Em todas as áreas de estudo, as redes formiga-membracídeo foram modulares, não aninhadas e apresentaram baixos valores de conectância (Capítulo 1: *Structure of mutualistic ant-treehopper interactions in the Brazilian Atlantic Forest*). A topologia das interações planta-membracídeo foi alterada pela fenologia, com maiores valores de especialização a nível de comunidade e espécies de membracídeos durante a fenofase reprodutiva. Durante a fenofase vegetativa, registrou-se uma maior riqueza de espécies de plantas e de membracídeos em comparação à fenofase reprodutiva. Em ambas as fenofases, as redes planta-membracídeo foram modulares e especializadas, com baixos valores de conectância e não aninhadas em todas as áreas estudadas. Os membracídeos utilizaram principalmente meristemas apicais e inflorescências como recurso, e Asteraceae foi a principal família botânica utilizada por esses insetos (Capítulo 2: *Phenological phases of the host plant shape plant-treehopper interaction networks*). Os resultados apontaram ainda que a perturbação antrópica presente nas áreas de estudo pode afetar a estrutura das redes de interações de maneiras distintas. Os antagonismos são mais susceptíveis à perda de habitat, porque são interações altamente especializadas e modulares, em comparação aos mutualismos facultativos, que podem ser considerados mais robustos devido à topologia das redes de interação ser menos especializada (Capítulo 3: *Structural response of plant-treehopper-ant interactions to anthropogenic changes in protected areas in the Brazilian Atlantic Forest*).

Palavras-chave: aninhamento, antagonismo, especialização, fenologia, herbivoria, interações ecológicas, mutualismo facultativo, redes formiga-membracídeo, redes planta-membracídeo.

Abstract

In natural communities, antagonistic (e.g. herbivory and parasitism) and mutualistic interactions (e.g. seed dispersal and pollination) are common and may serve as a basis to understand the relationships among species in the ecosystem. Highly numerous organisms such as insects, living in different types of habitat, can occupy several niches in the community and thus establish many interactions with other species. The structure of these interactions can be represented by complex ecological networks between species. Due to the high biodiversity in the Brazilian Atlantic Forest, the plant-treehopper-ant system is a good model to study interactions. In this system, the phytophagous insects (treehoppers) feed on plant sap (antagonism) and exude a sweet secretion (honeydew), establishing associations with ants, which can protect them from natural enemies and parasites (mutualism). Thus, this thesis aimed to know the topology of tritrophic interactions between plants, treehoppers and ants in the Atlantic Forest in southern Brazil. Therefore, we investigated how the following factors: (1) the recruitment power of ants, (2) the social behavior of treehoppers, (3) the phenology of plants and (4) the degree of human disturbance in the study areas, can change the architecture of plant-treehopper-ant interactions in this biome. Three Atlantic Forest protected areas, with different degrees of anthropogenic disturbance, were selected for the study in the state of Santa Catarina. Field observations and collecting specimens occurred during the warm period of the years 2013 and 2014. To describe the topology of the interactions studied, the structural metrics of ecological networks of connectance, nestedness, modularity, specialization of community and species were used. The results showed that the mutualism between ants and treehoppers are asymmetric interactions in which ant species that has greater recruitment power monopolize the honeydew produced by treehoppers. Ants of *Brachymyrmex*, *Camponotus*, *Crematogaster* and *Wasmannia* genera established interactions with the largest number of treehopper species. Social behavior of aggregation promoted that abundant species such as *Bolbonota* treehopper genus, interact with the largest number of species of ants. In all study areas, the ant-treehopper networks were modular, non-nested and had low connectance values (Chapter 1: *Structure of mutualistic ant-treehopper interactions in the Brazilian Atlantic Forest*). The phenology affects the topology of plant-treehopper interactions, contributing to the specialization of treehoppers during the reproductive phenophase. During vegetative phenophase, a higher species richness of plants and treehoppers were found compared to reproductive phenophase. In both phenophases, the plant-treehopper networks were modular and specialized, with low connectance values and not nested in all studied areas. Treehoppers used mainly apical meristems and inflorescences as a resource, and Asteraceae was the main botanical family used by these specialized insects (Chapter 2: *Phenological phases of the host plant shape plant-treehopper interaction networks*). The results also showed that the human disturbance present in the study areas may affect differently the structure of interaction networks. The antagonisms are more susceptible to habitat loss because they are highly specialized and modular interactions compared to facultative mutualism, which can be considered more robust due to the topology of interaction networks be less specialized (Chapter 3: *Structural response of plant-treehopper-ant interactions to anthropogenic changes in protected areas in the Brazilian Atlantic Forest*).

Keywords: ant-treehopper networks, antagonism, ecological interactions, facultative mutualism, herbivory, nestedness, phenology, plant-treehopper networks, specialization.

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Introdução geral

Plantas e insetos são os organismos mais numerosos nos ecossistemas, concentrando 80% de toda a biodiversidade de espécies conhecidas (CORNELISSEN & FERNANDES, 2003). Essa biodiversidade é composta principalmente por interações ecológicas entre as diferentes espécies (GUIMARÃES JR., 2009). Essas interações podem ser: (1) harmônicas (+ +), quando ambas as espécies envolvidas são beneficiadas pela associação, ou (2) desarmônicas (+ -), quando há prejuízo para alguma das espécies envolvidas.

As plantas podem funcionar como hospedeiras de diversas espécies de insetos, formando a base de uma unidade trófica nas comunidades terrestres (LEWINSOHN et al., 2012). As formigas arborícolas comumente forrageiam na superfície de plantas (BELCHIOR et al., 2016), sendo atraídas por estruturas como nectários extraflorais ou insetos herbívoros que produzem secreções, tendo como exemplos larvas de borboletas e hemípteros sugadores de seiva (DEL-CLARO & OLIVEIRA, 1999; OLIVEIRA et al., 2002; KAMINSKI et al., 2010; GADELHA et al., 2016). Essas formigas, que são atraídas por secreções de hemípteros, podem beneficiar as plantas ao atacar ou interromper a atividade de outros herbívoros (OLIVEIRA & DEL-CLARO, 2005; DEL-CLARO et al., 2016), estabelecendo assim interações indiretas vantajosas para as plantas (RICO-GRAY & OLIVEIRA, 2007). Além disso, a remoção de herbívoros que causam mais prejuízos às plantas resulta em menos danos, aumentando as taxas de crescimento e reprodução dessas hospedeiras (STYRSKY & EUBANKS, 2007). Outro benefício para as plantas é não haver necessidade de manter estruturas secretoras, que são gastos energéticos adicionais, uma vez que os hemípteros fornecem um recurso rico em carboidratos para as formigas (RICO-GRAY & OLIVEIRA, 2007), e essas interações persistem ao longo do tempo (DEL-CLARO et al., 2006).

Em contrapartida, a qualidade nutricional da planta pode alterar a composição das secreções produzidas pelos hemípteros, tornando esses herbívoros mais atrativos para as formigas (QUENTAL et al., 2005). Outro fator que pode determinar o estabelecimento de interações hemíptero-formiga é a quantidade de secreção produzida, assim, espécies que formam agregados concentram mais recurso e atraem mais formigas em comparação às espécies solitárias (STADLER & DIXON, 2008). Portanto, o sistema planta-hemíptero-formiga é um bom modelo para se estudar a biodiversidade de interações, uma vez que muitas espécies interagem sincronicamente, possibilitando combinar a história natural das espécies com estudos de comunidades (OLIVEIRA & DEL-CLARO, 2005; DEL-CLARO, 2008). Além disso, vários níveis tróficos podem ser observados nesse sistema, porque insetos herbívoros e inimigos naturais (e.g. aranhas predadoras e vespas parasitóides) interagem com plantas, hemípteros e formigas (MOREIRA & DEL-CLARO, 2005; RICO-GRAY & OLIVEIRA, 2007).

Antagonismos e mutualismos

Antagonismos são interações nas quais existem condições desfavoráveis para alguma das espécies envolvidas, caso da predação, parasitismo e herbivoria (ZANGERL & BAZZAZ, 1992, COLEY & BARONE, 1996; VÁZQUEZ et al., 2005; ALLESINA & PASCUAL, 2007; KROHLING et al., 2010). Essas interações afetam teias alimentares e a estrutura das espécies na comunidade e, geralmente, são associações mais estáveis em comparação aos mutualismos, sobretudo em ambientes tropicais (DOBSON et al., 2008; SCHOWALTER, 2011).

A herbivoria é definida como o consumo de partes da planta como folhas, caules, raízes, flores, frutos ou sementes por animais (STRAUSS & ZANGERL, 2002; SCHOWALTER, 2011). Essa interação pode ser considerada como: (1) parasitismo, quando o herbívoro ingere partes da planta, diminuindo seu *fitness*, ou (2) predação, quando o herbívoro ingere uma planta inteira, causando sua morte (CORNELISSEN & FERNANDES, 2003).

De acordo com a preferência alimentar, os insetos podem ser classificados em monófagos, oligófagos ou polífagos, considerando esses herbívoros como especialistas quando utilizam poucas plantas (caso dos monófagos e oligófagos) ou generalistas quando utilizam muitas plantas (caso dos polífagos) como recurso (SCHOONHOVEN et al., 2005). Menos de 10% das espécies de herbívoros se alimentam de plantas em mais de três famílias diferentes, portanto especialização de planta hospedeira é comumente observada (WARD et al., 2002; SCHOONHOVEN et al., 2005).

A herbivoria afeta o crescimento e sobrevivência das plantas, principalmente devido à forte pressão que os herbívoros causam em determinadas partes, como meristemas apicais e folhas jovens, que sofrem de cinco a 25 vezes mais danos quando comparados às folhas maduras (COLEY & BARONE, 1996). Devido à forte pressão exercida pelos insetos herbívoros, as plantas desenvolveram diferentes mecanismos de defesa química, biológica, mecânica e fenológica ao longo do tempo evolutivo (COLEY & BARONE, 1996; THOMPSON, 2013).

Os mutualismos são definidos como cooperação entre as espécies (BRONSTEIN, 2001; BRONSTEIN et al., 2006), nos quais interações como polinização, frugivoria e dispersão de sementes podem ser citadas como exemplos (GHAZOUL, 2005; PIGOZZO & VIANA, 2010; MELLO et al., 2013). Interações mutualísticas variam no grau de intimidade (ou força), podendo ser simbióticas ou facultativas (GUIMARÃES JR. et al., 2007). Como exemplo, interações entre formigas e plantas do gênero *Cecropia*, que possuem estruturas vegetais denominadas domácias, são simbióticas e altamente especializadas (OLIVEIRA et al., 2015). Por outro lado, mutualismos facultativos entre formigas e plantas, apresentam uma força de interação mais fraca (GUIMARÃES JR. et al., 2007).

Formigas (Hymenoptera: Formicidae) são organismos extremamente abundantes, especialmente em florestas tropicais (FITTKAU & KLINGE, 1973; FLOREN et al., 2002). A maioria das espécies desse grupo, utilizam plantas como substrato de forrageamento para a busca de alimento e de locais para nidificação (RICO-GRAY & OLIVEIRA, 2007). Plantas que possuem nectários extraflorais comumente estabelecem interações com formigas (DEL-CLARO, 2008; DEL-CLARO et al., 2016), principalmente das subfamílias Formicinae e Myrmicinae, que podem predar insetos herbívoros, diminuindo as taxas de herbivoria em ambientes tropicais (OLIVEIRA & PIE, 1998). Além das interações com plantas com nectários extraflorais, as formigas podem estabelecer mutualismos facultativos com insetos produtores de secreções adocicadas (OLIVEIRA & PIE, 1998), dentre eles os membracídeos (DEL-CLARO & OLIVEIRA, 1999; BLÜTHGEN et al., 2006a; DEL-CLARO, 2008). Nessa associação, as formigas são recompensadas com exsudato (*honeydew*), uma substância rica em nitrogênio, fósforo, potássio, aminoácidos e carboidratos (KAY et al., 2004, MORALEZ & BEAL, 2006; KATAYAMA et al., 2013) e em troca podem proteger os membracídeos contra predadores, aumentando as taxas de sobrevivência e fecundidade desses sugadores, dependendo do grau de agressividade da formiga (DEL-CLARO & OLIVEIRA, 1999; MOREIRA & DEL-CLARO, 2005; GUIMARÃES JR. et al., 2007).

Os membracídeos (Hemiptera: Membracidae) (Figura 1) preferencialmente sugam seiva elaborada de meristemas apicais, inflorescências e veias foliares, sendo observados nas partes mais jovens das plantas (LOPES, 1995). Esses fitófagos podem ser classificados de acordo com seu comportamento social em três categorias: (1) solitários, (2) agregados de ninfas e/ou adultos e (3) comportamento subsocial, com vários graus de cuidado parental, no qual duas ou mais fêmeas podem se reunir para proteger as posturas e as ninfas (WOOD, 1993; LIN, 2006). Em alguns casos, as fêmeas transferem o cuidado parental das ninfas para as formigas, com a finalidade de aumentar a quantidade de posturas e o seu potencial reprodutivo (ZINK, 2003; STADLER & DIXON, 2008). Esses insetos depositam ovos na superfície de plantas e as ninfas se desenvolvem até a fase adulta sobre suas hospedeiras (LIN, 2006). Os membracídeos apresentam um ciclo de vida curto e várias gerações, inclusive de espécies diferentes, podem compartilhar o recurso espacial e alimentar provido pelas plantas (WOOD, 1993).

Figura 1. Interações entre o membracídeo subsocial *Calloconophora* sp., formigas atendentes *Camponotus fastigatus* Roger, 1863 e a planta hospedeira *Piper aduncum* L. (Piperaceae) em Mata Atlântica, Santa Catarina, Brasil, em 2013 e 2014. Em destaque adulto e ninfas em mutualismo com formigas (a), adultos em cópula (b) e fêmea sobre a postura (c). Fotos de Yve E. A. Gadelha.

Estratégias de defesa das plantas contra herbivoria

As folhas jovens sofrem elevadas taxas de herbivoria, porque essas estruturas têm baixa dureza e concentram altas taxas de nitrogênio durante o seu desenvolvimento (COLEY & BARONE, 1996; KURSAR

& COLEY, 2003). As plantas podem adotar diferentes estratégias para escapar da herbivoria, utilizando mecanismos diretos ou indiretos. Diretamente, as estruturas morfológicas como tricomas e espinhos, ou o endurecimento das folhas podem formar uma primeira barreira física contra o ataque de insetos herbívoros (KURSAR & COLEY, 2003; HANLEY et al., 2007; WAR et al., 2012). Como defesa química, as plantas podem produzir metabólitos secundários (e.g. alcalóides, flavonóides ou compostos fenólicos) que afetam o crescimento e desenvolvimento dos insetos herbívoros (WAR et al., 2012).

Para escapar da herbivoria, as plantas podem ainda produzir folhas durante a época seca, na qual há menor abundância de insetos herbívoros em comparação ao período chuvoso (AIDE, 1993). Outra defesa de escape temporal é ter um rápido crescimento foliar, com produção de folhas menos nutritivas (e.g. com menores concentrações de nitrogênio) para saciar os herbívoros especialistas e diminuir a quantidade de nutrientes gastos pela planta durante a fase de brotação (KURSAR & COLEY, 2003). Além disso, os tecidos reprodutivos das plantas acumulam grandes quantidades de toxinas defensivas que repelem os herbívoros durante o período de reprodução (HOWE & JANDER, 2008) e, portanto, a fenofase (e.g. fase reprodutiva ou vegetativa da planta) pode ser outra estratégia de escape temporal.

De forma indireta, as plantas podem estabelecer mutualismos com formigas atendentes de hemípteros que excretam *honeydew*, principalmente afídeos e membracídeos, evitando a herbivoria (WAY, 1963; ZHANG et al., 2012; ZHANG et al., 2013). Estudos apontam que plantas sem formigas sofrem o dobro de danos e têm 50% mais herbívoros do que plantas com formigas (ROSUMEK et al., 2009). Especificamente, os mutualismos hemíptero-formiga diminuem significativamente a herbivoria e a abundância de outros insetos nas plantas (ZHANG et al., 2012). Além disso, essas interações tendem a ser mais fortes em regiões subtropicais e tropicais do que em ambientes temperados (ROSUMEK et al., 2009; ZHANG et al., 2012). Portanto, de uma forma geral, as estratégias diretas ou indiretas conferem imunidade às plantas ao ataque de insetos herbívoros (HOWE & JANDER, 2008).

O uso de redes complexas em estudos ecológicos

Em comunidades naturais, diferentes espécies interagem entre si gerando redes complexas (JORDANO, 1987). Essas redes ecológicas são compostas basicamente de vértices (ou pontos) que se unem entre si através de arestas (ou *links*). Em Ecologia, os vértices podem representar indivíduos, espécies, grupos funcionais ou guildas, e as arestas são equivalentes às diferentes formas de interações (e.g. planta-polinizador, planta-herbívoro, parasita-hospedeiro, presa-predador). Essas associações podem ser representadas em matrizes de interação, onde os *links* podem ser mensurados na forma binária (matrizes de presença/ausência) ou quantitativa (matrizes ponderadas), onde insere-se algum peso como o número de vezes que determinada interação foi observada (BASCOMPTE et al., 2003; JORDANO et al., 2003, 2009; GUIMARÃES JR., 2009; HAGEN et al., 2012; CORSO et al., 2015).

Em estudos de redes ecológicas, comumente são utilizados índices para descrever a estrutura das comunidades, como conectância (JORDANO, 1987), aninhamento (BASCOMPTE et al., 2003), modularidade (GUIMERÀ & AMARAL, 2005) e índices de especialização da comunidade H_2’e das espécies d’ (BLÜTHGEN et al., 2006b; 2007). Esses índices variam de acordo com o tipo de interação e grau de intimidade entre as espécies e, portanto, antagonismos e mutualismos apresentam padrões estruturais bem definidos (PIRES & GUIMARÃES JR., 2013).

Numa matriz de interação, a conectância é definida como a proporção de interações observadas em meio ao total de interações possíveis (JORDANO, 1987). O aninhamento é uma propriedade que nos diz o quanto as interações de um determinado conjunto de vértices são um subconjunto de interações do próximo conjunto de vértices mais conectado (BASCOMPTE et al., 2003). Se numa rede ecológica hipotética, os vértices são equivalentes às espécies de uma comunidade, o aninhamento perfeito ocorreria se todas as espécies com menos interações fossem um subconjunto das outras espécies que teriam o maior número de conexões (BASCOMPTE et al., 2003). Módulos, por sua vez, são grupos de vértices altamente conectados e que são frouxamente ligados a outros grupos de vértices numa rede ecológica (OLESEN et al., 2007). Espécies mais firmemente conectadas entre si podem formar módulos, compartilhando recursos entre si (GUIMARÃES JR. et al., 2007; TINKER et al., 2012). Em redes ecológicas, modularidade (ou compartimentalização) é a medida de quanto uma rede ecológica é organizada em módulos claramente delimitados (OLESEN et al., 2007).

Em termos estruturais, as redes mutualísticas são altamente aninhadas, com baixa conectância e modularidade (VÁZQUEZ et al., 2009). Além disso, essas interações são assimétricas, ou seja, certas espécies têm um maior grau de dependência em relação às outras

(BASCOMPTE et al., 2006; BASCOMPTE & JORDANO, 2007; BASTOLLA et al., 2009). Por outro lado, em redes antagonísticas observa-se alta modularidade (especialmente em interações parasita-hospedeiro que são simbióticas), com baixos valores de aninhamento e conectância, e também um elevado grau de especialização na comunidade (ROBINSON et al., 2015). Essa alta intimidade na interação leva à compartimentalização tanto em redes antagonísticas como mutualísticas (VAN VEEN et al., 2008; FONTAINE et al., 2011; ROBINSON et al., 2015). Entretanto, redes antagonísticas tendem a ser mais modulares do que as mutualísticas (PIRES & GUIMARÃES JR., 2013), apresentando mecanismos de rápida adaptação às perturbações externas e podendo conter esses efeitos em seus módulos (STOUFFER & BASCOMPTE, 2011; CLUNE et al., 2013; NUWAGABA et al., 2015).

