Universidade Federal de Uberlândia
Instituto de Biologia
Programa de Pós-Graduação em Ecologia e Conservação de Recursos Naturais

# REDES DE INTERAÇÃO ENTRE AVES FRUGÍVORAS E PLANTAS: PADRÕES DE INTERAÇÃO E INFLUÊNCIA DE ATRIBUTOS

ADRIANO MARCOS DA SILVA

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

**Orientadora**

**Prof.ª Dr.ª Celine de Melo**

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# Sumário

# RESUMO

A dispersão de sementes é um processo essencial para os ecossistemas, tendo diversas implicações para a diversidade vegetal e animal. Dentre os animais que dispersam sementes, as aves são os mais importantes em diversos ecossistemas. Essa tese teve como objetivos em nível de rede definir (1) qual forma de analisar a diversidade das aves mais influenciam na estrutura da rede de interação; (2) mensurar a complementariedade e a redundância nas redes de interação e (3) determinar se a presença de plantas congêneres, morfologicamente e nutricionalmente semelhantes, leva à formação de módulos na rede de interação.Em nível de espécie, os objetivos foram determinar (1) quais atributos morfológicos e comportamentais influenciam na seleção de frutos e intensidade das interações; (2) quais atributos de propensão à extinção mais influenciam na importância de uma espécie para a estrutura da rede de interação e (3) quais atributos determinam a contribuição de cada espécie para a estrutura modular da rede. O banco de dados com redes de interação entre aves frugívoras e plantas foi composto por redes coletadas da literatura ou de dados próprios e o banco de dados com atributos das aves composto por medições tiradas de indivíduos capturados ou em museu e de dados da literatura. Modelos lineares e análises de redes foram utilizadas como estatística. Em relação ao objetivo (1), a diversidade funcional foi o parâmetro de diversidade que melhor explicou a variação na estrutura da rede e abertura do bico foi o atributo que melhor explicou a seleção de frutos e a combinação de nível de frugivoria e massa corporal que melhor explicou a intensidade das interações. No objetivo (2), as redes analisadas apresentaram especialização e baixa redundância e a combinação entre nível de frugivoria e dependência de floresta melhor explicou a importância de cada espécie na estrutura da rede. No objetivo (3), usando redes ponderadas, módulos foram detectados em todas as redes de interação, mas nenhum dos atributos das aves foi relacionado com o seu papel dentro da estrutura modular.Esse trabalho demonstra que o conjunto de atributos de uma espécie de ave é determinante para o seu papel dentro de uma rede de interação de frugivoria e que conhecer tais atributos é um importante passo para definir estratégias de manejo e conservação. Destacamos ainda a importância da diversidade de atributos funcionais na estruturação das redes de interação, principalmente em comunidades com baixa redundância funcional.

**Palavras-chave:** dispersão de sementes; frugivoria; redes mutualísticas

# ABSTRACT

Seed dispersal is an essential ecosystems process, which has different implications for plant and animal diversity. Among the seed dispersal animals, birds are the most important vectors in several ecosystems. This thesis had three network-level goals: (1) which way to analyze the bird’s diversity most influence in the interaction network structure; (2) measuring the complementarity and redundancy in the interaction networks and (3) determining whether the presence of congeneric plants species that are morphologically and nutritionally similar, lead to the formation of interaction modules in the network. At species level, the goals were to determine (1) which morphological and behavioral traits influence in fruit selection and interactions intensity; (2) which extinction proneness traits most influence on the importance of each species to the structure of the interaction network and (3) which traits determine the contribution of each species to the modular structure of the network. The database were composed by interaction networks between frugivorous birds and plants that was collected from literature or own data and the bird’s traits consisted of measurements taken from individuals captured in mist-nets or museum and literature. Linear models and network analysis were used as statistical. In relation to the goal (1), functional diversity is the diversity parameter that best explained the variance in network structure of the network, gape width was the trait that best explained the fruit selection and the combination of frugivory level and body mass best explained the intensity of interactions. The goal (2), networks analyzed showed high specialization and low redundancy and the combination of level frugivory and forest dependence better explained the importance of each species in the network structure. The goal (3), using weighted networks, modules were detected in all interaction networks, but none of the birds traits were related to his role within the modular structure. This study demonstrates that the trait set of a bird species is crucial to its role within the frugivory interaction network and that knowing these traits is an important step to define conservation and management. We also highlight the importance of diversity of functional traits in the structuring of interaction networks, especially in communities with low functional redundancy.

**Key-words:** frugivory, mutualistic networks, seed dispersal

# APRESENTAÇÃO

A degradação e fragmentação de habitats são as principais ameaças à biota brasileira (MARINI; GARCIA, 2005), pois elimina e/ou modifica habitats adequados para muitas espécies de plantas e animais, inviabilizando a persistência de populações e alterando os padrões de interação entre as espécies (CADOTTE; CARSCADDEN; MIROTCHNICK, 2011). Dentre os organismos afetados, as aves naturalmente são um grupo sensível às alterações e distúrbios ambientais (SEKERCIOGLU; DAILY; EHRLICH, 2004), sendo os frugívoros um grupo particularmente vulnerável (GOMES et al., 2008). Essas aves frugívoras tem papel essencial para regeneração e manutenção das comunidades vegetais, atuando como dispersoras de sementes para várias espécies de angiospermas (JORDANO et al., 2006). Desta forma, estudos que nos ajude a entender melhor os padrões que influenciam no processo de dispersão de sementes por aves e sua importância na conservação de comunidades ecológicas são essenciais para traçar futuras estratégias de manejo e recuperação de áreas degradadas.

Na última década, a popularização do uso de análises de redes nos estudos de interações mutualísticas tem sido essencial para diversos avanços ecológicos (BASCOMPTE; JORDANO, 2014). Essa ferramenta propicia testar tanto hipóteses em nível de comunidade, como também determinar parâmetros específicos de cada espécie dentro da rede de interação. Desta forma, o objetivo geral dessa tese é, através de análises de redes, abordar a influência dos diferentes atributos das aves (morfológicos, comportamentais ou de propensão à extinção) no papel em que essas desempenham dentro do processo de frugivoria e dispersão de sementes.

A presente tese é estruturada em quatro capítulos. No **Capítulo I** é apresentada uma revisão bibliográfica sobre a principal ferramenta de análises (redes ecológicas) e sobre o modelo ecológico estudado (frugivoria e dispersão de sementes). No **Capítulo II** propõe-se descobrir qual a forma de análise de diversidade é mais determinante sobre a estrutura de redes de interação entre aves frugívoras e plantas e quais atributos morfológicos e comportamentais das aves mais influenciam na sua escolha de recurso e intensidade de interação. No **Capítulo III** busca-se respostas para quais os atributos de propensão à extinção estão presentes nas espécies de aves mais relevantes nas redes de interação entre aves frugívoras e plantas e sobre a redundância e complementariedade da comunidade de aves nessas interações. No **Capítulo IV**, aborda-se como a presença de espécies de plantas congêneres dentro de uma comunidade gera uma estrutura modular e quais os atributos das aves dentro dessa comunidade influenciam sua contribuição para essa modularidade. Os capítulos II ao IV são apresentados em formato de artigo e já na língua inglesa e com formatação das revistas onde foram ou serão submetidos.

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# Capítulo I

## INTRODUÇÃO GERAL

### FRUGIVORIA E DISPERSÃO DE SEMENTES

A dispersão de sementes representa uma etapa fundamental no ciclo reprodutivo das plantas (HARPER, 1977), pois conecta o final do evento reprodutivo do adulto com o estabelecimento do novo indivíduo (WANG; SMITH, 2002). Esse processo consiste na retirada das sementes (envolta por um fruto) da planta-mãe e o seu depósito em locais mais distantes, aumentando as chances de germinação e sobrevivência dos novos indivíduos devido à redução da competição e patógenos associados ao adensamento na base da planta-mãe e pelo encontro de sítios viáveis para germinação (HOWE; MIRITI, 2004; HOWE; SMALLWOOD, 1982). A dispersão é um processo demográfico que influencia na distribuição espacial, dinâmica de populações (JORDANO, 2002; NATHAN; MULLER-LANDAU, 2000), colonização de novos habitats e fluxo gênico (OUBORG; PIQUOT; VAN GROENENDAEL, 1999), com grandes implicações para sucessão, regeneração e conservação (JORDANO et al., 2006; WANG; SMITH, 2002), estando ainda intimamente ligado à história evolutiva e diversidade das plantas (RONCE, 2007).

