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Instituto de Ciências Biológicas
Programa de Pós-Graduação em
Ecologia e Evolução



LEONARDO LIMA BERGAMINI
TESE DE DOUTORADO

**CONSERVAÇÃO FILOGENÉTICA DE INTERAÇÕES EM
REDES ANTAGONISTAS BIPARTIDAS**

Orientador: Prof. Dr. Mário Almeida-Neto

GOIÂNIA – GO

Maio de 2017

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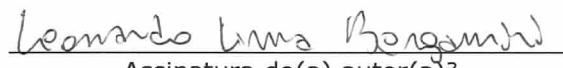
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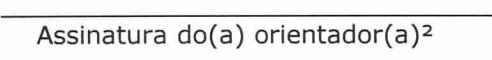
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TESE DE DOUTORADO

**CONSERVAÇÃO FILOGENÉTICA DE INTERAÇÕES EM
REDES ANTAGONISTAS BIPARTIDAS**

Tese apresentada à Universidade Federal
de Goiás, como parte das exigências do
Programa de Pós-graduação em Ecologia e
Evolução para obtenção do título de
Doutor.

Orientador: Prof. Dr. Mário Almeida-Neto

GOIÂNIA – GO

Maio de 2017



**SERVIÇO PÚBLICO FEDERAL
UNIVERSIDADE FEDERAL DE GOIÁS - UFG
INSTITUTO DE CIÊNCIAS BIOLÓGICAS - ICB
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E EVOLUÇÃO - PPGEE**

ATA DA SESSÃO PÚBLICA DE DEFESA DE TESE Nº 58

Aos vinte e seis dias do mês de maio de 2017, (26/05/2017), às quatorze horas (14h), no Auditório do ICB V, UFG, reuniram-se os componentes da banca examinadora: **Prof. Dr. Mário Almeida Neto, ICB-UFG; Prof. Dr. Adriano Sanches Melo, ICB-UFG, Prof. Dr. Marcus Vinicius Cianciaruso, ICB-UFG, Profa. Dra. Cecília Siliansky de Andreazzi, Fundação Osvaldo Cruz; Profa. Dra. Luísa Gigante Carvalheiro, UnB**; para, em sessão pública presidida pelo (a) primeiro(a) examinador(a) citado(a), procederem à avaliação da defesa de tese intitulada: **"Conservação filogenética de interações em redes antagonísticas bipartidas"**, em nível de doutorado, área de concentração em Ecologia e Evolução, de autoria de **Leonardo Lima Bergamini**, discente do Programa de Pós-Graduação em Ecologia e Evolução da Universidade Federal de Goiás. A sessão foi aberta pelo(a) presidente(a), que fez a apresentação formal dos membros da banca. A palavra, a seguir, foi concedida a(o) autor(a) da tese que, em cerca de 35 minutos, procedeu à apresentação de seu trabalho. Terminada a apresentação, cada membro da banca arguiu a(o) examinada(o), tendo-se adotado o sistema de diálogo sequencial. Terminada a fase de arguição, procedeu-se à avaliação da tese. Tendo-se em vista o que consta na Resolução nº 1127 de dezembro de 2012 do Conselho de Ensino, Pesquisa, Extensão e Cultura (CEPEC), que regulamenta o Programa de Pós-Graduação em Ecologia e Evolução, a tese foi APROVADA, considerando-se integralmente cumprido este requisito para fins de obtenção do título de Doutor(a) em Ecologia e Evolução pela Universidade Federal de Goiás. A conclusão do curso dar-se-á quando da entrega da versão definitiva da tese na secretaria do programa, com as devidas correções sugeridas pela banca examinadora, no prazo de trinta dias a contar da data da defesa. Cumpridas as formalidades de pauta, às 17 h e 10 min., encerrou-

se a sessão de defesa e, para constar, eu, Suely Ana Ribeiro, secretária executiva da Universidade Federal de Goiás - UFG, lavrei a presente ata que, após lida e aprovada, será assinada pelos membros da banca examinadora em três vias de igual teor.

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CONSERVAÇÃO FILOGENÉTICA DE INTERAÇÕES EM REDES ANTAGONISTAS BIPARTIDAS

Leonardo Lima Bergamini

Tese apresentada à Universidade Federal de Goiás como parte das exigências do Programa de Pós-Graduação em Ecologia e Evolução para a obtenção do título de Doutor.

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Examinadora

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RESUMO

Esta tese é composta de três capítulos apresentados em formato de artigos científicos, e aborda a conservação filogenética de interações ecológicas sob diferentes aspectos. Os três capítulos são apresentados em formato de artigos científicos. Citações e referências bibliográficas em todo o texto estão formatados de acordo as normas da revista Oikos, na qual uma versão do primeiro capítulo já se encontra publicado. Os materiais suplementares referidos nos textos de cada um dos capítulos se encontram nos anexos ao final da tese.

Começo com o texto de meu exame de qualificação, que faz uma breve apresentação sobre filogenética de comunidades. Ao abordar este tema mais geral esta introdução fornece uma visão complementar à literatura específica apresentada em cada um dos capítulos.

No primeiro capítulo, meus coautores e eu exploramos a correlação entre similaridade filogenética e similaridade no conjunto de antagonistas nas plantas e nos herbívoros em uma rede regional Asteraceae-endófagos de capítulos. Usando diferentes medidas para similaridade de antagonistas e diferentes recortes definidos por linhagens de herbívoros tentei detectar como a história evolutiva das espécies de plantas e espécies se reflete em suas interações tanto ao nível específico quanto nos módulos da rede. Nós mostramos que, além da similaridade composicional previamente reportada em outros estudos, espécies aparentadas também compartilham uma maior proporção da história filogenética de seus pares, tanto para as espécies recurso quanto para seus consumidores. A comparação entre os padrões encontrados para a rede como um todo com aqueles encontrados em sub-redes compostas de grupos mais filogeneticamente restritos de herbívoros fornece evidência de que a partição de recursos ocorre em maior parte em

níveis filogenéticos mais profundos, de modo que um sinal filogenético positivo na similaridade de hospedeiras é detectável mesmo entre consumidores muito próximos em sub-redes monofiléticas. A assimetria na força do sinal entre níveis tróficos é mais aparente na maneira com que os módulos da rede refletem a filogenia das espécies hospedeiras, tanto para a rede como um todo quanto para as sub-redes. Tomados em conjunto, estes resultados sugerem que processos evolutivos, como conservantismo filogenético e a história de colonizações independentes dos diferentes grupos de insetos devem ser as principais forças gerando a estrutura filogenética observada neste sistema planta-herbívoro em particular.

No segundo capítulo testo mais detalhadamente as contribuições relativas de diferentes processos ecológicos e da história evolutiva na formação da rede de interações Asteraceae-Tephritidae. Unindo uma abordagem estatística previamente utilizada na literatura de redes mutualísticas, um método de análise co-evolutiva e alguns novos métodos propostos neste trabalho mostrei o efeito marcante da filogenia neste sistema e discuti como os padrões desta rede de antagonistas diferem de outros sistemas.

No terceiro capítulo utilizei um conjunto de dados compilado da bibliografia sobre cofilogenia para testar a generalidade do padrão de conservação filogenética e da assimetria na força dessa conservação observados em outros sistemas. Usei uma abordagem meta-analítica para estimar tamanhos de efeito gerais para as correlações entre filogenia e interações e também para as assimetrias nessas correlações. Encontrei um padrão geral de conservação filogenética nos padrões de interação para ambos níveis tróficos com uma considerável heterogeneidade entre estudos. Por outro lado, a assimetria na força do sinal foi consistentemente pequena e não significativa em cada estudo individual, com um efeito geral positivo mas também pequeno. Meus resultados fornecem evidências convincentes de que a conservação de interações ecológicas é comum na

natureza, juntamente com uma representação quantitativa de sua heterogeneidade e da assimetria entre níveis tróficos.

Tomados em conjunto, os resultados dos três trabalhos ressaltam a importância da especialização para a estrutura das interações antagonistas e a presença marcante de restrições filogenéticas no estabelecimento destas interações. Espero que as contribuições apresentadas aqui, as questões que elas levantam, e as novas abordagens que utilizei ajudem a melhorar nossa compreensão dos processos que modulam a formação de redes ecológicas.

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INTRODUÇÃO GERAL

Texto sobre filogenética de comunidades apresentado como parte do exame de qualificação

A ecologia de comunidades se encontra na raiz da Ecologia, incluindo em seu escopo grande parte dos temas e questões abordados nos primeiros trabalhos dessa disciplina (Haeckel, 1886; Warming and Vahl, 1909; Warming, 1895). Na edição em inglês do primeiro livro especificamente dedicado à Ecologia, *Plantesamfund*, de Eugenius Warming (Warming, 1895), a formação das comunidades de plantas por espécies com diferentes formas de crescimento e as similaridades nas estratégias ecológicas entre espécies que ocorrem em ambientes semelhantes em partes diferentes do mundo são temas centrais (Warming and Vahl, 1909). Apesar de críticas recorrentes ao avanço da ecologia de comunidades, como por exemplo a noção de que a ecologia de comunidades tem falhado em estabelecer leis gerais (Lawton, 1999), o advento de novas abordagens vem permitindo a consolidação e o avanço deste fascinante ramo da ecologia (Simberloff, 2004; Vellend, 2010).

O surgimento de novos métodos (p.ex. Supertrees - Bininda-Emonds et al., 2002) e a sempre crescente disponibilidade de dados filogenéticos gerados a partir de métodos moleculares tem gerado novos meios de se atacar estas questões de longa data, em uma nova área chamada de “*Community phylogenetics*”, ou filogenética de comunidades (Cavender-Bares et al., 2009a; Mouquet et al., 2012; Schoener, 2011; Webb et al., 2002).

A COMUNIDADE ECOLÓGICA

Apesar de ser um dos termos mais utilizados em ecologia (Prado and El-Hani, 2013), e, talvez exatamente por isso, o conceito de comunidade ainda guarde

controvérsias quanto a sua definição. De modo geral, dois sentidos principais são atribuídos à comunidade ecológica. O primeiro é a ideia do nível organizacional, localizado como o próximo passo após a 'população' na hierarquia, muitas vezes didática, em que são divididos os objetos de estudo da biologia. Sob esse ponto de vista amplo, a comunidade biológica se refere a uma construção conceitual, o nível em que se expressam propriedades emergentes dos conjuntos de populações de organismos, como a riqueza de espécies, as distribuições de abundância, entre inúmeras outras.

No entanto, a enorme complexidade das comunidades naturais, decorrente da miríade de processos e fenômenos que nelas ocorrem apresenta dificuldades práticas e teóricas para seu estudo. Desta forma se faz necessária uma definição operacional deste conceito. Neste uso mais prático do termo comunidade se encontram diversas definições, com enfoques variados em diferentes aspectos e propriedades das comunidades. Algumas definições enfatizam a existência de interações entre os organismos, enquanto outras apenas enfocam o compartilhamento dos organismos de um mesmo ambiente. Outros autores, ainda, usam o termo comunidade quando o mais apropriado seria utilizar outros conceitos, como guilda (conjunto de organismos funcionalmente semelhantes) e assembleia (um conjunto de organismos definido taxonomicamente = taxocenose), entre outros.

A validade e utilidade desse conceito operacional de comunidade têm levantado discussões (p.ex. Magnusson, 2013 e respostas subsequentes). Parte da origem desses desentendimentos pode ser traçada aos primórdios da ecologia de comunidades, e se refere à discussão sobre a natureza das comunidades ecológicas. Um dos mais notáveis exemplos vem do debate oriundo do estudo de comunidades vegetais e a discussão sobre o grau de interdependência existente entre as espécies de uma comunidade. De um lado, as analogias categóricas de Clements, que defendia a repetitividade dos padrões de

sucessão como uma evidência da coerência estrutural das comunidades vegetais, e do outro a visão individualista defendida por Gleason, em que comunidades são apenas a sobreposição espacial das distribuições das espécies, marcaram um dos primeiros debates sobre a natureza das comunidades.

Outro ponto de contenda é a delimitação espacial das comunidades, sua arbitrariedade e como o enfoque em escalas locais pode ou não prejudicar a compreensão dos mecanismos que envolvem maiores escalas temporais e espaciais (Brooker et al., 2009; Ricklefs and Jenkins, 2011; Ricklefs et al., 2008). O que fica evidente nas diferentes definições e discussões sobre o conceito de comunidade são as diferenças na importância atribuída a diferentes processos. O maior reconhecimento da importância de processos regionais na estruturação de comunidades locais, por exemplo, foi um dos grandes avanços ao longo da história conceitual da ecologia de comunidades (Cornell and Lawton, 1992). Entretanto, ainda é um desafio entender como os processos em diferentes escalas atuam em conjunto, e esforços de pesquisa em escalas locais são cruciais para esse entendimento (Brooker et al., 2009).

Em meio às discussões sobre o conceito de comunidade e sobre a natureza das comunidades ecológicas, fica claro a ênfase em diferentes aspectos e processos. De maneira ampla, os processos envolvidos na formação e funcionamento das comunidades podem ser classificados em quatro grandes categorias (Vellend, 2010) análogas aos quatro grandes conceitos da genética de populações: deriva, dispersão, especiação e seleção. Sob essa visão, todos os fenômenos nas comunidades são resultados da interação desses quatro principais processos, atuando através das diferentes escalas temporais e espaciais. Como deriva se entendem os processos relacionados ao componente estocástico da demografia das populações, isto é, nascimentos e mortes. Os mecanismos agrupados sob o processo de dispersão são aqueles decorrentes da movimentação dos

indivíduos, que ligam as dinâmicas populacionais ao longo do espaço. A especiação diz respeito à diferenciação das populações em novas espécies, o processo que gera a diversidade constituinte das comunidades. Seleção inclui todos os processos relacionados à diferenças determinísticas na aptidão dos indivíduos, como as interações ecológicas dos indivíduos, que são influenciadas por diferenças entre os mesmos. Essa generalização é útil por fornecer uma perspectiva ampla das diferenças entre as visões de comunidades e reconhecer a existência de mecanismos relacionados a estes diferentes processos. Partindo desta ideia, temos um panorama de como diferentes linhas dentro da ecologia de comunidade enfocam esses diferentes processos, e como diferentes áreas tem proporcionado um avanço em entendê-los. A teoria neutra, por exemplo, estimulou uma grande discussão sobre a importância da deriva ecológica (Chave, 2004). Os processos relacionados à dispersão de indivíduos têm um grande papel nas teorias sobre metacomunidades (Leibold et al., 2004) e no desenvolvimento da ecologia de paisagens (Turner, 2005). O estudo das teias tróficas (Cohen et al., 2003) nas comunidades e das redes de interação (Ings et al., 2009), por outro lado, está mais ligado aos processos seletivos. Finalmente, abordagens que levam em conta os efeitos em maior escala (Ricklefs and Jenkins, 2011) e a história evolutiva dos organismos (Cavender-Bares et al., 2009) trazem um maior reconhecimento do papel da especiação e evolução nas comunidades.

Ao longo deste trabalho utilizei o termo comunidade para me referir a conjuntos de espécies que compartilham um determinado local em um determinado período de tempo. A composição taxonômica desses conjuntos é arbitrária, bem como a extensão espacial e temporal de cada comunidade. Isso não significa, entretanto, que o estudo de tais conjuntos não seja informativo, pelo contrário, sua definição é baseada na adequabilidade dos mesmos como sistemas propícios para responder certas questões

(Swenson et al., 2006). Em seguida veremos algumas das principais ideias em ecologia de comunidades, e como a inclusão de informações sobre a história evolutiva das espécies que as compõe tem propiciado novas abordagens para questões antigas e levantado novas questões.

MONTAGEM E DINÂMICA DE COMUNIDADES

Apenas um pequeno subconjunto das espécies existentes no planeta pode ser encontrado em certa região. E apenas um subconjunto dessas espécies coexiste em uma comunidade, seja ela uma floresta tropical ou uma comunidade de fitotelma. O processo pelo qual as comunidades locais são formadas a partir do conjunto de espécies disponíveis na região se chama montagem de comunidades, ou ainda coalescência de comunidades. Qual a importância relativa dos diferentes mecanismos e processos que levam à montagem de comunidades tem sido uma das questões fundamentais da ecologia de comunidades (Sutherland et al., 2013).

Os clássicos estudos dos padrões de co-ocorrência de espécies de pássaros em ilhas (Diamond, 1973) levaram a longos debates sobre a importância da exclusão competitiva como processo de montagem (Gotelli and McCabe, 2002), além de um grande desenvolvimento do uso de modelos nulos em ecologia (Gotelli, 2001). Desde então, grandes avanços têm sido feitos na compreensão da montagem de comunidades (Weiher et al., 2011). Dentre eles estão o desenvolvimento de abordagens que consideram explicitamente a dependência de escala na montagem de comunidades (Ricklefs, 2004), a inclusão de processos neutros nos modelos (Chave, 2004) e a busca experimental por mecanismos de coexistência (Chesson, 2000a).

Com os primeiros trabalhos no início dos anos 2000 (Webb, 2000; Webb et al., 2002), a análise da estrutura filogenética das comunidades passou a ser uma importante ferramenta para entender a montagem de comunidades. A premissa básica desta abordagem é a de que espécies mais parentadas devem ter uma maior similaridade em suas características ecológicas, sendo similarmente afetadas pelos filtros ambientais (Webb, 2000) e mais propícias à interações competitivas entre si. A partir desses pressupostos, duas principais predições podem ser feitas. A primeira é que filtros ambientais, isto é, características do ambiente que limitam o estabelecimento de alguma espécie com base na sua tolerância a tais características, levam a um padrão de convergência filogenética, de forma que as espécies presentes em uma comunidade local sejam mais parentadas do que seria esperado de uma comunidade formada por uma amostragem aleatória do conjunto regional, uma vez que espécies parentadas potencialmente apresentam tolerâncias similares. A segunda predição é que interações competitivas mediadas pela similaridade ecológica entre as espécies que levem à exclusão de espécies demasiadamente similares das comunidades locais deve gerar um padrão de uniformidade filogenética, com as espécies que coexistem localmente sendo mais uniformemente distribuídas ao longo da filogenia do que seria esperado por uma comunidade formada aleatoriamente.

Um grande corpo de literatura se formou baseado nestas predições (Vamosi et al., 2009). Enquanto o pressuposto de sinal filogenético nos traços das espécies, seja ele resultante de conservação de nicho ou apenas de evolução por movimento Browniano (Losos, 2008), parece ser comum em diferentes graus (Chamberlain et al., 2012), falta evidência empírica sobre a validade e generalidade da relação entre parentesco evolutivo e força das interações entre espécies. Além de existirem resultados mistos com diferentes grupos (Cahill et al., 2008; Fritschie et al., 2014), teorias modernas sobre coexistência

(Chesson, 2000b; HilleRisLambers et al., 2011) preveem diferentes resultados da exclusão competitiva dependendo dos traços mediando essa exclusão (Mayfield e Levine, 2010). A inclusão de informações sobre atributos conhecidamente importantes para as respostas das espécies, tanto para o ambiente quanto para as interações com outras espécies, pode permitir uma melhor interpretação dos padrões filogenéticos observados (McGill et al., 2006). Por outro lado, a demonstração destes padrões tem levantado questões interessantes, e, fatores inicialmente percebidos como problemas, como o efeito da escala filogenética e do tamanho do conjunto regional de espécies, tem se mostrado como oportunidades para testar a força de diferentes processos em diferentes escalas (Kraft et al., 2007).

Além da montagem de comunidades, os processos que governam a sua dinâmica temporal também são de grande interesse. Uma perspectiva evolutiva pode ajudar a simplificar parte da complexidade aparentemente intratável (Lawton, 1999) destes processos. Uma boa teoria explicando os diferentes padrões de sucessão, por exemplo, seria uma ótima ferramenta para o manejo e restauração de áreas degradadas. A sucessão ecológica é o processo de mudanças temporais na composição de uma comunidade a partir do momento em que ela se forma ou após algum distúrbio. A sucessão pode ocorrer em estágios aparentemente bem definidos em alguns sistemas, em que determinadas espécies ou grupos de espécies entram na comunidade em uma sequência previsível.

O papel relativo dos diferentes processos (e.g. interações entre as espécies, deriva ecológica, filtros ambientais) em determinar essa dinâmica depende do tipo de sucessão e do estágio sucesional em que a comunidade se encontra. Quando consideramos a sucessão secundária, por exemplo, é importante lembrar que pode existir um componente estocástico nos próprios distúrbios, embora características das espécies possam ter um

papel importante em determinar sua suscetibilidade aos distúrbios e o seu tipo de resposta (Lavorel et al., 1999).