Nas redes ecológicas, baixas conectividades geram redes altamente aninhadas e modulares e o inverso ocorre em altas conectividades (FORTUNA et al., 2010). A conectividade das espécies (ou simplesmente, o grau *k*) é uma propriedade da rede que está diretamente relacionada com alterações ambientais ou antrópicas. Se houver extinção de uma espécie altamente conectada (com maior número de interações), provavelmente haverá um maior impacto dentro da comunidade, pois os seus efeitos diretos e indiretos vão afetar as espécies a um ou dois *links* de distância e, consequentemente, a maioria das espécies na rede (DUNNE et al., 2002).

Portanto, estudos de redes de interação podem contribuir para a manutenção da biodiversidade e importantes serviços ecossistêmicos, e também podem ser utilizados como base para políticas de conservação e manejo de espécies. A gestão de ecossistemas baseada em estudos de redes ecológicas pode auxiliar de forma substancial a conservação e proteção de espécies, sobretudo em teias alimentares, que são a base da estrutura de uma comunidade (MCDONALD-MADDEN et al., 2015).

Mata Atlântica brasileira

A Mata Atlântica brasileira é um *hotspot* de biodiversidade mundial, mesmo tendo perdido 93% de sua cobertura florestal original (MYERS et al., 2000). Esse bioma tem altos níveis de endemismo, no entanto a elevada ocupação populacional humana, atividades econômicas e distúrbios antrópicos ameaçam essa biodiversidade (LAGOS & MULLER, 2007). A histórica supressão da cobertura vegetal da Mata Atlântica (iniciada depois do descobrimento do Brasil em 1500) contribuiu para a perda de habitat e aumento da fragmentação, restando apenas remanescentes nesse bioma (MMA, 2010).

Para garantir a proteção da biodiversidade ainda existente nos remanescentes, são necessárias políticas de conservação que visem a uso sustentável dos recursos da Mata Atlântica (PINTO et al., 2005). Dessa forma, a criação de unidades de proteção integral (como parques e reservas) foi fundamental para assegurar a proteção desses remanescentes (TABARELLI et al., 2005). A Lei federal nº 9.985/2000 possibilitou que mais de 800 reservas particulares fossem criadas em todo o Brasil, sendo que a maioria está localizada na Mata Atlântica (MMA, 2010). Assim, esse bioma tem o maior número de unidades de conservação da América do Sul (GALINDO-LEAL & CÂMARA, 2003).

Santa Catarina é o terceiro Estado brasileiro com maior área de remanescentes da Mata Atlântica, no qual a maior extensão de seu território é coberta por fragmentos de Floresta Ombrófila Densa (MEDEIROS, 2006). A área do Estado conta com 9.571.782 ha de vegetação e 23,2% de remanescentes florestais totais do bioma (FUNDAÇÃO SOS MATA ATLÂNTICA & INPE, 2014). Essa cobertura vegetal está subdividida em três fitofisionomias, de acordo com o mapa fitogeográfico do Estado: (1) Floresta Pluvial da Encosta Atlântica, (2) Floresta de Araucária e (3) Floresta Subtropical da bacia do Rio Uruguai (MEDEIROS, 2006). No entanto, segundo o último monitoramento realizado em remanescentes de Mata Atlântica para o período de 2012 a 2013, houve um aumento de 9% na taxa de supressão de vegetação, que foi liderada pelos Estados de Alagoas, Bahia e Ceará (FUNDAÇÃO SOS MATA ATLÂNTICA & INPE 2014).

Uma breve descrição das três unidades de conservação de Mata Atlântica em Santa Catarina que foram selecionadas para o estudo (Figura 2) será apresentada a seguir, sendo dois parques (Parque Estadual da Serra do Tabuleiro, em Santo Amaro da Imperatriz e Parque Nacional da Serra do Itajaí, em Blumenau) e uma reserva (Reserva Particular do Patrimônio Natural Chácara Edith, em Brusque).

Áreas de estudo

Parque Estadual da Serra do Tabuleiro (PAEST)

É a maior e mais antiga unidade de conservação de Santa Catarina, ocupando aproximadamente 1% do território do Estado, com uma extensão de 87.405 ha (VITALI & UHLIG, 2010;

BRÜGGEMANN, 2012; FATMA, 2016). Abrange áreas dos municípios de Florianópolis, Palhoça, Santo Amaro da Imperatriz, Águas Mornas, São Bonifácio, São Martinho, Imaruí e Paulo Lopes (Figura 2b). Fazem parte do Parque as ilhas do Siriú, dos Cardos, do Largo, do Andrade e do Coral, e os arquipélagos das Três Irmãs e Moleques do Sul. Esse parque possui uma elevada diversidade de habitats, porque é localizado em uma região estratégica e tem cinco das grandes formações vegetais do bioma Mata Atlântica (FATMA, 2016). Segundo classificação de Köppen, o clima da área de estudo é do tipo Cfa, mesotérmico úmido com verão quente, com precipitação média anual em torno de 1.200 mm e temperatura média anual 20,5°C (CECCA, 1997).

Parque Nacional da Serra do Itajaí (PNSI)

O parque compreende uma área de 57.374 há e abrange nove municípios, sendo eles: Blumenau, Indaial, Botuverá, Gaspar, Vidal Ramos, Apiúna, Guabiruba, Ascurra e Presidente Nereu. Ocorre sobre relevo extremamente ondulado, coberto por exuberante floresta atlântica (Figura 2c) principalmente primária e florestas secundárias, pastagens e alguns reflorestamentos. Representa 0,6% da área total do Estado de Santa Catarina e 2,5% da área remanescente de Mata Atlântica. Esse parque encontra-se totalmente inserido na região da Bacia Hidrográfica Itajaí. O clima da região é o mesotérmico úmido (Cfa subtropical úmido), com chuvas distribuídas uniformemente durante todos os meses do ano (MMA; ICMBio, 2009).

Reserva Particular do Patrimônio Natural Chácara Edith (RPPN Chácara Edith)

A reserva localiza-se no município de Brusque (Figura 2b), dentro da Bacia Hidrográfica Itajaí. Possui uma área de 280,66 km^2. Na região da reserva, podemos considerar o clima como Cfa, mesotérmico úmido com verão quente definido. A temperatura média anual é de 20°C, sendo a média de temperatura do mês mais quente 25°C e a temperatura do mês mais frio 16°C. A temperatura média é de 20°C, com máxima de 40°C e mínima de 5,3°C. A precipitação anual na região é de 1.390 mm, bem distribuída durante o ano (MMA & ICMBio, 2011).

Diante do exposto, esta tese buscou contribuir com a compreensão das interações entre plantas hospedeiras, membracídeos e formigas atendentes em Mata Atlântica no Estado de Santa Catarina, Brasil. A estrutura das interações mutualísticas formiga-membracídeo será apresentada no **primeiro capítulo**, onde serão avaliados o poder de recrutamento de operárias e o comportamento social dos membracídeos. A estrutura das interações antagonísticas planta-membracídeo será descrita no **segundo capítulo**, que verifica como a fenologia altera a topologia da herbivoria. Por fim, no **terceiro capítulo**, avalia-se como o grau de antropização existente nas unidades de conservação pode modificar a arquitetura das interações tritróficas entre os três componentes estudados.

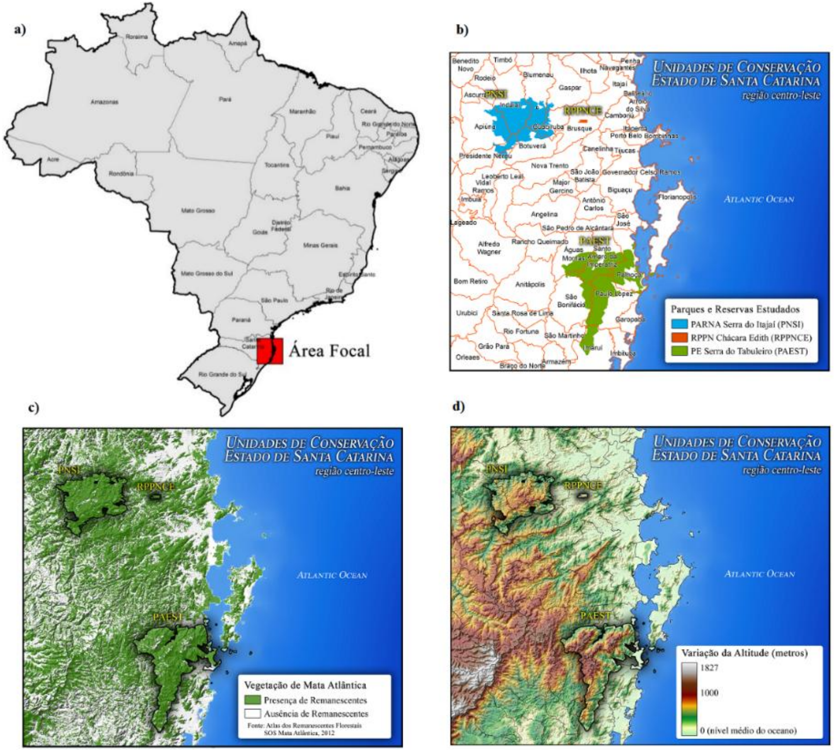

Figura 2. Áreas de estudo de Mata Atlântica selecionadas em Santa Catarina, sul do Brasil, destacando a área focal do estudo (a), localização das unidades de conservação (b), cobertura vegetal dos remanescentes (c) e altitude em metros (d).

Objetivo geral

- Conhecer e descrever a estrutura das interações entre plantas hospedeiras, membracídeos e formigas atendentes em remanescentes de Mata Atlântica do Estado de Santa Catarina, Sul do Brasil.

Objetivos específicos dos capítulos:

Capítulo 1 - Gadelha, Y. E. A., Dáttilo, W., Evangelista, E. & Lopes, B. C. 2016. Structure of mutualistic ant-treehopper interactions in the Brazilian Atlantic Forest. Journal of Tropical Ecology 32:250-259. DOI:10.1017/S0266467416000183. Artigo publicado no periódico **Journal of Tropical Ecology**.

- descrever a arquitetura das redes de interação formiga-membracídeo,
- investigar se a estratégia de recrutamento de formigas e o comportamento social dos membracídeos alteram a topologia das interações formiga-membracídeo na Mata Atlântica, e
- avaliar se o tamanho das agregações e comportamento social dos membracídeos afetam a coexistência de diferentes espécies de formigas nesse ambiente,

Capítulo 2 - Gadelha, Y. E. A., Lange, D., Dáttilo, W. & Lopes, B. C. 2016. Phenological phases of the host plant shape plant-treehopper interaction networks. Artigo submetido ao periódico **Ecological Entomology**.

- verificar a existência de variação temporal na estrutura das redes antagonísticas planta-membracídeo durante as diferentes fenofases das plantas hospedeiras, Capítulo 3 - Gadelha, Y. E. A., Halinski, R. & Lopes, B. C. 2016. Structural response of plant-treehopper and ant-treehopper interactions to anthropogenic changes in protected areas in the Brazilian Atlantic Forest. Artigo submetido ao periódico **Arthropod-Plant Interactions**.

- avaliar como as métricas das redes do sistema planta-membracídeo-formiga podem ser alteradas pelo grau de antropização existente em três áreas de estudo de Mata Atlântica, e
- testar quais propriedades estruturais das redes planta-membracídeo e formiga-membracídeo são afetadas pela antropização ao longo do tempo.

Capítulo 1..

Structure of mutualistic ant-treehopper interactions in the Brazilian Atlantic Forest

Artigo publicado no periódico **Journal of Tropical Ecology**

Structure of mutualistic ant-treehopper interactions in the Brazilian Atlantic Forest

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Abstract: Ant-treehopper mutualisms are centred on the availability of honeydew, a sugary fluid offered by treehoppers to attract ants, which respond by defending their hosts against predators and parasitoids. However, due to differences in the treehopper social behaviour (i.e. the amount of food resource available) ants can monopolize treehopper aggregations in many ways. Here we evaluated the topological structure of quantitative ant-treehopper interaction networks in three Brazilian Atlantic Forest localities. Moreover, we specifically investigated the role of ant recruitment strategy and treehopper behaviour in the structure of these networks. For this, we sampled ant-treehopper interactions along representative transects within each studied site and recorded the mean number of individuals of treehopper and ant species. We found that independent of variation in environmental factors among study sites, ant-treehopper networks were highly compartmentalized (Mean ± SD: $Q = 0.34 \pm 0.1$) when compared to null models, and exhibit low connectance ($C = 0.18 \pm 0.01$) and specialization ($H_2' = 0.36 \pm 0.08$) values. In addition, we also observed that larger aggregations of treehoppers interacted with the higher number of ant species and, ants that were locally dominant and showed massive recruitment interacted with a larger number of treehopper species. In summary, our results illustrate the importance of foraging strategies in shaping ecological interactions in tropical environments.

Key words: Ant-treehopper interaction, ecological networks, facultative mutualism, Membracidae, weighted nestedness.

INTRODUCTION

In tropical forests, a remarkable mutualistic interaction occurs between ants and honeydew-producing insects (e.g. aphids and treehoppers; Kaminski *et al.* 2010, Staab *et al.* 2014). Ant-treehopper mutualisms are centred on the availability of honeydew, an excretion rich in nitrogen, phosphorus, potassium, amino acids and carbohydrates (Katayama *et al.* 2013, Morales & Beal 2006). The sugary fluid offered by treehoppers attracts arboreal ants, providing defence against predators and parasitoids and, consequently, increasing treehopper survival and fecundity (Del-Claro & Oliveira 1999, Moreira & Del-Claro 2005).

Treehoppers (Hemiptera: Membracidae) display a wide range of behaviours, from solitary individuals to highly gregarious species that practice extended maternal care of eggs and nymphs (Lin 2006). Thus, gregarious species of treehopper concentrate more honeydew and, consequently, are more attractive to ants than solitary ones that are mostly dispersed. In some cases, treehoppers can be compared to extrafloral nectaries on plants, mainly because their short life cycle and aggregating behaviour offers a predictable and renewable food resource for tending-ants over time and space (Lin 2006, Wood 1993). Factors such as social behaviour and natural history of ant and treehopper species might provide the basis for explaining the establishment of mutualisms, especially in ant-treehopper systems. In fact, ant communities are strongly shaped by intraspecific competition; hence, the species foraging on hemipteran honeydew are more competitive than other common, non-facultative community members (Blüthgen & Fiedler 2004).

In the last decade, some studies showed that mutualistic networks were highly nested, in which species with fewer interactions were connected with species with the most interactions in cohesive subgroups (Bascompte *et al.* 2003). However, more recently, other authors noted that this pattern was associated with the type of existing matrix; therefore, nested networks can usually be found in binary matrices (Corso & Britton 2014, Staniczenko *et al.* 2013). Moreover, other studies found that the structural stability was positively associated with nestedness, species abundance and mutualistic strength (Feng & Takemoto 2014, Rohr *et al.* 2014, Suweis *et al.* 2013); nevertheless, nested networks do not increase community persistence (James *et al.* 2012, Strona & Veech 2015). Therefore, the use of quantitative metrics encourages ecologists to describe the structure of ecological networks

(Bellay *et al.* 2015, Robinson *et al.* 2015, Vizentin-Bugoni *et al.* 2016), including ant-plant networks (Dáttilo *et al*. 2014a).

In this study, we investigated whether ant recruitment strategy and treehopper behaviour can affect the topological structure of ant-treehopper interactions in the Brazilian Atlantic Forest. We hypothesized that ant species that recruit more workers are more likely to interact with gregarious treehopper species because greater abundance allows these ant species to discover and monopolize the food resource over space and time more frequently than other ant species. Moreover, we also assessed how the size of the aggregations and treehoppers' subsocial behaviour affected the co-existence of different species of ant in a given environment.

MATERIAL AND METHODS

Study site, data collection and specimen vouchering

This study was conducted in three natural reserve areas in the state of Santa Catarina, Southern Brazil: (1) Parque Estadual da Serra do Tabuleiro (PAEST) in Santo Amaro da Imperatriz (27° 43.708'S, 48° 48.493'W, 84,000 ha), (2) Parque Nacional da Serra do Itajaí (PNSI) in Blumenau (27° 03.442'S, 49° 05.280'W, 57,000 ha), and (3) Reserva Particular do Patrimônio Natural Chácara Edith (RPPN) in Brusque (27° 05.959'S, 48° 53.550' W, 510 ha). These locations are within the rain-forest phytogeographic zone, where the main vegetation includes large perennial trees, palms, epiphytes and lianas (Roderjan & Kuniyosshi 1988). According to the Köppen classification system, the climate in this region is subtropical humid (*Cf*), which is moderately hot and wet with no distinguishable dry season. Annual temperature means may range from 18°C to 22°C, while rainfall varies between 1600 mm and 1900 mm in areas below 700 m (PAEST and RPPN), and 2200 mm to 2500 mm in higher areas (PNSI) (Alvares *et al.* 2013, Pandolfo *et al.* 2002).

Field observations were made from January to April 2013, October-December 2013 and January-April 2014. We collected data every week along transects outlined from previously existing trails, between 8h00 and 16h00. We established six transects (1 km × 3 m) per reserve (18 in total) uniformly distributed along the same trail at every 500 m. These sets of transects were considered independent samples of treehoppers and tending-ants, yielding a distinct mutualistic network for each surveyed area. Mutualistic interactions consisted of individual observations made each time an ant was observed feeding on honeydew produced by treehoppers. The abundance of treehoppers was also recorded in each sample event, and these values were added as vectors to network bipartite graphs.

We sampled insects on all field visits. Treehoppers were manually collected with falcon tubes and killed with killing jars containing ethyl ether. Ants were collected manually with brushes and stored in 70% alcohol for later identification. After being properly processed and labelled, insect vouchers were taken to the Universidade Federal de Santa Catarina, in Florianópolis, Brazil (‘Coleção Entomológica, Departamento de Ecologia e Zoologia’). Treehoppers and ants were identified by the authors, Félix Baumgarten Rosumek and Dr. Albino Morimasa Sakakibara.

Network topology and statistical analyses

In the mutualistic networks presented here, nodes indicate the species of ant or treehopper, and the links between them correspond to the frequency of their interactions; i.e. the number of times ant species *a* was observed feeding on honeydew from treehopper species *t*. To estimate the structural patterns among these species, we assembled quantitative adjacency matrices b_{at} describing the interactions between ant (rows) and treehopper species (columns). Treehopper species were classified according to their social behaviour, based on Lin (2006) and Wood (1993).

Interaction networks were translated into bipartite graphs using the ‘Kamada-Kawai’ separate components in Pajek 4.01 (Batagelj & Mrvar 1998), which also displayed treehopper species abundance vectors. This layout method was set to optimize the position of each node separately, displaying the species according to their number of links and how they interact with other components in the network. The community structure was described based on several weighted quantitative metrics, which are specified below.