Existem diversas adaptações morfológicas que possibilitam diferentes formas de uma semente ser retirada e transportada da planta-mãe (VAN DER PIJL, 1982). Esse conjunto de adaptações para dispersão é chamada de síndrome de dispersão. Uma dessas formas é através do vento (anemocoria), sendo que as sementes com essa síndrome possuem estruturas alares, plumosas ou em formato de balão. Sementes podem também ser dispersas pela água (hidrocoria), através das enxurradas, chuvas ou rios ou então pela força gravitacional (barocoria). Existem também síndromes de dispersão em que as sementes são liberadas sem a intervenção de agentes externos, através da abertura espontânea dos frutos (autocoria). Mas a dispersão de sementes também pode ocorrer mediada por um vetor biótico, através da retirada do fruto por alguma espécie animal, evento conhecido como zoocoria (HOWE; SMALLWOOD, 1982). Nessa síndrome de dispersão, os animais determinam a distribuição espacial das espécies vegetais na paisagem (NATHAN; MULLER-LANDAU, 2000), sendo que normalmente é um método mais eficiente porque permite as sementes atingirem distâncias e locais não alcançáveis através de meios abióticos (BOLMGREN; ERIKSSON, 2010).

A dispersão zoocórica é um processo mutualístico entre plantas e animais em que o animal utiliza os recursos nutritivos oferecidos ao redor das sementes (JORDANO, 1987), que podem ser ricos em carboidratos, minerais, lipídios e proteínas (HERRERA, 1982). Os animais, por outro lado, podem transportar as sementes para outros locais. O processo de dispersão zoocórica é resultado da exploração recíproca entre as duas partes envolvidas, sendo interpretado como uma coevolução difusa entre grupos de agentes dispersores e plantas (CHARLES-DOMINIQUE, 1993; JANZEN, 1980). O dispersor pode afetar certos atributos da planta, e vice-versa, mas a coadaptação entre eles dificilmente ocorre em níveis taxonômicos menores (CHARLES-DOMINIQUE, 1993). A evolução da frugivoria propiciou um padrão de diversificação em larga escala de diversos clados envolvidos nesse processo, tanto de plantas como de animais (FLEMING, 2005).

A presença de frutos dispersos por animais é um dos principais fatores responsáveis pela alta diversidade de espécies vegetais (OLTIS, 2004). Frutos zoocóricos surgiram independentemente diversas vezes durante a história evolutiva das angiospermas, mesmo nas linhagens mais basais (FLEMING; KRESS, 2011). A hipótese da síndrome de dispersão afirma que frutos possuem conjunto de atributos, como cor, forma, odor, fenologia e valor nutricional que determinam seus agentes dispersores (HOWE; WESTLEY, 1988; JANSON, 1983). Frutos consumidos por animais visualmente guiados, como aves, tendem a possuir coloração mais contrastante, tamanho menor e serem inodoros (CAZETTA; SCHAEFER; GALETTI, 2009). Já frutos dispersos por agentes guiados pelo olfato, como mamíferos, tendem a ter coloração mais críptica e odor mais forte (WILLSON, 1993). A combinação dessas características não aleatórias implica que os agentes dispersores exercem pressão seletiva sobre os atributos dos frutos (GAUTIER-HION et al., 1985; HERRERA, 1985). Apesar disso, outros fatores como tolerância a sombra, predação de sementes e estratégia de germinação também selecionam os atributos dos frutos (FLEMING; KRESS, 2013).

Espécies de plantas com dispersão zoocóricas ocorrem praticamente em todos ambientes terrestres, predominando nas regiões tropicais (FLEMING; BREITWISCH; WHITESIDES, 1987; KISSLING; BÖHNING-GAESE; JETZ, 2009). Em florestas tropicais, mais de 90% das espécies vegetais podem ser zoocóricas. Essa proporção tende a diminuir em ambientes mais secos e sazonais (HOWE; SMALLWOOD, 1982). A proporção de frugívoros na avifauna mantém esse mesmo padrão, sendo que em florestas tropicais nas Américas e no sudeste Asiático os consumidores de frutos são mais representativos que em outros ambientes (KISSLING; BÖHNING-GAESE; JETZ, 2009). A distribuição temporal dos frutos não tende a ser muito regular ao longo do ano na maioria dos ambientes (FLEMING; BREITWISCH; WHITESIDES, 1987). Mesmo em florestas tropicais, onde a oferta de frutos é maior que o consumo durante quase todo ano, ocorrem meses com baixa de oferta (TERBORGH, 1986). Essa irregularidade no recurso é pressão para que animais frugívoros adotem comportamentos migratórios (LOISELLE; BLAKE, 1991) ou façam uso de recursos alternativos (SILVA; MELO, 2013).

A dispersão por vetores animais ocorre principalmente por endozoocoria, através da ingestão da semente que é eliminada posteriormente, por regurgito ou pelas fezes (TRAVESET et al., 2007). Menos comumente, as sementes podem ser dispersas por exozoocoria, ou seja, aderidas ao corpo do animal (SORENSEN, 1986). Uma ampla variedade de grupos animais dispersam sementes, inclusive alguns grupos de invertebrados, como minhocas (ZALLER; SAXLER, 2007), gafanhotos (DUTHIE; GIBBS; BURNS, 2006) e formigas (BREW; O’DOWD; RAE, 1989). Dentre os vertebrados, é incomum, mas possível a dispersão por peixes (GALETTI et al., 2008), répteis (VALIDO; NOGALES, 1994) e anfíbios (DA SILVA; DE BRITTO-PEREIRA, 2006). Mas os grupos animais mais importantes no processo de dispersão de sementes são os mamíferos (principalmente os primatas e morcegos) e as aves (FLEMING; KRESS, 2011).

As aves representam um dos mais bem sucedidos clados de vertebrados, com quase 10 mil espécies registradas (JETZ et al., 2012). Indivíduos desse grupo são facilmente reconhecidas por uma série de características bastante específicas, que em conjunto, contribuíram para sua ampla distribuição (GILL, 2007). O consumo de fruto evoluiu diversas vezes e de maneira independente e está amplamente distribuída na filogenia das aves, sendo reconhecido 10 ordens e ao menos 23 famílias (FLEMING; KRESS, 2013). Os Grupos mais basais, Paleognathae e Galloanserae, possuem espécies que consomem frutos, como os casuares e os cracideos. Diversas famílias de Neornithes, como Columbidae, Trogonidae, Ramphastidae e Bucerotidae tem frutos como parte importante de sua dieta. Mas os Passeriformes formam o grupo mais relevante na dispersão de sementes, por ser o mais diverso e abundante. Destacam-se na região neotropical as famílias Pipridae, Contingidae, Turdidae e Thraupidae (FLEMING; KRESS, 2011). Essa grande variedade de espécies consumindo frutos, associado com seu alto potencial de deslocamento e por normalmente eliminarem as sementes em condições viáveis para germinação (TRAVESET, 1998; TRAVESET; ROBERTSON; RODRÍGUEZ-PÉREZ, 2007), fez com que as aves sejam o grupo animal que mais influenciou na evolução dos frutos de diversas famílias de angiospermas (FLEMING; KRESS, 2011).

Nem todas as aves que consomem frutos tem sua dieta majoritariamente composta por esse recurso (IZHAKI; SAFRIEL, 1989), principalmente pela irregularidade na distribuição temporal e espacial, além de normalmente não suprirem toda a demanda nutricional de um vertebrado (FLEMING; BREITWISCH; WHITESIDES, 1987). Por isso, aves frugívoras consomem várias espécies de frutos, não se especializando em espécies ou famílias específicas (GITHIRU et al., 2002; MULLER-LANDAU; HARDESTY, 2005) e até consomem outros recursos para complementar a dieta, principalmente em épocas de escassez (CARNICER; JORDANO; MELIAN, 2009). Além disso, algumas espécies de insetívoros e granívoros consomem frutos oportunisticamente, seja para suprir a falta do seu recurso principal ou apenas para obter um recurso energético imediato (BORGHESIO; LAIOLO, 2004). Já algumas espécies onívoras também incluem frutos, apesar de fazerem uso de outros recursos (KISSLING; BÖHNING-GAESE; JETZ, 2009). A proporção de espécies altamente dependentes de frutos presentes em uma comunidade de aves é muito influenciada pela sazonalidade (SILVA; MELO, 2013) e grau de distúrbio do ambiente (MARKL et al., 2012).