Embora se reconheça que a dinâmica sucessional ocorre em todos os grupos de uma comunidade, a grande maioria dos trabalhos trata de sucessão das assembleias vegetais. Os principais modelos teóricos de sucessão, inclusive, são pensados para plantas. A existência de correlações negativas entre os atributos da história de vida das espécies é um elemento comum à maioria dos modelos, e gera previsões testáveis a respeito da estrutura filogenética e de sua mudança ao longo do tempo. Se os traços de história de vida das espécies são conservados ao longo das filogenias, espécies próximas devem responder de maneira similar durante a sucessão. Quais filtros atuam limitando o estabelecimento das espécies, entretanto, dependem do grupo em questão. Em um estudo com lianas, por exemplo, a estrutura da floresta em estágios sucessionais avançados atuou como um fator limitante ao estabelecimento de algumas espécies de lianas (Roeder et al., 2014), mostrando uma atuação dos processos sucessionais em um sentido diferente do observado para a comunidade de árvores.

Outra área que vem crescendo na filogenética de comunidades é o estudo da invasibilidade e resistência de comunidades a distúrbios. No contexto das invasões, observações sobre a relação taxonômica entre espécies nativas e invasoras levaram à hipótese de que espécies mais distantes seriam mais propensas a invadir uma comunidade, uma vez que sofreriam menos com o efeito da competição com as espécies presentes e com o compartilhamento de inimigos naturais. Resultados contrastantes sobre o efeito da distância filogenética sobre a invasibilidade (Jones et al., 2013), no entanto, nos mostram que essa relação é provavelmente mediada por outros processos, como a pressão de propágulos e estratégias de vida das espécies invasoras (Jones et al., 2013).

Resultados interessantes também vêm sendo obtidos no estudo de teias tróficas e redes de interação. Modelos teóricos que incluem o efeito do parentesco evolutivo na similaridade entre as espécies de uma teia trófica, por exemplo, tem tido relativo sucesso em reproduzir propriedades estruturais observadas na natureza (Cattin et al., 2004; Naisbit et al., 2012). Além disso, um efeito do parentesco na similaridade entre as espécies de uma teia trófica, têm sido encontradas em vários sistemas (p.ex. Rohr and Bascompte, 2014). Esses resultados indicam que processos evolutivos atuam não apenas na resposta das espécies ao meio abiótico, mas que também deixam um sinal detectável nas suas interações com o meio biótico. Entender quais são esses mecanismos e em quais circunstâncias eles atuam será um importante avanço.

MÉTODOS DA FILOGENÉTICA DE COMUNIDADES

O grande interesse sobre os padrões filogenéticos nas comunidades, propiciado pela maior disponibilidade de filogenias para diversos grupos, levou ao desenvolvimento de muitos métodos e métricas dedicados a esse tipo de questão. De modo amplo, as medidas disponíveis podem ser separadas em medidas de diversidade filogenética, seja diversidade alfa ou beta, e medidas de estrutura filogenética de comunidades.

Dentre os índices de diversidade alfa, um dos primeiros métodos que se utilizam de informação filogenética para medir a biodiversidade de comunidades é o índice de diversidade filogenética PD (Faith, 1992). Proposto para avaliar o valor de conservação da diversidade de reservas biológicas, o valor deste índice para uma comunidade é definido como a soma dos comprimentos de ramos necessários para conectar as espécies presentes naquela comunidade. Por ser uma soma de comprimentos de ramos, PD aumenta com a riqueza de espécies, o que o torna inadequado para situações em que se

tem interesse em avaliar a diversidade separadamente da riqueza de espécies. Para esses casos foram propostas medidas que variam independentemente da riqueza, como a distância média par a par (MPD – Webb, 2000) e a variabilidade filogenética das espécies (PSV - Helmus et al., 2007). Estes e outros índices foram revisados em Vellend et al. (2011), que mostra que todos eles são muito correlacionados e representam resultados equivalentes. Ao incorporar informação sobre o parentesco das espécies, índices de diversidade filogenética são boas alternativas a métricas mais simples, como a riqueza de espécies, para várias perguntas pois fornecem informações adicionais. Além da diversidade filogenética, outras características das comunidades representáveis como dendrogramas podem ser mensuradas com medidas análogas como, por exemplo, as medidas comumente aplicadas em estudos de diversidade funcional (McGill et al., 2006; Pavoine and Bonsall, 2011).

Medidas de beta diversidade filogenética, que medem mudanças na composição filogenética entre pares ou conjuntos de locais, são mais recentes. Uma das primeiras medidas deste tipo, o Unifrac (Lozupone and Knight, 2005), é definido como o complemento da proporção de comprimentos de ramos de uma árvore filogenética total que é compartilhada entre dois locais, proposto para filogenias moleculares obtidas de comunidades microbianas. Ives e Helmus (2010) propõe o PCD (*phylogenetic community dissimilarity*) e o compararam através de simulações com outras medidas de beta diversidade filogenética. Derivado a partir da covariância esperada entre as espécies das duas comunidades em um traço hipotético que evolui por movimento Browniano, o PCD inclui em sua formulação uma correção para o compartilhamento de espécies esperado ao acaso.

Trabalhos testando a estrutura filogenética de comunidades em relação ao conjunto regional compararam medidas de diversidade filogenética observadas com

aqueelas obtidas em conjuntos aleatórios formados a partir de um modelo nulo. As principais medidas para esse fim são o índice de parentesco líquido (NRI – uma medida homogeneizada dos valores médios de distância filogenética entre espécies de uma comunidade) e o índice do táxon mais próximo (NTI – similar ao NRI porém só considera a distância até a espécie mais próxima) (Webb, 2000; Webb et al., 2002). Estes índices são tamanhos de efeito obtidos a partir da comparação do valor observado (de distância filogenética média entre as espécies da comunidade ou dos valores de distância à espécie mais próxima) com uma distribuição nula, gerada a partir da formação de novos conjuntos espécies tiradas do conjunto regional ou pelo embaralhamento das legendas das pontas da filogenia, removendo os padrões de parentesco entre as espécies. Outros métodos para medir a estrutura filogenética incluem a correlação entre medidas de similaridade filogenética e medidas de similaridade ecológica (co-ocorrência, similaridade na composição de parceiros de interação) entre pares de espécies (Lovette and Hochachka, 2006; Slingsby and Verboom, 2006), o uso de modelos lineares mistos (Rafferty and Ives, 2013) e o uso de modelos lineares generalizados mistos (Ives and Helmus, 2011).

Todos estes métodos, no entanto, são sensíveis a diferenças em propriedades das árvores filogenéticas, como o padrão de diversificação (Vellend et al., 2011), balanço da árvore (Vellend et al., 2011), escala filogenética adotada (W. D. Pearse et al., 2013; Swenson et al., 2006) e, no caso das medidas baseadas em modelos nulos, na definição do conjunto regional de espécies e na escolha do modelo nulo (Vamosi et al., 2009). Por esse motivo, é importante um bom entendimento sobre como essas diferenças podem afetar a interpretação dos resultados.

CONSIDERAÇÕES FINAIS

A abordagem filogenética na ecologia de comunidades continua uma avenida promissora no caminho de uma visão cada vez mais integrada sobre como diferentes processos interagem em diferentes escalas para formar e manter as comunidades ecológicas. Os estudos sobre a estrutura filogenética de comunidades revelaram que a maioria das comunidades de plantas terrestres apresentam sinais de agrupamento filogenético (Vamosi et al., 2009). Um maior entendimento mecanicista desses padrões ainda é necessário, e abordagens experimentais (Fritschie et al., 2014) e a integração com estudos dos traços ecológicos (McGill et al., 2006), podem ser bons caminhos para se obter este maior entendimento.

A consideração de novas perspectivas teóricas deve levar a uma melhor compreensão das limitações da abordagem filogenética (Losos, 2011; Mayfield and Levine, 2010) e, por outro lado, permitir avanços no tratamento destas limitações. Várias linhas de pesquisa na interface entre a ecologia e a evolução mostram grandes prospectos de ideias inovadoras. Isso se aplica especialmente à programas de pesquisa integradores que, se utilizando de diferentes abordagens empíricas e metodológicas, e permitem uma maior integração entre dados e teorias em diferentes escalas.

Frentes de pesquisa que buscam esclarecer qual a importância da retroalimentação entre processos ecológicos e evolução (Johnson and Stinchcombe, 2007) também tem proporcionado uma mudança de percepção, ao demonstrar que processos evolutivos podem ter implicações importantes em escalas de tempo menor (Pelletier et al., 2009). Nesta mesma linha, novos trabalhos têm esclarecido a influência de processos ecológicos em processos evolutivos de grande escala (McPeek, 2008), assim como ressaltado a natureza dinâmica dessa inter-relação entre ecologia e evolução (Matthews et al., 2014).

Uma dessas áreas de desenvolvimento recente é a investigação da estrutura filogenética em teias tróficas e redes de interação. Trabalhos testando a correlação entre proximidade filogenética entre pares de espécies e seu papel nestas redes (ex. Pearse et al., 2013) têm revelado a presença de sinal filogenético e intrigantes e consistentes diferenças na força deste sinal entre os níveis tróficos e tipos de interação (Rohr and Bascompte, 2014).

Finalmente, os avanços proporcionados pela abordagem filogenética na ecologia de comunidades podem resultar em novas soluções para problemas práticos. A abordagem filogenética no entendimento das interações ao longo da sucessão vegetal (Verdú et al., 2010), por exemplo, pode fornecer ferramentas úteis para a restauração de comunidades ecológicas (Young et al., 2001). A aplicação desta abordagem também tem se mostrado promissora na biologia da conservação (Hartmann and André, 2013).

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CAPÍTULO 1- Múltiplas influências da estrutura filogenética sobre uma rede planta-herbívoro

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RESUMO

Os ecólogos estão cada vez mais cientes da inter-relação entre história evolutiva e processos ecológicos na moldagem dos padrões atuais de interações entre espécies. A inclusão de relações filogenéticas em estudos de redes de interação interespecíficas tem mostrado que espécies aparentadas comumente interagem com conjuntos similares de espécies. Notavelmente, o grau de conservantismo filogenético em interações ecológicas antagonistas é frequentemente maior entre espécies do nível trófico inferior do que entre aquelas do nível superior. Uma hipótese para explicar essa assimetria é a de que competição entre as espécies de consumidores promove partição de recursos e sobrepuja a manutenção da similaridade de dieta gerada pela inércia filogenética. Neste trabalho usamos uma rede planta-herbívoro regional composta de espécies de Asteraceae e insetos endófagos de capítulos para avaliar como a força do conservantismo filogenético em interações interespecíficas difere entre os dois níveis tróficos. Nós também avaliamos se a assimetria na força do sinal filogenético entre plantas e animais depende do grau total de parentesco entre os herbívoros. Nós mostramos que, além da similaridade composicional previamente reportada em outros estudos, espécies aparentadas também compartilham uma maior proporção da história filogenética de seus pares, tanto para as espécies recurso quanto para seus consumidores. A comparação entre os padrões encontrados para a rede como um todo com aqueles encontrados em sub-redes compostas de grupos mais filogeneticamente restritos de herbívoros fornece evidência de que a partição de recursos ocorre em maior parte em níveis filogenéticos mais profundos, de modo que um sinal filogenético positivo na similaridade de hospedeiras é detectável

mesmo entre consumidores muito próximos em sub-redes monofiléticas. A assimetria na força do sinal entre níveis tróficos é mais aparente na maneira com que os módulos da rede refletem a filogenia das espécies hospedeiras, tanto para a rede como um todo quanto para as sub-redes. Tomados em conjunto, estes resultados sugerem que processos evolutivos, como conservantismo filogenético e a história de colonizações independentes dos diferentes grupos de insetos devem ser as principais forças gerando a estrutura filogenética observada neste sistema planta-herbívoro em particular.

Manifold influences of phylogenetic structure on a plant-herbivore network

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Short running title: Phylogenetic structure in an herbivory network

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ABSTRACT

Ecologists are increasingly aware of the interplay between evolutionary history and ecological processes in shaping current species interaction patterns. The inclusion of phylogenetic relationships in studies of species interaction networks has shown that closely related species commonly interact with sets of similar species. Notably, the degree of phylogenetic conservatism in antagonistic ecological interactions is frequently stronger among species at lower trophic levels than among those at higher trophic levels. One hypothesis that accounts for this asymmetry is that competition among consumer species promotes resource partitioning and offsets the maintenance of dietary similarity by phylogenetic inertia. Here, we used a regional plant-herbivore network comprised of Asteraceae species and flower-head endophagous insects to evaluate how the strength of phylogenetic conservatism in species interactions differs between the two trophic levels. We also addressed whether the asymmetry in the strength of the phylogenetic signal between plants and animals depends on the overall degree of relatedness among the herbivores. We show that, beyond the previously reported compositional similarity, closely related species also share a greater proportion of counterpart phylogenetic history, both for resource and consumer species. Comparison of the patterns found in the entire network with those found in subnetworks composed of more phylogenetically restricted groups of herbivores provides evidence that resource partitioning occurs mostly at deeper phylogenetic levels, so that a positive phylogenetic signal in antagonist similarity is detectable even between closely related consumers in monophyletic subnetworks. The asymmetry in signal strength between trophic levels is most apparent in the way network modules reflect resource phylogeny, both for the entire network and for subnetworks. Taken together, these results suggest that evolutionary processes, such as phylogenetic conservatism and independent colonization history of the insect groups may be the main forces generating the phylogenetic structure observed in this particular plant-herbivore network system.

INTRODUCTION

Recent advances in ecophylogenetics have facilitated the investigation of the extent of phylogenetic conservatism in different types of species interactions (Rezende et al. 2007, Gómez et al 2010, Fontaine and Thebault 2015). The inclusion of phylogenetic relationships in studies of species interaction networks has shown that closely related species commonly interact with similar sets of species (e.g., Rezende et al. 2007, Gómez et al. 2010, Cagnolo et al. 2011, Krasnov et al. 2012, Martos et al. 2012, Naisbit et al. 2012, Elias et al. 2013). However, the strength of phylogenetic conservatism of interactions in ecological networks often differs between trophic levels in the same network. In antagonistic networks, the effect of phylogenetic relatedness on the compositional similarity of interactions is frequently stronger between resource species (i.e., species of lower trophic levels) than between consumer species (i.e., species of higher trophic levels) (Cagnolo et al. 2011, Jacquemyn et al. 2011, Krasnov et al. 2012, Martos et al. 2012, Naisbit et al. 2012, Elias et al. 2013, Fontaine and Thebault 2015). On the other hand, in plant–pollinator and plant–frugivore mutualistic networks, closely related animal species (higher trophic level) tend to share a larger proportion of plant species when compared to closely related plant species (lower trophic level) in relation to their pollinators or seed dispersers (Rezende et al. 2007).

The mechanisms generating the observed asymmetry in the phylogenetic signal between trophic levels are still not well understood. A theoretical study by Rossberg et al. (2006) on food webs suggests that a slower rate of evolution of defensive traits in the lower level could generate this difference between trophic levels. Another explanation for this asymmetry is that the effect of competitive interactions between consumer species is stronger than the effect of indirect interactions (e.g., predator-mediated apparent competition) between resource species, which then leads to a lower-than-expected

similarity in the dietary composition of closely related consumers (Elias et al. 2013). These effects could drive phylogenetic patterns in the topological structure of interaction networks, such as the formation of network modules, i.e. groups of species more densely connected among themselves than with other species from the same network (Prado and Lewinsohn 2004, Rezende et al. 2009, Krasnov et al. 2012). Finally, if asymmetry is driven by competition between consumers, it should be greater in networks of species with greater potential for competition. As phylogenetic conservatism in traits is common (Losos 2008, Wiens et al. 2010), and species with greater similarity are expected to share more resources (e.g., Fritschie et al. 2014, but see Cahill et al. 2008), the trophic-level differences in the phylogenetic conservatism of interactions should be higher in networks of closely related consumer species than in networks of phylogenetically distant species. Therefore, the asymmetry in the magnitudes of the correlations between phylogenetic and ecological similarities between trophic levels is expected to be higher for networks based on phylogenetically clustered consumers than for networks based on phylogenetically dispersed consumers.

Interactions between plants and herbivores have historically been used by ecologists as model systems to evaluate how evolution shapes current interaction patterns (e.g., Ehrlich and Raven 1964, Benson et al. 1975). For example, plant defense systems against natural enemies, such as chemical and physical barriers, tend to be phylogenetically conserved (Agrawal, 2007); therefore, herbivorous insects usually consume closely related plant species (Barone 1998, Morais et al. 2011). Similarly, because herbivore adaptations to feed and develop on their host plants are, at some level, also phylogenetically conserved, host plants that are more closely related are expected to have, on average, greater similarity in their herbivore faunas when compared to

phylogenetically distant host plants. Both patterns, however, can be masked to varying degrees by convergent evolution in both plant and herbivore traits (e.g., Becerra 1997).

In this study, we investigated the phylogenetic structure in the interactions of a well-studied system comprising plants of the family Asteraceae and their associated flower-head endophagous insects in remnants of Brazilian Cerrado (Fonseca et al. 2005, Almeida et al. 2006, Almeida-Neto et al. 2011). This was done by evaluating the phylogenetic patterns for both plants and herbivores at four organizational levels – within species, between species, within network modules and between network modules. The use of the entire set of herbivores, as well as phylogenetic subsets of herbivores, also allowed us to ascertain whether the asymmetry in the strength of the phylogenetic signal between plants and animals depends on the overall degree of relatedness among the herbivores. Specifically, we tested the following hypotheses: (i) host ranges of herbivore species tend to be phylogenetically clustered, while the herbivore assemblages associated to plant species tend to be phylogenetically dispersed; (ii) the strength of phylogenetic conservatism in species interactions is greater among plants (resources) than among herbivores (consumers); and (iii) for herbivores, phylogenetic conservatism in species interactions will be weaker when evaluated for subsets of the network containing only a given lineage, because of the higher potential for resource partitioning due to competition among closely related herbivores.

METHODS

Interaction network sampling

The Asteraceae and their flower-head endophagous insects comprise a well-defined and species-rich plant-herbivore system. In the Brazilian Cerrado savannas, flower-heads of the Asteraceae are used especially by Diptera (Tephritidae, Agromyzidae, and Cecidomyiidae), microlepidoptera (Tortricidae, Pterophoridae, Pyralidae, Gelechiidae, and Blastobasidae), and apionid weevils (*Apion* spp.) (Lewinsohn 1991, Fonseca et al. 2005, Almeida et al. 2006, Almeida-Neto et al. 2011).

Associations between Asteraceae and flower-head endophagous insects were assessed quantitatively in 20 remnants of Cerrado vegetation in southeastern Brazil (Almeida-Neto et al. 2011). The regional climate is characterized by rainy summers and dry winters and is classified as CWA in Köppen's (1948) system. The sampled sites were spaced from 0.6 to 41.4 km apart (mean distance = 16.3 km), at elevations ranging from 600 to 950 m.

Plants and insects were sampled from April to May 2003. The sampling design consisted of 15 transects of 30m × 5m, randomly allocated in relation to the edge of the areas. We sampled flower heads from at least 20 individuals of each Asteraceae species, collecting about 80 mL of flower-heads per individual plant whenever available. In the laboratory, the flower-head samples were kept in plastic containers covered with a mesh lid. Adult herbivore emergence was checked at least weekly for a period of two months. We spent about four person-hours collecting flower-heads in each period and site. Further information on sampling, vegetation, and studied areas can be found in Almeida-Neto et al. (2010, 2011).

For the purpose of this study, both species and their interactions were integrated into a single regional plant-herbivore network, depicting the presence or absence of

interactions between each plant-herbivore pair. We only included in the regional interaction network the plant and insect species that occurred in at least five (25%) of the sampled areas. By constructing the network in this way, we aimed to minimize the effect of spatial mismatch on the structure of plant-herbivore interactions. Among the 1210 plant-herbivore pairs included in our network, only 12 do not co-occur in at least one site.

Plant and insect phylogenies

Plant phylogeny was constructed by combining the information from a composite tree of the Asteraceae family (Funk et al. 2009) for most genera, with taxonomy serving as a surrogate for phylogenetic relationships of nodes for which no information was available. When even the taxonomy was unable to provide relationships, unresolved nodes were left as polytomies. Species were also attached as polytomies deriving from each genus.

Difficulties in the specific identification of the insect species, and the lack of a comprehensive phylogenetic hypothesis for the insect families comprising this study, led us to use an informal tree constructed by taxonomic substitution (*sensu* Bininda-Edmonds et al. 2001) of the available phylogenetic information. Starting with a purely taxonomic tree, we added information on the relationships between taxa whenever available (Supplementary material 1 Figure A1). We rendered both trees ultrametric by applying Grafen's transformation (Grafen 1989). We obtained similar results either by arbitrarily defining branch length as 1 (i.e., using the number of nodes between species as a measure of phylogenetic distance) or using Grafen's transformation on both phylogenies, so we only present the results of the branch lengths obtained by Grafen's transformation (see Supplementary material Appendix 1 Tables A1-A4 for the other results). We generated 300 trees with randomly resolved polytomies (RRT) for each group (plants and insects)

in order to assess the degree of phylogenetic uncertainty arising from polytomies (see Rangel et al. 2015). All analyses were performed in the original hypothesis containing the polytomies and on the 300 trees with randomly resolved polytomies. Final results from the RRT were used to compute 95% confidence intervals associated with phylogenetic uncertainty. Confidence intervals for DSI analysis are shown in the Supplementary material Appendix 1 Table A1.