We determined the total number of interactions (k), weighted connectance (C), web asymmetry, and quantitative network specialization H_2’ index (Blüthgen *et al.* 2006, 2007) using the networklevel function in bipartite package (Dormann *et al.* 2008) for the R software version 3.2.3. The degree of nestedness was measured according to the WNODF (Weighted Nestedness metric based on Overlap and Decreasing Fill, by Almeida-Neto & Ulrich 2011) and weighted modularity Q by Dormann & Strauss (2014), using the computemodules function, both also calculated in the bipartite package (Dormann *et al.* 2008) for R. WNODF values were normalized within the interval of 0 to 100, which encompassed zero to maximum nestedness, respectively. Modularity Q varied between zero (no modules within the network) and one (all modules in the network were mutually exclusive). The H_2’ index values were normalized within the interval of 0 to 1, which encompassed zero to maximum specialization, respectively.

A Z-test was performed to test the significance of the network metrics WNODF, Q and H_2’. The values of all metrics in the randomizations were used to determine the Z-score, which was the number of standard deviations in a datum above the mean of 100 randomized networks. Z-score values equal or greater than two were considered significantly nested, modular, or specialized (Almeida-Neto & Ulrich 2011, Blüthgen *et al.* 2006, Dormann & Strauss 2014). To compare indices of network structure of ant-treehopper systems between study sites, we listed the observed values for each study site and compared to the distribution of null models within these areas. This standardization permits us to compare across study sites.

To assess whether the mean number of workers recruited per ant species was related to the number of treehopper species with which they interacted, we used a general linear regression model (r^2) implemented in the stats package for R software for each surveyed area. The mean abundance of insects, and the links between them, were considered as independent and dependent variables, respectively, and were transformed into $\log_{10}$. The test was considered statistically significant when $P < 0.005$.

RESULTS

We found a total of 32 treehopper species over all of the studied areas and classified them into four subfamilies and ten tribes. Twelve of these species were not observed in association with ants and, therefore, were not included in the network matrices (Appendix 1). We recorded 20 treehopper species interacting with 47 ant species (Appendix 2). Regarding treehopper behaviour, 18 species were solitary, four were gregarious, and ten were subsocial (Appendix 1).

The species composition of network cores presented here was largely congruent in all of the study areas. In RPPN, the majority of interactions were centred on four treehopper species (*Bocydium globuliferum* (k = 17), *Bolbonota melaena* (k = 16), *Cyphonia clavata* (k

= 11) and *Cyphonia trifida* (k = 7)) and three ant species (*Crematogaster longispina* (k = 11), *Crematogaster nigropilosa* (k = 7) and *Camponotus fastigatus* (k = 6)) (Figure 1a). In this study area, we found *C. clavata* in aggregates of up to 30 nymphs tended by *Cephalotes pusillus* and *Wasmannia auropunctata*. A similar pattern was also noted in the aggregates of *B. melaena* that interacted with the highest number of tending-ant species.

In PAEST, components concentrating the highest number of interactions included four treehopper species (*Bolbonota melaena* (k = 12), *Bocydium globuliferum* (k = 9), *Enchenopa* sp. (k = 9) and *Cyphonia trifida* (k = 8)) and four ant species (*Camponotus fastigatus* (k = 7), *Crematogaster longispina* (k = 5), *Brachymyrmex* sp. 1 (k = 5) and *Crematogaster nigropilosa* (k = 4)). The second group recovered in this topology was represented by interactions between the subsocial treehopper *Leioscyta* sp. and *Crematogaster* sp. 1 ant (Figure 1b).

In PNSI, two treehopper species (*B. melaena* (k = 12) and *C. clavata* (k = 9)) and five ant species (*C. nigropilosa* (k = 5), *Camponotus melanoticus* Emery (k = 4), *Brachymyrmex* sp. 1 (k = 3), *Crematogaster moelleri* Forel (k = 2) and *W. auropunctata* (k = 2)) established the highest number of interactions, forming a central core in the network. These treehoppers were also the most abundant in this site, concentrating the majority of the observed interactions. A single peripheral group was comprised of solitary treehopper *C. trifida* and *Crematogaster* sp. 1 ant (Figure 1c).

We observed similar network structural properties across all of the studied sites. Connectance values were low (0.17-0.20), and the distribution of mutualistic interactions was distinctly asymmetrical (-0.33 to -0.38), with few treehopper species concentrating the highest number of interactions with ants. None of the networks was significantly nested (WNODF = 31.2-41.2, all $Z < 2$), and none of the values of H_2' in the three sites was significantly different ($H_2' = 0.27\text{-}0.42$, all $Z < 2$) from the null model. However, all networks were significantly modular when compared with the neutral patterns of ant-treehopper interactions (null models) ($Q = 0.26\text{-}0.46$, all $Z > 2$), with number of modules ranging from four to five modules (Table 1).

In all of the studied areas, ant and treehopper species that showed the highest number of interactions also showed the greatest abundances. Linear regression analyses indicated a significant correlation between the mean of species abundance and the number of existing interactions between treehoppers and ants (PAEST: $r^2 = 0.71$, PNSI: $r^2 = 0.72$, RPPN: $r^2 = 0.51$, all $P < 0.001$) (Figure 2a-c).

DISCUSSION

Our hypothesis was corroborated, as ant species with greater power of recruitment established the most mutualistic interactions with gregarious species of treehopper. Our results showed an interesting trend in the structural pattern of ant-treehopper mutualistic networks, once ant species with a magnitude of worker recruitment interacted with more treehopper species (Dáttilo *et al.* 2014b). One explanation for this pattern is that ants that are more competitive tend to monopolize available food resources, such as honeydew produced by treehoppers and extrafloral nectaries (Dáttilo *et al.* 2014b, Del-Claro & Oliveira 1999, Schoereder *et al.* 2010). These findings agreed with the abundance-asymmetry hypothesis, which assumes that asymmetry in network topology is associated with variation in abundance (Vázquez *et al.* 2007). Moreover, asymmetry is a common pattern in mutualistic networks, characterized by high heterogeneity in species dependence and low frequency of strong dependence, which may promote community coexistence and diversity (Bascompte *et al.* 2006).

Interestingly, in the core of highly interacting species, we found that gregarious and solitary species of treehopper and ant species that recruited more workers were the most abundant and had the largest number of links among themselves. At the core of our mutualistic networks, we mostly found the following species of treehopper and tending-ant: *B. melaena*, *C. clavata*, *B. globuliferum*, *C. fastigatus*, *C. longispina*, *C. nigropilosa*, *Brachymyrmex* sp. 1 and *W. auropunctata*. Although several treehopper species displayed consistent solitary or gregarious behaviour, it was unclear whether small aggregations of nymphs in species that were solitary as adults were affected by ecological circumstances or transitory facultative mutualistic benefits, as opposed to reflecting a genuine behavioural trait. On this topic, we provided new ecological observations on immature specimens of *C. clavata*, which were found in small aggregations tended by ants in two surveyed sites. The ant genera most frequently associated with treehoppers, *Brachymyrmex*, *Camponotus* and *Crematogaster*, included extreme omnivores that have ecophysiological adaptations to feed on extrafloral nectaries and honeydew (Fernández 2003, Longino 2003) and that are highly efficient at recruiting large numbers of individuals. Similarly, *W. auropunctata* workers are aggressive, polyphagous and usually associate with honeydew-producing hemipterans, showing greater abundance in areas where these sap-feeding insects are found (Naumann 1994, Wetterer & Porter 2003). In agreement with previous studies, our results indicated that ants exhibiting stronger recruiting force dominated resources offered by treehoppers (Blüthgen *et al.* 2000). It was previously shown that dominant ants may regulate local species diversity through competition, contributing to the structuring of ant communities (Blight *et al.* 2014). In contrast, a single aggregating treehopper species can alter the composition of the local ant community, causing an increased abundance of ant workers (Fagundes *et al.* 2013). Thus, the number of individuals in the aggregation may affect the number of interactions that treehoppers establish with their mutualistic partners. Here, we confirmed that recruitment was a key factor in mutualistic networks because ant species with more massive recruitment often interacted with more treehopper species.

We know that abiotic factors can alter the nutritional composition of the extrafloral nectaries, such as soil pH (Dáttilo *et al.* 2013a), temperature, precipitation (Rico-Gray *et al.* 2012) and plant phenology (Lange *et al.* 2013). Therefore, resources produced by these plant structures undergo significant variation in time and space (Rico-Gray 1993) and are less stable than honeydew. As such, food resources provided by sucking insects can change over time; therefore, it is a good nutritional investment for ants. This explains the role of massive recruitment and resource domination in structuring ant-treehopper networks. Moreover, despite environmental variation, it is possible that the core of highly interacting ant species feeding on treehoppers could remain unaltered over large space-time scales, as previously observed for ant-plant networks (Dáttilo *et al.* 2013b, Lange *et al.* 2013, Santos *et al.* 2014).

Our ant-treehopper networks showed a combination of strong, asymmetrical relations and low connectance values, features that can be found in several mutualistic systems (Lange & Del-Claro 2014, Mello *et al.* 2013). Low connectance values are often seen in species-rich communities, including plants, insects and vertebrates (Clemente *et al.* 2012, Passmore *et al.* 2012, Pigozzo & Viana 2010, Santos *et al.* 2010). Our mutualistic networks were not significantly nested, possibly because we used quantitative matrices to describe these interactions. For example, in ant-plant systems, Dáttilo *et al.* (2014a) observed that the nested pattern was different when comparing quantitative and binary matrices; therefore, quantitative networks were often non-nested. Staniczenko *et al.* (2013) also argued that mutualistic ecological networks were binary nested, but quantitative ones were non-nested. Our ant-treehopper networks were significant modular, showing that there is no group of ant species that feed specifically on a particular group of treehopper species, as previously demonstrated for plant-pollinator systems or interactions between pathogens, herbivores and their host plants (Barriga *et al.* 2015, Benítez-Malvido & Dáttilo 2015, Pigozzo & Viana 2010, Santos *et al.* 2010). These findings indicate that independently of variation in environmental factors among study sites, the patterns of organization of these interacting assemblages do not change.

Ant-treehopper networks yielded highly congruent results across the three surveyed sites in the Brazilian Atlantic Forest. They revealed the breadth of ecological factors that may contribute to ant-treehopper mutualisms, such as the magnitude of worker recruitment and treehoppers' social behaviour. Our results showed that ant-treehoppers interactions did not occur randomly, and these associations were highly asymmetrical, modular and non-nested. Honeydew was monopolized by aggressive and locally dominant ants that were capable of recruiting a stronger foraging workforce, as shown by the genera *Brachymyrmex*, *Camponotus*, *Crematogaster* and *Wasmannia*, and they were also able to establish interactions with a larger number of treehopper species. Indeed, obtaining valuable food items, such as honeydew, greatly depends on how efficiently ants can discover and dominate those resources. An important aspect of these mutualistic interactions resides in the fact that honeydew is a highly nutritious resource that is more stable over time and space than extrafloral nectaries, which are severely affected by phenological and environmental changes.

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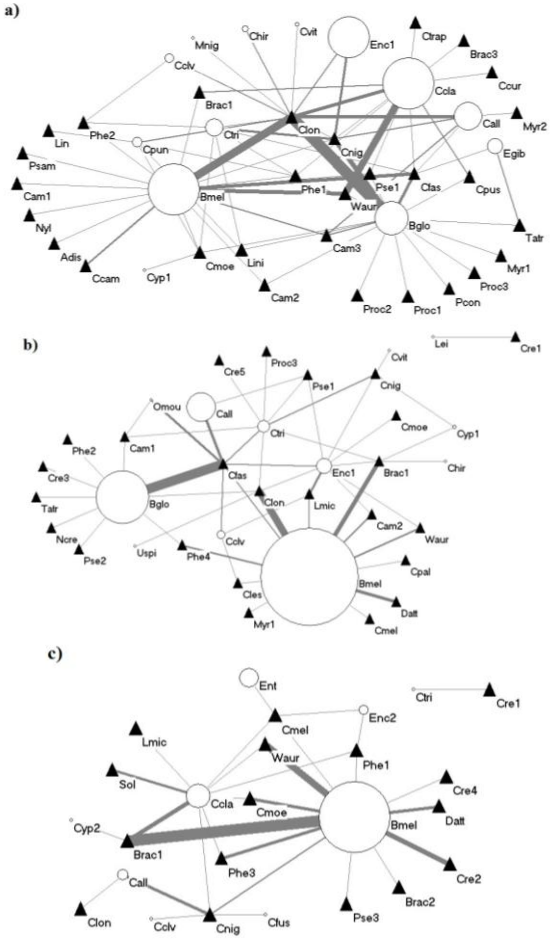


Figure 1. Interaction networks between treehoppers and ants species in Santa Catarina, Brazil, in 2013 and 2014: RPPN: Reserva Particular do Patrimônio Natural Chácara Edith, Brusque (a), PAEST: Parque Estadual da Serra do Tabuleiro, Santo Amaro da Imperatriz (b), and PNSI: Parque Nacional da Serra do Itajaí, Blumenau (c). The most important species are drawn closer to the centre of each diagram. The circles represent the abundance of each species of treehopper. The triangles represent the ant species. The size of the link is proportional to the number of times of occurrence of the interaction between species. Species codes use the first letter of the genus and the first three letters of the specific epithet. The codes are listed in Appendices 1 and 2.

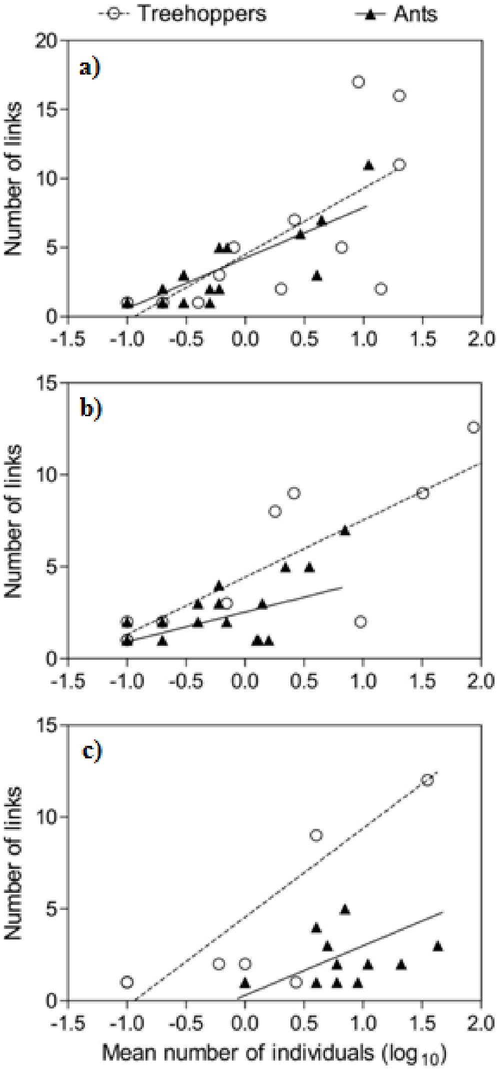


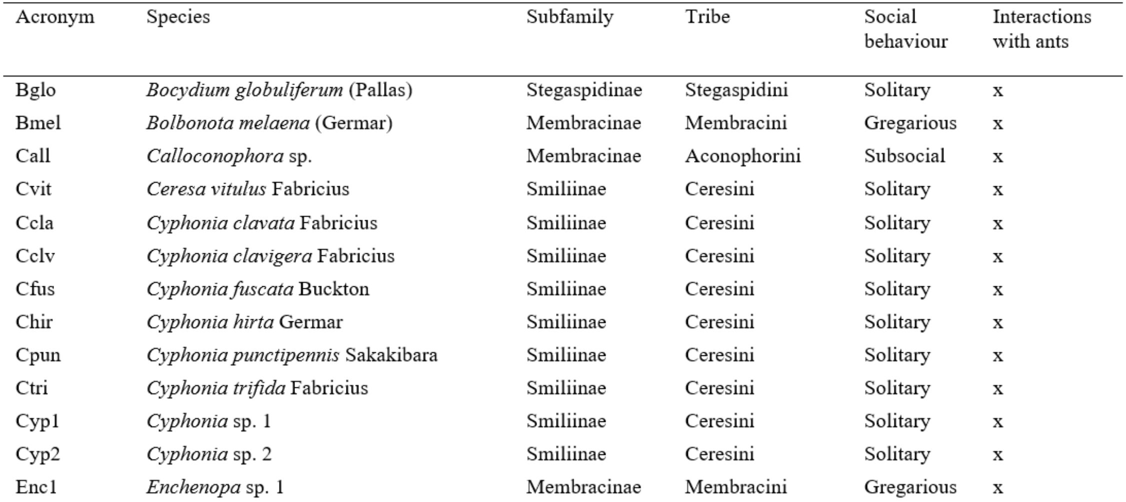
Figure 2. Linear regression (r^2) between mean number of individuals ($\log_{10}$) and number of links of treehopper and ant species. RPPN: treehoppers: $r^2 = 0.51$, $P < 0.001$; ants: $r^2 = 0.73$, $P < 0.001$ (a), PAEST: treehoppers: $r^2 = 0.71$, $P < 0.001$; ants: $r^2 = 0.36$, $P < 0.001$ (b), PNSI: treehoppers: $r^2 = 0.72$, $P < 0.001$; ants: $r^2 = 0.24$, $P = 0.05$ (c).

Table 1. Richness, abundance and descriptors of interaction networks between treehoppers and their tending-ants in three areas of the Atlantic Forest, Santa Catarina, Brazil, in 2013 and 2014. Study sites: RPPN: Reserva Particular do Patrimônio Natural Chácara Edith, Brusque, PAEST: Parque Estadual da Serra do Tabuleiro, Santo Amaro da Imperatriz, and PNSI: Parque Nacional da Serra do Itajaí, Blumenau

	Study sites		
	RPPN	PAEST	PNSI
Richness of plants	26	18	13
Richness of ants	29	24	13
Richness of treehoppers	13	12	9
Number of links between insects	302	191	110
Total abundance of ants	310	201	114
Total abundance of treehoppers	716	1573	420
Weighted connectance (C)	0.19	0.17	0.20
Nestedness (WNODF)	41.2	31.2	36.1
Z-value (WNODF)	-3.56	-5.11	-4.31
Modularity (Q)	0.30	0.46	0.26
Z-value (Q)	11.5	24.0	6.82
Number of modules	5	5	4
H_2’ index	0.27	0.40	0.42
Z-value (H_2’)	0.11	0.18	0.17
Web asymmetry	-0.38	-0.33	-0.33

Supporting Information

Appendix 1. List of acronyms (only for species that interacts with ants), species, subfamily, tribe, social behaviour and interactions with ants of Membracidae (Hemiptera) in Atlantic Forest in Santa Catarina, Brazil, in 2013 and 2014. Interactions with ants: x: present and -: absent.