Apesar de não ser uma forma de alimentação muito especializada, o consumo eficiente de frutos demanda das aves algumas adaptações morfológicas e comportamentais (CORLETT, 2011). As aves possuem visão tetra cromática, bastante sofisticada e com alta distinção de cores e contrastes (GOLDSMITH, 2006). Essa eficiência visual possivelmente surgiu para comunicação intraespecífica (HART; HUNT, 2007), mas sem dúvida a coloração dos frutos e seu contraste com o ambiente é utilizada pelas aves na detecção e seleção do recurso (CAMARGO et al., 2013). Ainda em relação às cores, o consumo de frutos também influencia na coloração das penas. Aves frugívoras tendem a ser mais coloridas devido à maior ingestão de carotenóides presentes nos frutos, que são matéria prima para colorações vermelho e amarelo nas penas (OLSON; OWENS, 2005).

O modo de forrageio por frutos varia entre os diferentes grupos de aves, mas se resumem em três formas: captura em voo, empoleirado ou no solo. Cada hábito favorece diferentes formatos de bico, asas e patas (MOERMOND; DENSLOW, 1985). Além disso, devido a grande diversidade morfológica de aves que consomem frutos regularmente, não é possível determinar um padrão comum para a morfologia externa das aves frugívoras. No entanto, é sabido que alguns atributos estão relacionados à captura e seleção de frutos, como formato da asa, que influencia o estrato preferencial de forrageio e a acessibilidade aos frutos (MOERMOND; DENSLOW, 1985); a abertura do bico, que limita o tamanho de frutos que podem ser engolidos (WHEELWRIGHT, 1985) e a massa corporal, que determina as necessidades energéticas e nutricionais da espécie (WOTTON; KELLY, 2012). Já em relação à morfologia interna, de forma geral, o trato digestivo das aves frugívoras tende a ser adaptado para a ingestão de altas taxas de carboidratos, apresentando intestino curto, moela fina e rápida passagem do alimento (STANLEY; LILL, 2002). Por sua vez, o tempo da passagem do alimento pelo corpo da ave é um fator essencial para determinar a distância que a semente será dispersa (WESTCOTT et al., 2005).

O consumo de frutos não significa que a semente retirada da planta-mãe será efetivamente dispersa, ou seja, resultará em um novo indivíduo (SCHUPP, 1993). Dessa forma, diferentes espécies de aves contribuem de maneira diferente para a dispersão das sementes, sendo que inclusive, muitas delas são predadoras de sementes, impossibilitando uma dispersão bem sucedida. A efetividade de uma espécie de ave como dispersora de sementes é resultado do produto de fatores quantitativos (valores numéricos da taxa de visitação e retiradas de frutos) e qualitativos (tratamento e deposição das sementes) (SCHUPP, 1993; SCHUPP; JORDANO; GÓMEZ, 2010). Desta forma, abundância e a dependência de frutos são importantes para definir o número de sementes que são potencialmente dispersas (VÁZQUEZ; MORRIS; JORDANO, 2005) e o modo de mandibulação (LEVEY, 1987), ingestão

(MOERMOND; DENSLOW, 1985), passagem pelo trato digestivo (TRAVESET, 1998) e local de deposição determinam a probabilidade da semente retirada germinar e gerar um novo indivíduo (WESTCOTT et al., 2005).

## ANÁLISES DE REDES APLICADAS AO MUTUALISMO ECOLÓGICO

Uma rede é a representação de um sistema composto de múltiplos elementos potencialmente conectados (BASCOMPTE; JORDANO, 2014). O conceito de rede de interação data do século XVIII, sendo criada por Leonard Euler em 1736, como proposta para a solução de um enigma existente na cidade russa de Kaliningrado. O problema consistia em provar que não existia um caminho possível para se passar pelas sete pontes da cidade apenas uma vez. Usando uma representação de grafo, Euler demonstrou a impossibilidade (Figura 1). Desde então, embasados também pelo trabalho de ERDÖS; RÉNYI (1959), as análises de redes se popularizaram em diversas áreas, como na física, sociologia, tecnologia e também nos estudos biológicos. Hoje, análises de rede são utilizadas em todos os níveis de organização biológica, desde estudos moleculares, como vias metabólicas, genes reguladores e interações protéicas até espécies animais e vegetais interagindo dentro de uma comunidade (PROULX; PROMISLOW; PHILLIPS, 2005).

Independente do sistema estudado, um grafo é composto por dois elementos. Um deles é o vértice (também chamado de nó ou ponto), querepresenta a unidade que esta sendo estudada (e.x. uma espécie, uma indivíduo, uma moléculas, uma área...) e o outro é a arestra (também chamado de conexão ou linha), que representa o tipo de conexão entre os vértices (e.x. interação, fluxo de energia...). Uma rede de interação pode ser classificada de duas formas. Ela pode ser unipartida, quando existe apena uma categoria de vértices e todos eles são potencialmente conectáveis entre si ou então bipartidas, quando existem dois grupos de vértices, e a conexão só ocorre entre vértices de grupos diferentes (Figura 2). As redes podem ainda ser binárias, quando as interações são diferenciadas apenas na ocorrência ou não, ou ponderadas, quando as interações tem algum valor quantitativo de intensidade. Seja qual for o estilo de rede, ela pode ser definida sobre a forma de uma matriz adjacente. Nas redes unipartidas, as linhas e colunas se repetem e nas bipartidas, cada grupo preenche ou as linhas ou as colunas.

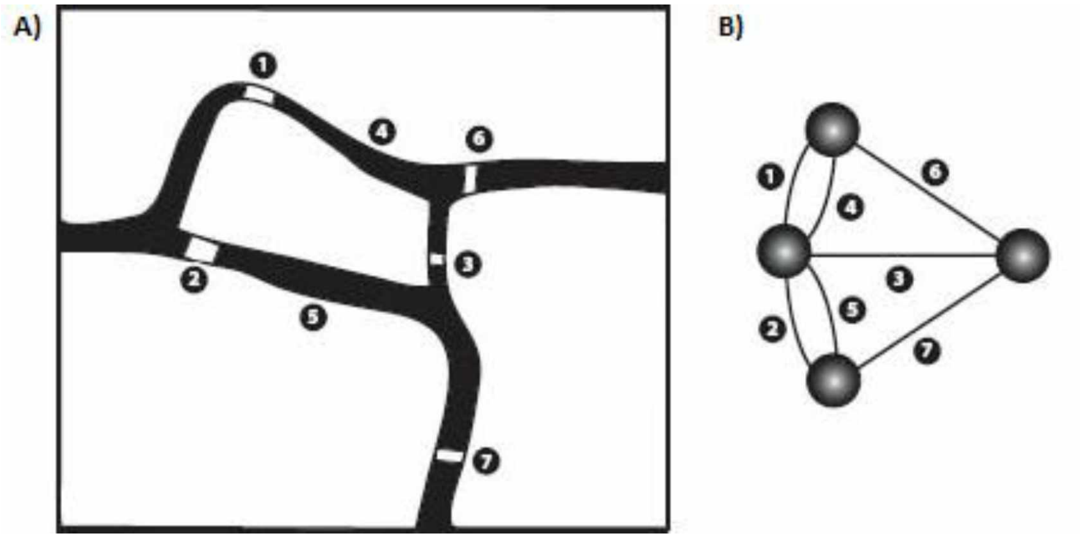
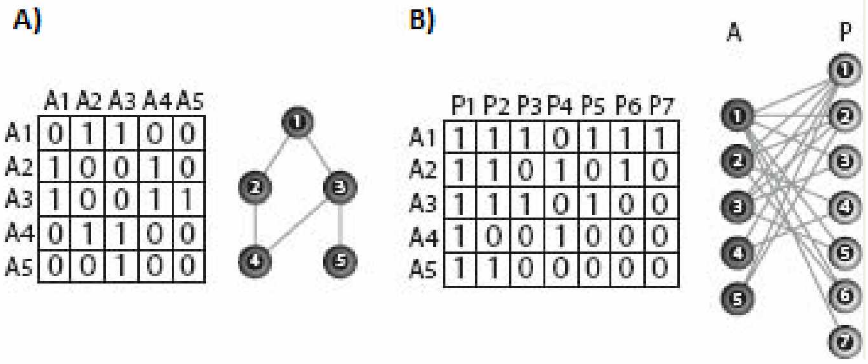


**Figura 1.** Problema das pontes de Kaliningrado (antiga Königsberg). A) Mapa esquemático da cidade no século XVII, sendo que cada número representa uma ponte, as porções brancas são as massas de terra e a escura é o rio Pregel. B) Representação da cidade em forma de grafo. Os vértices representam as massas de terra e as conexões representam as pontes. Retirado de BASCOMPTE; JORDANO (2014).