Data analysis

All analyses were applied to the entire data set and the following subsets: (i) interactions between tephritids (Diptera: Tephritidae) and their hosts, (ii) interactions between cecidomyiids (Diptera: Cecidomyiidae) and their hosts, and (iii) interactions between lepidopterans (Blastobasidae, Gelechiidae, Pyralidae, Pterophoridae, Tortricidae) and their hosts. Defining a subnetwork comprising the weevil species was not possible, due to the small number of species present. All procedures were implemented in the R environment (R Core Team 2014) using original code and functions from the packages *picante* (Kembel et al. 2010) and *bipartite* (Dormann et al. 2008).

We tested whether the overall network and the subnetworks show a modular pattern by using the QuanBimo algorithm (Dormann and Strauss 2013), implemented by the computeModules function in the R package *bipartite*. For the modularity analysis we included interaction frequencies, which improves the detection of modules (Schleuning et al. 2014). This simulated annealing procedure allows the detection of modules in quantitative bipartite networks, and provides a modularity measure (Q) that compares the frequency of within vs. between module interactions. For each network, we applied the algorithm and the resulting Q value was used as the modularity estimate. This estimate was then compared to those obtained from 100 random networks created using a null

model with fixed marginal totals in order to obtain a z-value. This null model maintains the interaction frequency patterns for each species, randomizing only the resource use pattern.

We tested whether the set of plants used by a given herbivore species, and likewise the set of herbivores that develop in a given plant species, is composed of species related to a greater or lesser extent than would be expected from a null set of the same size. This is measured using an analog of the recently proposed DSI-S index (Jorge et al. 2014), which measures the degree of phylogenetic clustering in a given set of species in comparison to randomly assembled sets. The DSI-S index is computed as the z-score obtained by the comparison between the observed mean phylogenetic distance between the species in the group and the distances obtained by shuffling the species' positions along the phylogeny 999 times. The same test was applied to the set of plants in the same module, and the set of herbivores in the same module to assess the phylogenetic clustering of modules. The mean species-level and module-level DSI-S values of each subnetwork were then compared with the expected null value of 0 with one sample t-tests (Kembel and Hubbell 2006).

We also tested the effect of phylogenetic distance on counterpart dissimilarity by computing correlation coefficients between the phylogenetic distance matrices of the species and two metrics of counterpart overlap for each group. The first metric was purely compositional, defined as follows: we first computed the Jaccard dissimilarity in the counterpart composition of a given pair of plants/insects and then calculated a z-value by comparing the observed value with the mean and standard deviation of 500 null values obtained by randomly selecting two sets of the same size from all insect and plant species from the regional network. The second metric was also a null model standardized dissimilarity, calculated using the UniFrac index (Lozupone and Knight 2005). The

UniFrac between two sets of species measures the proportion of evolutionary history present exclusively in each set in relation to the total amount comprised by both. In a phylogenetic tree comprising all species from the two sets, the UniFrac is defined as the ratio between the sum of branch lengths that leads to species exclusive to either set and the total sum of branch lengths in the entire tree. The UniFrac between each pair of species was compared to null values generated by the following null model: first we keep the counterparts of species A constant, randomly reassign the interactions of species B and compute the Unifrac; then we keep the interactions of species B and shuffle the interactions of species A. The null value was then defined as the mean of these two values. This procedure separates the effects of the phylogenetic pattern within the counterparts of each species from the patterns arising from the phylogenetic relationships between the species. The use of the standardized dissimilarity measures, both for the compositional dissimilarity and the UniFrac, avoids the undesired effects of counterpart richness differences between pairs of species as well as the inherent cap on maximum dissimilarity values. By looking at the phylogenetic component of counterpart sharing we aim to better explore the interaction patterns of both groups. The observed values of correlation between phylogenetic distance and each of the counterpart overlap measures were then compared to those obtained in 999 null correlations using a null model that randomly relocates species along the phylogeny. We also tested if the relatedness between a pair of species affects the probability of both species being in the same network module by adjusting binomial GLMs. Model coefficients were tested against the same null models previously described.

Data deposition

Data available from the Dryad Digital Repository:

<http://dx.doi.org/10.5061/dryad.c3v62> > (Bergamini et al. 2016).

RESULTS

A total of 13011 adult herbivores were reared from 1373 individual plants. The regional plant-herbivore network was composed of 157 interactions between 55 species of flower-head feeding insects and 22 species of host plants. The insect species belong to six families and 16 genera, while the host plants belong to six tribes and 12 genera within the Asteraceae family. The species richness of herbivores and plants, respectively, was 23 and 19 for the Tephritidae-Asteraceae subnetwork, 6 and 17 for the Lepidoptera-Asteraceae subnetwork, and 16 and 11 for the Cecidomyiidae-Asteraceae subnetwork. The number of plant-herbivore interactions for each insect group was 67, 18 and 47, for the Tephritidae, Cecidomyiidae and Lepidoptera subnetworks, respectively.

Phylogenetic clustering of host plant ranges and herbivore assemblages

In the entire network, as expected, the host-plant species used by each herbivore species comprised, on average, a subset of species more closely related than random subsets of host-plant species of the same size ($t = 7.98$, $df = 26$, $p < 0.001$, Fig. 1). A similar pattern was observed in the Tephritidae subnetwork, with a strong degree of phylogenetic clustering in the plants consumed by the tephritid species ($t = 8.9$, $df = 13$, $p < 0.001$, Fig. 1). The species in the Lepidoptera and Cecidomyiidae subnetworks also showed consistent positive DSI-S values, but their mean phylogenetic aggregation could not be tested due to the small sample sizes.

The subsets of herbivore species on each host-plant species did not show phylogenetic clustering when all insect groups were combined ($t = 1.6$, $df = 16$, $p = 0.100$, Fig. 1). However, contrary to what would be expected if more closely related herbivores showed resource partitioning, separate analyses of the three subnetworks revealed significant clustering of the herbivores sharing the same host species (Tephritidae: $t =$

7.28, $df = 14$, $p < 0.001$; Lepidoptera: $t = 12.67$, $df = 12$, $p < 0.001$; Cecidomyiidae: $t = 7$, $df = 5$, $p < 0.001$; Fig. 1).

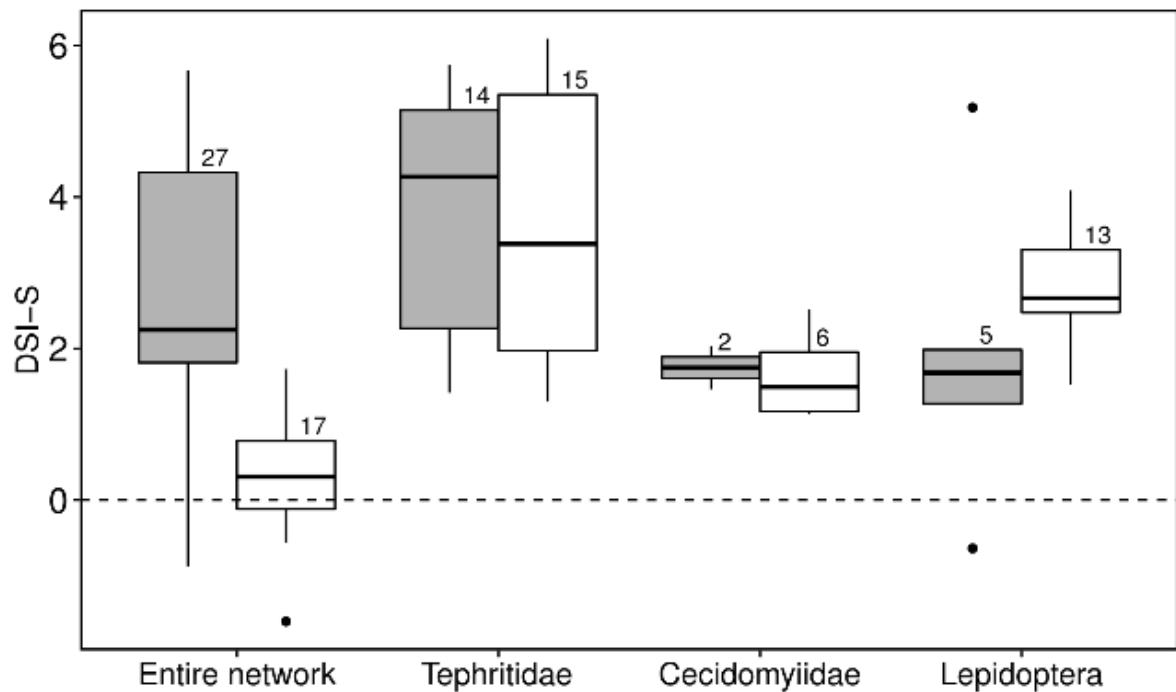


Figure 1 – Boxplot of the DSI-S values of the counterpart of each insect species (grey boxes) and the counterparts of each plant species (white boxes), for each of the subsets considered. Positive values mean higher than expected phylogenetic clustering of the counterpart set. Horizontal lines represent the median values, boxes the interquartile range, vertical lines the 95% percentiles and dots the outliers. Sample sizes are shown above each box.

Compositional and phylogenetic similarity of host plants and herbivore assemblages

The overall influence of phylogenetic relatedness between herbivores on the compositional (i.e., taxonomic) similarity of their host plants was positive but weak across the entire network (Table 1, Fig. 2a). A stronger pattern was found, however, for the effect of phylogenetic closeness between herbivores on the phylogenetic similarity of their host plant species (Table 1, Fig. 2b). In subnetworks we found significant positive relationships between the phylogenetic relatedness of the herbivores and the phylogenetic similarity of their host plants for the subnetworks composed of the Tephritidae and

Cecidomyiidae, but not for the Lepidoptera subnetwork (Table 1, Figs. 2d-2f). Thus, both Tephritidae and Cecidomyiidae showed a pattern contrary to our hypothesis, with increased phylogenetic conservatism of interactions when analyzed as subnetworks.

Host plants showed a different pattern than herbivores in the entire network, with a positive correlation between host-plant phylogenetic distance and both the compositional and phylogenetic disimilarity of their herbivore assemblages (Table 1, Fig. 3). Both the subnetwork composed of the Tephritidae and that composed of the Lepidoptera showed significant positive relationships between host-plant phylogenetic proximity and compositional and phylogenetic similarity of herbivores (Table 1, Figs. 3c, 3d, 3g, 3h). For the Cecidomyiidae subnetwork, only the phylogenetic similarity of herbivores increased with increasing phylogenetic proximity between host plant species (Table 1, Fig. 3f).

Table 1 – Correlations between phylogenetic distance and the two metrics of compositional overlap (Jaccard and Unifrac) for each subnetwork and trophic level. 95% confidence intervals due to phylogenetic uncertainty associated with polytomies are shown in parenthesis.

Herbivore group	Jaccard			Unifrac		
	r	z-value	p-value	r	z-value	p-value
All herbivores						
Plant pairs	0.40	4.89 (4.75 – 5.22)	<0.001	0.29	3.67 (3.63 – 4.20)	<0.001
Herbivore pairs	0.08	2.11 (1.86 – 2.62)	0.014	0.11	2.37 (2.11 – 2.77)	0.011
Tephritidae						
Plant pairs	0.21	2.65 (2.67 – 3.19)	<0.001	0.70	8.60 (8.98 – 10.83)	<0.001
Herbivore pairs	0.10	1.36 (0.37 – 4.73)	0.076	0.44	5.90 (3.67 – 8.05)	0.001
Cecidomyiidae						
Plant pairs	0.14	1.03 (0.88 – 1.17)	0.164	0.57	4.10 (3.82 – 4.95)	<0.001
Herbivore pairs	0.13	1.44 (0.73 – 1.43)	0.087	0.22	2.35 (1.86 – 3.00)	0.021
Lepidoptera						
Plant pairs	0.23	1.75 (1.71 – 1.90)	0.038	0.34	2.41 (2.06 – 2.34)	0.011
Herbivore pairs	0.23	0.75 (0.03 – 1.15)	0.277	-0.46	-1.39 (-1.88 - -0.58)	0.085

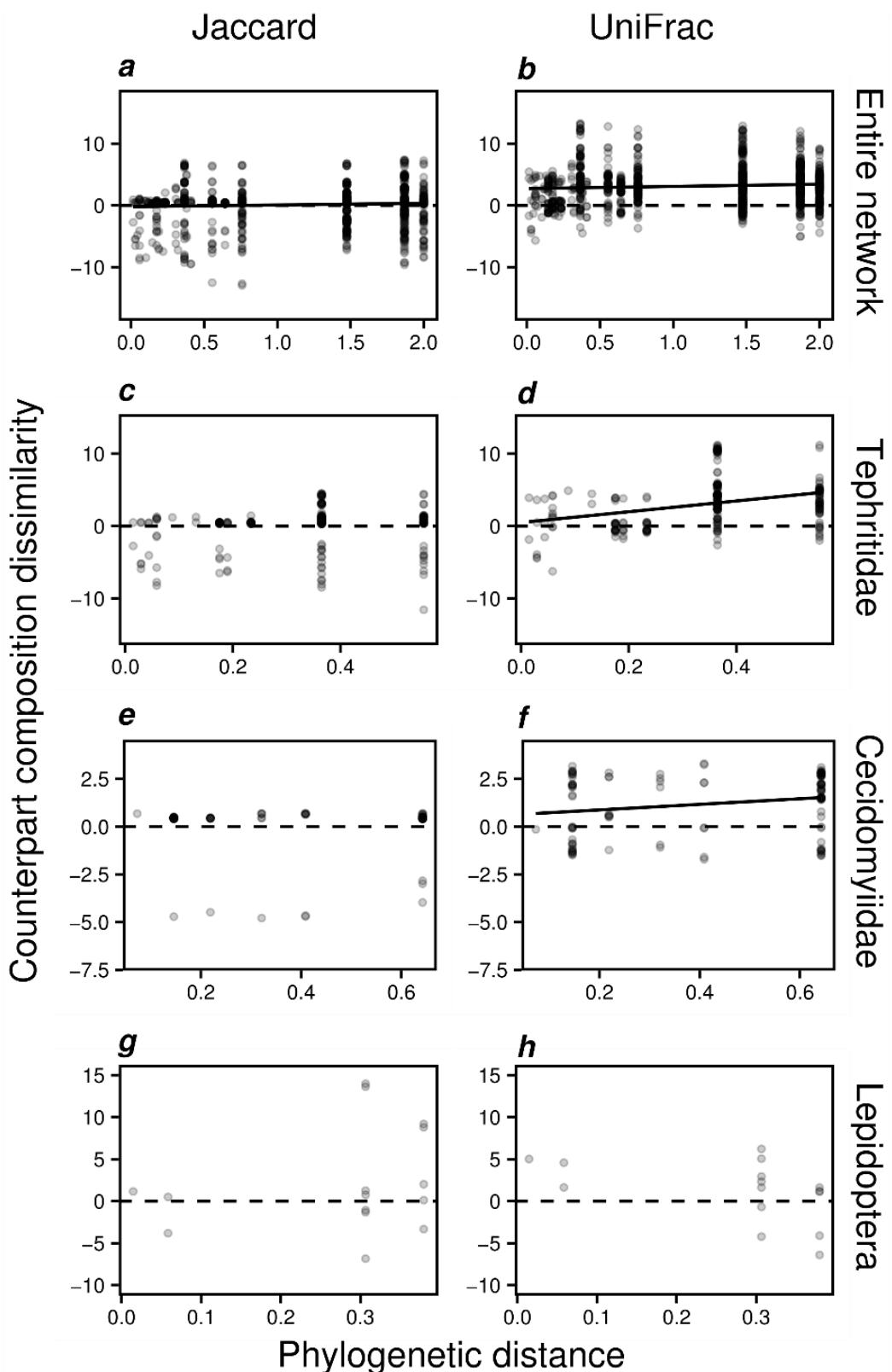


Figure 2 – Correlations between phylogenetic distance between pairs of species (x axis) and the two metrics of compositional distance z-values (Jaccard: b, d, f, h; UniFrac: a, c, e, g), for the pairs of endophage species for each subset (entire network: a, b; Tephritidae: c, d; Cecidomyiidae: e, f; Lepidoptera: g, h). Significant correlations are depicted by the regression line. Dashed line at zero added for better visualization.

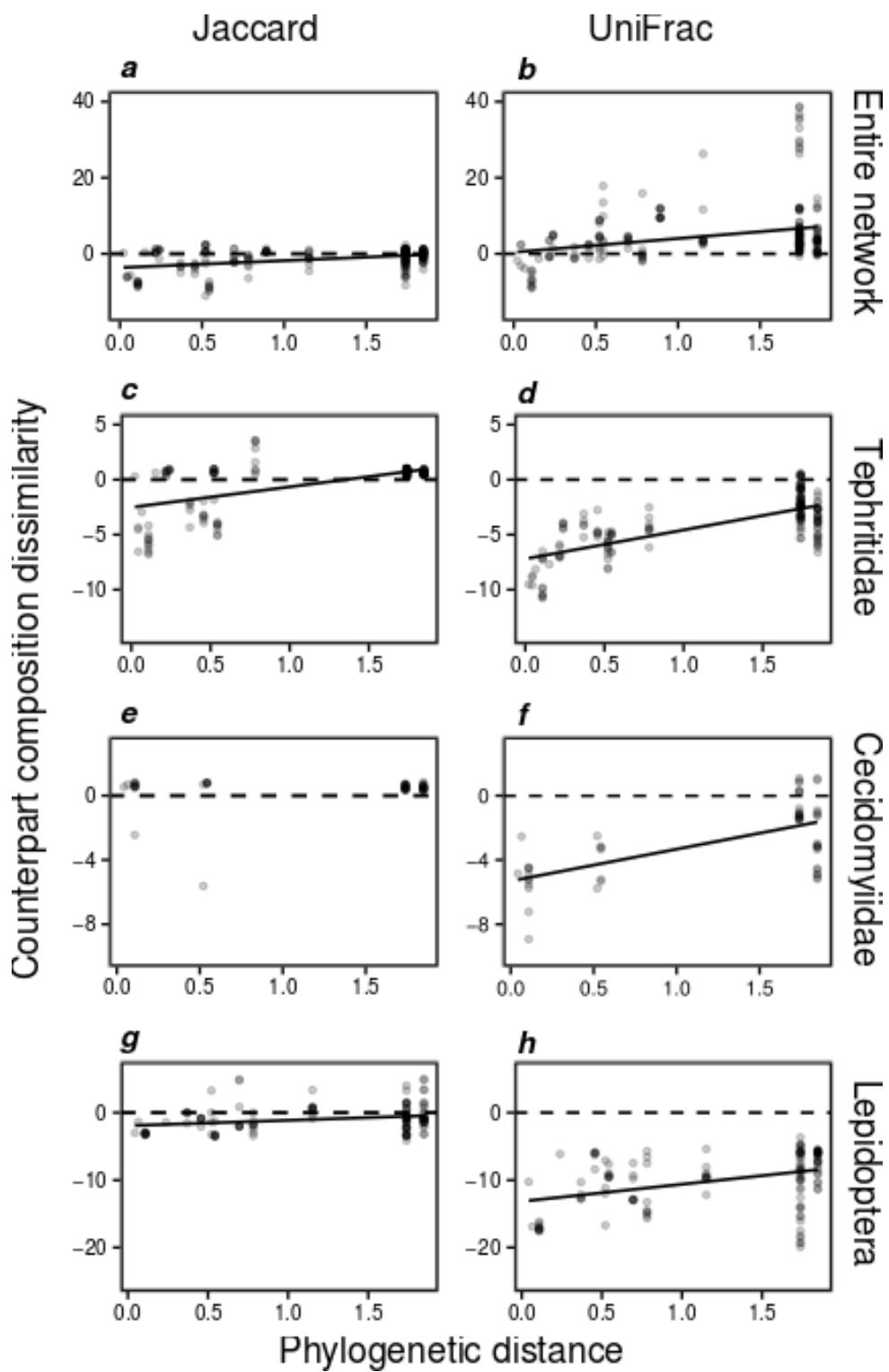


Figure 3 – Correlations between phylogenetic distance between pairs of species (x axis) and the two metrics of compositional distance z-values (Jaccard: a, e, c, g; Unifrac: b, d, f, h), for the pairs of plant species for each subset (entire network: a, b; Tephritidae: c, d; Cecidomyiidae: e, f; Lepidoptera: g, h). Significant correlations are depicted by the regression line. Dashed line at zero added for better visualization.

Phylogenetic patterns within network modules

Both the entire network and the three subnetworks showed significant modularity with the number of modules ranging from 6 to 12 (see Fig. 5, and Supplementary Material 1, Table A5 for details). However, many modules comprised only one interaction, which reduced the number of modules with sufficient data for testing. We did not find phylogenetic clustering of herbivores within the same module in the entire network ($t = 0.85$, $df = 3$, $p = 0.460$, Fig. 4). However, both the Tephritidae ($t = 3.71$, $df = 4$, $p = 0.02$, Fig. 4) and the Cecidomyiidae subnetworks showed significant phylogenetic clustering ($t = 6.21$, $df = 4$, $p = 0.003$, Fig. 4). The Lepidoptera subnetwork had only one module with two species, which precluded statistical tests for this group (Fig. 4).