Acronym	Species	Subfamily	Tribe	Social behaviour	Interactions with ants
Bglo	*Bocydium globuliferum* (Pallas)	Stegaspidinae	Stegaspidini	Solitary	x
Bmel	*Bolbonota melaena* (Germar)	Membracinae	Membracini	Gregarious	x
Call	*Calloconophora* sp.	Membracinae	Aconophorini	Subsocial	x
Cvit	*Ceresa vitulus* Fabricius	Smiliinae	Ceresini	Solitary	x
Ccla	*Cyphonia clavata* Fabricius	Smiliinae	Ceresini	Solitary	x
Cclv	*Cyphonia clavigera* Fabricius	Smiliinae	Ceresini	Solitary	x
Cfus	*Cyphonia fuscata* Buckton	Smiliinae	Ceresini	Solitary	x
Chir	*Cyphonia hirta* Germar	Smiliinae	Ceresini	Solitary	x
Cpun	*Cyphonia punctipennis* Sakakibara	Smiliinae	Ceresini	Solitary	x
Ctri	*Cyphonia trifida* Fabricius	Smiliinae	Ceresini	Solitary	x
Cyp1	*Cyphonia* sp. 1	Smiliinae	Ceresini	Solitary	x
Cyp2	*Cyphonia* sp. 2	Smiliinae	Ceresini	Solitary	x
Enc1	*Enchenopa* sp. 1	Membracinae	Membracini	Gregarious	x

Enc2	*Enchenopa* sp. 2	Membracinae	Membracini	Gregarious	x
Ent	*Entylia* sp.	Smiliinae	Polyglyptini	Subsocial	x
Egib	*Erechtia gibbosa* (De Geer)	Membracinae	Talipedini	Subsocial	x
Lei	*Leioscyta* sp.	Membracinae	Membracini	Subsocial	x
Mnig	*Micrutalis nigromarginata* Funkhouser	Smiliinae	Micrutalini	Solitary	x
Omou	*Ochropepla mourei* (Sakakibara)	Membracinae	Hoplophorionini	Subsocial	x
Uspi	*Umbonia spinosa* Fabricius	Membracinae	Hoplophorionini	Subsocial	x
-	*Alchisme* sp.	Membracinae	Hoplophorionini	Subsocial	-
-	*Enchophyllum* sp.	Membracinae	Membracini	Gregarious	-
-	*Germariana terminalis* (Fonseca)	Darninae	Cymbomorphini	Solitary	-
-	*Hypsoprora* sp.	Membracinae	Hypsoprorini	Solitary	-
-	*Leioscyta* sp. 2	Membracinae	Membracini	Subsocial	-
-	*Lycoderes* sp. 1	Stegaspidinae	Stegaspidini	Solitary	-
-	*Lycoderes* sp. 2	Stegaspidinae	Stegaspidini	Solitary	-
-	*Micrutalis tripunctata* (Fairmaire)	Smiliinae	Micrutalini	Solitary	-
-	*Notocera brachycera* (Fairmaire)	Membracinae	Hypsoprorini	Solitary	-
-	*Potnia* sp.	Membracinae	Hoplophorionini	Subsocial	-
-	*Talipes appendiculatus* (Fonseca)	Membracinae	Talipedini	Subsocial	-
-	*Paraceresa* sp.	Smiliinae	Ceresini	Solitary	-

Appendix 2. List of acronyms, species and subfamilies of Formicidae (Hymenoptera) in the Atlantic Forest in Santa Catarina, Brazil, in 2013 and 2014.

Acronym	Species	Subfamily
Adis	*Acromyrmex disciger* (Mayr)	Myrmicinae
Brac1	*Brachymyrmex* sp. 1	Formicinae
Brac2	*Brachymyrmex* sp. 2	Formicinae
Brac3	*Brachymyrmex* sp. 3	Formicinae
Catr	*Camponotus atriceps* (Smith)	Formicinae
Ccam	*Camponotus cameranoi* Emery	Formicinae
Cfas	*Camponotus fastigatus* Roger	Formicinae
Cles	*Camponotus lespesii* Forel	Formicinae
Cmel	*Camponotus melanoticus* Emery	Formicinae
Cam1	*Camponotus* sp. 1	Formicinae
Cam2	*Camponotus* sp. 2	Formicinae
Cam3	*Camponotus* sp. 3	Formicinae
Ctra	*Camponotus trapezoideus* Mayr	Formicinae
Cpal	*Cephalotes pallidicephalus* (Smith)	Myrmicinae
Cpus	*Cephalotes pusillus* (Klug)	Myrmicinae
Ccur	*Crematogaster curvispinosa* Mayr	Myrmicinae
Clon	*Crematogaster longispina* Emery	Myrmicinae
Cmoe	*Crematogaster moelleri* Forel	Myrmicinae
Cnig	*Crematogaster nigropilosa* Mayr	Myrmicinae
Cre1	*Crematogaster* sp. 1	Myrmicinae
Cre2	*Crematogaster* sp. 2	Myrmicinae
Cre3	*Crematogaster* sp. 3	Myrmicinae
Cre4	*Crematogaster* sp. 4	Myrmicinae
Cre5	*Crematogaster* sp. 5	Myrmicinae
Datt	*Dolichoderus attelaboides* (Fabricius)	Dolichoderinae
Lmic	*Linephitema micans* (Forel)	Dolichoderinae
Lini	*Linepithema iniquum* (Mayr)	Dolichoderinae

Lin	*Linepithema* sp. Mayr	Dolichoderinae
Myr1	*Myrmelachista* sp. 1	Formicinae
Myr2	*Myrmelachista* sp. 2	Formicinae
Ncre	*Neoponera crenata* (Roger)	Ponerinae
Nyl	*Nylanderia* sp.	Formicinae
Phe1	*Pheidole* sp. 1	Myrmicinae
Phe2	*Pheidole* sp. 2	Myrmicinae
Phe3	*Pheidole* sp. 3	Myrmicinae
Phe4	*Pheidole* sp. 4	Myrmicinae
Pcon	*Procryptocerus convergens* (Mayr)	Myrmicinae
Psam	*Procryptocerus sampaioi* Forel	Myrmicinae
Proc1	*Procryptocerus* sp. 1	Myrmicinae
Proc2	*Procryptocerus* sp. 2	Myrmicinae
Proc3	*Procryptocerus* sp. 3	Myrmicinae
Pse1	*Pseudomyrmex* sp. 1	Pseudomyrmecinae
Pse2	*Pseudomyrmex* sp. 2	Pseudomyrmecinae
Sol	*Solenopsis* sp.	Myrmicinae
Tatr	*Tapinoma atriceps* Forel	Dolichoderinae
Waur	*Wasmannia auropunctata* (Roger)	Myrmicinae

Capítulo 2……………………………………………………………

Phenological phases of the host plant shape plant-treehopper interaction networks

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Phenological phases of the host plant shape plant-treehopper interaction networks

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Abstract. 1. Several studies have recently focused on the structural pattern of plant-insect interaction networks. However, insects and plants have dynamic cycles and differ in their level of specialisation over time. Thus, it is expected that sap-sucking insects, like treehoppers, and plants will not share similar patterns of interactions in all phenophases of the host plants.

2. We postulated that phenology could change the structure of plant-treehopper networks, which will be more specialised during the reproductive phenophase than the vegetative one, mainly because of high concentrations of toxic compounds in the reproductive phenophase. Here, we used quantitative metrics derived from graph theory to describe, for the first time, the variations in the structure of plant-treehopper interactions during the phenophases of host plants in a Brazilian Atlantic Forest.

3. The central core of the highly interacting treehopper species was composed by the genera *Bocydium*, *Bolbonota* and *Cyphonia*. On the other hand, the central core of the highly interacting plant species was comprised of *Baccharis*, *Eupatorium* and *Vernonia*, all Asteraceae plants, where treehoppers were observed mainly feeding on the apical meristems and inflorescences. In both phenophases, plant-treehopper networks had low connectance values and exhibited a modular and non-nested pattern. However, during the reproductive phenophase, we

recorded lower species richness of plants and treehoppers and higher levels of specialisation compared to the vegetative phenophase.

4. In short, our findings demonstrate that phenological phases of the host plant can be a remarkable mechanism that shapes plant-treehopper interactions in a tropical rainforest.

Keywords. Atlantic forest, ecological networks, herbivory, host specialisation, phenology, plant-insect interactions.

Introduction

Herbivory is defined as the consumption of any plant part, including foliage, stems, roots, flowers, fruits or seeds by animals (Schowalter, 2011). Insects are the primary herbivores in many ecosystems, exhibiting specialised host-use patterns as result of adaptations to plant defences (Augustyn *et al.*, 2013). Certain insects feed by removing chunks of plant tissue (chewing) and others extract sap from their hosts (sucking), often reducing plant fitness (Strauss & Zangerl, 2002). The majority of phytophagous insects feed on the same plant families, thus specialisation of host plants are frequently observed (Futuyma & Mitter, 1996).

The impact of herbivory on plants depends of what plant part is consumed and which herbivores are involved, thus vegetative parts are more easily replaced than reproductive counterparts because of the plasticity of plants, and chewing insects might cause major damage by removing large amounts of plant tissue versus sucking insects (Strauss & Zangerl, 2002). Furthermore, apical meristems are more nutritious (rich in nitrogen) and have fewer secondary chemical defence compounds, promoting the growth of insects and higher fertility rates (Schoonhoven *et al.*, 2005), therefore young tissues usually have greater vulnerability to attack by herbivore insects (War *et al.*, 2012). In addition, the reproductive parts have high concentrations of toxic compounds, and because of defence strategies, these plant tissues are likely to be attacked by less herbivores compared with vegetative parts (Zangerl & Bazzaz, 1992; Zangerl & Rutledge, 1996; Kaplan *et al.*, 2008).

As a result of the strong pressure exerted by herbivorous insects in tropical regions, plants have developed unique chemical, biological, mechanical and phenological defence mechanisms over evolutionary time (Coley & Barone, 1996; Strauss & Zangerl, 2002; Thompson, 2013). In the case of phenological defence, plants can alter the quality and quantity of food resources available to their herbivorous asynchronously with the life cycle of them, affecting the abundance of their populations, mainly of species with short life (Yukawa, 2000; Yukawa & Akimoto, 2006; Vilela *et al.*, 2014). Thus, phenology may modify plant-herbivore interactions over the time (Boege & Marquis, 2005; Yang & Rudolf, 2010) because the foliar defences change according to the variation of plant phenophases (Calixto *et al.*, 2015). Yet, the relationship between host plant phenology and insect herbivory performance might be considered a variable of plant-animal interactions, possibly vulnerable to local spatial and temporal variability (Hunter, 1992).

Treehoppers (Hemiptera: Membracidae) are herbivorous insects that suck sap in apical meristems and inflorescences of herbaceous and shrubby plants (Wood, 1993; Del-Claro & Oliveira, 1999; Lin, 2006; Fagundes *et al*., 2016). This preference for particular parts of plants is explained by the short and fragile buccal apparatus of these phytophagous insects, which choose tissues where the conductive vessels are closer to the surface to facilitate feeding (Funkhouser, 1950; Wood, 1993). The herbivores have a short life cycle, ranging from 50 to 70 days in mean (Kopp & Yonke, 1973; Linares *et al*., 2010; Torrico-Bazoberry *et al*., 2014), and several generations of these insects, including those of different species, may share among them the space and food resources provided by plants (Wood, 1993). A number of species exhibit highly subsocial behaviour with maternal care, while other species range from solitary behaviour (nymphs and/or adults) to gregarious species (eggs, adults and nymphs), all sharing the same plant branch (Wood, 1993). Treehoppers have a strong relationship with their plants of choice and their entire life cycle is associated with hosts' feeding and reproduction (Funkhouser, 1950; Lin, 2006). Certain species of membracids alter their plants over the life cycle (Torrico-Bazoberry *et al*., 2014), and as such the nymphs may migrate from the host with eggs (where they are laid) to feed on another plant and then return to the first plant to oviposition (Funkhouser, 1950).

Interactions between plants and herbivorous insects may be antagonistic because the insect feeding brings about loss of plant tissues and/or fitness (Coley & Barone, 1996). Insect feeders depend directly or indirectly on plant taxa, therefore they are more vulnerable to plant species loss (Pocock *et al*., 2012). These plant-herbivore associations tend to be more specialised than mutualistic ones (e.g., ant-plant or pollinator-plant) mainly based on the degree of intimacy between herbivores with their host plants (Pires & Guimarães Jr, 2013). Plant-herbivore systems generally have a majorly modular structure (i.e., groups of herbivore species strongly associated with a particular set of plant species) (Cagnolo *et al*., 2011; Robinson *et al*., 2015) and this compartmentalization may favour the stability of antagonistic interactions (Fortuna *et al*., 2010) because environmental changes can be quickly absorbed by the functional subunits of the networks (Clune *et al*., 2013; Nuwagaba *et al*., 2015).

In this study, we sought to verify how the phenological changes of host plants affect the structure of plant-treehopper interaction networks. Whereas the reproductive parts of plants have greater amounts of defensive toxic compounds against herbivores (Kaplan *et al*., 2008), we anticipated that during the reproductive phenophase, few phytophagous species would have the ability to feed on the plants. As a result, we postulated that phenology could alter the structure of plant-treehopper networks, which should be more specialised during the reproductive phenophase than the vegetative phenophase of the host plants.

Materials and methods

Study area

We conducted the fieldwork in the State of Santa Catarina, Southern Brazil. We selected tree-protected areas in the east of the State, specifically in the following municipalities: Parque Estadual da Serra do Tabuleiro (PAEST, Santo Amaro da Imperatriz, 27°43.708’S, 48°48.493’W; 84,000 hectares), Parque Nacional da Serra do Itajaí (PNSI, Blumenau, 27°03.442’S, 49°05.280’W; 57,000 hectares) and Reserva Particular do Patrimônio Natural Chácara Edith (RPPNCE, Brusque, 27°05.959’S, 48°53.550’W; 510 hectares). The primary vegetation of the selected areas contained large perennial trees, palms, epiphytes and lianas (Roderjan & Kuniyosshi, 1988). The climate in the region was subtropical humid (Cf) by the Köppen classification system, and moderately hot and wet with no distinguishable dry season, with annual temperature means varying from 18°C to 22°C. The rainfall ranges from between 1,600 mm and 1,900 mm in areas below 700 m (PAEST and RPPNCE), and 2,200 mm to 2,500 mm in higher areas (PNSI) (Pandolfo *et al*., 2002; Alvares *et al*., 2013).

Sampling and specimen collection

We carried out field observations in the warm period of the years 2013 (from January to April, and from October to December) and 2014 (from January to April). We always compiled data and insect specimen in the morning period (8 to 12 h) along transects arranged in the existing trails in the study areas. We selected six transects per area measuring 1,000 m × 3 m distributed along the trails at every 500 m. All these sets of transects (18 in total) were considered an independent sample of plant-treehopper interactions, producing an interaction network for each study area for each phenophase studied. Antagonistic interactions consisted of individual observations made each time a treehopper (adult or nymph) was seen feeding on the host plant or adults on aggregations with eggs and nymphs. All existing plants in the transects were inspected for treehoppers (gregarious or solitary) and their feeding behaviour was observed over the course of two to three minutes.

During all field expeditions, the treehoppers were manually sampled using Falcon tubes and sacrificed with jars containing ethyl ether. For each plant species, we collected three to five branches of 30 to 40 cm in length for identification of species and deposition to the herbarium. We classified the i) reproductive phenophase when we noted evidence of the presence of a flower bud, flower, inflorescence and/or fruits, and the ii) vegetative phenophase when the host plant did not feature at least one of these morphological structures (d'Eça-Neves & Morellato, 2004; Locatelli & Machado, 2004). After being processed and labelled, insect and plant specimens were deposited at Universidade Federal de Santa Catarina (Coleção Entomológica, Departamento de Ecologia e Zoologia, and Herbário Flor, Departamento de Botânica), in Florianópolis, Brazil.

Network analysis

Within the antagonistic interaction networks described here, nodes correspond to plants or treehoppers species, and the links between them are related to the frequency of their interactions, i.e., the number of times a treehopper species, *t*, was observed feeding on a plant species, *p*. In order, to estimate the structural patterns among these species, we assembled quantitative adjacency matrices, b_{pt}, illustrating the interactions between plant (rows) and treehopper species (columns). To compute all networks metrics, we used the bipartite package (Dormann *et al.*, 2009) for R software, version 3.2.4 (R Core Team, 2016). Interaction networks were translated into bipartite graphs using the plotweb and sortweb functions in R software.

In order to portray the structure of our plant-treehopper networks within each study site and phenophase, we determined the weighted connectance (C), species' degree (k), linkage density (marginal totals-weighted diversity of interactions per species), vulnerability, WNODF to estimate the nestedness (*sensu* Almeida-Neto & Ulrich, 2011) and weighted modularity (Q) (Dormann & Strauss, 2014) using the networklevel and computemodules functions in R software. WNODF values were normalized within the interval of zero (non-nested) to 100 (maximum nestedness) and Q ranged between zero (network with no modules) and one (maximum modularity).

We assessed the degree of specialisation within each study site and phenophase using the network specialisation H_2' index (*sensu* Blüthgen *et al.*, 2006). This index characterizes the degree of compartmentalisation between the two parts of the entire network (community). We also verified the specialisation index (d') for each plant and treehopper species. Both indexes are quantitative, derived from Shannon entropy, and range from zero (extreme generalization) to one (extreme specialisation) (Blüthgen *et al.*, 2006, 2007).

Statistical analysis

We performed the z-test to test the significance of the metrics, WNODF and Q, for all networks. The values of these metrics in randomizations were used to determine the z-score, which is the number of standard deviations from a reference point above the mean of 100 randomized networks. We considered the z-score values equal or greater than two significantly nested or modular (Almeida-Neto & Ulrich, 2011; Dormann & Strauss, 2014). We evaluated the statistical significance of the H_2' index by a Monte Carlo simulation with 10,000 iterations using Patefield's algorithm (Patefield, 1981).

Finally, to assess the effort of sampling the plant-treehopper community, we determined the effectiveness of interaction accumulation curves for each study site and phenophase with the Jackknife 1 richness estimator. The effectiveness was estimated by percentages, taking into account the number of observed and expected interactions in the vegan package (Oksanen *et al.*, 2016) for R software. Interaction curves reduce the number of missing cells in interaction matrices using total interactions and explaining missed interactions (Falcão *et al.*, 2016; Jordano, 2016).

Results

We observed 32 species of treehopper belonging to four subfamilies, Membracinae being the most expressive (13 genera), followed by Smiliinae (five genera), Stegaspidinae (two genera) and Darninae (only one genus) (Appendix 1). We collected these treehoppers from 36 species of plants that were distributed across nine families, with Asteraceae possessing the largest number of species (11 genera), followed by Moraceae and Melastomataceae (two genera each), along with Boraginaceae, Clethraceae, Clusiaceae, Malpighiaceae, Piperaceae and Ulmaceae (all featuring one genus) (Appendix 2).

During the vegetative phenophase, we observed a larger number of interactions between species of plants and treehoppers compared to the reproductive phenophase (Table 1). All networks had low weighted connectance values (C = 0.08-0.13) and were not significantly nested (WNODF = 25.65-30.20, Z < 2) (Table 1). The communities were significantly specialized (H_2' = 0.52-0.57, $P < 0.001$) and networks were modular (Q = 0.34-0.49, Z > 2) (Table 1). Compared with the reproductive phenophase, we found a higher linkage density (2.30-3.57) in the vegetative phenophase, as well greater vulnerability of plant-treehopper networks (1.82-3.20) (Table 1). During this phenophase, the central core of the networks was formed by five species of treehoppers and four host plants, all Asteraceae (*Bocydium globuliferum* (k = 17, d' = 0.59), *Cyphonia trifida* (k = 15, d' = 0.50), *Cyphonia clavata* (k = 12, d' = 0.56), *Bolbonota melaena* (k = 12, d' = 0.63), *Enchenopa* sp. 1 (k = 12, d' = 0.34), *Vernonia tweediana* (k = 13, d' = 0.26), *Eupatorium* sp. (k = 11, d' = 0.37), *Vernonia scorpioides* (k = 10, d' = 0.53), *Baccharis conyzoides* (k = 8, d' = 0.14)) (Fig. 1a, 1b and 1c; Appendices 1 and 2). In RPPNCE, we noted the peripheral group was formed by two treehopper species, *Calloconophora* sp. (d' = 0.94) and *Lycoderes* sp. 2 (d' = 0.40), and the host plant, *Piper aduncum* (Fig. 1a). Another peripheral group was formed in the PAEST network, with the interaction between the treehopper, *Calloconophora* sp., and the host plant, *P. aduncum* (Fig. 1b). The interaction between the plant, *Baccharis* sp., and the treehopper *Enchenopa* sp. 2 (d' = 0.82), formed another peripheral group in PNSI (Fig. 1c). Regarding the morphological parts most utilised by treehoppers, *B. melaena* and *Enchenopa* sp. 1 demonstrated a preference for sucking apical meristems whereas *B. globuliferum*, *C. trifida* and *C. clavata* consumed internodes.