Interpretar um sistema complexo utilizando as ferramentas disponibilizadas pelas análises de rede permite a representação visual do mesmo, além de fornecer um mecanismo de medir atributos de cada vértice ou do sistema como um todo (POULIN, 2010). Outra vantagem é a possibilidade de encontrar propriedades emergentes dentro do sistema, ou seja, encontrar padrões gerais que não seria possível se cada elemento fosse analisado separadamente (HELENO et al., 2014). Análises de rede permitem ainda operacionalizar diversas variáveis teóricas, tanto em nível de rede, atribuindo valores para diversos parâmetros que descrevem a estrutura da rede de interação (SEBASTIÁN-GONZÁLEZ et al., 2015) como também em nível de vértice, atribuindo valores à diversas características que um vértice tem dentro daquela rede (DORMANN, 2011). Essa operacionalização de variáveis é essencial para se testar hipóteses, tanto através de comparações entre sistemas já estudados, mas principalmente através da comparação de dados observados com dados gerados via modelos nulos (BASCOMPTE; JORDANO, 2014).



| | A1 | A2 | A3 | A4 | A5 |
|---|---|---|---|---|---|
| A1 | 0 | 1 | 1 | 0 | 0 |
| A2 | 1 | 0 | 0 | 1 | 0 |
| A3 | 1 | 0 | 0 | 1 | 1 |
| A4 | 0 | 1 | 1 | 0 | 0 |
| A5 | 0 | 0 | 1 | 0 | 0 |

| | P1 | P2 | P3 | P4 | P5 | P6 | P7 |
|---|---|---|---|---|---|---|---|
| A1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 |
| A2 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| A3 | 1 | 1 | 1 | 0 | 1 | 0 | 0 |
| A4 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| A5 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |

**Figura 2.** A) Matriz de adjacência e grafo representando uma rede de interações unipartida. B) Matriz de adjacência e grafo representando uma rede de interações bipartidas. Retirado de BASCOMPTE; JORDANO (2014).

Pensar interações ecológicas como uma rede de interações não é algo novo em ecologia, visto que as comunidades ecológicas são formadas por diversas espécies que estão envolvidas em diversos tipos de interações, sua aplicação se torna bastante óbvia (BASCOMPTE; JORDANO, 2007). Trabalhos clássicos da década de 40 e 50 já utilizavam essa abordagem para descrever interações tróficas entre espécies (LINDENMAN, 1942; ODUM, 1956). Mas o número de trabalhos utilizando redes de interação para estudos ecológicos tem aumentado intensamente nas últimas décadas (HELENO et al., 2014). Por muitos anos, essas análises foram utilizadas na ecologia apenas para estudos de teias alimentares (COHEN, 1978; PAINE et al., 1980; PIMM, 1980), mas recentemente outros tipos de interações ecológicas também passaram a ser analisadas como redes de interações (PROULX; PROMISLOW; PHILLIPS, 2005). Apesar de poderem ser classificadas de diversas formas diferentes, estudos com redes ecológicas são normalmente agrupados em três categorias: redes predador-presa, redes parasito-hospedeiro e redes mutualísticas (INGS et al., 2009). Redes mutualísticas, por sua vez, envolvem relações de exploração mútua em que os dois parceiros são potencialmente beneficiados (TOBY KIERS et al., 2010), sendo representadas por interações entre animais e plantas, como frugívoras-frutos, nectarívoros-flores e formigas-plantas (BASCOMPTE; JORDANO, 2014).

Uma rede mutualística é bipartida, em que um dos grupos é o animal e o outro o vegetal, sendo que estudos envolvendo os processos de polinização e dispersão de sementes são os mais abordados (BASCOMPTE; JORDANO, 2014). Jordano (1987) em estudo seminal aplicou os primeiros conceitos de rede de interação em relações mutualísticas, analisando questões sobre número de parceiros com que cada espécie interage e a importância de cada espécie para seu conjunto de parceiros. Apesar disso, apenas duas décadas depois que os primeiros trabalhos (BASCOMPTE et al., 2003; FONSECA; GANADE, 1996; JORDANO; BASCOMPTE; OLESEN, 2003; MEMMOTT, 1999; VÁZQUEZ; AIZEN, 2004) abriram as portas para que as análises de rede passaram a ser amplamente utilizadas em estudos de interações mutualísticas plantas-animais. Estudos tradicionais de interação mutualísticas entre aves frugívoras e plantas tradicionalmente focam na relação entre uma espécie vegetal e sua assembleia de consumidores (e.x. GONÇALVES et al., 2015; HERRERA; JORDANO, 1981; MELO; BENTO; OLIVEIRA, 2003; MELO; OLIVEIRA, 2009; PIZO, 1997) ou em um frugívoro e as espécies de planta por ele consumidas (e.x. RAGUSA-NETTO, 2013; SILVA; MELO, 2011). Mas estudos abordando as interações de mesma natureza dentro de uma comunidade, realizados por meio da perspectiva de redes, propiciaram uma nova forma de entender e estudar processos ecológicos e evolutivos da interação de frugivoria e dispersão de sementes (CARLO; YANG, 2011).

Nos últimos anos, várias redes de interações animal-planta foram analisadas através de parâmetros que descrevem a estrutura de uma rede, sendo observado que elas não são formadas aleatoriamente e que ocorrem diversos padrões em comum (BASCOMPTE; JORDANO, 2007; VAZQUEZ et al., 2009). O padrão de número de interações que uma espécie realiza em redes mutualísticas é muito heterogêneo, sendo que maioria das espécies possuem poucos parceiros (normalmente chamados de especialistas) e poucas interações e algumas poucas espécies possuem diversos parceiros (normalmente chamadas de generalistas) e concentram maior parte das interações (JORDANO; BASCOMPTE; OLESEN, 2003; VAZQUEZ;

AIZEN, 2003). Dessa forma, as interações apresentam uma alta assimetria de dependência, sendo que dependência é a importância (seja na dispersão ou na nutrição) que uma espécie animal tem para as espécies vegetais, e vice-versa (VÁZQUEZ; MORRIS; JORDANO, 2005). Essa assimetria normalmente ocorre porque se uma espécie de planta é importante para uma espécie animal, esse animal não será importante para essa planta (VÁZQUEZ; AIZEN, 2004), sendo que esse padrão favorece a coexistência em longo prazo e facilita a manutenção da diversidade (BASCOMPTE, 2006).

Um dos padrões mais recorrentes nas redes de interação é o aninhamento (BASCOMPTE et al., 2003; Figura 3A). Uma rede aninhada apresenta três características: (1) um grupo de espécies concentra a maioria das interações, interagindo muito entre si e com as outras espécies da rede; (2) as espécies com poucas interações interagem preferencialmente com espécies com muitas interações e (3) não há interações entre as espécies com poucas interações. O aninhamento está relacionado com a estabilidade da comunidade e prevenção de extinções secundárias (BASCOMPTE et al., 2003; BURGOS et al., 2007; TYLIANAKIS et al., 2010). Isso porque uma pequena proporção das espécies está envolvida em um grande número de interações, aumentando a redundância e criando formas alternativas do sistema se manter, além disso, os especialistas interagem com espécies que tendem a ser menos flutuantes e mais estáveis, favorecendo a permanência dos especialistas (BASCOMPTE et al., 2003; BASCOMPTE; JORDANO, 2007).

Algumas redes de interação mutualísticas apresentam padrão modular, ou seja, existem conjuntos de espécies que tendem a interagir mais entre si do que com as outras espécies (OLESEN et al., 2007;

Figura 3B). A formação de módulos pode ser resultado de diversos fatores ecológicos e evolutivos como diversidade de espécies (MARTÍN GONZÁLEZ et al., 2012; OLESEN et al., 2007), compatibilidade entre parceiros (MARUYAMA et al., 2014), fatores macroecológicos (DALSGAARD et al., 2013; SCHLEUNING et al., 2014) e para evitar competição entre espécies próximas (Silva et al. 2016). A compartimentalização das redes tem importante relação com a conservação, visto que distúrbios tendem a ficar concentrados dentro do módulo, não espalhando por toda a rede (TYLIANAKIS et al., 2010).