Overall, we did not detect significant phylogenetic clustering of host plants within modules ($t = 1.14$, $df = 3$, $p = 0.35$, Fig. 4). However, in accordance with our expectations, some modules had host plants that were more closely related than would be expected by chance (Supplementary Material 1, Table A2). A separate evaluation of each subnetwork revealed phylogenetic clustering of the host plants only for the Tephritidae subnetwork (Fig. 4). For the Lepidoptera subnetwork, we found phylogenetic clustering of host plants in a single module. Phylogenetic clustering of host plants within modules was not tested for the Cecidomyiidae subnetwork because only one module had more than one plant species.

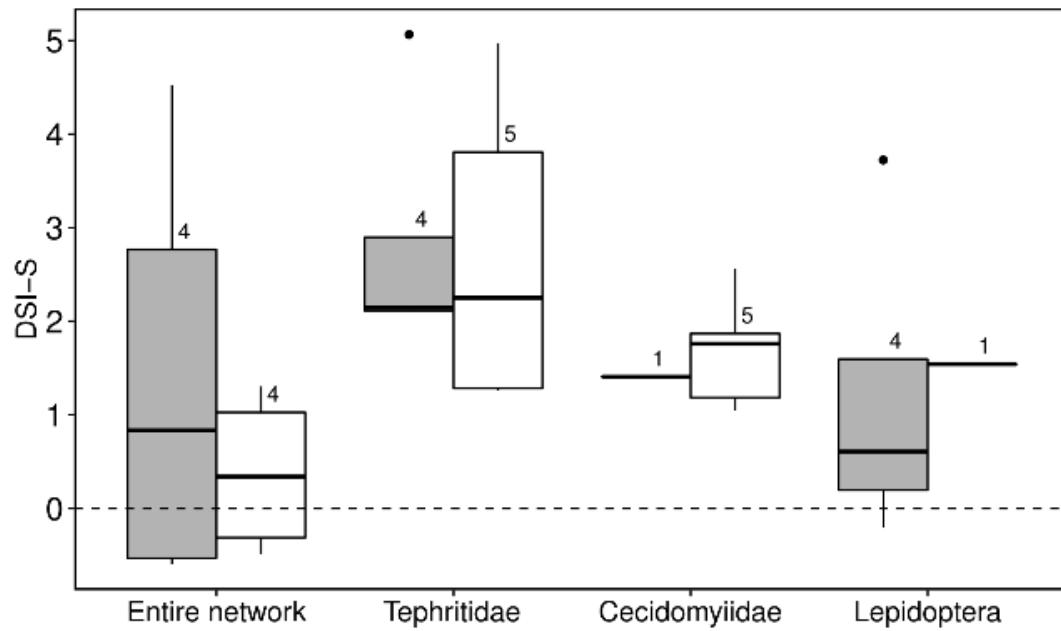


Figure 4 - Boxplot of the DSI-S values of the plant species (grey boxes) and insect species (white boxes) in the same module, for each of the subsets considered. Positive values mean higher than expected phylogenetic clustering of the species in the module. Horizontal lines represent the median values, boxes the interquartile range, vertical lines the 95% percentiles and dots the outliers. Sample sizes are shown along each box. In the Lepidoptera subset there was only one module with more than one insect species and in the Cecidomyiidae subset there was only one module with more than one plant species, for these cases the horizontal lines represent the DSI-S values of that particular module.

Patterns between network modules

The co-affiliation of host-plant species pairs to the same module was greater between plant species that were more closely related, both for the entire network and for the Tephritidae and Lepidoptera subnetworks (Table 2, Fig. 5). This result shows that, although the presence of unrelated species in a given module may have led to an overall absence of phylogenetic clustering of the plants in each module, closely related plants are still more likely to belong to the same module. By contrast, herbivores showed no relationship between phylogenetic relatedness and module co-affiliation (Table 2).

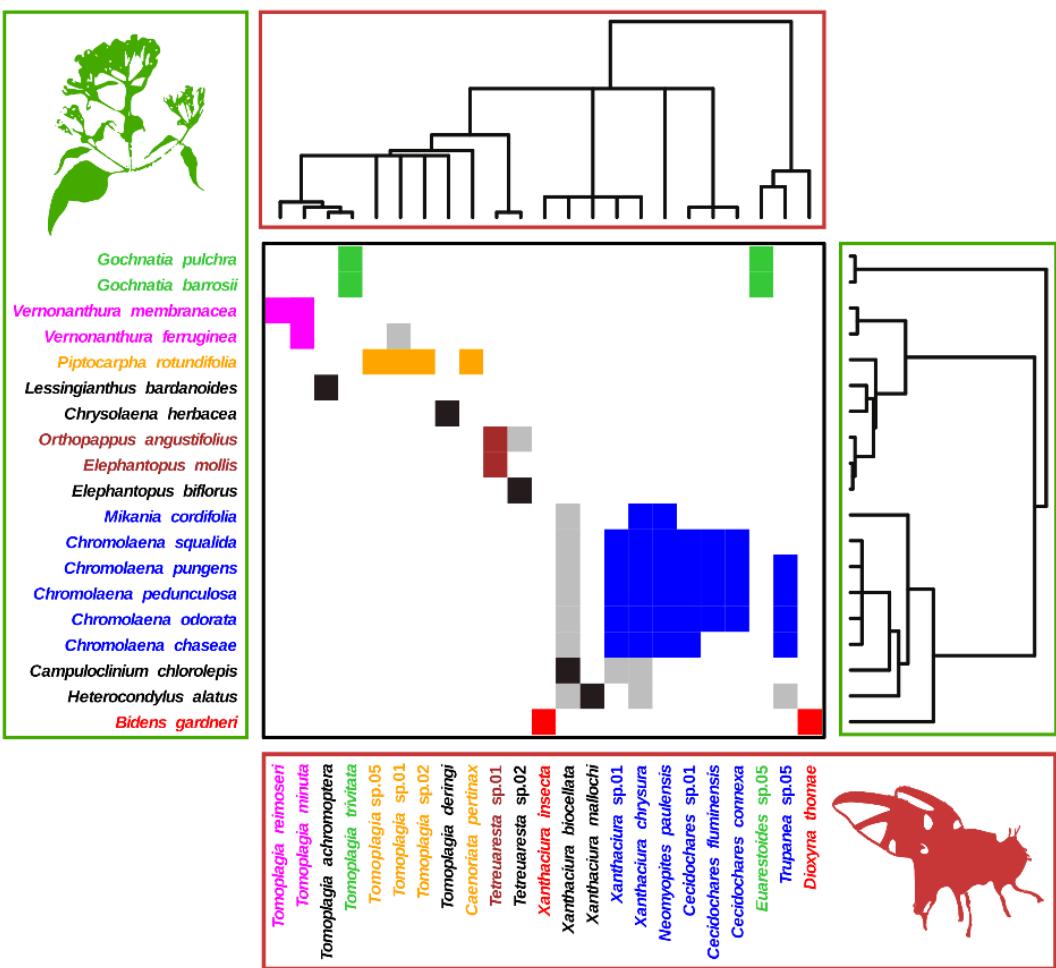


Figure 5 - Module affiliations for each species in the Tephritidae subnetwork. Tephritidae species are shown on the bottom with their phylogeny shown on the top. Asteraceae hosts are shown on the left with their phylogeny shown on the right. Colors mark species and interactions that belong to each module. Species in black belong to modules that contain only one interaction. Interactions between species that belong to different modules are shown in grey.

Table 2 – Results from the binomial GLMs modelling the relationship between phylogenetic distance of species pairs and the probability that both belong to the same module. 95% confidence intervals due to phylogenetic uncertainty associated with polytomies are shown in parenthesis.

Herbivore group	Coefficient	z-value	p-value
All herbivores			
Plant pairs	-0.66	-2.01 (-2.26 - -1.90)	0.028
Herbivore pairs	0.01	-0.24 (-0.37 - -0.08)	0.494
Tephritidae			
Plant pairs	-4.59	-10.86 (-12.78 - -11.19)	<0.001
Herbivore pairs	-1.01	-1.29 (-3.73 - -0.59)	0.133
Cecidomyiidae			
Plant pairs	-1.52	-0.55 (-0.50 - -0.20)	0.318
Herbivore pairs	-4.01	-1.41 (-1.43 - -0.85)	0.087
Lepidoptera			
Plant pairs	-0.62	-1.89 (-2.14 - -1.80)	0.027
Herbivore pairs	2.84	-0.20 (-0.32 - -0.12)	0.500

Phylogenetic uncertainty

Phylogenetic uncertainty resulting from polytomies had no qualitative impact on the final results, since no confidence interval overlapped zero in any case that was statistically significant in the results with polytomies (Table 1, Table 2; Supplementary material Appendix 1 Table A1). DSI-S values for modules or species with significant aggregation varied, on average, 16.56% for the Asteraceae and 21.72% for the endophages. Likewise, statistically significant correlations across all analyses (Jaccard, Unifrac and Module co-occurrence) showed an average associated uncertainty of 16.73% for the Asteraceae and 46.68% for the endophages.

DISCUSSION

In this study, we integrated phylogenetic/taxonomic information in a well-defined plant-herbivore network to evaluate to what extent the compositional and phylogenetic similarities of interactions between herbivorous insects or between host plants are influenced by phylogenetic relatedness of either plants or herbivores. Our results show that, in the entire network, whereas herbivores use phylogenetically clustered sets of host plants, plants are not associated to phylogenetically aggregated sets of herbivores. This asymmetry in phylogenetic clustering of interactions between herbivores and plants is probably a result of the inclusion of disparate lineages of insects that evolved this feeding mode and independently colonized this group of host plants. Evidence for this explanation comes from results for more restricted phylogenetic sets of herbivores (the Cecidomyiidae, Lepidoptera, and Tephritidae), in which species sets of each insect group were, on average, more closely related than would be expected by chance. These results are consistent with a high phylogenetic conservatism of traits mediating interactions among species. Susceptibility of plants to pathogens, for example, has been shown experimentally to be phylogenetically conserved (Gilbert and Webb 2007), probably as a result of the conservatism of defense traits observed among all the angiosperms (Agrawal 2007). There are, however, examples of how convergent traits can mediate plant-herbivore interactions, independent of plant phylogeny (Becerra 1997, Kergoat et al. 2005).

We also demonstrated the presence of a positive relationship between phylogenetic relatedness and the interaction similarity between species pairs from the same trophic level in most subnetworks. Additionally, our inclusion of phylogenetic information in the measures of interaction similarity resulted in an improved signal for the herbivore pairs. This was the case both for herbivore and plant partitions in the

Cecidomyiidae subnetwork, an insect group that did not show correlations between pure compositional similarity and phylogenetic distance. Most cecidomyiids are highly specialized, utilizing a single host plant species (Carneiro et al., 2009). Monophagy was also common among cecidomyiid species in our study system; therefore, no compositional overlap was possible between most species pairs. Even so, a greater phylogenetic similarity was observed between cecidomyiids associated to highly related plants. It is possible, therefore, that even in cases where no phylogenetic signal in ecological similarity is apparent (e.g., Rezende et al., 2007, Cagnolo et al., 2011, Elias et al., 2013) a phylogenetic signal might still exist in the shared partners' evolutionary history. The differences in signal strength between the purely compositional and the phylogenetically weighted measures of similarity can also shed some light on the detailed patterns of counterpart-sharing between species. For example, a stronger signal in phylogenetic similarity can be caused either by higher divergence in the partners of distantly related species or by higher convergence of the partners of closely related species. Future analysis of the phylogenetic component of ecological similarity between pairs of interacting species and studies exploring additional approaches (e.g. Ives and Godfray 2006) should be helpful to further test these hypotheses.

In agreement with the patterns found in other antagonistic systems (Cagnolo et al. 2011, Krasnov et al. 2012, Elias et al. 2013, Fontaine and Thebault 2015), the strength of the phylogenetic signal was consistently greater for the host-plant species than for the herbivore insects, with higher correlation coefficients. This asymmetry was more evident when looking at the modules present in the network. Despite the phylogenetic conservatism in the ecological interactions at the species level for most insect groups tested, closely related herbivores frequently belonged to different network modules. For the plants, however, even though some modules contained distant relatives, closely

related plants were more commonly found in the same module. This finding shows that the module structure is mainly driven by the plant clades and that the herbivore lineages are distributed in different modules. This result is in line with previously reported taxonomic patterns in module structure in the same system (Prado and Lewinsohn, 2004).

There were, however, important differences between the entire network and the subnetworks. Contrary to what was expected if competition between consumers was the main driver of phylogenetic signal asymmetry, the observed phylogenetic conservatism in plant use was greater when we considered subnetworks composed of phylogenetically more restricted insect groups of herbivores. More closely related herbivores in these subnetworks shared a higher proportion of hosts than was observed for the entire network. This result suggests that competition between related consumers is not the only major driver of phylogenetic signal asymmetry at this scale. A recent study on the correlation between phylogenetic distance and individual level co-occurrence in flea communities (Krasnov et al. 2014) also demonstrated significant co-occurrence of pairs of closely related fleas, which indicates a prevalence of environmental, or host, filtering in determining the composition of flea assemblages on individual hosts. The parasitic lifestyle of endophagous insects also imposes numerous restrictions on host use that probably increase the influence of those kinds of filters. It seems more likely, therefore, that other processes such as differences in the colonization history between herbivore lineages and contrasting rates of evolution between resources and consumer have a greater role in determining the observed phylogenetic patterns.

Taken together, our results show the pervasive presence of phylogenetic effects in different levels of network organization. The importance of plant evolutionary history in shaping host use by herbivores has long been recognized (Ehrlich and Raven 1964, Benson et al. 1975), but the integration of phylogenetic information into plant-herbivore

studies has been hampered by the scarcity of well-resolved phylogenetic hypotheses for many insect groups. Recent advances in phylogenetic methods have triggered new improvements in our understanding of how species interactions are constrained by historical processes (Symons and Beccaloni 1999, Weiblen et al. 2006, Mouquet et al. 2012, Jorge et al. 2014). Although the phylogenetic hypotheses used here were constructed by the combination of information from different sources and did not include information on branch lengths, the patterns observed are probably robust enough to withstand these shortcomings as general results were unaltered even using different branch length representations and uncertainty associated with polytomies had no qualitative impact on final results. By gaining a better understanding of the role of phylogenetic constraints in defining species interactions, many new applications, such as the prediction of novel interactions (e.g., Pearse and Hipp, 2009, Ness et al. 2011, Pearse et al. 2013) will become possible.

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CAPÍTULO 2 - Avaliando a importância relativa de fatores ecológicos e filogenéticos para a estrutura de uma rede planta-herbívoro

RESUMO

Elucidar o quanto diferentes fatores afetam a probabilidade de interação entre espécies é um passo importante em direção a um entendimento mecanicista da formação de redes ecológicas. Uma abordagem possível para testar a importância relativa destes efeitos é a representação dos diferentes fatores em matrizes de probabilidade de interação. Entretanto, como salientado por Vázquez et al. (2009), traduzir as relações filogenéticas em matrizes de probabilidade de interação ainda é problemático. Neste estudo, resolvemos esta lacuna usando uma modificação de uma análise co-evolutiva baseada em Procrustes. Além disso, aplicamos uma abordagem baseada em modelos de modo a permitir uma comparação direta dos tamanhos de efeito de cada fator testado. Exemplificamos nossa nova abordagem ao testar o quanto as interações e as propriedades de uma rede planta-herbívoro extensamente estudada podem ser previstas por processos ecológicos e evolutivos. Nossos resultados mostram que, para esta diversa rede planta-herbívoro, os padrões de interação das espécies aparentadas a uma determinada espécie combinados com informações sobre padrões de ocorrência espaço-temporal e de abundância das espécies explicam a maior parte da variação na frequência de interação entre pares de espécies. Entretanto, nenhuma das matrizes de probabilidade de interação foi capaz de reproduzir a estrutura altamente modular e especializada observada na rede. Uma melhor compreensão das condições que mediam a importância relativa de diferentes processos deverá melhorar nossa habilidade de inferir e prever quais interações irão ocorrer, e também melhor antecipar os impactos de mudanças ambientais sobre as interações existentes.

Assessing the relative importance of ecological and phylogenetic factors for the structure of plant-herbivore interactions

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ABSTRACT

Elucidating the extent to which different factors affect the probability of interaction between species is an important step towards a mechanistic understanding of how ecological networks are set. One proposed way to test for the relative importance of ecological and evolutionary effects is their representation as interaction probability matrices. However translating phylogenetic relatedness into interaction probability matrices is still problematic. In this study, we address this shortcoming by using a modified Procrustes-based coevophylogenetic analysis. In addition, we applied a model-based framework to allow a direct comparison of the effect sizes of each tested factor. We exemplify our new approach by testing the extent to which interactions and network properties of an extensively studied plant-herbivore assemblage are predicted by ecological and evolutionary processes. Our results show that, for this diverse herbivore-plant network, the interaction patterns of the relatives of a given species combined with information on the spatio-temporal occurrence and abundance patterns of the species explain most of the variation in the frequency of interaction between pairs of species. However, no interaction probability matrix was able to reproduce the highly modular and specialized network structure observed. A better understanding of the conditions that mediate the relative importance of different processes may also improve our ability to infer and predict which interactions should actually occur, and also to better anticipate the impacts of environmental change in existing interactions

INTRODUCTION

Understanding why some species are more likely to interact with each other is a fundamental question in Ecology (Sutherland et al. 2013). This question has been investigated using the signal, strength, and frequency of interspecific interactions in different systems (Connel 1983, Lewinsohn et al. 2006, Melia et al. 2007, Ings et al. 2008, Verdú et al. 2010). By using network-based approaches to study ecological interactions, many studies have found community-level patterns in the distribution and similarity of interactions among species (e.g., Dunne et al. 2002, Bascompte et al. 2003, Araújo et al. 2015). Recently, there has been a growing interest in investigating the fine structure of ecological networks by focusing on species-specific traits and phylogenetic relatedness (Cagnolo et al. 2011, Kaiser-Bunbury et al. 2014).

A basic question regarding the fine structure of interaction networks is why some of the possible links are not observed. Unobserved links can result from different ecological and evolutionary processes that make some interactions impossible or that reduce their probability between certain species pairs. For example, it is obvious that there can be no direct interaction if the individuals do not meet each other, such as in species pairs with mismatched spatial distributions, different phenological patterns or even different diurnal activity times (Olesen et al. 2011). Following this reasoning, it is expected that species that co-occur more frequently are more likely to interact than those species that have mismatched temporal or spatial distributions (Maruyama et al. 2014). Likewise, more abundant species are more likely to interact, both due to chance alone (Vázquez et al. 2009) and to positive demographical effects that result from the interactions, thus favoring species with more interactions (e.g., in mutualistic interactions, Suweis et al. 2013).

Absent links in ecological networks can also result from trait-related constraints, also referred to as forbidden links (Jordano et al. 2003; Vázquez 2005, Olesen et al. 2011, Vizentin-Bugoni et al. 2014). Furthermore, because there is commonly some degree of phylogenetic conservatism in species traits (Kraft et al. 2007, Vamosi et al. 2009), it is expected that closely related species will interact with similar counterpart species. There is, indeed, plenty of evidence for phylogenetic conservatism in ecological interactions across many taxa (Rezende et al. 2007, Gómez et al. 2010, Minoarivelo et al. 2014, Rohr and Bascompte 2014).

Elucidating the extent to which different factors affect the probability of interaction between species is an important step towards a mechanistic understanding of how ecological networks are formed. The relative importance of trait-related factors in determining network structure, for instance, is probably mediated by the degree of intimacy of the interaction (Guimaraes et al. 2007). Interactions involving tight adaptations and intimate lifestyles are expected to impose many trait-related constraints, increasing the potential role of phylogenetic conservatism in shaping interaction networks (Anderson 1993, Krasnov et al. 2014). Opportunistic interactions, on the other hand, are expected to be less constrained by phylogenetically-structured traits, and therefore should reflect mechanisms that increase the probability of encounter between two individuals, such as co-occurrence and species abundances (Burns 2007, Vázquez et al. 2009).

One proposed way to test for the relative importance of these effects is their representation as interaction probability matrices (Vázquez et al. 2009). This approach has been applied on pollinator-plant networks with some interesting insights (Vázquez et al. 2009, Vizentin-Bugoni et al. 2014, Maruyama et al. 2014, Olito and Fox 2015). It has been shown, for example, that morphological attributes of the species can have a greater importance than abundance patterns in structuring the interaction network (Vizentin-

Bugoni et al. 2014). There is also evidence that the ability to describe network structural patterns is decoupled from the ability to describe pairwise interactions (Vázquez et al. 2009, Vizentin-Bugoni et al. 2014, Maruyama et al. 2014, Olito and Fox 2015). For example, Vázquez et al. (2009) models were able to reproduce partially the nestedness of the observed networks, despite not providing a good fit for the pairwise interactions. However, as stressed by Vázquez et al. (2009), the proposed method does not take directly into account the relative importance of phylogenetic relatedness. In this study, we address this shortcoming by using a modified Procrustes-based coevolutionary analysis (Balbuena et al. 2013), which applies Procrustes analysis to compare the shape of the parasite and host phylogenies. In addition, we applied a model-based framework to allow a direct comparison of the effect sizes of different possible determinants of network structure. We exemplify our new approach by testing the extent to which interactions and network properties of an extensively studied plant-herbivore assemblage are predicted by ecological and evolutionary patterns.