In the reproductive phenophase, we observed a decreased richness of treehopper and plants species in all study areas (Table 1). During the first year of sampling, we found eight species of plants possessed inflorescence (*Elephantopus mollis, Erechtites valerianifolia, Eupatorium laevigatum, Eupatorium picturatum*, *Garcinia gardneriana*, *Miconia latecrenata*, *Solidago chilensis* and *V. tweediana*), where six belonged to the Asteraceae, and the reproductive period of these extended from January to May and from October to December. The following year, we found three species of plants with inflorescences in addition to those already mentioned, all belonging to Asteraceae (*B. conyzoides*, *Eupatorium pedunculosum* and *Vernonia eriolepis*), however the reproduction period of these plants extended between the months from January to April 2014 (Appendix 2).

During this phenophase, all networks had low values of weight connectance (C = 0.06-0.10) and were not significantly nested (WNODF = 14.90-31.62, Z < 2), however the networks were significantly modular (Q = 0.50-0.67, Z > 2) and community specialisation was higher (H_2' =

0.67-0.90, $P < 0.001$) at all study sites (Table 1). We noted both lower linkage density (1.47-2.05) and vulnerability of antagonistic networks (1.34-2.19) within the reproductive phenophase (Table 1). The central cores of the networks were formed with three treehopper and three host plants species, all Asteraceae (*B. melaena* (k = 11, d' = 0.55), *C. trifida* (k = 7, d' = 0.70), *C. clavata* (k = 4, d' = 0.64); *V. tweediana* (k = 9, d' = 0.34), *Conyza bonariensis* (k = 7, d' = 0.78), *E. laevigatum* (k = 5, d' = 0.40)) (Fig. 1d, 1e and 1f; Appendices 1 and 2). In RPPNCE, we observed two peripheral groups, the first being formed by the interaction between the treehopper, *Calloconophora* sp. (d' = 0.98), and the plant, *P. aduncum*, while the second group was between the treehopper, *Micrutalis tripunctata*, and the plant, *Cordia monosperma* (Fig. 1d). During this phenophase, the treehopper species, *B. melaena*, *B. globuliferum* and *Ochropepla mourei* mainly used the inflorescences despite most of these insects being observed at internodes and nodes. In general, the highest values of the specialisation index d' were determined in the peripheral species of plant-treehopper networks in both phenophases studied. The interaction accumulation curves for both phenophases had similar effectiveness values, ranging from 62 to 66% (Table 1; Appendix 3).

The herbivore species, *B. globuliferum*, *B. melaena*, *Calloconophora* sp., *C. clavata*, *C. trifida*, *M. tripunctata* and *Ochropepla mourei*, had enhanced specialisation in both phenophases (Appendix 1). We observed aggregations of adults and nymphs of these treehopper species on seven species of *Eupatorium*, four *Vernonia* species, three of *Baccharis* and two of *Conyza*, all Asteraceae plants. Furthermore, during the vegetative phenological phase, the treehopper species, *Alchisme* sp., *Enchenopa* sp. 2, *Micrutalis nigromarginata* and *Potnia* sp. were more specialised (Appendix 1). On the other hand, we found the treehoppers, *Cyphonia* sp. 2, *Enchenopa* sp. 1, *Entylia* sp. and *Erechtia gibbosa*, were more specialised during reproductive phenophase (Appendix 1).

Discussion

In this study, we showed that plant phenology is an ecological factor responsible for structuring plant-treehopper networks. We also found that in the reproductive phenophase, interaction networks had greater specialisation versus networks during the vegetative phenophase. Many studies have demonstrated that insect-plant interactions may be affected by plant phenology, causing biotic changes in the abundance, richness and performance of herbivore insects (Vilela *et al.*, 2014; Belchior *et al.*, 2016; Del-Claro *et al.*, 2016; Velasque & Del-Claro, 2016). In fact, these temporal variations may change the properties of interaction networks (e.g., nestedness and specialisation) (Lange *et al.*, 2013), as also shown in this study for phenological phases.

We observed that the majority of treehopper species feed on Asteraceae plants. Other authors have also made note of most treehopper fauna being restricted to just a few families, including Asteraceae (Lopes, 1995), in tropical environments, like Caatinga and Brazilian Cerrado (Del-Claro & Oliveira, 1999; Moreira & Del-Claro, 2005; Creão-Duarte *et al.*, 2012; Fagundes *et al.*, 2016), and temperate regions (Wood, 1993; Lin, 2006; Harvey & Wheeler Jr, 2015). High specificity of the host plant (index d' was approximately one for both species) was determined in the interaction between the plant, *P. aduncum* (Piperaceae), and treehoppers of genus *Calloconophora* in our study. Other work has provided evidence that nymphs of the treehopper genus, *Calloconophora*, feed on inflorescences of *Piper* (Piperaceae), and pointed out that these plants can be the host of treehoppers in tropical regions (Vanin *et al.*, 2008; Lencioni-Neto, 2011).

By definition, the treehoppers included in this study could be classified as polyphagous, using a wide variety of hosts (*sensu* Schoonhoven *et al.*, 2005). These herbivores were observed on herbaceous and shrubby plants, mainly species of the genera, *Baccharis*, *Eupatorium* and *Vernonia*. Plants of these genera share similar chemical compositions and a variety of secondary metabolites, such as flavonoids present in both *Baccharis* and *Vernonia* (Verdi *et al.*, 2005; Sayuri *et al.*, 2010; Machado *et al.*, 2013). This may be an indication that treehoppers prefer Asteraceae hosts on a chemical basis and the habitat of these plants (Lopes, 1995; Del-Claro & Oliveira, 1999; Fagundes & Fernandes, 2011). Furthermore, species of herbaceous plants have a greater variation in chemical composition and life cycle compared to woody plants, while specialist insects are more adapted to this change and can better exploit resources than generalist insects (Schoonhoven *et al.*, 2005). Further, high levels of toxic compounds observed in young leaves are tolerated by herbivores specialists that employ these chemical substances in their own defence (Schoonhoven *et al.*, 2005; Vilela *et al.*, 2014), consequently making these herbivores less preyed upon (Schoonhoven *et al.*, 2005).

In this study, we observed a greater tendency toward specialisation of plant-treehopper interactions during the reproductive phenophase compared to the vegetative. Within the reproductive phenophase, the networks were more simplified (with a diminished richness of interactions and species) in two of the three study areas (RPPNCE and PAEST) that together contained nearly half the species of treehoppers interacting with fewer species of plants at a lower linkage density. In PNSI, we observed the same number of species of plants and treehoppers interacting in both phenophases, however, there was also lower linkage density during the reproductive period. These findings may be related to the defence of phenological escape, whereby plants must avoid herbivory (Vilela *et al.*, 2014; Velasque & Del-Claro, 2016). As reproductive structures are more valuable for plants than vegetative parts (Cousens *et al.*, 2008), the time to invest in reproductive structures should be lower in the case of herbivores. However, herbivores may be specialised for the reproductive phenophase of plants, feeding exclusively on flowers or seeds of their host (Navarro-Cano *et al.*, 2015). In insect-plant interactions, species that visit flowers are typically specialists rather than other species of herbivores that are usually leaf feeders (Kuppler *et al.*, 2016). Herbivores can still migrate from plant to plant over time (Vilela *et al.*, 2014), especially treehoppers that migrate from plant to plant to feed or oviposition (Funkhouser, 1950). Therefore, the variation in phenological phases of plants may be related to defence against herbivores, rendering plant-treehopper relationships more specialized.

We did not find any nestedness in networks evaluated in this research. Nestedness is commonly a feature in general interactions involving non-symbiotic relationships, such as mutualistic interactions (Díaz-Castelazo *et al.*, 2010; Santos *et al.*, 2010; Clemente *et al.*, 2012; Dáttilo *et al.*, 2014; Lange & Del-Claro, 2014). The modular structure and absence of or low nestedness values is common in plant-herbivore systems (Cagnolo *et al.*, 2011; López-Carretero *et al.*, 2014). Antagonistic network consumers (herbivores) are highly specialised, spending most of their life cycle on hosts (plants) (van Veen *et al.*, 2008). According to same authors, these interactions are generally more modular and less nested than antagonistic networks with species possessing no symbiotic interactions. Host plant specialisation of herbivores is extremely common and, according to López-Carretero *et al.* (2014), could be promoted evolutionarily for two reasons: (1) the benefits conferred by foraging specialist behaviour overcome the difficulties of herbivores having to choose suitable hosts in locations with high diversity, such as tropical forests, and/or (2) specialisation for hosts that do not have many associated herbivores, avoiding competition for resources. According to the author, these two forms of promotions of specialisation between plants and herbivores remain unexploited by plant defences. However, whatever the reasons, more intimate interactions, like those involving plants and herbivores, are associated with high specialisation and modularity (Cagnolo *et al.*, 2011; Pires & Guimarães Jr, 2012; López-Carretero *et al.*, 2014; Benítez-Malvido & Dáttilo, 2015). This pattern is also observed in mutualistic interactions where more closely related species lead to low values of nestedness in networks (Ollerton *et al.*, 2003; Dáttilo, 2012; Thompson *et al.*, 2013). Thus, variations in the architecture of ecological networks may be attributed to the type of interaction and the degree of specialisation of the species in the studied community (Robinson *et al.*, 2015).

Ecological systems can be highly dynamic across time and space, where new interactions may occur and/or the old ones might be lost (Bascompte, 2010; Lange & Del-Claro, 2014; López-Carretero *et al.*, 2014). The use of interaction accumulation curves in ecological studies may help explain how biological systems actually behave, solving problems of sampling interactions and limitations of biological inventories (Jordano, 2015). Here, we observed that the interaction accumulation curves exhibited a great sampling effort for both evaluated phenophases, showing that the plant-treehopper system is dynamic. As observed in other studies involving ant-plant and plant-pollinator networks, only 60% of interactions were registered in the field, and this was despite a greater sampling effort (Chacoff *et al.*, 2012; Falcão *et al.*, 2016). Accumulation curves for interactions are robust tools for evaluating sampling completeness in ecological networks (Falcão *et al.*, 2016), whereas this shows that even with a large sampling effort, certain interactions were not observed only because they are rare (Chacoff *et al.*, 2012). In sum, our results demonstrate that phenology may be a contributing factor to the structure of plant-treehopper interactions and the architecture of these associations tend to be more specialised in reproductive phenophase compared with vegetative phenophase in the Brazilian Atlantic forest.

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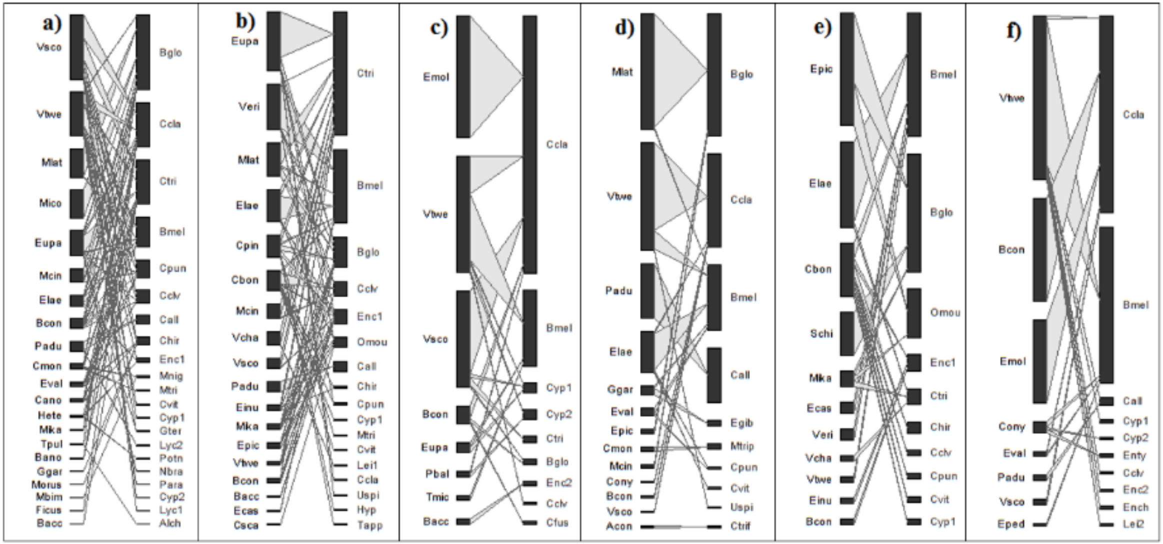


Fig 1. Interaction networks between host plants and treehoppers species in the Brazilian Atlantic Forest, Santa Catarina, Brazil, in 2013 and 2014, during the vegetative phenophase: (a) RPPNCE, (b) PAEST and (c) PNSI, and reproductive phenophase: (d) RPPNCE, (e) PAEST and (f) PNSI. The left side shows the plant and the right side shows the treehopper species. The size of the link is proportional to the number of times of occurrence of the interaction between species. Species codes were made using the first letter of the genus and the first three letters of the specific epithet. The codes are listed in Appendices 1 and 2.

Table 1. Richness, descriptors and number of interactions expected by Jackknife 1 estimator between host plant and treehopper antagonistic networks, in three study sites in Atlantic Forest, Santa Catarina, Brazil, in 2013 and 2014. Study sites: RPPNCE (Reserva Particular do Patrimônio Natural Chácara Edith), PAEST (Parque Estadual da Serra do Tabuleiro) and PNSI (Parque Nacional da Serra do Itajaí). Significant values are highlighted in **bold**.

	RPPNCE		PAEST		PNSI	
	Phenophase of host plant					
	Vegetative	Reproductive	Vegetative	Reproductive	Vegetative	Reproductive
Richness of plants	21	13	18	11	8	8
Richness of treehoppers	21	10	17	10	9	10
Linkage density	3.39	1.47	3.57	2.05	2.30	1.66
Vulnerability	3.20	1.34	2.28	2.19	1.82	1.39
Weighted connectance (C)	0.08	0.06	0.10	0.10	0.13	0.09
Nestedness (WNODF)	27.98	14.90	30.20	24.25	25.65	31.62
Z-value (WNODF)	-11.51	-9.43	-8.14	-3.88	-6.22	-6.06
Modularity (Q)	**0.49**	**0.67**	**0.48**	**0.56**	**0.34**	**0.50**
Z-value (Q)	40.08	32.24	33.65	10.77	13.18	18.98
Number of modules	6	8	5	4	4	4
Specialisation (H_2')	**0.52**	**0.90**	**0.56**	**0.67**	**0.57**	**0.88**
P-value (H_2')	P<0.001	P<0.001	P<0.001	P<0.001	P<0.001	P<0.001
Number of observed interactions	72	21	57	19	18	18
Number of expected interactions	108	33	86	30	29	29
Sampling effectiveness (%)	66.6	63.3	66.2	66.2	62.0	65.5

Supporting Information

Appendix 1. List of acronyms, species, subfamily of Membracidae (Hemiptera), abundance (number of individuals) of adults and nymphs, and index of specialisation per species (d’) during vegetative (v) and reproductive (r) phenofase of the host plants in Atlantic Forest in Santa Catarina, Brazil, in 2013 and 2014. In **bold** are values equal or greater than 0.50.

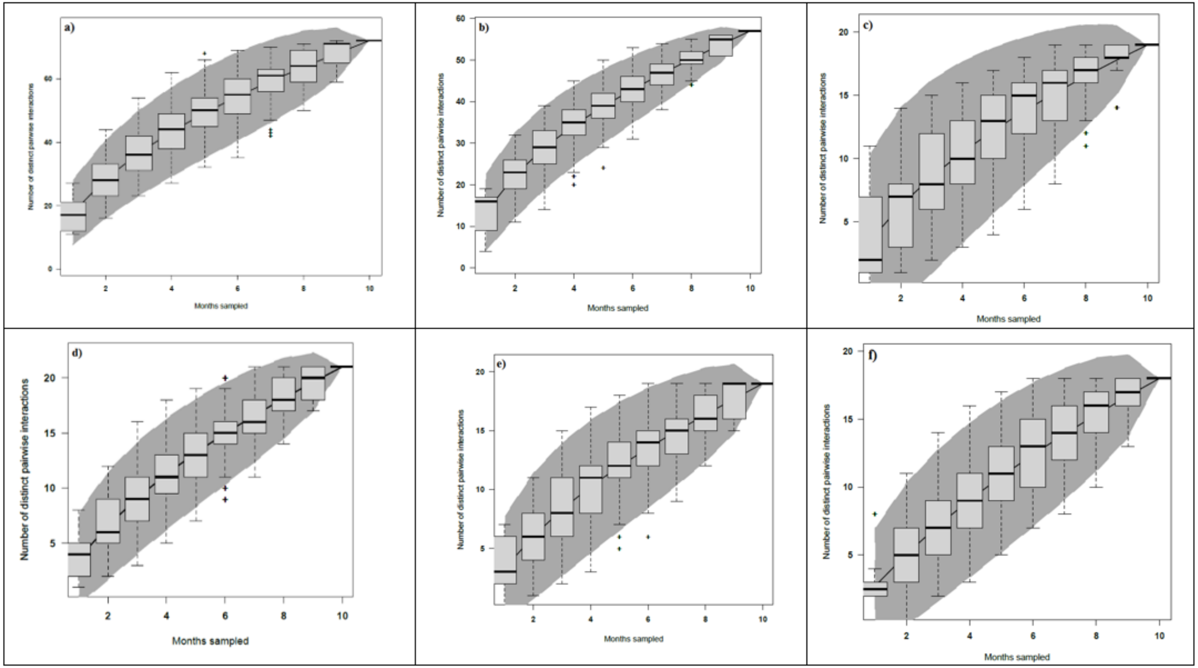
Acronym	Species	Subfamily	Abundance of adults/ nymphs	d’ index (v)	d’ index (r)
Alch	*Alchisme* sp.	Membracinae	1/-	**0.78**	-
Bglo	*Bocydium globuliferum* (Pallas)	Stegaspidinae	342/170	**0.59**	**0.98**
Bmel	*Bolbonota melaena* (Germar)	Membracinae	195/1612	**0.63**	**0.55**
Call	*Calloconophora* sp.	Membracinae	80/125	**0.98**	**0.94**
Cvit	*Ceresa vitulus* Fabricius	Smiliinae	6/-	0.23	0.22
Ccla	*Cyphonia clavata* Fabricius	Smiliinae	405/162	**0.56**	**0.64**
Cclv	*Cyphonia clavigera* Fabricius	Smiliinae	62/-	0.32	0.09
Cfus	*Cyphonia fuscata* Buckton	Smiliinae	1/-	0.28	-
Chir	*Cyphonia hirta* Germar	Smiliinae	30/-	0.47	0.41
Cpun	*Cyphonia punctipennis* Sakakibara	Smiliinae	55/-	0.37	0.29
Ctri	*Cyphonia trifida* Fabricius	Smiliinae	363/19	**0.50**	**0.70**
Cyp1	*Cyphonia* sp. 1	Smiliinae	11/-	0.18	0.09
Cyp2	*Cyphonia* sp. 2	Smiliinae	6/-	0.27	**0.67**
Enc1	*Enchenopa* sp. 1	Membracinae	57/85	0.34	**0.82**

Enc2	*Enchenopa* sp. 2	Membracinae	2/5	**0.82**	0.00
Ench	*Enchophyllum* sp.	Membracinae	1/-	-	0.00
Enty	*Entylia* sp.	Smiliinae	1/26	-	**0.67**
Egib	*Erechtia gibbosa* (De Geer)	Membracinae	9/21	-	**0.94**
Gter	*Germariana terminalis* (Walker)	Darninae	2/-	0.00	-
Hyp	*Hypsoprora* sp.	Membracinae	1/-	0.31	-
Lei1	*Leioscyta* sp. 1	Membracinae	1/-	0.40	-
Lei2	*Leioscyta* sp. 2	Membracinae	1/-	0.40	0.00
Lyc1	*Lycoderes* sp. 1	Stegaspidinae	1/-	0.01	-
Lyc2	*Lycoderes* sp. 2	Stegaspidinae	2/-	0.40	-
Mnig	*Micrutalis nigromarginata* Funkhouser	Smiliinae	5/-	**0.79**	-
Mtri	*Micrutalis tripunctata* (Fairmaire)	Smiliinae	8/-	**0.57**	**1.00**
Nbra	*Notocera brachycera* (Fairmaire)	Membracinae	1/-	0.01	-
Omou	*Ochropepla mourei* (Sakakibara)	Membracinae	129/97	**0.76**	**0.70**
Para	*Paraceresa* sp.	Smiliinae	1/-	0.00	-
Potn	*Potnia* sp.	Membracinae	1/4	**0.68**	-
Tapp	*Talipes appendiculatus* (Fonseca)	Membracinae	1/-	0.31	-
Uspi	*Umbonia spinosa* Fabricius	Membracinae	2/-	0.01	0.00

Appendix 2. List of acronyms, species, families and index of specialisation per species (d’) during vegetative (v) and reproductive (r) phenofase of the host plants in the Atlantic Forest in Santa Catarina, Brazil, in 2013 and 2014. In **bold** are values equal or greater than 0.50.