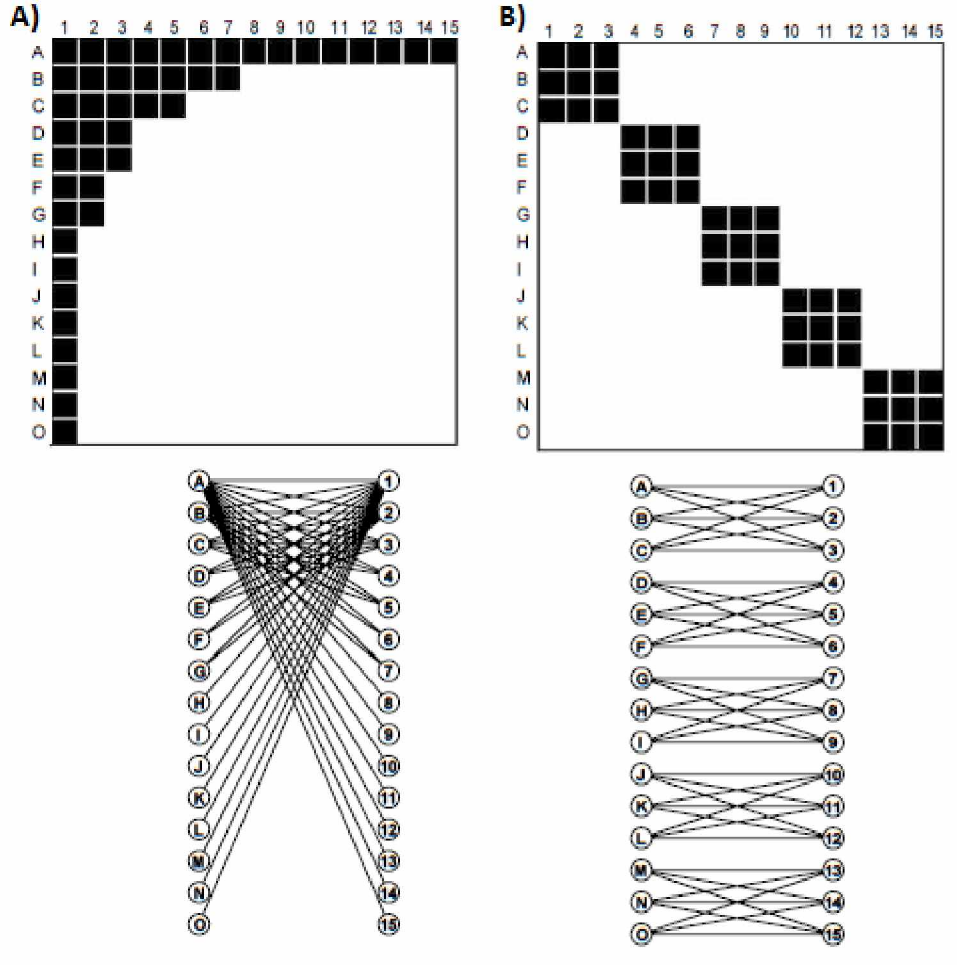


**Figura 3.** A) Matriz de adjacência e grafo representando uma rede de interações aninhada. B) Matriz de adjacência e grafo representando uma rede de interações modularizada. Adaptado de LEWINSOHN et al. (2006).

Além de descrever e caracterizar a estrutura geral da rede de interação, existem diversas ferramentas que permitem analisar o papel que cada vértice tem dentro da rede através do seu padrão de interações (DORMANN, 2011). A importância de cada espécie tem dentro daquela comunidade não é a mesma, sendo que a perda de algumas espécies pode ser muito mais impactante para o sistema do que a perda de outras. Desta forma, mensurar essa importância é muito relevante na determinação de espécies-chave e espécies prioritárias para conservação (VIDAL et al., 2014). Mas o papel de uma espécie pode ser entendido de diversas formas, como sua especialização complementar (BLÜTHGEN; MENZEL; BLÜTHGEN, 2006), sua importância para conectar módulos ou dentro do módulo que ela está inserida (OLESEN et al., 2007), o tanto que ela contribui para o padrão de aninhamento da rede (ALARCO; WASER; OLLERTON, 2008) ou então o qual próximo ela está das outras espécies (MARTÍN GONZÁLEZ; DALSGAARD; OLESEN, 2010).

Mas além de trazer informações sobre a rede e seus vértices, um dos maiores desafios que tenta ser solucionado com essa ferramenta é entender os processos evolutivos e ecológicos responsáveis pelos padrões das interações entre espécies (THOMPSON, 2006; VAZQUEZ et al., 2009). Devido a tendência de conservação de nicho entre espécies próximas, é esperado que essas tenham padrões de interação semelhante, ou seja, a fatores filogenéticos podem influenciar na estrutura da rede (REZENDE et al., 2007). De forma geral, a estrutura da rede e resultado de eventos de interação individuais definidos pela combinação de dois processos: interações neutras e compatibilidade de atributos (VAZQUEZ et al., 2009). Uma interação neutra é aquela que ocorre através do encontro aleatório entre indivíduos, sem nenhum tipo de preferência ou escolha, ou seja, a probabilidade de duas espécies interagirem é fruto de suas abundâncias relativas, sendo que espécies mais abundantes irão interagir mais frequentemente que espécies menos abundantes (KRISHNA et al., 2008; VÁZQUEZ; CHACOFF; CAGNOLO, 2009; VÁZQUEZ; MORRIS; JORDANO, 2005). Já uma interação ocorrendo por compatibilidade de atributos é resultante da correspondência de atributos fenotípicos envolvidos na interação, como compatibilidade de tamanho das estruturas envolvidas ou nos padrões fenológicos (MARUYAMA et al., 2014; VIZENTIN-BUGONI; MARUYAMA; SAZIMA, 2014).

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# Capítulo II

## TRAIT DIVERSITY INFLUENCES STRUCTURE AND SPECIES ROLES IN PLANT-FRUGIVORE NETWORKS

DIVERSIDADE DE ATRIBUTOS INFLUENCIA NA ESTRUTURA E NO PAPEL DAS ESPÉCIES EM REDES DE INTERAÇÃO PLANTA-FRUGÍVORO

Formatação de acordo com o periódico: Oecologia

## Abstract

There are several ways to express the diversity in a community and some of these ways may be related with the diversity and patterns of interactions, which generated the structure of plant-frugivore networks. We aim to known the bird diversity index that have more influence in network structure and the bird traits that are most related with species roles. There were selected 10 weighted plant-frugivore bird's network from Brazil and collected data of morphological and behavioral traits of birds registered. As diversity index we utilized functional diversity, phylogenetic diversity, species richness and evenness. As network-level metrics we utilized connectance, nestedness, modularity and specialization and as specie-level metrics we selected specialization and species strength. We run linear models between diversity indexes and network level metrics and between bird traits and specie level metrics. The model containing functional diversity was the one that best explain the variance of connectance and modularity. Nestedness and specialization were not related with any diversity index. Gape width were the trait that best explained the variance of specie specialization and the model contain frugivory degree and body mass best explain species strength. We conclude that trait diversity has great influence in the structure of network and that specific bird traits are determinant in the roles that a species play within the network.

**Key-words:** frugivory, functional diversity, mutualistic interactions, phylogenetic diversity, seed dispersal.

## Resumo

Existem diversas formas de expressar a diversidade em uma comunidade e algumas dessas estão relacionadas com a diversidade e padrões de interações, o que gera a estrutura das redes planta-frugívoros. Nosso objetivo foi determinar o índice de diversidade que tem mais influência na estrutura da rede e os atributos que são mais relacionados com o papel da espécie. Foram selecionadas 10 redes ponderadas de interações entre planta-aves frugívoras do Brasil e foram compilados dados de atributos morfológicos e comportamentais das aves registradas. Como índices de diversidade foram utilizados diversidade funcional, diversidade filogenética, riqueza de espécies e equitabilidade. Como as métricas em nível de rede foram utilizadas conectância, aninhamento, modularidade e especialização, e como métricas em nível de espécies selecionamos especialização e força da espécie. Rodamos modelos lineares entre índices de diversidade e métricas em nível de rede e entre os atributos de aves e métricas em nível de espécie. O modelo contendo diversidade funcional foi o que melhor explicou a variação na conectância e modularidade. Aninhamento e especialização não foram relacionadas com qualquer índice de diversidade. Abertura do bico é o atributo que melhor explicou a variação na especialização da espécie e o modelo contendo nível de frugivoria e massa corporal foi o que melhor explicou a força da espécie. Concluiu-se que a diversidade de atributos tem grande influência na estrutura da rede e que atributos das aves são determinantes no papel que uma espécie desempenha dentro da rede.

## 1. Introduction

The increase of anthropogenic land-use, such as via urbanisation and agricultural activities, are transforming the natural landscapes in the neotropic (Chapin III et al. 2000), leading to alterations in overall species diversity (Morris 2010) and generating gaps in ecosystem functioning (Cadotte et al. 2011). In spite of the undeniable importance of biological diversity to overall ecosystem functions (Loreau et al. 2001; Hooper et al. 2005), measuring this diversity has been a major ecological challenge, not only in the collection of field data, but also in data analysis and interpretation (Duelli and Obrist 2003). Classical diversity indices, such as the Shannon index or even absolute species richness, assume that all species and individuals are ecologically equivalent within the community (Magurran 2005). However, each species plays different roles in ecosystem functioning according to their morphological, behavioural and evolutionary attributes (Maglianesi et al. 2014). The concept of functional and phylogenetic diversity becomes more important as essential tools to fill this lack in biodiversity measurement (Cadotte et al. 2011), to evaluate complementarity and convergence patterns in ecological assemblages through the diversity of traits that influence specific ecological functions (Violle et al. 2007) and through the accumulated evolutionary history of a community (Faith 2013).