METHODS

Study system

Here we analyze the interactions between Asteraceae plants found in 20 Cerrado areas and their flower-head endophagous Tephritidae species. Flower head samplings were conducted in each area in three different periods (April-May 2003; August-September 2003; January-February 2004), totaling about four person-hours collecting flower-heads per period and site. A maximum of 80mL of flower heads per individual were sampled from up to 35 individuals per plant species at each site and sampling period. Adults of endophagous tephritid flies were reared in the laboratory, providing precise plant-endophagous associations along with counts of emerging individuals per sample.

Independent estimates of densities for each plant species were obtained by counting the number of individuals found in 15 rectangular plots of $30\text{m} \times 5\text{m}$ in each area. Further details on the sampling methods can be found elsewhere (Almeida-Neto et al. 2010, 2011). The plant-herbivore interaction network comprised 37 species of Asteraceae and 39 species of endophagous Tephritidae (Table S1). Considering only the plant-herbivore species pairs that co-occurred in the same site in at least one sampling, we included in our models 913 possible pairwise interactions. As expected from previous observations in this type of plant-herbivore interactions, the network is specialized ($H^2 = 0.67$), with very low connectance (Weighted connectance = 0.04) and moderately high modularity ($Q = 0.48$).

Data analysis

We constructed a phylogenetic hypothesis for the Asteraceae species in our study by attaching each species to the respective genus node in an Asteraceae family tree (Funk et al. 2009). For nodes for which there was no information available, we used taxonomic information whenever possible. We adopted a similar procedure for the tephritid species complementing the taxonomic information with available phylogenetic relationships from different sources (Korneyev 1999, Yotoko et al. 2005).

We then computed matrices describing the probability of interaction between each tephritid-plant species pair based on spatial overlap (matrix S), temporal overlap (matrix T), species abundance (matrix Ab) and the interaction patterns of phylogenetically related species (Phylo). The spatial (S) and temporal (T) interaction probability matrices were calculated by dividing the number of co-occurrences (site or sampling periods, respectively) between the species in the pair by the number of occurrences of the species

with the least occurrences among them. In this way, pairs with higher spatial or temporal overlap had higher values in the interaction probability matrix.

The abundance-based matrix (Ab) was calculated as the product of the abundances of the species in each pair. For the Asteraceae species, we used the total number of individuals sampled along all the sites and sampling periods as surrogate measure of abundance, while for the tephritid species the abundance was measured as the number of individuals that emerged from all the samples. Constructed in this way, both abundance measures also reflect information on temporal and spatial incidence. In order to use the abundance measures as interaction probability measures we rescaled them by dividing the values by the sum of observed values for each group. This matrix then described pairs consisting of highly abundant plants and tephritids as more likely to interact than pairs of rare species.

The quantitative estimates of interaction probability based on the interaction patterns of related species (*Phylo*) was obtained using an adaptation of the Procrustes approach proposed in Balbuena et al. (2013), in the following steps (see figure 1 for a graphical representation of the procedure): (1) First, as in Balbuena et al. (2013), we computed the principal coordinates from the phylogenetic distance matrices for each group. Each species was then represented in a multidimensional space by the point given by the respective PCo coordinates. Since the number of species was different between the groups, we only retained the first n PCo axes, where n is the number of species for the group with the least species from the two. Coordinates of species with multiple interactions were replicated accordingly, so each interacting pair of species was represented by their own pair of points. (2) For each focal endophagous species in turn, we computed the Procrustean transformation of the endophagous species coordinates that minimized the distances between all the other endophagous species, excluding the focal

species, and their hosts. (3) We then applied this transformation matrix to the coordinates of the focal species and calculated the Euclidean distance between the transformed coordinates and the coordinates of the plant species. (4) The more conserved are the interactions along the phylogenies of both groups (i.e., the more closely related endophagous interacting with closely related plants), the smaller the distance between the transformed coordinates of the focal species and the coordinates of the plant species that it interacts with. Thus, if the interactions are conserved in both groups, interaction probability between a given pair of species should be inversely proportional to this distance measure. Therefore, we converted those distances in interaction probability estimates by computing the inverse of the distance value and rescaling all values by the sum of the values for each group. We also tested alternative conversions using squared distances and obtained similar results (Supplementary Material).

Here we present a new approach to test the relative contribution of each of the tested factors in explaining the observed pattern of interactions. Aiming to allow for a more flexible parameterization of the importance of each interaction probability matrix, we used Poisson generalized linear mixed models (GLMMs) to model the observed frequency of interaction as a function of the temporal, spatial, abundance and phylogenetic interaction probabilities. By analyzing only species that co-occurred in at least one site and one sampling, we only modelled species pairs that could potentially interact. We also accounted for the variation between different plant and endophagous species by adding the species' identities as random effects in the model. In this way, we were able to estimate the importance of each factor to the observed interaction pattern. We computed the marginal and conditional R^2_{GLMM} as indices of goodness-of-fit (Nakagawa and Schielzeth 2013).

In order to compare this new method to the previously existing approach proposed by Vázquez et al. (2009), we simulated theoretical interaction matrices using compound interaction probability matrices describing all possible combination of the five individual probability matrix (Insect abundance, Plant abundance, Spatial overlap, Temporal overlap and Phylogenetic probability). The compound interaction probability matrices were generated by multiplying element wise the individual probability matrices. We then used each combination of probabilities to generate 1000 matrices, using the algorithm proposed in Vázquez et al. (2009), from which three different quantitative measures of network structure were calculated – Weighted Modularity (QuanBinMo – Dormann and Strauss 2014), Weighted Connectance (Tylianakis et al. 2007), and Network Specialization (H2 – Bluthgen et al. 2006). We then assessed the ability of each matrix combination in predicting the observed interaction patterns by comparing the observed values of network structures with the mean and 95% CI of the simulated values. We also compared the fit between each probability matrix combination and the observed interactions by calculating AIC values from the multinomial likelihoods as proposed in Vázquez et al. (2009). In the original formulation, the number of parameters k is defined as the number of matrices combined to obtain the probability values. We also present, in the Supplementary Material, a more conservative approach considering the number of species involved in each comparison, as proposed by Vizentin-Bugoni et al. (2014). Additionally, we built an interaction probability matrix derived from the fitted values of the GLMM. We then used this model-derived probability matrix (matrix M) to generate simulated matrices and to compute network metrics in the same way as the other matrices. To calculate the AIC value in the same way as the other matrix combinations described above we defined the number of parameters k as the number of estimated parameters in the model. All analyses were performed in the R statistical environment (R core Team,

2014), using original code, code from Balbuena et al. 2013, and functions from the packages *bipartite* (Dormann et al. 2009), *ggplot2* (Wickham 2009), *lme4* (Bates et al. 2015), *MuMIn* (Bartón 2009), *picante* (Kembel et al. 2010), and *vegan* (Oksanen et al. 2015).

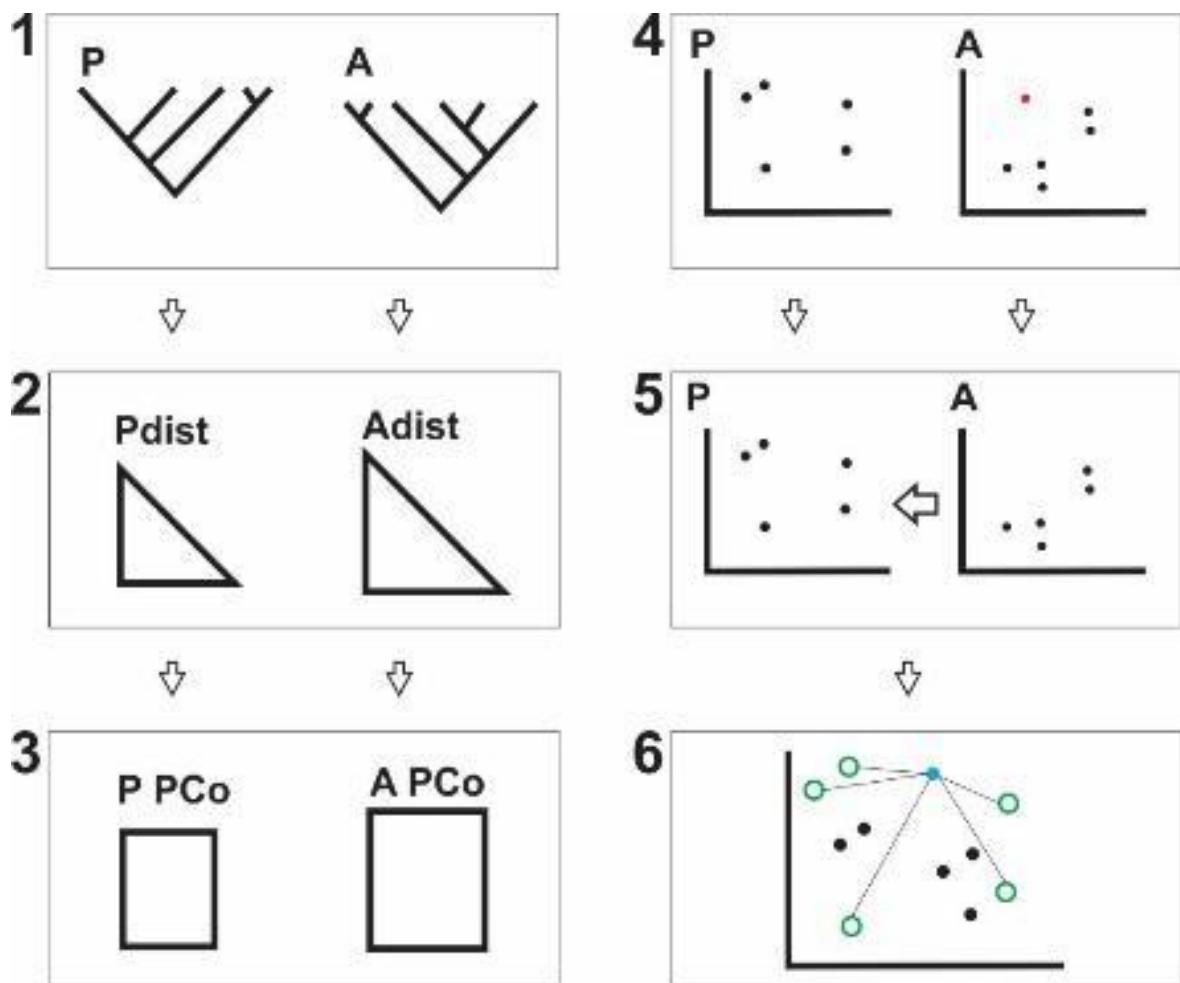


Figure 1 – Flowchart of the steps used to obtain quantitative estimates of interaction probability based on the interaction patterns of related species. 1 - Plant (P) and animal phylogenies (A) are used to compute 2 - phylogenetic distance matrices (Pdist) and (Adist). 3 – Species are then represented by their distance's principal coordinates (PPCo and APCo). Following Balbuena et al. 2013, coordinates for species with multiple interactions are duplicated so that each unique interaction is represented as a pair of coordinates. In order to avoid including the interaction information of the focal species in its own interaction probability values, we use a leave-one-out approach. One of the animal species is removed (red dot in 4) and a Procrustes analysis is performed to find the transformation that best overlays the animal coordinates onto the plant coordinates (5). 6 - The transformation matrix found by the Procrustes analysis is applied to the coordinates of the focal species (the blue dot) and the distances between the focal species and all plant species (green hollow dots) are computed. The inverse of these distances is then used as an estimate of the probability of interaction between the focal species and each plant species.

RESULTS

We found significant effects of all five components of interaction probability in the GLMM.(abundance, spatial overlap, temporal overlap, and phylogenetic proximity). The frequency of interactions between the tephritid flies and the plant species that co-occurred in the same site most frequently was higher ($Z = 194.05$, $p < 0.0001$, Table 1, Fig. 2), as well as for those pairs that had greater temporal overlap ($Z = 33.96$, $p < 0.001$, Fig. 2). We also found a striking phylogenetic signal, with more interactions between a given focal tephritid species and the plants closely related to the host plants of the focal species relatives ($Z = 52.03$, $p < 0.001$, Table 1, Fig. 2). More abundant species also had more interactions, both for the insects ($Z = 2.39$, $p = 0.017$, Table 1, Fig. 2) and for the plants ($Z = 2.97$, $p = 0.003$, Table 1, Fig. 2).

Table 1 – GLMM estimates for the effects of the predictor variables on the interaction frequencies between all plant-herbivore pair. Marginal $R^2_{\text{GLMM}} = 0.51$, Conditional $R^2_{\text{GLMM}} = 0.88$.

Fixed Effects	Z-value	P
Intercept	-36.69	<0.001
Phylogenetic signal	52.03	<0.001
Temporal overlap	33.96	<0.001
Spatial overlap	194.05	<0.001
Plant abundance	2.97	0.003
Insect abundance	2.39	0.017

Random Effects	Variance	Standard Deviation
Plants (37 spp.)	3.26	1.81
Insects (39 spp.)	2.70	1.64

Despite the positive effects of all variables in the model, individual probability matrices and their combinations were not able to reproduce the properties of the observed network, since no set of predictor variables resulted in metric distributions encompassing the observed values (Fig. 3). The observed values of network specialization and modularity were higher than those from all simulated matrices, whereas the observed weighted connectance was lower (Fig. 3). Although the probabilities derived from the fitted values of the GLMM were among the closer to the observed values for the three variables (Figure 3), those model-based metrics did not encompass the observed values. The GLMM fit probability matrix presented the best AIC value among all probability matrices and their combinations (Table 2). The second-best AIC was obtained by the PST matrix, but its difference to the best one was large ($\Delta\text{AIC} = 97$, Table 2).

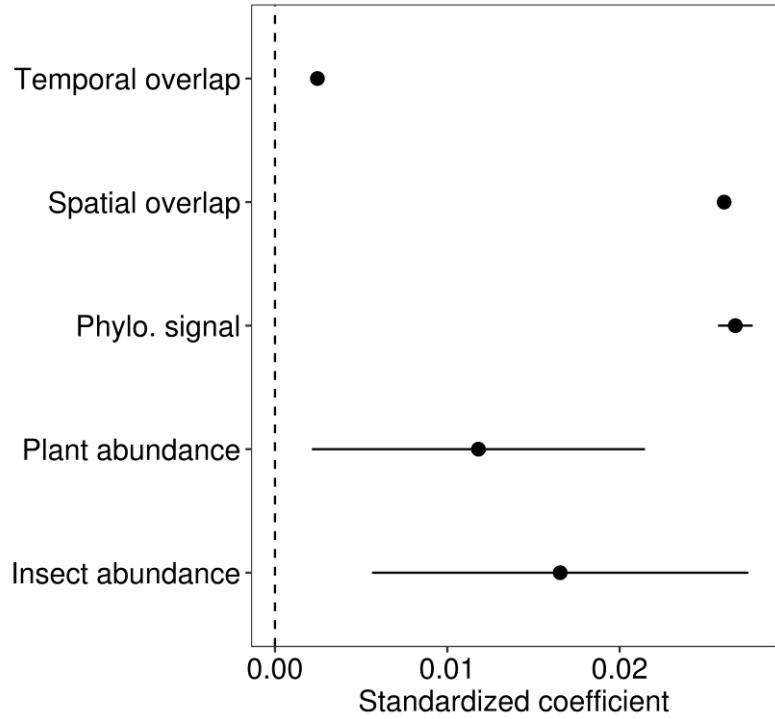


Figure 2 – Standardized coefficients for the effects of insect abundance, plant abundance, phylogenetic signal, spatial and temporal overlap on interaction probability between Asteraceae and Tephritidae species. Horizontal lines represent 1.96 times the standard errors of the coefficients. Dashed line at zero added for better visualization.

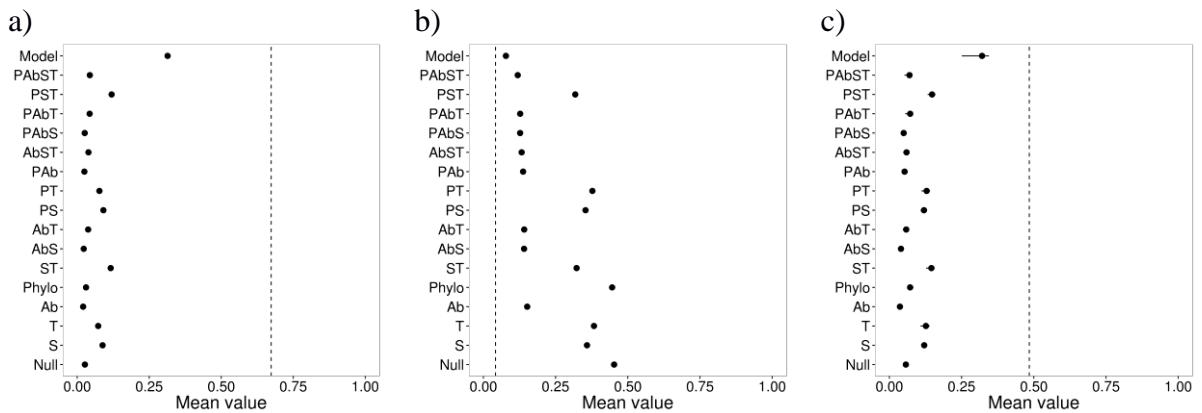


Figure 3 – Mean (dots) and 95% confidence intervals (spreads – note that most of the intervals were too small to be visible in the figure) for the values of network specialization (a), weighted connectance (b), and modularity (c) for each probability matrix and their combinations (Model – matrix derived from the GLMM fitted values, P – phylogenetic probability matrix, Ab – abundance probability matrix, T – temporal overlap probability matrix, S – spatial overlap probability matrix, Null – null probability matrix, Letter combinations – the element wise product of the respective matrices). The dashed lines indicate the values in the observed network.

Table 2 – Log likelihood and AIC values for the fit of each probability matrix to the observed interaction values, ordered by their difference to the best fit (ΔAIC). Model – matrix derived from the GLMM fitted values, Phylo/P – phylogenetic probability matrix, Ab – abundance probability matrix, T – temporal overlap probability matrix, S – spatial overlap probability matrix, Null – null probability matrix, Letter combinations – the element wise product of the respective matrices. Number of parameters calculated as proposed in Vázquez et al. 2009. Alternative calculation as in Vizentin-Bugoni et al. 2014 are presented in the Supplementary Material Table S2.2 and Table S3.

Probability matrix	Log Likelihood	Number of parameters	AIC	ΔAIC
Model	-248.61	8	513.22	0.00
PST	-302.22	3	610.44	97.22
ST	-317.67	2	639.34	126.13
PS	-321.83	2	647.66	134.44
S	-337.31	1	676.62	163.40
PT	-336.40	2	676.80	163.58
T	-352.94	1	707.88	194.66
P	-363.01	1	728.02	214.80
Null	-379.71	1	761.42	248.20
PAbT	-512.48	3	1030.96	517.74
AbT	-514.48	2	1032.96	519.74
PAb	-519.62	2	1043.24	530.02
AbST	-520.21	3	1046.42	533.21
Ab	-522.25	1	1046.49	533.27
PAbST	-519.30	4	1046.60	533.38
PAbS	-525.97	3	1057.94	544.72
AbS	-527.58	2	1059.15	545.93

DISCUSSION

The new approach proposed here has allowed us to incorporate the relative contributions of phylogenetic conservatism and ecological factors in determining species-specific interactions. Our results show that, for this diverse herbivore-plant network, the interaction patterns of the relatives of a given species combined with information on the spatio-temporal occurrence and abundance patterns of the species explain most of the variation in the frequency of interaction between pairs of species.

There is plenty of evidence for a strong imprint of phylogenetic history in the observed interaction patterns in plant-herbivore networks (Cagnolo et al. 2011, Elias et al. 2013), including the Cerrado Asteraceae-Tephritidae system studied here (Jorge et al. 2015, Bergamini et al. 2017). Our results show that this pattern remains even after controlling for abundance and co-occurrence patterns, that probably include phylogenetic structure themselves (Bartomeus et al. preprint). There must be, therefore, additional phylogenetically structured effects mediating interaction patterns, such as plant defense traits (Agrawal 2011) and codiversification patterns (Althoff et al. 2014). The incorporation of trait-matching rules can be readily made using this analytical approach, as has been demonstrated in some other studies (Vizentin-Bugoni et al. 2014, Olito and Fox 2015). Future work that incorporates species attributes alongside phylogenetic patterns should be able to attain further insight in the relative importance of macroevolutionary processes such as codiversification (Althoff et al. 2014), diversification rates, and speciation patterns (Chamberlain et al 2014).