Acronym	Species	Family	d’ index (v)	d’ index (r)
Acon	*Ageratum conyzoides* L.	Asteraceae	-	**0.71**
Bacc	*Baccharis* sp.	Asteraceae	**0.57**	-
Bano	*Baccharis anomala* DC	Asteraceae	0.09	-
Bcon	*Baccharis conyzoides* (Less.) DC	Asteraceae	0.14	0.46
Cpin	*Calea pinnatifida* (Brown) Banks ex Steudel	Asteraceae	0.24	-
Cony	*Conyza* sp.	Asteraceae	-	0.37
Cbon	*Conyza bonariensis* (L.) Cronquist	Asteraceae	0.49	**0.78**
Emol	*Elephantopus mollis* Kunth	Asteraceae	**0.51**	0.43
Eval	*Erechtites valerianifolia (*Link ex Spreng.) DC	Asteraceae	0.37	0.18
Ecas	*Eupatorium casarettoi* (Rob.) Steyerm	Asteraceae	0.00	0.13
Einu	*Eupatorium inulifolium* Kunth	Asteraceae	0.20	0.37
Elae	*Eupatorium laevigatum* Lam.	Asteraceae	0.31	0.40
Eped	*Eupatorium pedunculosum* Hooker & Amott	Asteraceae	-	0.00
Epic	*Eupatorium picturatum* Malme	Asteraceae	**0.64**	0.47
Eupa	*Eupatorium* sp.	Asteraceae	0.37	-
Mika	*Mikania* sp.	Asteraceae	0.24	0.44
Pbal	*Pterocaulon balansae* Chodat	Asteraceae	0.36	-

Schi	*Solidago chilensis* Meyen	Asteraceae	-	0.45
Vcha	*Vernonia chamissonis* Less.	Asteraceae	0.40	**0.71**
Veri	*Vernonia eriolepis* Gardner	Asteraceae	0.49	0.00
Vsco	*Vernonia scorpioides* (Lam) Pers.	Asteraceae	**0.53**	0.19
Vtwe	*Vernonia tweediana* Baker	Asteraceae	0.26	0.34
Cano	*Cordia anomala*	Boraginaceae	0.34	-
Cmon	*Cordia monosperma* (Jacq.) Roem. & Schult	Boraginaceae	**0.50**	**1.00**
Csca	*Clethra scabra* Pers.	Clethraceae	**0.54**	-
Ggar	*Garcinia gardneriana* (Planch. & Triana) Zappi	Clusiaceae	0.40	**0.76**
Hete	*Heteropterys* sp.	Malpighiaceae	**0.51**	-
Mbim	*Miconia bimucronata* (DC.) Kuntze	Melastomataceae	**0.71**	-
Mcin	*Miconia cinnamomifolia* (DC.) Nand.	Melastomataceae	0.22	0.26
Mico	*Miconia* sp.	Melastomataceae	**0.54**	-
Mlat	*Miconia latecrenata* (DC.) Naudin.	Melastomataceae	0.36	**0.93**
Tpul	*Tibouchina pulchra* Cogn.	Melastomataceae	0.40	-
Ficus	*Ficus* sp.	Moraceae	0.02	-
Morus	*Morus* sp.	Moraceae	0.40	-
Padu	*Piper aduncum* L.	Piperaceae	**1.00**	**0.98**
Tmic	*Trema micrantha* (L.) Blume	Ulmaceae	0.14	-



Appendix 3. Interaction accumulation curves between host plants and treehoppers species in the Brazilian Atlantic Forest, Santa Catarina, Brazil, in 2013 and 2014, during the vegetative phenophase: (a) RPPNCE, (b) PAEST and (c) PNSI, and reproductive phenophase: (d) RPPNCE, (e) PAEST and (f) PNSI.

Capítulo 3..

Structural response of plant-treehopper-ant interactions to anthropogenic changes in protected areas in the Brazilian Atlantic Forest

Artigo submetido ao periódico **Arthropod-Plant Interactions**
(formatação de acordo com os moldes da revista)

Structural response of plant-treehopper-ant interactions to anthropogenic changes in protected areas in the Brazilian Atlantic Forest

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Abstract In the plant-treehopper-ant system, we observe phytophagous insects feeding on the sap of plants (antagonism) while also establishing associations with ants, which can offer protection from natural enemies and parasites (mutualism). Anthropisation is a factor that can change species composition and interactions within ecological communities. Our goal was to determine if the degree of anthropisation could modify the structural properties of antagonistic (plant-treehopper) and mutualistic (ant-treehopper) networks over time in three protected areas in the Brazilian Atlantic Forest. We analysed structural metrics of annual quantitative matrices for each study area with different degrees of environmental disturbance. The topology of the antagonistic and mutualistic networks was described by the indices weighted connectance, nestedness, modularity, specialisation of community H_2’, vulnerability and linkage density. To test if anthropogenic disturbances affect the structural properties of interaction networks over time (per month), we used generalised linear mixed models. Our results show that plant-treehopper networks are more modular and specialised in comparison to ant-treehopper networks in areas with a higher degree of disturbance. In contrast, the values of vulnerability and linkage density of plant-treehopper networks were higher compared to ant-treehopper networks, likely due to the facultative mutualistic nature of this interaction. We conclude that anthropisation affects the two types of interactions studied in different ways, i.e., antagonisms appear to be more vulnerable to environmental disturbances than mutualisms.

Key words Antagonism, anthropisation, ecological networks, facultative mutualism, specialisation, vulnerability.

Introduction

The structure and composition of biological communities are subject to change due to human activities and environmental fragmentation, at both local and landscape levels (Tylianakis et al. 2008; Schüepp et al. 2014; Osorio et al. 2015). These changes may affect the type and strength of interactions between species, resulting in structural changes in interaction networks (Tylianakis et al. 2008). Another process that can contribute to changing the structure is deforestation, which leads to the homogenisation of interactions (Laliberté and Tylianakis 2010). Human action can also affect factors such as abundance, composition and species richness, which consequently can alter properties of networks such as connectance, linkage density, vulnerability, specialisation and diversity of interactions (Blüthgen et al. 2006; Tylianakis et al. 2007; Vázquez et al. 2009). Moreover, we can find different patterns of interaction between species in different environments, i.e., the same species may behave differently in different environments (Tylianakis et al. 2007). Monitoring of human impacts is therefore essential to establishing management strategies and conservation of tropical environments (Gray et al. 2014).

Tropical environments suffer from deforestation and are a good model with which to investigate how ecological interactions are structured in communities (Laliberté and Tylianakis 2010). In the Brazilian Atlantic Forest, we have found an interesting ecological model with which to study these anthropogenic changes: the interactions between host plants, treehoppers and tending-ants (Wood 1993; Lin 2006). In this system, we observe phytophagous insects feeding on the sap of plants (antagonism) while also establishing associations with ants, which can offer protection from natural enemies and parasites (mutualism) (Del-Claro and Oliveira 1999; Lin 2006).

Mutualisms (+/+) are cooperative interactions in which different species benefit from skills combined for mutual benefit (Bronstein et al. 2006; Leigh Jr 2010). Depending on the degree of dependence between the partners, mutualisms can be symbiotic or facultative (Guimarães Jr et al. 2016), promoting asymmetry and networks with a nested structure (Thompson 2006). In a nested network, species with fewer connections interact with subgroups that contain species with the highest number of interactions (Bascompte et al. 2006). Some authors suggest that nestedness confers greater robustness to human disturbance on mutualistic networks, due to asymmetries (Memmott et al. 2004; Piazzon et al. 2011), and this property promotes the coexistence of a large number of species (Bastolla et al. 2009; Thébault and Fontaine

2010). Recent studies indicate, however, that this property does not contribute to an increase in species richness and that is not related to the persistence of these species in the community (James et al. 2012; Strona and Veech 2015).

Similar to mutualisms, antagonistic interactions are related to the degree of intimacy of interaction (Pires and Guimaraes Jr. 2013). Antagonisms (+/-) are compartmentalised interactions which are highly specialised, because these interactions have a greater degree of dependence between the partners, as observed in insect-plant and host-parasite communities (Schädler et al. 2007; Morris et al. 2014). Due to this specialised structure, antagonisms present mechanisms for rapid adaptation to environmental perturbations, because it is simpler reprogram networks with functional subunits than nested mutualistic networks (Clune et al. 2013; Nuwagaba et al. 2015). Herbivorous insects that are more specialised in the plant species they require, however, are more vulnerable to extinction if their hosts have a higher probability of being deleted from the environment (Moir et al. 2011).

Our study aims to assess how much the metrics of networks such as the plant-treehopper-ant system can be changed by the degree of human disturbance in three Atlantic Forest areas in southern Brazil. Our hypothesis is that in areas with a higher degree of environmental disturbance, the mutualistic networks are highly nested and antagonistic networks have a specialised and modular structure, when compared to preserved areas. Specifically, in this study, we aimed to answer the following questions: (1) Does the topology of ant-treehopper and plant-treehopper networks differ between the three study areas with different levels of anthropisation? (2) Does the higher degree of human disturbance promote specialisation and vulnerability of plant-treehopper networks? (3) Do areas with less disturbance contribute to the establishment of a greater number of interactions between species of host plants, treehoppers and tending-ants, and, consequently, lead to more robust interaction networks?

Material and Methods

Study sites, data and specimen collection

We selected three study sites in the Atlantic Forest in Santa Catarina State, Southern Brazil: (1) Parque Estadual da Serra do Tabuleiro (PAEST), in Santo Amaro da Imperatriz (27° 43.708’S, 48° 48.493’W, 84,000 ha); (2) Parque Nacional da Serra do Itajaí (PNSI), in Blumenau (27° 03.442’S, 49° 05.280’W, 57,000 ha); and (3) Reserva Particular do

Patrimônio Natural Chácara Edith (RPPNCE), in Brusque (27° 05.959'S, 48° 53.550'W, 510 ha).

The region encompassing the areas that were studied is within the phytogeographic area of the Atlantic Forest and the main vegetation consists of large perennial trees, palms, epiphytes and lianas (Roderjan and Kuniyosshi 1988). The climate in this region is subtropical humid (Cf), which is moderately hot and wet with no distinguishable dry season, according to the Köppen classification system (Alvares et al. 2013). Annual temperature means range from 18°C to 22°C, while rainfall varies between 1,600 mm and 1,900 mm in areas below 700 m (PAEST and RPPNCE), and between 2,200 mm and 2,500 mm in areas at higher altitudes (PNSI) (Pandolfo et al. 2002; Alvares et al. 2013).

In PAEST (Fig. 1a), we observed a high degree of human disturbance, as there are developments of the Hotel Caldas da Imperatriz in this protected area (PA). This is the largest and oldest PA of Santa Catarina, occupying approximately 1% of the territory of the State (Vitali and Uhlig 2010). Ecotourism activities are practiced in this area, which has pavement, as well as hiking for tourists on the main trail, recreation and leisure activities during holidays and weekends (Soldateli 2003). The PNSI (Fig. 1b) has an intermediate degree of human disturbance, because in this area there are buildings next to the headquarters, and a part of the area was used for recreation and leisure for visitors before officially becoming a PA in 2009 (MMA and ICMBio 2009). At this study site, public visitation generally has several impacts, such as accumulation of garbage, fishing and the capture of wild animals without authorisation (MMA and ICMBio 2009). RPPNCE (Fig. 1c) is considered to be the most preserved area because of historical protection since the creation of the reserve in the 1930s (Adami 2002). In this PA, visits are carried out in a controlled way, such as conducted educational activities for students from the city of Brusque and nearby cities, as well as research activities of universities and industry events organised by institutions and trade in the region (MMA and ICMBio 2011).

In the first year of sampling (2013), field observations were carried out from January to April and from October to December. In the second year of sampling (2014), observations occurred between January and April only. We collected data weekly along transects outlined by previously existing trails, between the hours of 8h00 and 16h00. We determined six transects (1 km × 3 m) per reserve (18 in total) uniformly distributed along the same trail, every 500 m. These sets of transects were considered to be independent samples of plants, treehoppers and ants, producing a distinct interaction network for each surveyed area. For each year of sampling, we produced structure proprieties for each interaction (antagonistic and mutualistic). Antagonistic interactions consisted of individual observations made each time a treehopper (adult or nymph) was seen feeding on the host plant, or when adults were observed with the presence of eggs and/or nymphs. Mutualisms consisted of individual observations made every time an ant was seen feeding on honeydew produced by treehoppers.

We sampled ants and treehoppers from all field expeditions. Ants were collected manually with brushes and stored in 70% alcohol for later identification. Treehoppers were manually collected with falcon tubes and killed with killing jars containing ethyl ether. After being properly processed and labelled, insect and plant vouchers were deposited in the Universidade Federal de Santa Catarina, in Florianópolis, Brazil (Coleção Entomológica, Departamento de Ecologia e Zoologia; Herbário Flor, Departamento de Botânica).

Topology of interaction networks

In the antagonistic and mutualistic networks presented here, nodes indicate the species of treehoppers/plants or ants/treehoppers and links between them correspond to the frequency of interactions, i.e., the number of times a treehopper species *t* was observed feeding on a plant species *p* or on aggregations in a plant species, or the number of times a species of ant *a* was observed feeding on honeydew produced by treehopper *t*. In order to estimate the structural patterns among these species, we assembled quantitative matrices. Antagonisms describe the interactions between plant (rows) and treehopper species (columns) b_{pt}, whereas mutualisms describe the interactions between ant species (rows) and treehoppers (columns) b_{at}. The community structure has been described based on several metrics, which are specified below.

In order to describe the structure of our plant-treehopper and ant-treehopper networks, we determined the weighted connectance (C); the degree of nestedness, measured according to the WNODF (Weighted Nestedness metric based on Overlap and Decreasing Fill) proposed by Almeida-Neto and Ulrich (2011); and weighted modularity Q, following the methods of Dormann and Strauss (2014), using the networklevel and computemodules functions in the bipartite package (Dormann et al. 2009) of software R version 3.2.3 (R Core Team 2016). WNODF values were normalised within the interval of zero to 100, ranging from zero to maximum nestedness. Modularity Q varied between zero (no modules within the network) and one (all modules in the network were mutually exclusive).

To describe the topology of the networks, we calculated the following structural properties: web asymmetry; links per species (sum of links divided by number of species); linkage density (marginal totals-weighted diversity of interactions per species); vulnerability; robustness; and interaction evenness in the bipartite package for software R. We also used the same package to assess the degree of specialisation of networks using the H_2' index (Blüthgen et al. 2006). This index characterises the degree of compartmentalisation between the two parts of the entire network (community). This quantitative index is derived from the Shannon entropy, which ranges from zero (extreme generalisation) to one (extreme specialisation) (Blüthgen et al. 2007).

Statistical analysis

A Z-test was performed to test the significance of network metrics WNODF and Q. The values of all metrics in randomisations were used to determine the Z-score, which is the number of standard deviations from a reference point above the mean of 100 randomised networks. Z-score values equal to or greater than two were considered significantly nested or modular (Blüthgen et al. 2006; Almeida-Neto and Ulrich 2011; Dormann and Strauss 2014). The statistical significance of the H_2' index was assessed by Monte Carlo simulation with 10,000 iterations, using the Patefield’s algorithm (Patefield 1981).

Finally, to see if the degree of anthropisation of the study sites changed the structure of antagonistic and mutualistic networks, we used generalised linear mixed models (GLMM) with the negative binomial function. We treated the metrics of networks as the response variable and the time (per month) with fixed effect in the study sites with higher (PAEST) and lower degree (RPPNCE) of human disturbance as the explanatory variable (adapted from Geslin et al. 2013). We applied GLMM with the package lmer (Bates et al. 2015) in software R. To evaluate these interactions, we selected the seven following structural metrics: links per species, linkage density, interaction evenness, H_2' index, robustness of higher species (ants/treehoppers), robustness of lower species (plants/treehoppers) and vulnerability of lower species. These properties were selected because they indicate the fragility and robustness of interaction networks, indicating how the topology of antagonistic and mutualistic can be affected by environmental disturbance.

Results

Structure of antagonistic networks (plant-treehopper)

In both years of data collection in PAEST, we observed that plant-treehopper networks were significantly modular (2013: Q = 0.51; 2014: Q = 0.50, both Z > 2), with the number of modules ranging between five and six, and specialised (2013: H_2'= 0.54; 2014: H_2'= 0.68, both P < 0.0001). In PNSI, values of modularity were significantly higher (2013: Q = 0.54; 2014: Q = 0.63, both Z > 2), with the number of modules between four and seven, and community-level specialisation (2013: H_2'= 0.56; 2014: H_2'= 0.70, both P < 0.0001), when compared to PAEST. In RPPNCE, antagonistic networks had significantly lower values of modularity (2013: Q = 0.35; 2014: Q = 0.42, both Z > 2), ranging from three to four modules, and high specialisation of the community for both years of sampling (2013: H_2'= 0.69; 2014: H_2'= 0.62, both P < 0.0001), when compared to the other two study sites (Table 1). In all studied areas, the networks possessed low weighted connectance values (C = 0.07 to 0.16) and were not significantly nested (WNODF = 10.49 to 27.25, all Z < 2) (Table 1). The mean number of links per species was 1.34 and linkage density was 2.60 between species of plants and treehoppers, and the vulnerability of networks was higher in disturbed areas (Table 1).