Trait-based diversity measures are usually more informative than species richness or composition (Mcgill et al. 2006), especially when one is interested in ecological functioning and interactions (Hooper et al. 2005). The use of functional traits approach report species' roles and their potential interactive partners (Moran and Catterall

2010), mediating pairwise interactions between species through trait-matching, as bird gape width and fruit size, for instance (Olesen et al. 2010). Besides, at a community scale, the diversity of traits in the assemblage should also be manifested in the diversity of interactions, which may influence the architecture of the mutualistic networks (Chamberlain et al. 2014). In this context, the use of network analyses in species-rich environments is useful to measure whole community patterns that shape the stability and resilience of species interactions (Fortuna and Bascompte 2006).

The network architecture is defined by the density and pattern of interactions (Newman and Girvan 2004) and can be interpreted through several metrics, such as: connectance, the proportion of realised interactions from of all possible interactions between the species of a network (Jordano 1987); nestedness, when specialists species interacting with subsets of species interacting with more generalist species (Bascompte et al. 2003); modularity, the tendency of certain species to organise in subgroups that interact more among themselves than with species outside the group (Krause et al. 2003); and complementary specialisation, the overlap in interactive species among different partners across the entire community (Blüthgen et al. 2006). The network analysis can also describe the role that each species plays in the community (Martín González et al. 2010). At the species level, specialisation or generalisation can be interpreted in various ways (Dormann 2011), but the most usual are related to proportional resource utilisation in relation to resource availability (Blüthgen et al. 2006). The network approach applied to plant-animal interactions shed light to mutualistic studies (Proulx et al. 2005), bringing important insights on seed dispersal interactions (Vidal et al. 2014; Sebastián-González et al. 2015).

Seed dispersal by animals occurs in most terrestrial environments, especially in the tropics (Moermond and Denslow 1985; Kissling et al. 2009), where most plants rely on animals to disperse their seeds (Howe and Smallwood 1982). Among seed dispersers, birds are the most important taxon for several angiosperm families because of their abundance and range of functional traits (Fleming and Kress 2011). Since the diversity of functional traits in the assemblage of frugivorous birds are closely related to the efficiency of seed dispersal services in the community (Moran et al. 2004; Garcia and Martinez 2012), it is important to determine which bird traits are more important to fruit foraging behaviour. Among the morphological traits, gape width is essential because it constrains the range of fruit sizes that birds are able to consume (Wheelwright 1985); wing shape is related to preferred foraging strata and fruit accessibility (Moermond and Denslow 1985); and body mass influences diet and nutritional requirements (Wotton and Kelly 2012). As for behavioural traits, the frugivory level determines the dependence and choice on fruit (Moermond and Denslow 1985) and migratory behaviour could be important, since migratory species have different proportions of fruits in the diet compared to their resident counterparts (Boyle et al. 2011).

The different pool of traits and evolutionary history of birds in a community may be reflected in network architecture. As network metrics are influenced by the balance of generalist and specialist species in the network (Lewinsohn et al. 2006), we expect that these metrics are related to different aspects of diversity of fruit-eating bird assemblages. In this sense, we had two hypotheses at different hierarchical levels: (1) At the network-level: we tested the hypothesis that functional diversity is the diversity index that better explains the architecture of plant-frugivore networks, as it is directly related with the amplitude of functional traits in the community, being determinant to pairwise interactions (Moran et al. 2004). (2) At the specie-level: we tested the hypothesis that gape width and frugivory level better explain the roles of bird species within the network, as they impose a threshold on fruits that can be consumed (Wheelwright 1985) and determine the dependence on fruits (Moermond and Denslow 1985), respectively, being the main predictors of frugivory birds diet composition (Moran and Catterall 2010).

## 2. Material and methods

### (a) Data set

We selected a data set of 10 weighted interaction networks between fleshy-fruited plants and frugivore birds from Central and Southeast Brazil (table S1).The data set came from published studies or our own data, being all from Brazilian Cerrado or Atlantic Forest. Despite that other animal groups can act as seed dispersers, the data focused only on fruit consumption by birds, which are the most important taxa for this ecological service (Fleming and Kress 2011). The networks selected were from the only plant-frugivore weighted networks collected in Brazil that we had access. Our data focused to this country because the accessibility of bird's morphological data knowledge about the natural history were restricted on these region.

The interaction between frugivore birds and plants in the networks analysed were recorded through seeds presence in faecal samples or direct observation of birds eating fruits. The sampling effort was different between studies, but always covered the main fruiting period in each area.

Datasets were organised as matrices, being rows and column representing species and cells filled with interactions. Elements *aij* represent the number of interactions between bird *i* and plant *j*. If *aij*= 0, no interaction was registered. The quantitative factors were the number of feeding visits of a bird species in each plant species (for networks made with direct observations) or the number of faecal samples with a specific type of seed (for networks made with captured birds). For diversity metrics that demand abundance data, we used the species degree, since our goals did not involve patterns of whole communities, but only the presence in the community of plant-frugivore bird interactions. For instance, an insectivore species that consumed few fruits would be a rare species considering frugivory interactions, even if it was a very abundant species.

### (b) Bird traits and phylogeny

To relate the network role of birds to their functional traits, we gathered data on morphological and behavioural traits of birds registered in the considered networks. The morphological traits were taken from 3-5 individuals collected in mist nets or specimens in museums. Body mass was measured with a dynamometer (of different capacities, according to bird size) or with data from the literature (Dunning 2008). From the beaks of each species, we measured length, width (considered as gape width) and height. The wing lengths were measured with a digital calliper as the distance between the bend of the wing and the longest primary feather of the right wing. The fruit-eating birds were classified into three frugivory level, following (Kissling et al. 2007) as obligate frugivores: species for which fruits are the main food resource in the diet; partial frugivores: species that, besides fruit, utilise other major food items in their diet; and opportunistic fruit-eaters: granivorous or insectivorous species that occasionally eat fruits as a supplementary food resource. Data on food preferences of birds were gathered from (Sick 1997; del Hoyo et al. 2015). Finally, we classified the migratory behaviour of the bird species as: resident, sedentary species that remain year-round in the same area; nomad, species that perform irregular movements in response to resource availability; and migratory, species that make short or long and well-defined seasonal movements. Movement information was gathered from (Nunes and Tomas 2008; del Hoyo et al. 2015) and personal observations.

To account for phylogeny, we used trees generated by http://birdtree.org/ (Jetz et al. 2012) for the bird species in each network, using the (Hackett et al. 2008) backbone. This website provides samples trees from a pseudo-posterior distribution, which allowed us to construct a majority-rule consensus tree based on 500 trees, according to (Holder et al. 2008), considering a branching event when it occurs in >50% of the trees and considering politomy when the branch is below 50%. We used R 3.1.2 using the package APE for the consensus analyses.

### (c) Diversity analyses

For each network, we calculated four types of diversity analysis: species richness, functional diversity, phylogenetic diversity and evenness. Species richness was measured as the absolute number of bird species registered in each network. To measure evenness, we used the Pielou index (Pielou 1967), which allowed to determine how close the number of interactions of each species in the network was through the derivation of a Shannon-Wiener diversity index.

We utilised a distance-based framework to compute multidimensional functional diversity (Villéger et al. 2008), represented as functional dispersion (FDis). FDis measured the mean distance of individual species to the centroid of all species in the community, defined by a set of traits (Laliberté and Legendre 2010). This index was weighted by relative abundance, represented by the number of interactions of each species, reducing the effect of rare species with extreme trait values (Laliberté and Legendre 2010). To measure the FDis of fruit-eating bird assemblages, we used traits that influenced fruit consumption: beak length, width and height, wing length, body mass, frugivory level and migratory behaviour. To measure phylogenetic diversity of the bird assemblage in each area, we utilised the phylogenetic species evenness (PSE), which is a weighted version of the phylogenetic species variability. This metric summarised the degree to which species in a community were phylogenetically related, balanced to abundance (Helmus et al. 2007). All diversity analyses were carried out with R 3.1.2 using the packages FD and PICANTE.