Although we did not include species pairs with zero overlap in the model, we still found that species pairs that co-occur more frequently also have a higher number of interactions. Despite the small number of temporal units, we also found a relationship between temporal overlap and interaction frequency. The positive effects of spatial and

temporal overlap may reflect the turnover in plant composition and a tight coupling between the occurrence of the herbivores and their hosts. Various biotic and abiotic factors can lead to the turnover in plant composition, including anthropic habitat modification (Almeida-Neto et al. 2011). A low co-occurrence between species that do not interact puts further constraints on host-switches and promotes the maintenance of the specialization in the network (Lion and Gandon 2015). There remains to be tested whether this pattern also is reflected in spatial modularity in the network.

Although all of the tested factors showed an effect on the frequency of interaction between species pairs, no interaction probability matrix was able to reproduce the highly modular and specialized network structure observed. This result contrasts with what is commonly observed in studies on mutualistic networks (Vázquez et al. 2009, Vizentin-Bugoni et al. 2014, Olito and Fox 2015), where at least some network properties are well predicted by simple null models. Another difference between previously reported studies and this one is that while the evidence for mutualistic networks points towards a strong effect of species abundances (Vázquez et al. 2009), in our system matrices that included the species abundance were among the worst in explaining interaction patterns. Both results can be explained by the high intimacy found in the interactions between endophagous insects and their hosts, which leads to specialized interactions and consequently to weaker roles of the abundance of the species (Nobre et al. 2016).

Considered along the high degree of specialization and modularity observed in this network (Bergamini et al. 2017, Almeida-Neto et al. 2011), the positive effects of the abundance of both the insects and the plants indicate that, overall, abundant host plants also have abundant herbivores. Since the information on plant abundance was collected independently from the network data, in order for an abundant plant species to consistently show high interaction numbers, their herbivore species must be highly

abundant as well. This pattern is consistent with the expectations of the resource concentration hypothesis (Root 1973), that predicts higher herbivore abundances on abundant host plants because of patch selection behavior and local population dynamics.

In our model, we chose to add plant and insect identities as random factors in order to mitigate the use of pairwise comparisons as observation units. While the inclusion of a phylogenetic covariance matrix in the model (as in Rafferty and Ives 2013) would better account for the non-independence of the species in the pairwise comparisons, the approach we developed allows for a more direct comparison between the magnitudes of the effects of phylogenetically structured processes and the ecological processes. This was possible because the relationships between both plants and insects were reframed as a component of the phylogenetic interaction probability matrix, and so its effects could be estimated in the same way as the other main effects in the model. Additionally, this choice also allowed the use of the matrix to generate simulated networks and investigate higher-level structural patterns. One of the advantages of a model-based approach is the possibility of modeling more complex relationships (Warton et al. 2015), such as polynomial expansions and interactions between the variables. This possibility stimulates the formulation and testing of specific hypothesis and provides a new step in tackling the need for more flexible phylogenetic statistical approaches in community ecology (Rafferty and Ives 2013). Nevertheless, future work in simulated data is warranted to better analyze the properties of our model in different situations, such as varying levels of phylogenetic signal in interaction patterns and abundance distributions in both groups.

Our new approach allowed the evaluation of the relative importance of distinct factors in structuring interaction networks. By gathering this kind of information in more systems, novel insights about the structure of ecological interactions may emerge. A better understanding of the different conditions that mediate the relative importance of

different processes may also improve our ability to infer and predict which interactions should actually occur (Morales-Castilla et al. 2015, Pearse and Altermatt 2015), and also to better anticipate the impacts of environmental change in existing interactions (Peralta 2016).

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CAPÍTULO 3 – Assimetria entre níveis tróficos no sinal filogenético em interações ecológicas: uma análise global de redes de antagonistas

RESUMO

Conservação filogenética em interações ecológicas tem sido demonstrada empiricamente em vários sistemas, juntamente com assimetrias consistentes na força deste sinal. Em redes de antagonistas, por exemplo, interações são usualmente mais conservadas entre espécies do nível trófico inferior, enquanto espécies do nível trófico superior apresentam variados graus de troca de hospedeiros. Entre as explicações propostas para este padrão emergente de assimetria estão os efeitos de deslocamento de nicho trófico entre consumidores aparentados e diferenças nas taxas evolutivas entre traços relacionados ao ataque e à defesa. Neste trabalho aproveitamos a ampla literatura sobre cofilogenia e métodos de reconciliação de árvores filogenéticas para investigar a generalidade do padrão assimétrico em diferentes sistemas de antagonistas. Para cada nível trófico em cada uma das 102 redes compiladas, medimos o sinal filogenético nos padrões de interação usando a correlação de Pearson entre a matriz de distância filogenética e os valores z de distâncias Unifrac entre todos os pares de espécies. Avaliamos a assimetria na força do sinal com tamanhos de efeito Q de Cohen. Usamos uma meta análise de efeitos aleatórios para estimar tamanhos de efeito gerais para as correlações entre filogenia e interações e também para as assimetrias nessas correlações. Usamos um modelo de meta-regressão para testar os efeitos da intimidade da interação, escala espacial dos estudos e diferenças de riqueza entre os níveis tróficos. Encontramos um padrão geral de conservação filogenética nos padrões de interação para ambos níveis tróficos com uma considerável heterogeneidade entre estudos. Por outro lado, a assimetria na força do sinal foi consistentemente pequena e não significativa em cada estudo individual, com um efeito geral positivo mas também pequeno. Não detectamos efeitos de nenhum dos moderadores testados. Nossos resultados fornecem evidências convincentes de que a conservação de interações ecológicas é comum na natureza, juntamente com uma representação quantitativa de sua heterogeneidade e da assimetria entre níveis tróficos.

Asymmetric phylogenetic signal in ecological interactions between trophic levels: a worldwide analysis of antagonistic networks

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Short running title: Asymmetric phylogenetic signal in antagonistic interactions

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ABSTRACT

Phylogenetic signal in ecological interactions has been empirically demonstrated in various systems, along with consistent asymmetries in the strength of this signal. In antagonistic networks, for instance, interactions are usually more conserved among the species of the lower trophic level, while the species of the higher trophic level show varying degrees of host switching. Among the explanations proposed for this emerging asymmetric pattern are the effects of trophic niche displacement among related consumers and differences in evolutionary rates among attack- and defense-related traits. Here we take advantage of the ample literature on cophylogeny and tree reconciliation methods to investigate the generality of the asymmetric pattern among different antagonistic interaction systems. For each trophic level in each of the 102 compiled networks, we measured phylogenetic signal in interaction patterns using the Pearson correlation between the phylogenetic distance matrix and the z-value of the UniFrac interaction similarity matrix between all species pairs. We assessed the asymmetry in signal strength with Cohen's Q effect sizes. We used a random-effects meta-analysis approach to estimate the overall effect sizes for the phylogenetic signal in each trophic level and signal asymmetry. We also used a meta-regression model to test the effects of interaction intimacy, study spatial scale and richness differences between trophic levels. We found a general pattern of phylogenetic signal in interaction patterns for both trophic levels with considerable between-study heterogeneity. On the other hand, strength asymmetry was consistently small and non-significant in each individual study, with a positive but also small overall effect size. We did not detect effects for any of the tested moderators. Our results provide compelling evidence that conservatism of ecological interactions is widespread in nature, along with a quantitative depiction of its heterogeneity and asymmetry between trophic levels.

INTRODUCTION

Phylogenetic signal in ecological interactions is a theoretical expectation under the observation that interaction-relevant traits are phylogenetically structured (Losos 2008). Accordingly, a pattern of increased sharing of interacting species among more closely related species has been empirically demonstrated in various systems, including both antagonistic and mutualistic ecological networks (Goméz et al. 2010, Rohr and Bascompte 2014). In addition to phylogenetic signal, many studies have also shown asymmetries in the strength of the phylogenetic signal across trophic levels (Rezende et al. 2007, Elias et al. 2013). In antagonistic networks, for instance, interactions are usually more conserved among the species of the lower trophic level, while the species of the higher trophic level show varying degrees of host switching (Rohr and Bascompte 2014).

Among the explanations proposed for this asymmetric pattern are the effects of trophic niche displacement among related consumers (Elias et al. 2013) and differences in evolutionary rates among attack- and defense-related traits (Rossberg et al. 2006). Other ecological mechanisms may also play an important role in structuring interaction networks. For example, even if there is selective pressure leading to resource use diversification among consumers, highly specialized and intimate interactions may impose stronger constraints on consumer evolution (Pires and Guimarães Jr. 2012, Krasnov et al. 2014). Therefore, the degree of intimacy and specialization of the interaction may be a crucial determinant of signal strength asymmetry. Additionally, ecological differences between the interacting groups, such as disparate generation times and reproductive strategies, could also lead to differences in diversification patterns (Cardillo et al. 2003, Philimore et al. 2006, Smith and Donoghue 2008), and ultimately affect the rate at which resource use and prey vulnerability evolve (Rossberg et al. 2006). Lastly, besides reflecting the possible imprints of diversification patterns on the conservatism of ecological interactions, differences in species richness between interacting clades may also lead to differences in statistical power in detecting such patterns.

Besides the effects of phylogenetic constraints, contemporaneous processes such as meta-community dynamics (Leibold et al. 2004, Poisot et al. 2012) may also play a role in interaction network establishment by modifying local species abundances and their temporal and spatial co-occurrences (Vazquéz et al. 2009). The extent of these effects, however, should be less pronounced when observing the interaction patterns at larger scales (Leibold et al. 2004, Burkle and Alarcón 2010). Finally, interaction patterns themselves may influence microevolutionary processes (Guimarães Jr et al. 2007, 2011), which, in turn, may influence phylogenetic patterns (Arnold et al. 2001).

A major challenge in conducting a comprehensive review of phylogenetic patterns in antagonistic interactions is the lack of phylogenetic data. This kind of data, however, is frequently produced in studies investigating cophylogenetic patterns between sets of interacting species. Thus, here we take advantage of the ample literature on cophylogeny and tree reconciliation methods to investigate the generality of the asymmetric pattern among different antagonistic interaction systems. Additionally, using this large and comprehensive compilation of primary data, we address some preliminary hypotheses on what mechanisms might be responsible for the pervasive presence of asymmetric phylogenetic signals between trophic levels. Specifically, we test for the influence of the following factors on the degree of phylogenetic signal in interaction patterns and the asymmetry of this signal between trophic levels: i) the spatial scale considered in the study, ii) the intimacy of the interaction, and iii) differences in species richness between trophic levels.

METHODS

Data compilation

We conducted a literature search for studies presenting bipartite antagonistic interactions as well as the phylogenies of both interacting groups. We included in our analysis studies that described the interactions at species level with at least five species at each trophic level. Networks of viruses and their

hosts were not included because delimitation in virus is not directly comparable to species delimitation in other groups, and horizontal gene transfer is common among viruses and their hosts (Liu et al. 2011).

We performed the search in Scopus database using two strategies. The first was to apply the following search terms: ((cophylog* OR codiver* OR cospeciat* OR tanglegr* OR coevolut*) AND (parasit* OR host OR antagonis* OR herbiv* OR folivo*)).

The second search strategy involved evaluating the studies cited in a recent review article about coevolution (de Vienne et al. 2013) and all studies that cited the eleven statistical methods reviewed in this same article (Brooks 1981, Page 1990, Ronquist 1995, Charleston 1998, Huelsenbeck et al. 2000, Legendre 2002, Merkle and Middendorf 2005, Light and Hafner 2008, Schardl et al. 2008, Hommola et al. 2009, Conow et al. 2010). Both searches were conducted using the Scopus database on July 26, 2016.

From each study, binary interaction matrices and phylogenies were extracted either from available supplementary materials, through manual input (in the case of the interaction matrices), or with the aid of the tree capturing software TreeSnatcher Plus (Laubach and Haeseler 2007). The degree of intimacy was obtained from system descriptions in the source studies, and categorized into three levels: 1 – interactions that occur with short-term contact between counterparts; 2 – interactions that involve long term contact between counterparts but without physiological integration; and 3 – interactions where the contact is prolonged and internal. We also categorized studies according to their spatial scale. This was done with a three-level categorical variable: local level – interaction data that was obtained from direct sampling in an area of up to 1×10^3 Km²; regional level – studies where interaction data comes from compilations or samplings of areas between 1×10^3 Km² and 5×10^5 Km²; and global level – studies where interaction data comes from compilations or samplings of areas greater than 5×10^5 Km².

Statistical analyses

First, for each trophic level in each network, we computed a simple measure of phylogenetic signal in the interactions based on the Pearson correlation between the phylogenetic distance matrix and the null-model obtained z-value of the phylogenetic dissimilarity matrix between all species pairs (as in Bergamini et al. 2017). The UniFrac dissimilarity between two host species, for example, is defined as the ratio between the sum of branch lengths that leads to parasites species exclusive to either host and the total sum of branch lengths in the entire parasite tree. We used the Fisher transformation of the correlation coefficients as effect-size measures. Then, we measured the asymmetry in phylogenetic signal using the Cohen's q statistic (the difference between two Fisher-transformed correlation coefficients – Cohen 1988):

$$q = \frac{1}{2} \log \frac{1+r_1}{1-r_1} - \frac{1}{2} \log \frac{1+r_2}{1-r_2},$$

where r_1 is lower trophic level correlation coefficient (i.e., how similar are the sets of parasites of closely related hosts) and r_2 is the higher trophic level correlation coefficient (i.e., how similar are the diets of closely related consumers). Positive values indicate networks where the phylogenetic signal is stronger for resource species, negative values indicate networks where the phylogenetic signal is stronger for consumer species, and values close to zero indicate networks where signal strength is similar between both levels. We used the number of species (Koricheva et al. 2013) as the number of data points for the calculation of the variances for both the correlations and the Cohen's q statistic:

$$\begin{aligned} \text{var}(r) &= \frac{1}{n-3} \\ \text{var}(q) &= \frac{1}{n_1-3} + \frac{1}{n_2-3}, \end{aligned}$$

where $\text{var}(r)$ is the variance for the correlation between phylogenetic distances and UniFrac z-values for the n species in each trophic level, and $\text{var}(q)$ is the variance of the Cohen's q statistic where one of the trophic levels has n_1 species and the other has n_2 species.

We used a random-effects meta-analysis to estimate the overall effect sizes for the correlations and for the q statistic. We used the Egger et al.'s (1997) regression test as an indicator of publication bias. Finally, we adjusted the meta-regression models using categorical spatial scale of the study (local, regional, and global), and degree of intimacy of the interaction as moderators for the correlations. Variation between q values was modeled with the same variables plus the difference in species richness between trophic levels (higher trophic level richness minus lower trophic level richness). All analyses were performed in the R statistical environment (R core Team 2014), using original code and functions from the packages *bipartite* (Dormann et al. 2009), *ggplot2* (Wickham 2009), *metafor* (Viechtbauer 2010), *picante* (Kembel et al. 2010), and *vegan* (Oksanen et al. 2015).

RESULTS

Our search returned 458 articles, from which 178 presented the interactions and phylogenies for both groups. From those, 86 articles fitted the remaining selection criteria of having five or more species in both trophic levels and not involving viruses, encompassing the 102 data sets used in the analyses (Supplementary Material 1). The included works were published between 1995 and 2016 and included data on a range of antagonistic interaction types, such as plant-herbivore, endoparasites and their hosts, and flea-mammal systems. Species richness was usually lower in the lower trophic level (mean richness difference = 3.2 ± 13.4 species) and ranged from 5 to 106 species (Supplementary Material 1).

As could be expected, given the coevolution focus of the primary studies, there was greater proportion of highly intimate, endogenous interactions (65% of the studies) with fewer cases of ectoparasites (27% of the studies) and even fewer short term interactions (8%) such as external leaf-chewers.

While local studies were less common in our dataset (11%), the number of regional and global studies were similar (47% and 42%, respectively).

We did not find evidence of publication bias for any of the effect size measures (Lower trophic level $r - z = 0.43$, $p = 0.670$; Higher trophic level $r - z = 0.12$, $p = 0.906$; Cohen's $q - z = 1.20$, $p = 0.231$). Both lower and higher trophic level correlations showed a moderate-to-high positive overall correlation between the phylogenetic distance matrix and the null-model obtained z -value of the UniFrac dissimilarity matrix between all species pairs (Lower trophic level $r = 0.463$ [0.396 | 0.525], $\tau = 0.31$, $z = 11.89$, $p < 0.001$; Higher trophic level $r = 0.376$ [0.304 | 0.444], $\tau = 0.319$, $z = 9.52$, $p < 0.001$; Figure 1). Despite being statistically significant, the overall effect size for the asymmetry was very small (Cohen's $q = 0.080$ [0.01 | 0.149], $\tau = 0$, $z = 2.29$, $p = 0.022$, Figure 1), with individual studies presenting broad and overlapping confidence intervals (Fig. 1, Supplementary Material 1).

Although we found considerable between-study heterogeneity in lower level ($Q = 268.33$, $p < 0.001$, $I^2 = 60.22\%$ [42.38% | 66.43%]) and higher level ($Q = 308.96$, $p < 0.001$, $I^2 = 65.78\%$ [50.54% | 71.65%]) correlations, the moderators included in the meta-regression had very poor explanatory power (Lower level $QM = 1.85$, $p = 0.763$; Higher level $QM = 2.93$, $p = 0.561$; Table 1). For the asymmetry, on the other hand, there was no heterogeneity ($Q = 40.00$, $p > 0.999$, $I^2 = 0\%$ [0% | 0%]) to be explained by the moderators ($QM = 3.51$, $p = 0.622$, Table 1).

Table 1 – Results from the meta-regression analysis for the three effect size measures. Significant values are presented in bold.

Response	Moderator	Estimate [lower CI upper CI]	Z	p
Lower level r	Intercept	0.45 [0.10 0.80]	2.49	0.013
	Intimacy (level 2)	0.16 [-0.20 0.51]	0.85	0.397
	Intimacy (level 3)	0.05 [-0.29 0.38]	0.28	0.782
	Scale (local)	-0.03 [-0.32 0.27]	-0.17	0.864
	Scale (regional)	-0.04 [-0.22 0.14]	-0.45	0.654
Higher level r	Intercept	0.39 [0.01 0.77]	2.04	0.042
	Intimacy (level 2)	0.10 [-0.28 0.49]	0.51	0.607
	Intimacy (level 3)	0.07 [-0.29 0.43]	0.39	0.697
	Scale (local)	-0.12 [-0.40 0.16]	-0.84	0.401
	Scale (regional)	-0.13 [-0.30 0.05]	-1.41	0.160
Cohen's q	Intercept	0.08 [-0.25 0.42]	0.49	0.625
	Intimacy (level 2)	0.03 [-0.32 0.37]	0.14	0.887
	Intimacy (level 3)	-0.06 [-0.38 0.26]	-0.36	0.720
	Scale (local)	0.07 [-0.17 0.31]	0.61	0.542
	Scale (regional)	0.09 [-0.07 0.25]	1.09	0.275
	Richness difference	0 [0.00 0.01]	1.12	0.265

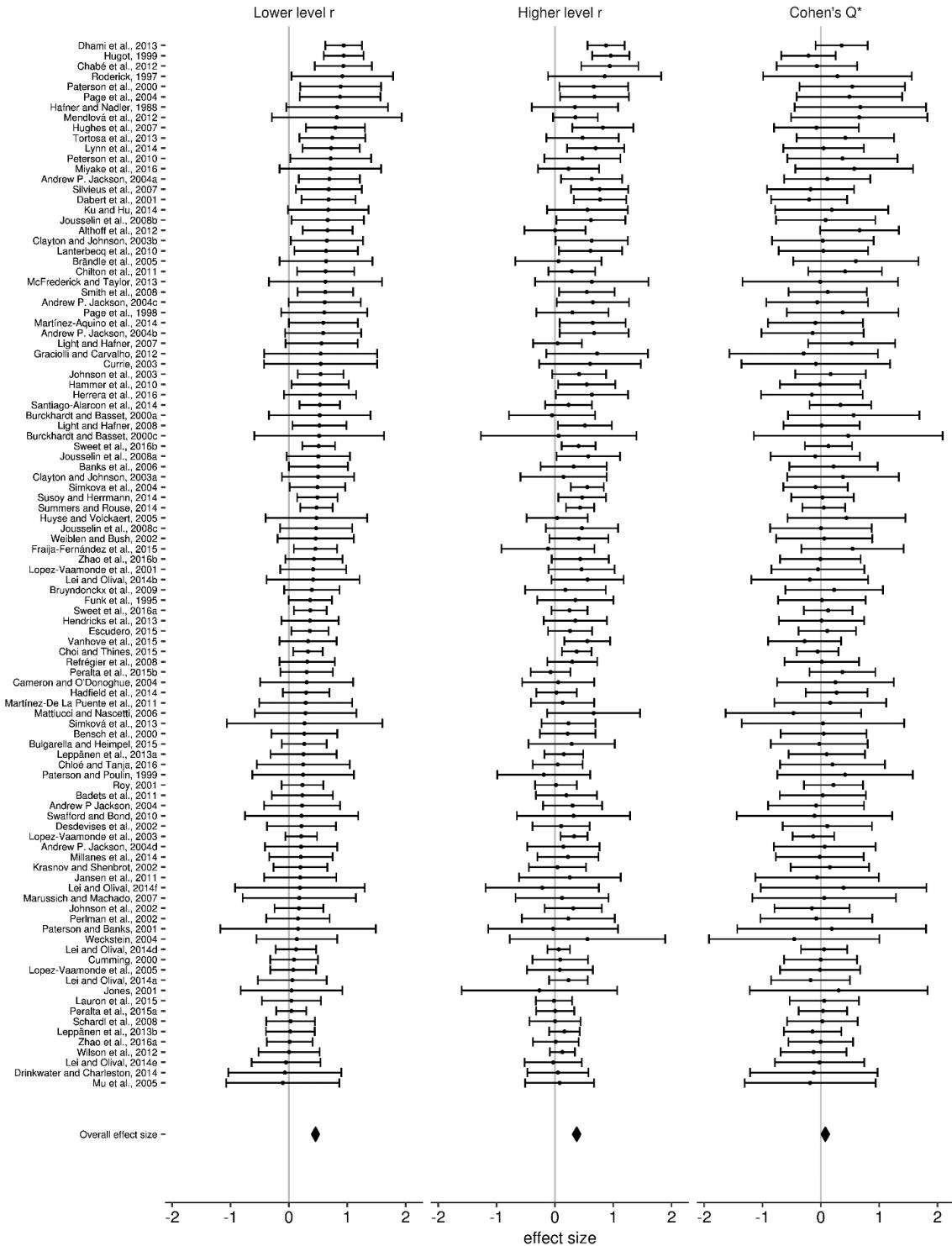


Figure 1 – Forest plot showing each study's observed effect size (points) with $\pm 1.96 \times \text{SE}$ confidence intervals (whiskers) and the random-effects model overall effect size (diamonds at the bottom). Diamonds' width represent the 95% confidence interval. References that provided more than one dataset are shown with letters after the year. All values were back-transformed from Fisher's Z values to correlation coefficients to allow easier interpretation.