Structure of mutualistic networks (ant-treehopper)

In PAEST, ant-treehopper networks had a significantly modular structure in both years of data collection (2013: Q = 0.33; 2014: Q = 0.23, both Z > 2), with the number of modules ranging from four to six, but there was significant specialisation in the studied community only in 2013 (H_2'= 0.34, P < 0.0001). In PNSI, the community was modular (2013: Q = 0.38; 2014: Q = 0.29, both Z > 2) and specialised (2013: H_2'= 0.51; 2014: H_2'= 0.31, both P < 0.0001) in relation to the expectation of null models. In RPPNCE, we observed significantly higher specialisation only in 2013 (H_2' = 0.48, P < 0.0001) and significant modularity values (2013: Q = 0.42; 2014: Q = 0.17, both Z > 2) for the community (Table 2). At all study sites, mutualistic networks had higher weighted connectance values (C = 0.13 to 0.21) and nestedness (WNODF = 16.75 to 39.28, all Z < 2) than did antagonistic networks (Table 2). The mean number of links per species was 1.14 and the mean linkage density between ants and treehoppers species was 3.29, higher than that observed in plant-treehopper networks (Table 2). Moreover, there was a greater annual variation in vulnerability of mutualistic networks (Table 2).

Generalised linear mixed models

The degree of anthropisation in the study sites affected interactions differently. Over time, the following metrics of plant-treehopper antagonistic networks were significantly affected by the degree of environmental disturbance: links per species (GLMM, AIC = 51.6, P = 0.09), robustness of species of treehoppers (GLMM, AIC = 47.8, P = 0.02) and vulnerability of species of plants (GLMM, AIC = 51.6, P = 0.07) (Appendix 1). The structural properties of the ant-treehopper mutualistic networks were not significantly affected by human disturbance of study areas (Appendix 2).

Discussion

Our hypothesis, that in areas with a higher degree of human disturbance, the mutualistic networks are highly nested and antagonistic networks have a specialised and modular structure, was corroborated in part, because we observed that antagonistic networks were more modular and specialised than were mutualistic networks in areas with a higher degree of anthropisation. The structure of ant-treehopper networks were non-nested and showed low values of modularity and specialisation of the community.

The structures of plant-treehopper and ant-treehopper networks showed different patterns in relation to the different levels of anthropisation in the studied areas. This difference can be explained by the structure of the interaction, because antagonistic networks are more compartmentalised than mutualistic ones, and this topology can contribute to the persistence of food webs (Bascompte 2010; Stouffer and Bascompte 2011). In the most disturbed areas (PAEST and PNSI), we observed an increase in vulnerability of antagonistic interactions when compared to most preserved area (RPPNCE). In addition, properties such as modularity and specialisation of networks were significantly higher in all study sites. One explanation for higher specialisation values of plant-treehopper networks is that sap-sucking insects generally use herbaceous and shrubby plants as a resource, are more common in disturbed areas, and have a preference for certain morphological parts, such as apical meristems, leaf veins and inflorescences (Wood 1993; Lopes 1995; Lin 2006).

Our plant-treehopper networks showed a structure typically found in other antagonistic interactions, such as host-parasite and plant-herbivore (Maunsell et al. 2015; Osorio et al. 2015; Poulin et al. 2016). Antagonistic networks have a topology that is essentially specialised, because herbivores co-evolved with their host plants, which developed defence strategies (such as trichomes and chemical compounds) to repel the action of insects (Fürstenberg-Hägg et al. 2013). The intimacy between treehoppers and host plants (Guimarães Jr et al. 2016) may explain the specialised and modular structure of the plant-treehopper interaction network.

Considering the level of specialisation of herbivores, we can point out that antagonistic networks are more vulnerable to habitat loss (Cagnolo et al. 2009) than mutualistic ones. The specialised structure of these trophic interactions in the Atlantic Forest was more sensitive to human disturbance and, therefore, antagonisms appear to be more fragile than mutualistic interactions. The GLMM analysis showed that three properties of antagonistic plant-treehopper networks have changed over time in relation to the degree of anthropisation: links per species, robustness of treehoppers and vulnerability of plants. These network properties may change due to antagonistic interactions presenting a greater fragility compared to facultative mutualism because antagonisms are symbiotic interactions (Pires and Guimarães Jr. 2013). In our study, the species of herbivores and plants were directly affected by the degree of anthropisation, so the antagonistic networks were apparently more vulnerable and susceptible to loss of species and links, because they are specialised interactions (Ramírez-Flores et al. 2015). Indeed, generalist species are less vulnerable, because they have more interactions with other species, so the loss of a link has a smaller effect than it would for specialist species that are less connected (Montoya et al. 2009). Robustness is a metric that is highly sensitive to sampling completeness (Kaiser-Bunbury et al. 2010; Tylianakis et al. 2010) and is related to network generalisation (Pocock et al. 2012); thus symbiotic mutualistic interactions appear to be more fragile to species extinction (Bartomeus 2013).

Our ant-treehopper mutualistic networks were not significantly nested, likely because we used quantitative matrices to describe the topology of these interactions. This non-nested pattern has been observed in other studies about mutualism structure (Staniczenko et al. 2013; Dáttilo et al. 2014; Cuartas-Hernández and Medel 2015; Robinson et al. 2015), which point out empirically that this property does not increase species richness and persistence of these interactions (James et al. 2012; Strona and Veech 2015). On the other hand, the vulnerability of ant-treehopper networks did not show a pattern well established in all study sites, therefore this property does not appear to be altered by the degree of anthropisation. Because the mutualism studied here was facultative (Lin 2006), the community of tending-ants and treehoppers was not modular or specialised.

The ant-treehopper networks studied here showed a less specialised and vulnerable structure in comparison to plant-treehopper networks. In ant-plant-treehopper systems in the Brazilian Cerrado, Fagundes et al. (2016) observed that ant-treehopper interactions are a subset of the associations between extrafloral nectaries, tending-ants and ant-treehopper networks exhibiting low nestedness and high specialisation. In the Brazilian Atlantic Forest, Gadelha et al. (2016) observed that the structure of mutualism between ants and treehoppers was extremely compartmentalised, but with low values of specialisation. Ants therefore interact differently with plants than they do with other insects (Fagundes et al. 2016).

Our results show that human disturbance can affect the structure of ecological interaction networks in the Atlantic Forest differently. Antagonisms appear to be more susceptible to habitat loss, because they are more specialised and modular interactions compared to facultative mutualism, whereas mutualisms can be considered more robust due to the topology of interaction networks being less vulnerable and specialised. The conservation and management of studied communities can provide useful information for establishing public politics to develop optimal conservation strategies, especially as that is one of the goals of protected areas. More studies involving the description of the structure of ecological networks in relation to anthropogenic factors are key to increasing knowledge of how interactions can be affected within an ecological community.

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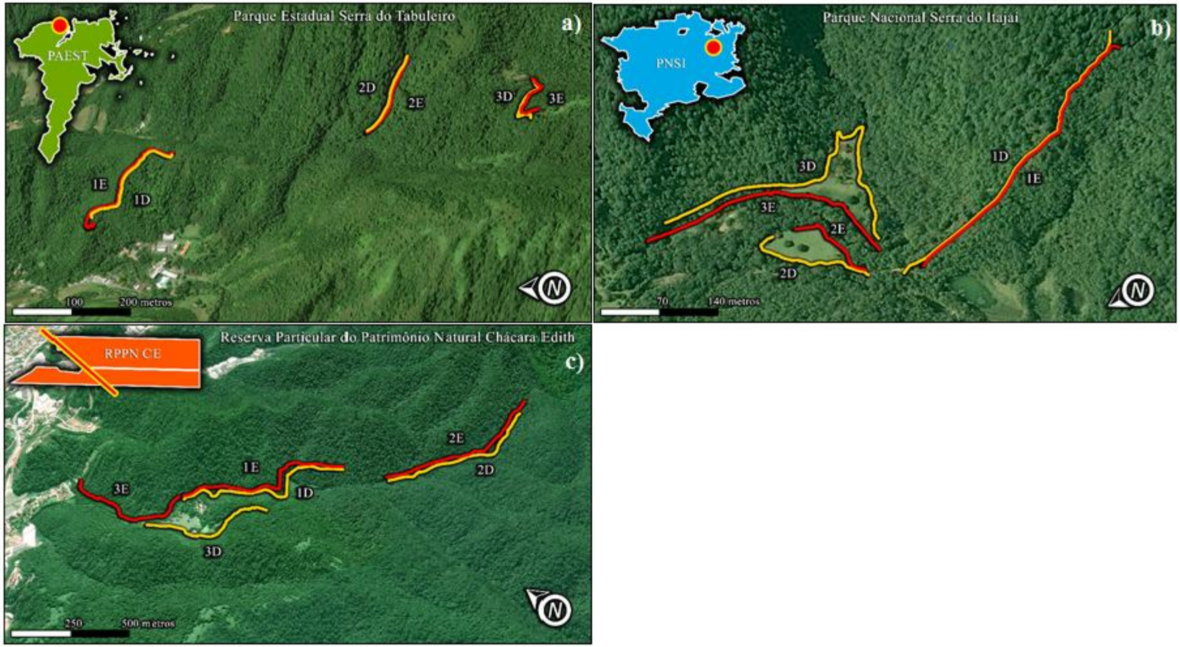
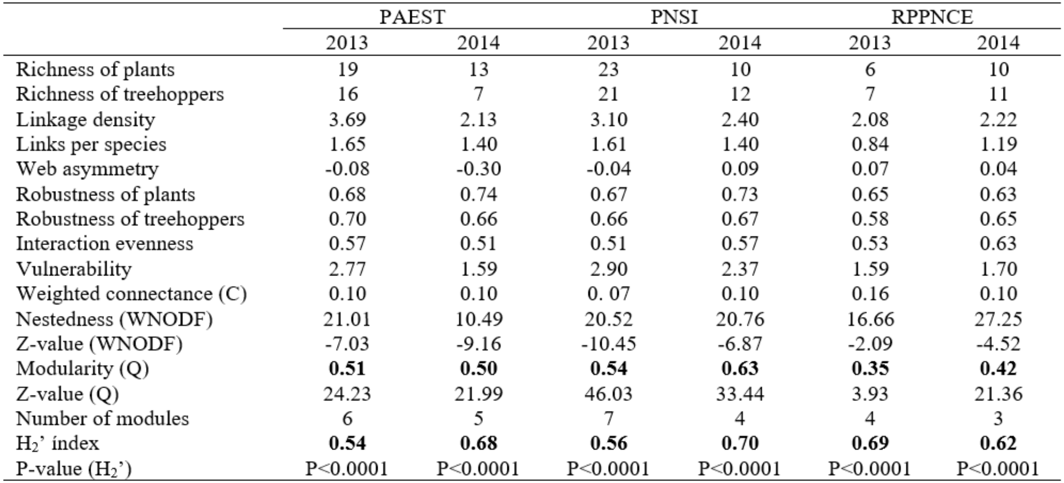


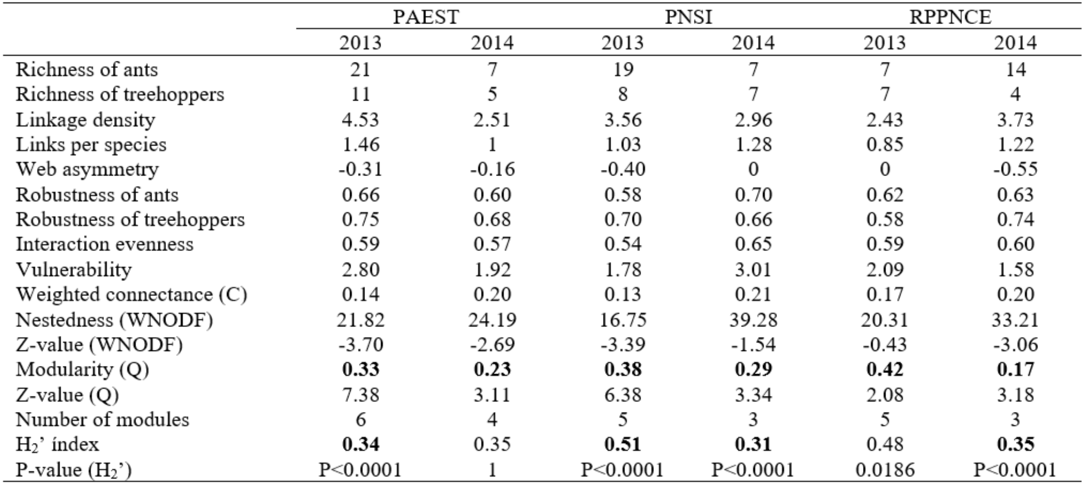
Fig. 1 Maps of transects of study areas in Santa Catarina, Brazil, in 2013 and 2014: a) Parque Estadual da Serra do Tabuleiro (PAEST), b) Parque Nacional da Serra do Itajaí (PNSI) and c) Reserva Particular do Patrimônio Natural Chácara Edith (RPPNCE). Numbers with inicial D or/and E corresponding to existing trails used for sampling

Table 1 Richness and descriptors of antagonistic networks between plants and treehoppers in three study areas with different levels of anthropisation in the Brazilian Atlantic Forest, Santa Catarina, Brazil, in 2013 and 2014. Study sites: PAEST (Parque Estadual da Serra do Tabuleiro), PNSI (Parque Nacional da Serra do Itajaí) and RPPNCE (Reserva Particular do Patrimônio Natural Chácara Edith). Significant values are highlighted in **bold**



	PAEST		PNSI		RPPNCE	
	2013	2014	2013	2014	2013	2014
Richness of plants	19	13	23	10	6	10
Richness of treehoppers	16	7	21	12	7	11
Linkage density	3.69	2.13	3.10	2.40	2.08	2.22
Links per species	1.65	1.40	1.61	1.40	0.84	1.19
Web asymmetry	-0.08	-0.30	-0.04	0.09	0.07	0.04
Robustness of plants	0.68	0.74	0.67	0.73	0.65	0.63
Robustness of treehoppers	0.70	0.66	0.66	0.67	0.58	0.65
Interaction evenness	0.57	0.51	0.51	0.57	0.53	0.63
Vulnerability	2.77	1.59	2.90	2.37	1.59	1.70
Weighted connectance (C)	0.10	0.10	0. 07	0.10	0.16	0.10
Nestedness (WNODF)	21.01	10.49	20.52	20.76	16.66	27.25
Z-value (WNODF)	-7.03	-9.16	-10.45	-6.87	-2.09	-4.52
Modularity (Q)	**0.51**	**0.50**	**0.54**	**0.63**	**0.35**	**0.42**
Z-value (Q)	24.23	21.99	46.03	33.44	3.93	21.36
Number of modules	6	5	7	4	4	3
H_2’ índex	**0.54**	**0.68**	**0.56**	**0.70**	**0.69**	**0.62**
P-value (H_2’)	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001

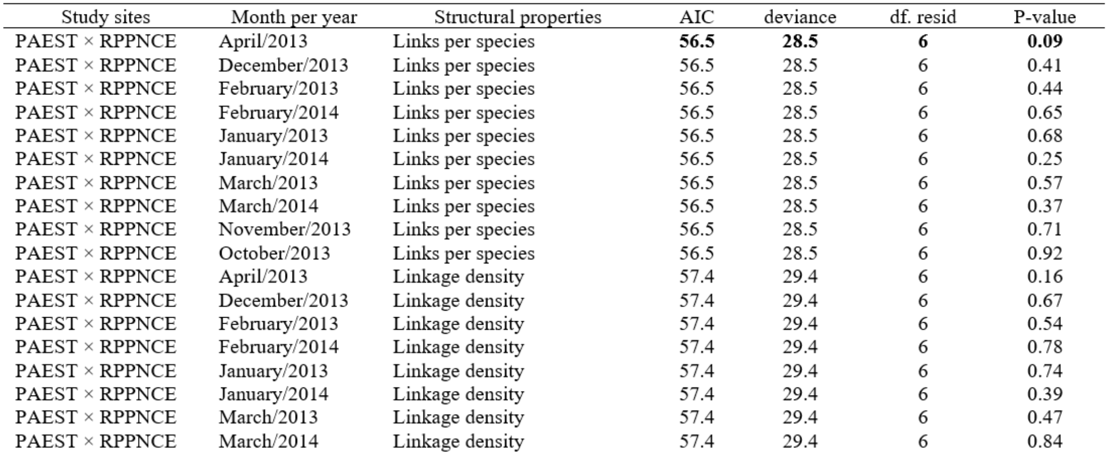
Table 2 Richness and descriptors of mutualistic networks between tending-ants and treehoppers in three study areas with different levels of anthropisation in the Brazilian Atlantic Forest, Santa Catarina, Brazil, in 2013 and 2014. Study sites: PAEST (Parque Estadual da Serra do Tabuleiro), PNSI (Parque Nacional da Serra do Itajaí) and RPPNCE (Reserva Particular do Patrimônio Natural Chácara Edith). Significant values are highlighted in **bold**



	PAEST		PNSI		RPPNCE	
	2013	2014	2013	2014	2013	2014
Richness of ants	21	7	19	7	7	14
Richness of treehoppers	11	5	8	7	7	4
Linkage density	4.53	2.51	3.56	2.96	2.43	3.73
Links per species	1.46	1	1.03	1.28	0.85	1.22
Web asymmetry	-0.31	-0.16	-0.40	0	0	-0.55
Robustness of ants	0.66	0.60	0.58	0.70	0.62	0.63
Robustness of treehoppers	0.75	0.68	0.70	0.66	0.58	0.74
Interaction evenness	0.59	0.57	0.54	0.65	0.59	0.60
Vulnerability	2.80	1.92	1.78	3.01	2.09	1.58
Weighted connectance (C)	0.14	0.20	0.13	0.21	0.17	0.20
Nestedness (WNODF)	21.82	24.19	16.75	39.28	20.31	33.21
Z-value (WNODF)	-3.70	-2.69	-3.39	-1.54	-0.43	-3.06
Modularity (Q)	**0.33**	**0.23**	**0.38**	**0.29**	**0.42**	**0.17**
Z-value (Q)	7.38	3.11	6.38	3.34	2.08	3.18
Number of modules	6	4	5	3	5	3
H_2’ índex	**0.34**	0.35	**0.51**	**0.31**	0.48	**0.35**
P-value (H_2’)	P<0.0001	1	P<0.0001	P<0.0001	0.0186	P<0.0001

Supporting Information

Appendix 1 Summary of generalised linear mixed model (GLMM) of the effect of antropisation on structural properties of antagonistic networks between plants and treehoppers in two study sites with higher (PAEST) and lower level (RPPNCE) of perturbation. Study sites: PAEST (Parque Estadual da Serra do Tabuleiro) and RPPNCE (Reserva Particular do Patrimônio Natural Chácara Edith). Significant values are highlighted in **bold**



Study sites	Month per year	Structural properties	AIC	deviance	df. resid	P-value
PAEST × RPPNCE	April/2013	Links per species	**56.5**	**28.5**	**6**	**0.09**
PAEST × RPPNCE	December/2013	Links per species	56.5	28.5	6	0.41
PAEST × RPPNCE	February/2013	Links per species	56.5	28.5	6	0.44
PAEST × RPPNCE	February/2014	Links per species	56.5	28.5	6	0.65
PAEST × RPPNCE	January/2013	Links per species	56.5	28.5	6	0.68
PAEST × RPPNCE	January/2014	Links per species	56.5	28.5	6	0.25
PAEST × RPPNCE	March/2013	Links per species	56.5	28.5	6	0.57
PAEST × RPPNCE	March/2014	Links per species	56.5	28.5	6	0.37
PAEST × RPPNCE	November/2013	Links per species	56.5	28.5	6	0.71
PAEST × RPPNCE	October/2013	Links per species	56.5	28.5	6	0.92
PAEST × RPPNCE	April/2013	Linkage density	57.4	29.4	6	0.16
PAEST × RPPNCE	December/2013	Linkage density	57.4	29.4	6	0.67
PAEST × RPPNCE	February/2013	Linkage density	57.4	29.4	6	0.54
PAEST × RPPNCE	February/2014	Linkage density	57.4	29.4	6	0.78
PAEST × RPPNCE	January/2013	Linkage density	57.4	29.4	6	0.74
PAEST × RPPNCE	January/2014	Linkage density	57.4	29.4	6	0.39
PAEST × RPPNCE	March/2013	Linkage density	57.4	29.4	6	0.47
PAEST × RPPNCE	March/2014	Linkage density	57.4	29.4	6	0.84