### (d) Network analyses

The connectances were measured as the realised proportion of possible links in the network. The values can range from zero (network with any link) to one (fully connected network). To obtain the nestedness, we utilised WNODF (Almeida-Neto and Ulrich 2011), an algorithm that quantified nestedness in weighted networks based on overlap and decreasing fill. The default values of WNODF range from 0 for non-nested to 100 for fully nested, but, to fit the values to the statistical analyses, they were divided by 100. To obtain the modularity in the networks, we used the algorithm QuanBiMo (Dormann and Strauss 2014). This algorithm detected the presence of modules in weighted bipartite networks based on a hierarchical representation of species link weights and optimal allocation to modules (Dormann and Strauss 2014). As the results of modularity Q are stochastic, they may have slight variations in each run. We ran the algorithm 10 times independently (with $10^8$ swaps) and used the maximum value. The modularity Q can range from 0 (a random number of links between species within a module) to 1 (maximum degree of modularity). Finally, specialisation at the network level was measured with the H’2 algorithm, which is mathematically related and derived from Shannon entropy (Blüthgen et al. 2006). This index was based on a comparison between the observed frequency distribution of interactions and the expected probability distribution, assuming all species interacted in proportion to their frequencies (Blüthgen et al. 2007). H’2 can range between 0 and 1 for extreme generalisation and specialisation, respectively.

At the species level, we utilised two metrics to describe each species in each network: specialisation and species strengths. These metrics were chosen as they represent different aspects of species roles in the network, one based on with whom the interaction occurs and other on the number of interactions. To measure specialisation at the species level, we utilised the d’ index (Blüthgen et al. 2006), which determined that opportunistic species used all niches in the same proportion as their availability, and specialist species used rare resources disproportionately more. The d’ ranged from 0 (perfect opportunist) to 1 (disproportionate specialist). The species strengths were measured as the sum of all the dependencies of plant species in relation to a bird species (Vázquez et al. 2005). All network analyses were carried out with R 3.1.2 using the package Bipartite.

### (e) Statistical analyses

We used β regression models to analyse the effect of each diversity index on the network metrics using the betareg R package. As our response variable values were continuous and ranged from 0 to 1, the β regression was the most appropriate method. As predictor variables, we used species richness, evenness, FDis and PSE. As response variables, we used connectance, nestedness, modularity and specialisation. For each of the response variables, we ran the models separately. We compared models with all possible combinations of predictors, including a null model (a model containing only the intercept), according to Akaike’s Information Criteria corrected for small sample sizes (Bolker et al. 2009).

To assess which bird traits most influenced species roles in the networks, we utilised a generalised linear mixed model (GLMM). As fixed factors, we included body mass, gape width, wing length, frugivory level and migratory behaviour and, as a random factor, we included the network where the species was recorded. For response variables, we used specialisation (d’) and species strength, and the model was run separately for each. We calculated models for all possible combinations of predictor variables, including a null model. Models were compared according to Akaike’s information criterion.

## 3. Results

In all ten bird-plant networks, 87 bird species (17.4 + 11.3 per network) and around 150 plant species (19.8 + 7.76 per network) were registered, connected by 3400 interactions spread through 170 links. The Passeriformes represented 82% (n=71) of the bird species consuming fruits and accounted for 92.5% (n=3145) of the feeding records. Among the morphology of studied birds, most species (85%, n=74) weighed less than 100 g and 82.8% (n=72) had a gape width smaller than 10 mm. Among the behaviours, 42.5% (n=26) of the bird species were partial frugivores and 64% (n=55) were resident.

Regarding the association among diversity indices and network level metrics (Table 1), modularity was best explained by the model containing only the functional diversity of bird species (AICcw=0.420), with the more functionally diverse networks tending to be more modular (figure 1). The variable connectance was also best explained by functional diversity (AICcw=0.370), despite that the model containing species richness also had a high explanatory power

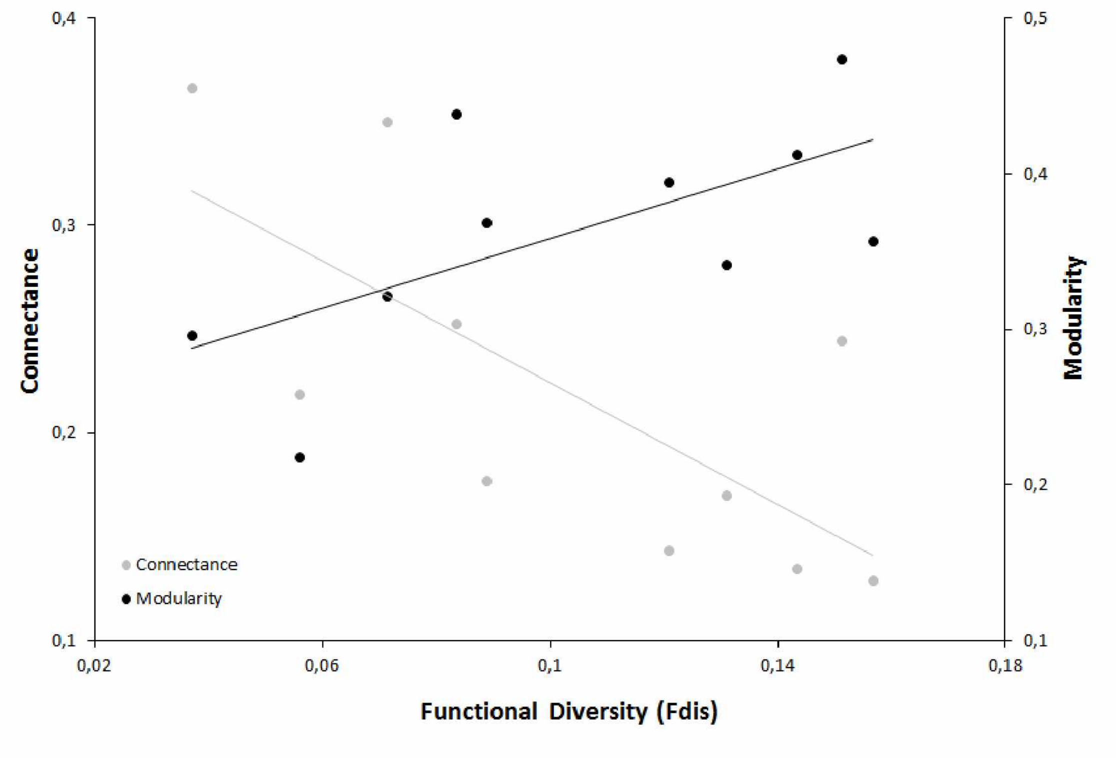
(AICcw=0.345). However, in contrast to modularity, connectance was negatively related to the predictor variables (figure 1). Nestedness and specialisation performed better with the model including only the intercept than with any model containing diversity indices.

Among the influence of birds' morphological and behavioural traits on the role that each species played on the bird-plant networks (table 2), specialisation (d') was better explained by the model containing only gape width (AICcw=0.416), which was present in all models that better fit the relationship between the variables. In this way, the bird species with larger gape widths tended to be more specialised than species with narrow gapes (figure 2a).

**Table 1.** Comparison of different statistical models generated by β regression explaining the influence of different diversity indexes (specie richness, evenness, functional and phylogenetic diversity) on network metrics. To each response variable were ran models with all possible combinations variables, including the null model (intercept). Here are just models with ΔAICc≤ 2.

| Model | AICc | ΔAICc | AICc weight |
|---|---|---|---|
| **Connectance** | | | |
| Functional | -21.0 | 0.0 | 0.370 |
| Richness | -20.9 | 0.1 | 0.345 |
| Phylogenetic | -19.5 | 1.6 | 0.169 |
| **Nestedness** | | | |
| Intercept | -20.6 | 0.0 | 0.614 |
| **Modularity** | | | |
| Functional | -19.8 | 0.0 | 0.420 |
| Intercept | -18.8 | 1.0 | 0.251 |
| Richness | -17.8 | 2.0 | 0.154 |
| **Specialization** | | | |
| Intercept | -2.0 | 0.0 | 0.597 |

**Fig. 1.** Relationships between functional diversity (Fdis) and network metrics (connectance and modularity) in 10 plant-frugivore networks.