* Cohen's q values on the graph are back-transformed, while those presented in the text are not.

DISCUSSION

In agreement with previous reports, our meta-analysis showed a general pattern of phylogenetic signal in interaction patterns for both trophic levels, with considerable between-study heterogeneity. On the other hand, strength asymmetry was consistently small and non-significant in each individual study, with a positive but also small overall effect size. We did not detect effects for any of the tested moderators.

Our findings contribute to the growing body of evidence that shows a pervasive role of phylogenetic constraints in determining interaction patterns (Cattin et al 2004, Goméz et al. 2010, Rohr and Bascompte 2014). Using a phylogeny-based measure of dissimilarity has allowed us to assess the strength of the phylogenetic signal even for interactions with a high degree of monophagy, because even if a species pair shares no resources or consumers there may still be some degree of conservatism in the form of shared resource or consumer branches. This fills a gap in the data available along the specialization gradient, providing a broader basis for the formulation of explanations and hypothesis that aim at understanding when and how the relative importance of phylogenetic constraints varies.

Our dataset was predominantly composed of specialized interactions, chosen as study systems in the primary studies precisely because they were expected to have higher potential for coevolution (de Vienne et al. 2013). In this sense, the common presence of phylogenetic signal in interaction patterns for both trophic levels is an expected result. However, the inability of interaction intimacy to address heterogeneity in effect sizes indicates that other factors might be driving this variation, at least along the intimacy degree range considered here. Other reports on asymmetric phylogenetic conservatism in different interaction types (Rohr and Bascompte 2014, Naisbit et al 2012, Bersier and Kehrli 2008, Fontaine and Thébault 2015) have different methodological approaches and differ on the source used for phylogenetic information, making comparisons of the results difficult. Future work using the same

approach with different datasets should be able to better compare patterns found in food webs (Bersier and Kehrli 2008, Naisbit et al 2012), mutualistic bipartite interactions (Rezende et al. 2007), and the antagonistic bipartite networks presented here.

While regional and global studies usually aimed to compile recorded interactions for all members of the focal group, local studies that sampled only interactions from a given locality probably represent a filtered subset of the existing interactions. Furthermore, local networks are subject to disruptions caused by anthropic disturbances (Burkle and Alarcón 2010, Gonzalez et al. 2011) that may lead to the loss of species and interactions (Burkle et al. 2013, Araújo et al. 2014), modifying interaction patterns and the degree of phylogenetic signal (Peralta et al. 2014). Nevertheless, we found no effect of study scale on either the correlations or the asymmetry. Therefore, the extent to which changes in the observation scale affect the perceived patterns may be highly variable between antagonist systems. Further work is needed to identify and assess the factors responsible for this variation.

Although we observed a tendency for stronger interaction phylogenetic signal at the lower trophic level, intra-study uncertainties were high and the overall effect-size was small. It is important to note that this result, in contrast with a scenario of low phylogenetic signal at both levels, is due to an almost-as-high level of phylogenetic signal for the higher trophic level. As discussed in the preceding paragraphs, our dataset encompasses interaction types not previously assessed in other works (Rohr & Bascompte 2014, Naisbit et al 2012, Bersier and Kehrli 2008, Fontaine and Thébaud 2015), and for which phylogenetic constraints might be stronger for the higher trophic levels. This observation underscores the need to consider the broad specialization spectrum of interactions.

Even though our dataset portrays a range of richness differences between trophic levels, there was no relationship between richness difference and degree of asymmetry. Similar richness values between levels are expected under a scenario of strict co-speciation, which should also lead to strong

phylogenetic signal and small asymmetry. It is now widely recognized, however, that different patterns of coevolution involving duplications, host-switches and sequential evolution are common (de Vienne et al. 2013) with widely variable resulting patterns of richness values and ecological interaction conservatism.

New efforts to explain the variation in phylogenetic signal strength could be made by testing the effects of additional moderators. Using more detailed operational measures of interaction intimacy (Guimarães Jr. et al. 2007, Pires and Guimarães Jr. 2012) or considering differences in the demographic impact of the interaction among trophic levels and different systems (Weiberg et al. 1986, Bond 1994, McPeek and Peckarsky 1998) could also yield further insights. The effects of macro-evolutionary processes on network properties, such as differences in diversification rates and speciation patterns between lineages, have only recently begun to be investigated. For plant-pollinator mutualistic networks, for example, it has been shown that tree properties can influence network structure (Chamberlain et al. 2014a, b), with less balanced plant phylogenies associated with less connected networks. Similar mechanisms may also be at work in antagonistic networks, affecting the structure of the networks and, consequently, the differences in signal strength among trophic levels. In this sense, further theoretical work and more data, including dated phylogenies, are needed to direct the formulation and to test new hypotheses.

Here we have shown more evidence that phylogenetic signal in ecological interactions is common in nature, along with a quantitative depiction of its heterogeneity and asymmetry between trophic levels. Future work building upon results from different systems should focus on exploring explanations for the observed heterogeneity in effect-sizes and the degree of asymmetry in different contexts. Simulation models are also a promising avenue of theoretical research (Rossberg et al. 2006, Costa et al. 2016), along with more directed empirical work (e.g., Elias et al. 2013). There is also plenty of room for advances in our understanding of how network patterns themselves affect evolutionary process (Pelletier

et al. 2009, Guimarães et al. 2011), potentially leading to insights into the mechanisms behind the observed patterns.

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CONSIDERAÇÕES FINAIS

Passando pela modulação dos nichos fundamentais das espécies, pelos impactos nos processos demográficos até as pressões seletivas que se refletem nos processos evolutivos, as interações interespecíficas permeiam todos os processos e padrões observados nas comunidades ecológicas. Em um cenário de crescentes impactos sobre os sistemas naturais, onde se faz necessária a manutenção da biodiversidade e dos serviços que ela provê para garantir o bem-estar humano, entender os mecanismos por trás das interações ecológicas é fundamental para conservar e manejar esses sistemas. Ao longo dos três capítulos desta tese, mostramos como a história evolutiva das espécies pode ser uma importante pista para entender a formação de redes de antagonistas especializados. De maneira complementar à abordagem observacional utilizada aqui, que permite detectar padrões e apontar caminhos, a integração dos dados levantados com avanços teóricos é fundamental. Diversas aplicações podem se servir de uma boa compreensão das interações antagonistas como por exemplo o controle biológico de pragas agrícolas, controle e manejo de doenças parasitárias, previsão e mitigação dos impactos causados por alterações ambientais e restauração de ecossistemas. Esperamos que as contribuições apresentadas aqui, as questões que elas levantam, e as novas abordagens que utilizamos ajudem a melhorar nossa compreensão dos processos que modulam a formação de redes ecológicas.

ANEXOS

Anexo 1 – Arquivo do Word contendo o material suplementar do capítulo 1.

Supplementary material

Appendix 1

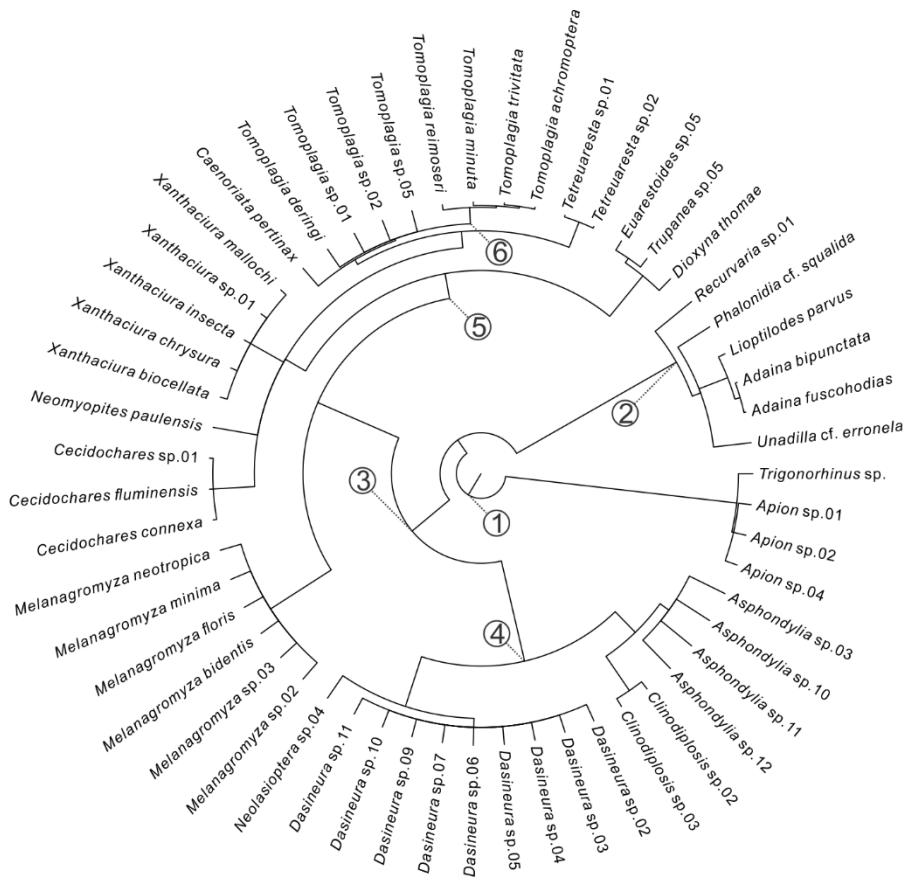


Figure A1 – Phylogenetic tree of the 55 species of flower head insects studied in this work. (1) relationships between orders follow Ishiwata et al. (2011); (2) relationships between Lepidoptera families follow Regier et al. (2013); (3) relationships between Diptera families follow Wiegmann et al. (2011); (4) relationships between Cecidomyiidae genera follow Joy (2013); (5) relationships between Tephritidae subfamilies and tribes follow Komeyeye (1999), Han and Ro (2009); (6) relationships between *Tomoplagia* species follow Yotoko et al. (2005).

Table A1 – DSIS values for each species with more than one antagonist. Values computed with branch lengths set to 1 and values computed with branch lengths computed by Grafen's transformation gave similar results (correlation between values = 0.89). Ast= Asteraceae, endo = Endophages.

Subnetwork	Trophic level	Taxon name	Number of counterparts	DSI-S	
				(Branch length 1)	DSI-S
Cecidomyiidae	ast	<i>Asphondylia</i> sp.12	2	2.01	2.04
Cecidomyiidae	ast	<i>Clinodiplosis</i> sp.03	2	0.90	1.46
Cecidomyiidae	endo	<i>Chromolaena odorata</i>	2	0.99	1.13
Cecidomyiidae	endo	<i>Chromolaena pedunculosa</i>	2	1.13	1.17
Cecidomyiidae	endo	<i>Chromolaena pungens</i>	2	1.01	1.17
Cecidomyiidae	endo	<i>Gochnertia pulchra</i>	2	2.18	2.00
Cecidomyiidae	endo	<i>Mikania cordifolia</i>	2	1.62	1.82
Cecidomyiidae	endo	<i>Vernonanthura membranacea</i>	3	2.99	2.52
Lepidoptera	ast	<i>Adaina bipunctata</i>	7	4.57	5.18
Lepidoptera	ast	<i>Lioptilodes parvus</i>	2	-0.03	-0.64
Lepidoptera	ast	<i>Phalonidia cf. squalida</i>	12	-0.01	1.98
Lepidoptera	ast	<i>Recurvaria</i> sp.01	11	-0.73	1.68

Subnetwork	Trophic level	Taxon name	Number of counterparts	DSI-S	
				(Branch length 1)	DSI-S
Lepidoptera	ast	<i>Unadilla cf. erronela</i>	14	-0.24	1.27
Lepidoptera	endo	<i>Bidens gardneri</i>	3	1.74	2.47
Lepidoptera	endo	<i>Campuloclinium chlorolepis</i>	2	1.09	1.67
Lepidoptera	endo	<i>Chromolaena chaseae</i>	4	1.97	3.30
Lepidoptera	endo	<i>Chromolaena odorata</i>	4	1.97	3.30
Lepidoptera	endo	<i>Chromolaena pedunculosa</i>	4	1.97	3.30
Lepidoptera	endo	<i>Chromolaena pungens</i>	4	1.97	3.30
Lepidoptera	endo	<i>Chromolaena squalida</i>	4	1.97	3.30
Lepidoptera	endo	<i>Conyza canadensis</i>	2	1.34	1.71
Lepidoptera	endo	<i>Mikania cordifolia</i>	3	1.98	2.66
Lepidoptera	endo	<i>Piptocarpha rotundifolia</i>	3	1.74	2.47
Lepidoptera	endo	<i>Vernonanthura ferruginea</i>	3	1.74	2.47
Lepidoptera	endo	<i>Vernonanthura membranacea</i>	5	2.56	4.09
Lepidoptera	endo	<i>Viguiera arenaria</i>	2	0.82	1.53
Tephritidae	ast	<i>Cecidochares connexa</i>	4	4.28	4.27

Subnetwork	Trophic level	Taxon name	Number of counterparts	DSI-S	
				(Branch length 1)	DSI-S
Tephritidae	ast	<i>Cecidochares fluminensis</i>	4	4.28	4.27
Tephritidae	ast	<i>Cecidochares</i> sp.01	5	5.24	5.08
Tephritidae	ast	<i>Euarestoides</i> sp.05	2	1.99	2.14
Tephritidae	ast	<i>Neomyopites paulensis</i>	6	4.86	5.17
Tephritidae	ast	<i>Tetreuaresta</i> sp.01	2	1.86	2.33
Tephritidae	ast	<i>Tetreuaresta</i> sp.02	2	1.78	2.26
Tephritidae	ast	<i>Tomoplagia minuta</i>	2	1.98	2.28
Tephritidae	ast	<i>Tomoplagia</i> sp.01	2	0.91	1.42
Tephritidae	ast	<i>Tomoplagia trivitata</i>	2	1.99	2.14
Tephritidae	ast	<i>Trupanea</i> sp.05	5	4.25	4.39
Tephritidae	ast	<i>Xanthaciura biocellata</i>	8	4.98	5.74
Tephritidae	ast	<i>Xanthaciura chrysura</i>	8	4.98	5.74
Tephritidae	ast	<i>Xanthaciura</i> sp.01	6	5.09	5.39
Tephritidae	endo	<i>Bidens gardneri</i>	2	0.52	1.30
Tephritidae	endo	<i>Campuloclinium chlorolepis</i>	3	3.52	3.38

Subnetwork	Trophic level	Taxon name	Number of counterparts	DSI-S	
				(Branch length 1)	DSI-S
Tephritidae	endo	<i>Chromolaena chaseae</i>	6	4.32	4.90
Tephritidae	endo	<i>Chromolaena odorata</i>	8	5.75	6.09
Tephritidae	endo	<i>Chromolaena pedunculosa</i>	8	5.75	6.09
Tephritidae	endo	<i>Chromolaena pungens</i>	8	5.75	6.09
Tephritidae	endo	<i>Chromolaena squalida</i>	7	6.45	5.81
Tephritidae	endo	<i>Gochnativa barrosoii</i>	2	-1.02	1.33
Tephritidae	endo	<i>Gochnativa pulchra</i>	2	-1.02	1.33
Tephritidae	endo	<i>Heterocondylus alatus</i>	4	2.80	3.61
Tephritidae	endo	<i>Mikania cordifolia</i>	3	3.12	2.85
Tephritidae	endo	<i>Orthopappus angustifolius</i>	2	2.33	2.16
Tephritidae	endo	<i>Piptocarpha rotundifolia</i>	4	4.41	3.67
Tephritidae	endo	<i>Vernonanthura ferruginea</i>	2	1.50	1.84
Tephritidae	endo	<i>Vernonanthura membranacea</i>	2	2.03	2.10
Entire Network	ast	<i>Adaina bipunctata</i>	7	4.80	5.34
Entire Network	ast	<i>Apion sp.02</i>	4	4.23	4.14

Subnetwork	Trophic level	Taxon name	Number of counterparts	DSI-S	
				(Branch length 1)	DSI-S
Entire Network	ast	<i>Asphondylia</i> sp.12	2	2.02	2.02
Entire Network	ast	<i>Cecidochares connexa</i>	4	4.32	4.10
Entire Network	ast	<i>Cecidochares fluminensis</i>	4	4.32	4.10
Entire Network	ast	<i>Cecidochares</i> sp.01	5	5.14	4.98
Entire Network	ast	<i>Clinodiplosis</i> sp.03	2	0.89	1.43
Entire Network	ast	<i>Euarestoides</i> sp.05	2	2.00	2.25
Entire Network	ast	<i>Lioptilodes parvus</i>	2	-0.06	-0.65
Entire Network	ast	<i>Melanagromyza bidentis</i>	8	0.42	2.42
Entire Network	ast	<i>Melanagromyza minima</i>	2	0.55	0.90
Entire Network	ast	<i>Melanagromyza neotropica</i>	3	0.47	1.88
Entire Network	ast	<i>Melanagromyza</i> sp.02	2	-0.16	-0.87
Entire Network	ast	<i>Melanagromyza</i> sp.03	2	2.08	2.19
Entire Network	ast	<i>Neomyopites paulensis</i>	6	4.74	4.92
Entire Network	ast	<i>Phalonidia cf. squalida</i>	12	0.02	2.04
Entire Network	ast	<i>Recurvaria</i> sp.01	11	-0.71	1.74
Entire Network	ast	<i>Tetruaresta</i> sp.01	2	1.89	2.23

Subnetwork	Trophic level	Taxon name	Number of counterparts	DSI-S	
				(Branch length 1)	DSI-S
Entire Network	ast	<i>Tetreuaresta</i> sp.02	2	1.91	2.26
Entire Network	ast	<i>Tomoplagia minuta</i>	2	2.08	2.19
Entire Network	ast	<i>Tomoplagia</i> sp.01	2	0.89	1.43
Entire Network	ast	<i>Tomoplagia trivitata</i>	2	2.00	2.25
Entire Network	ast	<i>Trupanea</i> sp.05	5	4.15	4.51
Entire Network	ast	<i>Unadilla cf. erronela</i>	14	-0.26	1.31
Entire Network	ast	<i>Xanthaciura biocellata</i>	8	5.02	5.68
Entire Network	ast	<i>Xanthaciura chrysura</i>	8	5.02	5.68
Entire Network	ast	<i>Xanthaciura</i> sp.01	6	5.03	5.27
Entire Network	endo	<i>Bidens gardneri</i>	9	2.11	1.08
Entire Network	endo	<i>Campuloclinium chlorolepis</i>	6	1.57	0.78
Entire Network	endo	<i>Chromolaena chaseae</i>	13	1.17	-0.12
Entire Network	endo	<i>Chromolaena odorata</i>	15	1.70	1.20
Entire Network	endo	<i>Chromolaena pedunculosa</i>	17	1.82	0.49
Entire Network	endo	<i>Chromolaena pungens</i>	16	1.56	0.34

Subnetwork	Trophic level	Taxon name	Number of counterparts	DSI-S	
				(Branch length 1)	DSI-S
Entire Network	endo	<i>Chromolaena squalida</i>	14	2.31	0.43
Entire Network	endo	<i>Conyza canadensis</i>	2	1.42	1.62
Entire Network	endo	<i>Gochnatia barrosii</i>	4	-2.38	-0.57
Entire Network	endo	<i>Gochnatia pulchra</i>	6	-1.59	-0.08
Entire Network	endo	<i>Heterocondylus alatus</i>	5	1.93	1.73
Entire Network	endo	<i>Mikania cordifolia</i>	11	0.74	-1.60
Entire Network	endo	<i>Orthopappus angustifolius</i>	3	0.16	0.22
Entire Network	endo	<i>Piptocarpha rotundifolia</i>	8	0.22	0.31
Entire Network	endo	<i>Vernonanthura ferruginea</i>	8	-0.80	-0.14
Entire Network	endo	<i>Vernonanthura membranacea</i>	12	-1.48	-0.25
Entire Network	endo	<i>Viguiera arenaria</i>	3	0.51	-0.04

Table A2 – DSI-S values for each module with more than one antagonist. Values computed with branch lengths set to 1 and values computed with branch lengths computed by Grafen's transformation gave similar results (correlation between values = 0.93). Ast= Asteraceae, endo = Endophages.