PAEST × RPPNCE	November/2013	Linkage density	57.4	29.4	6	0.40
PAEST × RPPNCE	October/2013	Linkage density	57.4	29.4	6	0.70
PAEST × RPPNCE	April/2013	Interaction evenness	61.1	33.1	6	0.18
PAEST × RPPNCE	December/2013	Interaction evenness	61.1	33.1	6	0.80
PAEST × RPPNCE	February/2013	Interaction evenness	61.1	33.1	6	0.73
PAEST × RPPNCE	February/2014	Interaction evenness	61.1	33.1	6	0.71
PAEST × RPPNCE	January/2013	Interaction evenness	61.1	33.1	6	0.89
PAEST × RPPNCE	January/2014	Interaction evenness	61.1	33.1	6	0.56
PAEST × RPPNCE	March/2013	Interaction evenness	61.1	33.1	6	0.47
PAEST × RPPNCE	March/2014	Interaction evenness	61.1	33.1	6	0.89
PAEST × RPPNCE	November/2013	Interaction evenness	61.1	33.1	6	0.63
PAEST × RPPNCE	October/2013	Interaction evenness	61.1	33.1	6	0.86
PAEST × RPPNCE	April/2013	H_2’ índex	59.7	31.7	6	0.67
PAEST × RPPNCE	December/2013	H_2’ índex	59.7	31.7	6	0.93
PAEST × RPPNCE	February/2013	H_2’ índex	59.7	31.7	6	0.74
PAEST × RPPNCE	February/2014	H_2’ índex	59.7	31.7	6	0.84
PAEST × RPPNCE	January/2013	H_2’ índex	59.7	31.7	6	0.83
PAEST × RPPNCE	January/2014	H_2’ índex	59.7	31.7	6	0.64
PAEST × RPPNCE	March/2013	H_2’ índex	59.7	31.7	6	0.59
PAEST × RPPNCE	March/2014	H_2’ índex	59.7	31.7	6	0.96
PAEST × RPPNCE	November/2013	H_2’ índex	59.7	31.7	6	0.60
PAEST × RPPNCE	October/2013	H_2’ índex	59.7	31.7	6	0.73
PAEST × RPPNCE	April/2013	Robustness of treehoppers	**47.8**	**19.8**	**6**	**0.02**
PAEST × RPPNCE	December/2013	Robustness of treehoppers	47.8	19.8	6	0.82
PAEST × RPPNCE	February/2013	Robustness of treehoppers	47.8	19.8	6	0.72
PAEST × RPPNCE	February/2014	Robustness of treehoppers	47.8	19.8	6	0.81
PAEST × RPPNCE	January/2013	Robustness of treehoppers	47.8	19.8	6	0.96
PAEST × RPPNCE	January/2014	Robustness of treehoppers	47.8	19.8	6	0.61

PAEST × RPPNCE	March/2013	Robustness of treehoppers	47.8	19.8	6	0.76
PAEST × RPPNCE	March/2014	Robustness of treehoppers	47.8	19.8	6	0.90
PAEST × RPPNCE	November/2013	Robustness of treehoppers	47.8	19.8	6	0.80
PAEST × RPPNCE	October/2013	Robustness of treehoppers	47.8	19.8	6	0.36
PAEST × RPPNCE	April/2013	Robustness of plants	57.8	29.8	6	0.38
PAEST × RPPNCE	December/2013	Robustness of plants	57.8	29.8	6	0.70
PAEST × RPPNCE	February/2013	Robustness of plants	57.8	29.8	6	0.77
PAEST × RPPNCE	February/2014	Robustness of plants	57.8	29.8	6	0.73
PAEST × RPPNCE	January/2013	Robustness of plants	57.8	29.8	6	0.95
PAEST × RPPNCE	January/2014	Robustness of plants	57.8	29.8	6	0.53
PAEST × RPPNCE	March/2013	Robustness of plants	57.8	29.8	6	0.81
PAEST × RPPNCE	March/2014	Robustness of plants	57.8	29.8	6	0.91
PAEST × RPPNCE	November/2013	Robustness of plants	57.8	29.8	6	0.79
PAEST × RPPNCE	October/2013	Robustness of plants	57.8	29.8	6	0.91
PAEST × RPPNCE	April/2013	Vulnerability of plants	**51.6**	**23.6**	**6**	**0.07**
PAEST × RPPNCE	December/2013	Vulnerability of plants	51.6	23.6	6	0.80
PAEST × RPPNCE	February/2013	Vulnerability of plants	51.6	23.6	6	0.59
PAEST × RPPNCE	February/2014	Vulnerability of plants	51.6	23.6	6	0.92
PAEST × RPPNCE	January/2013	Vulnerability of plants	51.6	23.6	6	0.78
PAEST × RPPNCE	January/2014	Vulnerability of plants	51.6	23.6	6	0.47
PAEST × RPPNCE	March/2013	Vulnerability of plants	51.6	23.6	6	0.58
PAEST × RPPNCE	March/2014	Vulnerability of plants	51.6	23.6	6	0.80
PAEST × RPPNCE	November/2013	Vulnerability of plants	51.6	23.6	6	0.59
PAEST × RPPNCE	October/2013	Vulnerability of plants	51.6	23.6	6	0.33

Appendix 2 Summary of generalised linear mixed model (GLMM) of the effect of antropisation on structural properties of mutualistic networks between ants and treehoppers in two study sites with higher (PAEST) and lower level (RPPNCE) of perturbation. Study sites: PAEST (Parque Estadual da Serra do Tabuleiro) and RPPNCE (Reserva Particular do Patrimônio Natural Chácara Edith). Significant values are highlighted in **bold**

Study sites	Month per year	Structural properties	AIC	deviance	df. resid	P-value
PAEST × RPPNCE	April/2013	Links per species	57.9	29.9	6	0.36
PAEST × RPPNCE	December/2013	Links per species	57.9	29.9	6	0.86
PAEST × RPPNCE	February/2013	Links per species	57.9	29.9	6	0.95
PAEST × RPPNCE	February/2014	Links per species	57.9	29.9	6	0.92
PAEST × RPPNCE	January/2013	Links per species	57.9	29.9	6	0.81
PAEST × RPPNCE	January/2014	Links per species	57.9	29.9	6	0.64
PAEST × RPPNCE	March/2013	Links per species	57.9	29.9	6	0.92
PAEST × RPPNCE	March/2014	Links per species	57.9	29.9	6	0.93
PAEST × RPPNCE	November/2013	Links per species	57.9	29.9	6	0.78
PAEST × RPPNCE	October/2013	Links per species	57.9	29.9	6	0.53
PAEST × RPPNCE	April/2013	Linkage density	56.2	28.2	6	0.35
PAEST × RPPNCE	December/2013	Linkage density	56.2	28.2	6	0.76
PAEST × RPPNCE	February/2013	Linkage density	56.2	28.2	6	0.78
PAEST × RPPNCE	February/2014	Linkage density	56.2	28.2	6	0.95
PAEST × RPPNCE	January/2013	Linkage density	56.2	28.2	6	0.79
PAEST × RPPNCE	January/2014	Linkage density	56.2	28.2	6	0.58
PAEST × RPPNCE	March/2013	Linkage density	56.2	28.2	6	0.93
PAEST × RPPNCE	March/2014	Linkage density	56.2	28.2	6	0.84
PAEST × RPPNCE	November/2013	Linkage density	56.2	28.2	6	0.90

PAEST × RPPNCE	October/2013	Linkage density	56.2	28.2	6	0.71
PAEST × RPPNCE	April/2013	Interaction evenness	57.6	29.6	6	0.58
PAEST × RPPNCE	December/2013	Interaction evenness	57.6	29.6	6	0.68
PAEST × RPPNCE	February/2013	Interaction evenness	57.6	29.6	6	0.64
PAEST × RPPNCE	February/2014	Interaction evenness	57.6	29.6	6	0.85
PAEST × RPPNCE	January/2013	Interaction evenness	57.6	29.6	6	0.43
PAEST × RPPNCE	January/2014	Interaction evenness	57.6	29.6	6	0.96
PAEST × RPPNCE	March/2013	Interaction evenness	57.6	29.6	6	0.87
PAEST × RPPNCE	March/2014	Interaction evenness	57.6	29.6	6	0.45
PAEST × RPPNCE	November/2013	Interaction evenness	57.6	29.6	6	0.75
PAEST × RPPNCE	October/2013	Interaction evenness	57.6	29.6	6	0.84
PAEST × RPPNCE	April/2013	H_2’ índex	59.5	31.5	6	0.20
PAEST × RPPNCE	December/2013	H_2’ índex	59.5	31.5	6	0.44
PAEST × RPPNCE	February/2013	H_2’ índex	59.5	31.5	6	0.41
PAEST × RPPNCE	February/2014	H_2’ índex	59.5	31.5	6	0.49
PAEST × RPPNCE	January/2013	H_2’ índex	59.5	31.5	6	0.71
PAEST × RPPNCE	January/2014	H_2’ índex	59.5	31.5	6	0.54
PAEST × RPPNCE	March/2013	H_2’ índex	59.5	31.5	6	0.88
PAEST × RPPNCE	March/2014	H_2’ índex	59.5	31.5	6	0.38
PAEST × RPPNCE	November/2013	H_2’ índex	59.5	31.5	6	0.46
PAEST × RPPNCE	October/2013	H_2’ índex	59.5	31.5	6	0.84
PAEST × RPPNCE	April/2013	Robustness of treehoppers	54.0	26.0	6	0.52
PAEST × RPPNCE	December/2013	Robustness of treehoppers	54.0	26.0	6	0.51
PAEST × RPPNCE	February/2013	Robustness of treehoppers	54.0	26.0	6	0.46
PAEST × RPPNCE	February/2014	Robustness of treehoppers	54.0	26.0	6	0.71
PAEST × RPPNCE	January/2013	Robustness of treehoppers	54.0	26.0	6	0.51
PAEST × RPPNCE	January/2014	Robustness of treehoppers	54.0	26.0	6	0.93
PAEST × RPPNCE	March/2013	Robustness of treehoppers	54.0	26.0	6	0.59
PAEST × RPPNCE	March/2014	Robustness of treehoppers	54.0	26.0	6	0.44

PAEST × RPPNCE	November/2013	Robustness of treehoppers	54.0	26.0	6	0.92
PAEST × RPPNCE	October/2013	Robustness of treehoppers	54.0	26.0	6	0.69
PAEST × RPPNCE	April/2013	Robustness of ants	59.7	31.7	6	0.71
PAEST × RPPNCE	December/2013	Robustness of ants	59.7	31.7	6	0.93
PAEST × RPPNCE	February/2013	Robustness of ants	59.7	31.7	6	0.74
PAEST × RPPNCE	February/2014	Robustness of ants	59.7	31.7	6	0.65
PAEST × RPPNCE	January/2013	Robustness of ants	59.7	31.7	6	0.75
PAEST × RPPNCE	January/2014	Robustness of ants	59.7	31.7	6	0.84
PAEST × RPPNCE	March/2013	Robustness of ants	59.7	31.7	6	0.78
PAEST × RPPNCE	March/2014	Robustness of ants	59.7	31.7	6	0.60
PAEST × RPPNCE	November/2013	Robustness of ants	59.7	31.7	6	0.70
PAEST × RPPNCE	October/2013	Robustness of ants	59.7	31.7	6	0.63
PAEST × RPPNCE	April/2013	Vulnerability of ants	52.0	24.0	6	0.23
PAEST × RPPNCE	December/2013	Vulnerability of ants	52.0	24.0	6	0.65
PAEST × RPPNCE	February/2013	Vulnerability of ants	52.0	24.0	6	0.62
PAEST × RPPNCE	February/2014	Vulnerability of ants	52.0	24.0	6	0.85
PAEST × RPPNCE	January/2013	Vulnerability of ants	52.0	24.0	6	0.77
PAEST × RPPNCE	January/2014	Vulnerability of ants	52.0	24.0	6	0.73
PAEST × RPPNCE	March/2013	Vulnerability of ants	52.0	24.0	6	0.54
PAEST × RPPNCE	March/2014	Vulnerability of ants	52.0	24.0	6	0.95
PAEST × RPPNCE	November/2013	Vulnerability of ants	52.0	24.0	6	0.81
PAEST × RPPNCE	October/2013	Vulnerability of ants	52.0	24.0	6	0.64

Conclusão geral

Diante dos resultados apresentados nos capítulos desta tese, pode-se concluir que as interações tritróficas entre plantas hospedeiras, membracídeos e formigas atendentes em Mata Atlântica são estruturadas por fatores como: (1) comportamento social dos membracídeos, (2) recrutamento de operárias, (3) fenologia das plantas, e (4) nível de antropização das áreas de estudo (Figura 3).

A estrutura das redes de interações mutualísticas formiga-membracídeo é semelhante às outras interações facultativas como associações entre formigas e plantas, por exemplo. No núcleo central dessas redes observou-se um maior número de espécies solitárias de membracídeos do que espécies gregárias (Tabela 1). Além disso, as espécies mais abundantes de membracídeos dominaram as interações mutualísticas com formigas. As espécies de formigas que apresentaram um maior poder de recrutamento de operárias dominaram o *honeydew* produzido pelos membracídeos, sendo este um recurso mais estável no tempo e espaço comparado aos nectários extraflorais (Capítulo 1).

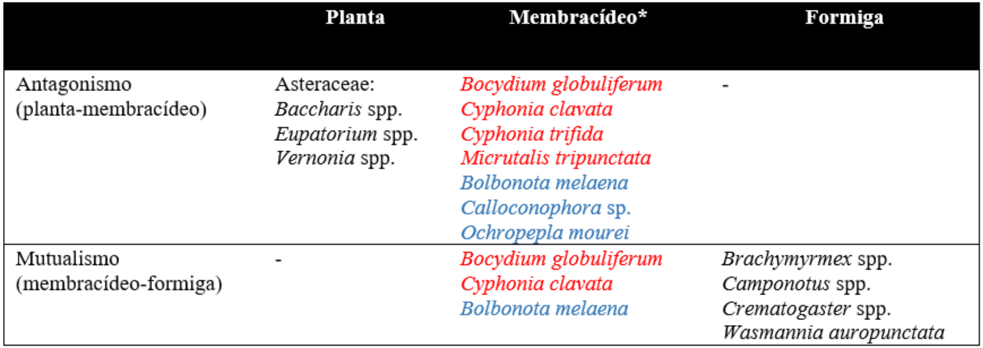
Em relação às interações antagonísticas planta-membracídeo estudadas aqui, as redes foram altamente especializadas e modulares. A especialização de plantas hospedeiras foi mais evidente durante a fenofase reprodutiva, na qual a riqueza de espécies foi menor comparada à fenofase vegetativa. Mais de 80% da fauna observada de membracídeos foi registrada em plantas da família Asteraceae, demonstrando a preferência desses fitófagos por plantas herbáceas e arbustivas dos gêneros *Baccharis*, *Eupatorium* e *Vernonia* (Tabela 1) (Capítulo 2).

A perturbação antrópica presente nas áreas de estudo afetou as interações antagonísticas e mutualísticas de formas distintas. Em áreas mais antropizadas, os antagonismos foram mais vulneráveis à perda de espécies, porque são interações mais especializadas e modulares em comparação aos mutualismos. Por outro lado, os mutualismos entre formigas e membracídeos são interações facultativas, portanto não há maior dependência entre as espécies, tornando a estrutura dessas associações menos frágil à perda de *links* e de espécies (Capítulo 3).

Esses resultados apontaram que a estrutura das interações tritróficas planta-membracídeo-formiga pode ser afetada por fatores bióticos e abióticos de diferentes maneiras (Figura 3), porque o tipo de interação pode contribuir para a fragilidade dessas associações em Mata Atlântica. A preservação apenas de espécies não é suficiente para manter o equilíbrio da biodiversidade em um bioma. Portanto, estratégias de conservação de biomas com forte grau de antropização humana podem considerar o uso de redes ecológicas como ferramentas úteis para descrever e entender as interações dentro da comunidade.

Os dados registrados nessa tese (Figura 3) podem servir de comparação para estudos de interações em outros ambientes como cerrado e caatinga brasileiros. Como perspectivas futuras, estudos biogeográficos que enfoquem o uso das famílias botânicas mais utilizadas por membracídeos podem esclarecer diferenças entre ambientes tropicais e temperados.

Tabela 1. Principais gêneros e/ou espécies observadas no núcleo das redes de interações ecológicas (antagonismo e mutualismo) no sistema planta-membracídeo-formiga em Mata Atlântica, Santa Catarina, Brasil. *Espécies solitárias de membracídeos (em vermelho), gregárias ou subsociais (em azul).



	Planta	**Membracídeo***	**Formiga**
Antagonismo (planta-membracídeo)	Asteraceae: *Baccharis* spp. *Eupatorium* spp. *Vernonia* spp.	*Bocydium globuliferum* *Cyphonia clavata* *Cyphonia trifida* *Micrutalis tripunctata* *Bolbonota melaena* *Calloconophora* sp. *Ochropepla mourei*	-
Mutualismo (membracídeo-formiga)	-	*Bocydium globuliferum* *Cyphonia clavata* *Bolbonota melaena*	*Brachymyrmex* spp. *Camponotus* spp. *Crematogaster* spp. *Wasmannia auropunctata*

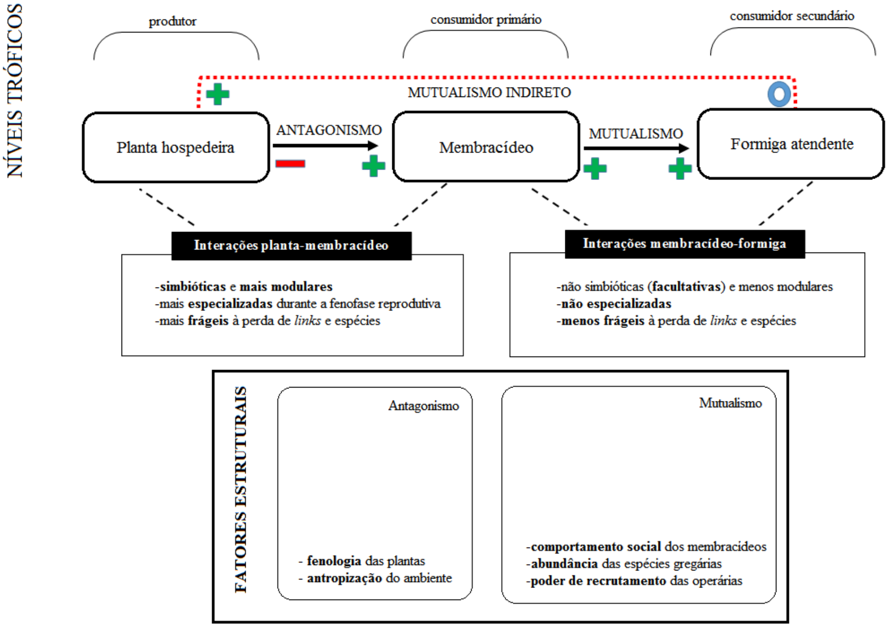


Figura 3. Quadro descrevendo os diferentes níveis tróficos, interações ecológicas e os fatores que estruturam o sistema planta-membracídeo-formiga em Mata Atlântica, Santa Catarina, Brasil.

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