Sub Network	Trophic level	Module	Number of species	DSI-S (Branch length 1)	DSI-S
Cecidomyiidae	ast	9	2	0.93	1.41
Cecidomyiidae	endo	2	2	1.10	1.18
Cecidomyiidae	endo	4	2	0.98	1.04
Cecidomyiidae	endo	7	2	2.26	1.87
Cecidomyiidae	endo	8	2	1.64	1.76
Cecidomyiidae	endo	10	3	2.98	2.56
Lepidoptera	ast	2	5	0.37	0.33
Lepidoptera	ast	3	4	3.37	3.72
Lepidoptera	ast	5	3	-1.09	-0.21
Lepidoptera	ast	12	4	0.07	0.89
Lepidoptera	endo	5	2	1.06	1.54
Tephritidae	ast	1	2	1.85	2.11
Tephritidae	ast	4	6	4.69	5.07
Tephritidae	ast	7	2	2.02	2.18

Sub Network	Trophic level	Module	Number of species	DSI-S (Branch length 1)	DSI-S
Tephritidae	ast	8	2	1.97	2.11
Tephritidae	endo	1	2	0.42	1.28
Tephritidae	endo	4	7	5.18	4.98
Tephritidae	endo	8	2	-1.04	1.26
Tephritidae	endo	10	4	4.34	3.81
Tephritidae	endo	11	2	2.03	2.25
Entire Network	ast	3	3	-0.73	-0.51
Entire Network	ast	4	2	1.80	2.18
Entire Network	ast	5	5	4.12	4.52
Entire Network	ast	6	6	-0.29	-0.59
Entire Network	endo	3	6	-1.56	-0.49
Entire Network	endo	5	14	1.69	0.93
Entire Network	endo	6	27	-0.97	1.31
Entire Network	endo	7	2	-0.73	-0.25

Table A3– Correlations between phylogenetic distance and the two metrics of compositional overlap (Jaccard and Unifrac) for each subnetwork and trophic level. Ast= Asteraceae, endo = Endophages.

Sub Network	Trophic Level	Dissimilarity Measure	r	Z-value	p
Tephritidae	endo	Jaccard	0.308	3.864	0.001
	ast	Jaccard	0.602	8.164	0.001
Tephritidae	endo	unifrac	0.405	5.555	0.001
	ast	unifrac	0.682	9.130	0.001
Lepidoptera	endo	Jaccard	0.208	0.670	0.261
	ast	Jaccard	0.235	2.415	0.008
Lepidoptera	endo	unifrac	-0.269	-0.835	0.273
	ast	unifrac	0.321	3.459	0.002
Cecidomyiidae	endo	Jaccard	0.030	0.308	0.392
	ast	Jaccard	0.116	0.900	0.235
Cecidomyiidae	endo	unifrac	0.162	1.567	0.042
	ast	unifrac	0.562	4.272	0.001
Entire Network	endo	Jaccard	0.114	3.131	0.002

Sub Network	Trophic Level	Dissimilarity Measure	<i>r</i>	Z-value	<i>p</i>
Entire Network	ast	Jaccard	0.420	6.713	0.001
Entire Network	endo	unifrac	0.145	3.602	0.001
Entire Network	ast	unifrac	0.327	5.171	0.001

Table A4 - Results from the binomial GLMs modelling the relationship between phylogenetic distance of species pairs and the probability that both belong to the same module, for each subnetork and trophic level. Ast= Asteraceae, endo = Endophages.

Sub Network	Trophic Level	Beta	Z-value	p
Lepidoptera	ast	-0.084	-2.289	0.015
Lepidoptera	endo	0.000	-0.090	0.401
Cecidomyiidae	ast	-0.100	-0.187	0.375
Cecidomyiidae	endo	-0.089	-0.464	0.383
Tephritidae	ast	-0.501	-13.156	0.001
Tephritidae	endo	-0.407	-3.923	0.001
Entire Network	ast	-0.126	-3.652	0.004
Entire Network	endo	-0.003	-0.183	0.448

Table A5 – Modularity values for the entire network and the subnetworks. Z-values were computed as the difference between the observed value and the mean of 999 simulations, divided by the standard deviation of the 999 simulations.

Subnetwork	Observed Modularity value (Q)	Z-value
Entire Network	0.651	297.16
Tephritidae	0.458	148.01
Lepidoptera	0.460	25.17
Cecidomyiidae	0.687	127.88

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Anexo 2 – Arquivo do Word contendo o material suplementar do capítulo 2.

Supplementary material 1 – Analysis results using the inverse of the squared distances for the estimation of interaction probabilities based on the interaction patterns of related species.

Table S1.1 – GLMM estimates for the effects of the predictor variables on the interaction frequencies between all plant-herbivore pair. Marginal $R^2_{GLMM} = 0.50$, Conditional $R^2_{GLMM} = 0.88$.

Fixed Effects

Variable	Z-value	P
Intercept	-24.03	<0.001
Spatial overlap	29.27	<0.001
Temporal overlap	6.46	<0.001
Insect abundance	2.45	0.014
Plant abundance	2.92	0.003
Phylogenetic conservatism	50.65	<0.001

Random Effects

Group	Variance	Standard Deviation
Insects (39 spp.)	2.68	1.64
Plants (37 spp.)	3.40	1.84

Table S1.2 – Log likelihood and AIC values for the fit of each probability matrix to the observed interaction values, ordered by their difference to the best fit (Δ AIC). Model – matrix derived from the GLMM fitted values, P – phylogenetic probability matrix, Ab – abundance probability matrix, T – temporal overlap probability matrix, S – spatial overlap probability matrix, Null – null probability matrix, Letter combinations – the element wise product of the respective matrices. Number of parameters calculated as in Vizentin-Bugoni *et al.* 2014. Phylogenetic probability matrix calculated using the inverse of squared distances.

Probability matrix	Log Likelihood	Number of parameters	AIC	Δ AIC
Model	-248.75	8	513.51	0.00
S	-337.31	77	828.62	315.11
P	-350.58	77	855.17	341.66
T	-352.94	77	859.88	346.38
Null	-379.71	77	913.42	399.91
PS	-310.85	154	929.71	416.20
ST	-317.67	154	943.34	429.84
PT	-324.05	154	956.10	442.59
PST	-291.20	231	1044.40	530.90
Av	-522.25	77	1198.49	684.99
AbT	-514.48	154	1336.96	823.45
PAb	-522.13	154	1352.26	838.75
AbS	-527.58	154	1363.15	849.65
PAbT	-515.25	231	1492.51	979.00
AbST	-520.21	231	1502.42	988.92
PAbS	-529.40	231	1520.79	1007.28
PAbST	-523.04	308	1662.09	1148.58

Table S2 – Log likelihood and AIC values for the fit of each probability matrix to the observed interaction values, ordered by their difference to the best fit (Δ AIC). Model – matrix derived from the GLMM fitted values, P – phylogenetic probability matrix, Ab – abundance probability matrix, T – temporal overlap probability matrix, S – spatial overlap probability matrix, Null – null probability matrix, Letter combinations – the element wise product of the respective matrices. Number of parameters calculated as in Vizentin-Bugoni *et al.* 2014. Phylogenetic probability matrix calculated using the inverse of the distances.

Probability matrix	Log Likelihood	Number of parameters	AIC	Δ AIC
Model	-248.61	8	513.22	0
S	-337.31	77	828.62	315.40
T	-352.94	77	859.88	346.67
P	-363.01	77	880.02	366.80
Null	-379.71	77	913.42	400.20
ST	-317.67	154	943.34	430.13
PS	-321.83	154	951.66	438.44
PT	-336.40	154	980.80	467.58
PST	-302.22	231	1066.44	553.23
Ab	-522.25	77	1198.49	685.27
AbT	-514.48	154	1336.96	823.74
Pab	-519.62	154	1347.24	834.02
AbS	-527.58	154	1363.15	849.93
PAbT	-512.48	231	1486.96	973.74
AbST	-520.21	231	1502.42	989.21
PAbS	-525.97	231	1513.94	1000.72
PAbST	-519.30	308	1654.60	1141.38

Anexo 3 – Arquivo do Word contendo o material suplementar do capítulo 3.

Supplementary Table 1 – Citations, effect sizes, and moderator variables for each of the 106 datasets included in the analyses. References that provided more than one dataset are shown with letters after the year.

Citation	HL rich.	LL. rich	Intimacy	Scale	LL zcor	LL var(zcor)	HL zcor	HL var(zcor)	q	var(q)
Dhami et al., 2013	41	42	3	regional	1.74	0.026	1.36	0.026	0.37	0.052
Hugot, 1999	41	36	3	global	1.73	0.030	1.94	0.026	-0.22	0.057
Chabé et al., 2012	19	19	3	global	1.69	0.063	1.75	0.063	-0.07	0.125
Roderick, 1997	7	8	1	local	1.56	0.200	1.27	0.250	0.29	0.450
Paterson et al., 2000	14	11	2	regional	1.41	0.125	0.81	0.091	0.60	0.216
Page et al., 2004	14	11	2	global	1.36	0.125	0.83	0.091	0.54	0.216
Hafner and Nadler, 1988	10	8	2	regional	1.18	0.200	0.36	0.143	0.82	0.343
Mendlová et al., 2012	29	6	3	regional	1.16	0.333	0.37	0.038	0.79	0.372
Hughes et al., 2007	17	18	2	global	1.09	0.067	1.17	0.071	-0.08	0.138
Tortosa et al., 2013	13	15	2	regional	0.96	0.083	0.52	0.100	0.45	0.183
Lynn et al., 2014	19	19	3	regional	0.91	0.063	0.87	0.063	0.05	0.125
Peterson et al., 2010	12	11	3	global	0.90	0.125	0.51	0.111	0.39	0.236
Miyake et al., 2016	17	8	3	local	0.89	0.200	0.24	0.071	0.65	0.271
Andrew P. Jackson, 2004a	17	17	3	global	0.85	0.071	0.74	0.071	0.11	0.143
Silvius et al., 2007	19	15	3	local	0.84	0.083	1.02	0.063	-0.18	0.146
Dabert et al., 2001	22	21	2	global	0.83	0.056	1.03	0.053	-0.20	0.111
Ku and Hu, 2014	11	11	3	regional	0.82	0.125	0.63	0.125	0.19	0.250
Jousselin et al., 2008b	14	13	3	regional	0.80	0.100	0.72	0.091	0.08	0.191
Althoff et al., 2012	17	24	1	regional	0.80	0.048	0.00	0.071	0.80	0.119
Clayton and Johnson, 2003b	13	13	2	global	0.78	0.100	0.74	0.100	0.03	0.200
Lanterbecq et al., 2010	16	16	3	global	0.75	0.077	0.71	0.077	0.04	0.154
Brändle et al., 2005	10	9	3	regional	0.75	0.167	0.06	0.143	0.69	0.310
Chilton et al., 2011	27	19	3	regional	0.74	0.063	0.30	0.042	0.44	0.104
McFrederick and Taylor, 2013	7	7	2	regional	0.74	0.250	0.75	0.250	-0.01	0.500
Smith et al., 2008	20	20	2	local	0.73	0.059	0.62	0.059	0.12	0.118

Citation	HL rich.	LL. rich	Intimacy	Scale	LL zcor	LL var(zcor)	HL zcor	HL var(zcor)	q	var(q)
Andrew P. Jackson, 2004c	13	13	3	global	0.72	0.100	0.78	0.100	-0.06	0.200
Page et al., 1998	13	10	2	global	0.70	0.143	0.31	0.100	0.39	0.243
Martínez-Aquino et al., 2014	15	14	3	regional	0.68	0.091	0.77	0.083	-0.09	0.174
Andrew P. Jackson, 2004b	14	12	3	global	0.67	0.111	0.82	0.091	-0.14	0.202
Light and Hafner, 2007	25	13	2	local	0.63	0.100	0.05	0.045	0.59	0.145
Graciolli and Carvalho, 2012	8	7	2	regional	0.61	0.250	0.91	0.200	-0.30	0.450
Currie, 2003	8	7	3	regional	0.61	0.250	0.70	0.200	-0.09	0.450
Johnson et al., 2003	21	28	2	global	0.61	0.040	0.44	0.056	0.17	0.096
Hammer et al., 2010	19	19	2	global	0.60	0.063	0.61	0.063	-0.01	0.125
Herrera et al., 2016	13	13	3	global	0.60	0.100	0.75	0.100	-0.15	0.200
Santiago-Alarcon et al., 2014	27	35	3	global	0.59	0.031	0.24	0.042	0.35	0.073
Burckhardt and Basset, 2000a	10	8	3	regional	0.59	0.200	-0.05	0.143	0.64	0.343
Light and Hafner, 2008	21	21	2	regional	0.58	0.056	0.57	0.056	0.01	0.111
Burckhardt and Basset, 2000c	5	6	3	regional	0.58	0.333	0.07	0.500	0.51	0.833
Sweet et al., 2016b	48	52	2	global	0.56	0.020	0.43	0.022	0.13	0.043
Jousselin et al., 2008a	16	16	3	regional	0.56	0.077	0.65	0.077	-0.10	0.154
Banks et al., 2006	15	18	2	global	0.56	0.067	0.33	0.083	0.22	0.150
Clayton and Johnson, 2003a	10	13	2	global	0.55	0.100	0.15	0.143	0.40	0.243
Simkova et al., 2004	51	20	3	regional	0.54	0.059	0.63	0.021	-0.09	0.080
Susoy and Herrmann, 2014	26	35	3	global	0.53	0.031	0.51	0.043	0.03	0.075
Summers and Rouse, 2014	69	53	3	global	0.51	0.020	0.46	0.015	0.05	0.035
Huyse and Volckaert, 2005	17	8	3	regional	0.51	0.200	0.04	0.071	0.47	0.271
Jousselin et al., 2008c	13	13	3	regional	0.51	0.100	0.50	0.100	0.00	0.200
Weiblen and Bush, 2002	18	12	3	regional	0.50	0.111	0.44	0.067	0.06	0.178
Fraijsa-Fernández et al., 2015	9	31	3	global	0.49	0.036	-0.12	0.167	0.61	0.202
Zhao et al., 2016b	19	19	3	global	0.46	0.063	0.47	0.063	-0.01	0.125
Lopez-Vaamonde et al., 2001	15	15	3	global	0.44	0.083	0.49	0.083	-0.05	0.167
Lei and Olival, 2014b	13	9	3	regional	0.44	0.167	0.63	0.100	-0.19	0.267
Bruyndonckx et al., 2009	11	20	2	regional	0.42	0.059	0.18	0.125	0.23	0.184
Funk et al., 1995	12	31	1	regional	0.38	0.036	0.37	0.111	0.02	0.147
Sweet et al., 2016a	43	52	2	global	0.38	0.020	0.26	0.025	0.13	0.045

Citation	HL rich.	LL. rich	Intimacy	Scale	LL zcor	LL var(zcor)	HL zcor	HL var(zcor)	q	var(q)
Hendricks et al., 2013	16	19	2	regional	0.38	0.063	0.37	0.077	0.01	0.139
Escudero, 2015	30	41	3	global	0.38	0.026	0.27	0.037	0.11	0.063
Vanhove et al., 2015	28	19	3	local	0.34	0.063	0.63	0.040	-0.29	0.103
Choi and Thines, 2015	63	63	3	global	0.34	0.017	0.39	0.017	-0.05	0.033
Refrégier et al., 2008	24	20	3	global	0.32	0.059	0.31	0.048	0.02	0.106
Peralta et al., 2015b	36	22	3	local	0.31	0.053	-0.07	0.030	0.39	0.083
Cameron and O'Donoghue, 2004	13	9	3	regional	0.31	0.167	0.06	0.100	0.26	0.267
Hadfield et al., 2014	35	27	2	regional	0.31	0.042	0.03	0.031	0.28	0.073
Martínez-De La Puente et al., 2011	16	9	3	local	0.30	0.167	0.13	0.077	0.16	0.244
Mattiucci and Nascetti, 2006	9	8	3	global	0.29	0.200	0.80	0.167	-0.51	0.367
SimkovÁj et al., 2013	21	5	3	regional	0.28	0.500	0.24	0.056	0.04	0.556
Bensch et al., 2000	20	15	3	global	0.27	0.083	0.22	0.059	0.05	0.142
Bulgarella and Heimpel, 2015	10	29	1	local	0.27	0.038	0.30	0.143	-0.03	0.181
Leppänen et al., 2013a	38	15	3	regional	0.26	0.083	0.16	0.029	0.10	0.112
Chloé and Tanja, 2016	24	9	3	regional	0.25	0.167	0.05	0.048	0.20	0.214
Paterson and Poulin, 1999	9	8	2	global	0.25	0.200	-0.19	0.167	0.44	0.367
Roy, 2001	33	33	3	global	0.24	0.033	0.02	0.033	0.22	0.067
Badets et al., 2011	17	17	3	global	0.24	0.071	0.20	0.071	0.03	0.143
Andrew P Jackson, 2004	18	12	3	global	0.23	0.111	0.31	0.067	-0.08	0.178
Swafford and Bond, 2010	7	7	1	regional	0.22	0.250	0.33	0.250	-0.11	0.500
Desdevises et al., 2002	19	14	3	regional	0.22	0.091	0.11	0.063	0.11	0.153
Lopez-Vaamonde et al., 2003	75	55	3	regional	0.21	0.019	0.34	0.014	-0.13	0.033
Andrew P. Jackson, 2004d	13	13	3	global	0.21	0.100	0.15	0.100	0.07	0.200
Millanes et al., 2014	17	16	3	global	0.21	0.077	0.23	0.071	-0.02	0.148
Krasnov and Shenbrot, 2002	19	21	2	global	0.20	0.056	0.04	0.063	0.16	0.118
Jansen et al., 2011	8	13	1	regional	0.20	0.100	0.26	0.200	-0.07	0.300
Lei and Olival, 2014f	7	6	3	regional	0.19	0.333	-0.22	0.250	0.41	0.583
Marussich and Machado, 2007	9	7	3	regional	0.18	0.250	0.12	0.167	0.06	0.417
Johnson et al., 2002	19	25	2	global	0.17	0.045	0.33	0.063	-0.15	0.108
Perlman et al., 2002	9	16	3	global	0.16	0.077	0.24	0.167	-0.08	0.244
Paterson and Banks, 2001	6	5	2	regional	0.16	0.500	-0.03	0.333	0.19	0.833

Citation	HL rich.	LL. rich	Intimacy	Scale	LL zcor	LL var(zcor)	HL zcor	HL var(zcor)	q	var(q)
Weckstein, 2004	5	11	2	regional	0.14	0.125	0.63	0.500	-0.49	0.625
Lei and Olival, 2014d	106	35	3	regional	0.12	0.031	0.07	0.010	0.06	0.041
Cumming, 2000	20	26	2	regional	0.09	0.043	0.09	0.059	0.00	0.102
Lopez-Vaamonde et al., 2005	15	28	3	regional	0.07	0.040	0.09	0.083	-0.01	0.123
Lei and Olival, 2014a	38	14	3	regional	0.06	0.091	0.24	0.029	-0.18	0.119
Jones, 2001	5	8	1	local	0.05	0.200	-0.27	0.500	0.32	0.700
Lauron et al., 2015	43	18	3	regional	0.04	0.067	-0.02	0.025	0.06	0.092
Peralta et al., 2015a	39	61	3	local	0.04	0.017	0.01	0.028	0.04	0.045
Schardl et al., 2008	23	25	3	global	0.03	0.045	0.00	0.050	0.03	0.095
Leppänen et al., 2013b	59	25	3	regional	0.02	0.045	0.17	0.018	-0.14	0.063
Zhao et al., 2016a	28	28	3	global	0.01	0.040	0.02	0.040	0.00	0.080
Wilson et al., 2012	87	17	1	regional	0.00	0.071	0.13	0.012	-0.13	0.083
Lei and Olival, 2014e	19	14	3	regional	-0.05	0.091	-0.03	0.063	-0.02	0.153
Drinkwater and Charleston, 2014	17	7	3	global	-0.07	0.250	0.05	0.071	-0.12	0.321
Mu et al., 2005	14	7	3	global	-0.10	0.250	0.08	0.091	-0.18	0.341

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