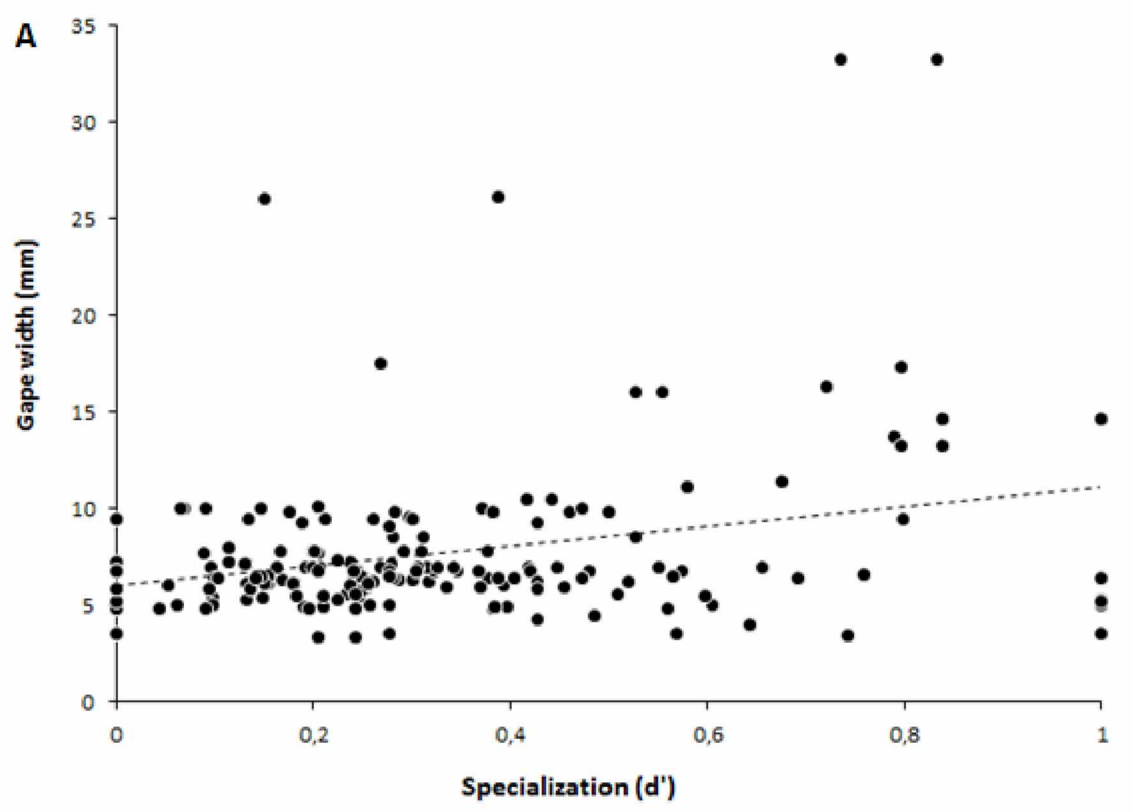


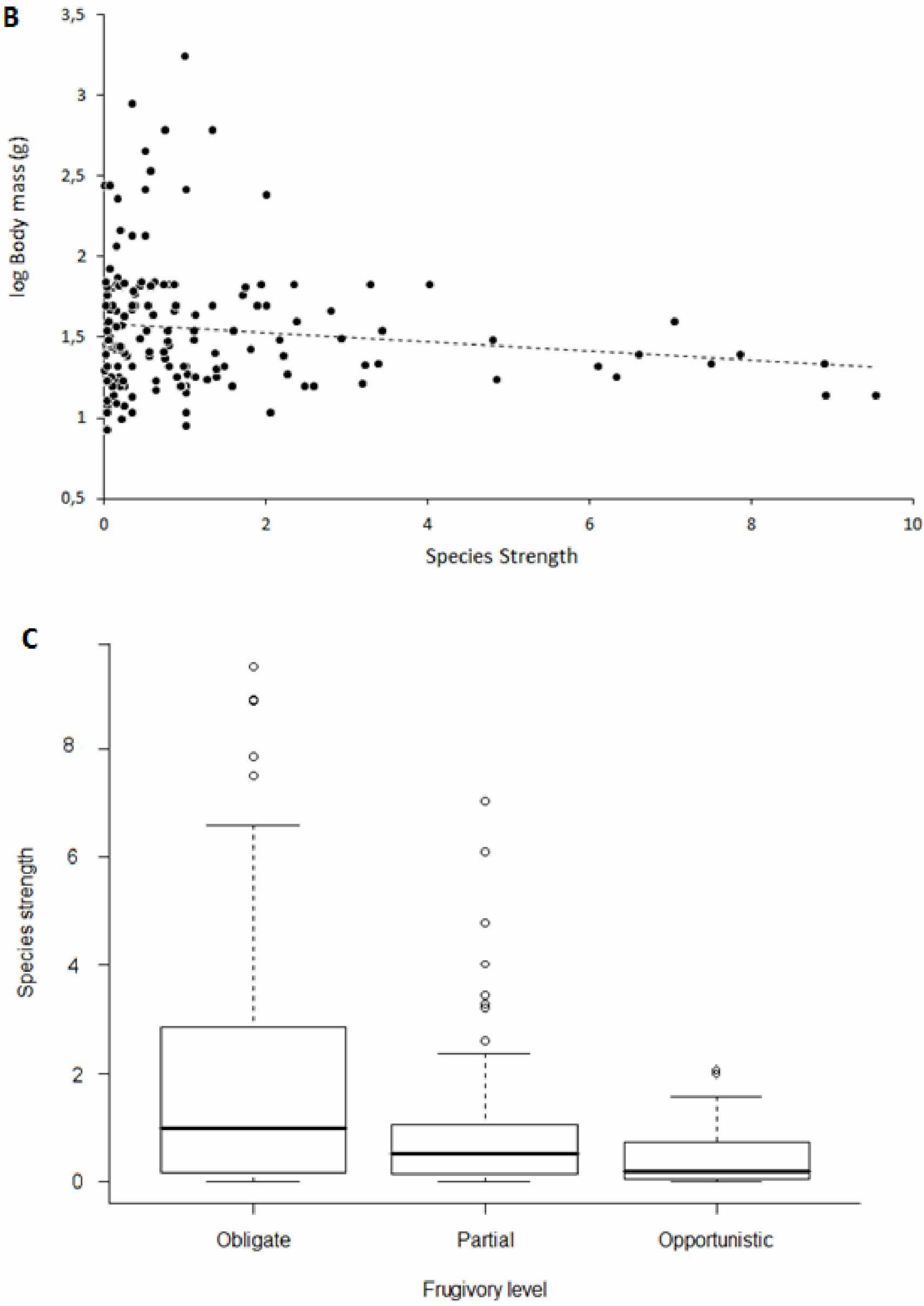
Species strength was better explained by the model that included frugivory level and body mass (AICcw=0.281), as frugivory level was present in the best models. Body mass was negatively related to species strength (figure 2b), and the obligate frugivores had a higher species strength than partial and opportunistic frugivores (figure 2c), as the small bodied and most fruit dependent species were more relevant in the network.

**Table 2.**Comparison of different statistical models generated by Generalized Linear Mixed Model explaining the influence of birds traits on specialization and species strength. To each response variable were ran models with all possible combinations of predictor variables, including the null model (intercept). Here are just models with ΔAICc$\leq$ 2.

| Model | AICc | ΔAICc | AICcweight |
|---|---|---|---|
| **Specialization d’** | | | |
| Gape | -19.0 | 0.00 | 0.416 |
| Gape + migratory | -17.4 | 1.59 | 0.188 |
| Gape + mass | -17.3 | 1.71 | 0.177 |
| **Species strength** | | | |
| Frugivory level + mass | 687.7 | 0.00 | 0.281 |
| Frugivory level + mass + migratory | 688.7 | 1.04 | 0.167 |
| Frugivory level + gape | 689.1 | 1.41 | 0.139 |
| Frugivory level | 689.5 | 1.83 | 0.113 |

**Fig. 2.** Relationship between species level metrics and birds traits included in the best predictor models. **A:** gape width (in mm) and specialization (d’); **B:** body mass (in g) and species strength; **C:** Boxplot of species strength of obligated, partial and opportunistic frugivores.





## 4. Discussion

### (a) Diversity indices on network architecture

The contribution of diversity indices to networks metrics supported the proposed hypothesis that bird functional diversity is the best diversity predictor for network metrics, as the models formed by this variable best explained the variance in connectance and modularity. On the other hand, nestedness and specialisation did not respond to any diversity index. In plant-pollinator networks analyses, (Chamberlain et al. 2014) found that functional and phylogenetic diversity of plants was associated with increased nestedness, but no animal diversity pattern influenced in network structure. Also, in plant-pollinator networks, complementary specialisation did not change in response to plant diversity (Fründ et al. 2010).

Analyses in simulated networks found that modularity was very enhanced by trait complementarity and the increase of this variable decreased connectance (Minoarivelo and Hui 2016). This theoretical result was in agreement with ours, since vast diversity of traits in the community may promoted trait complementarity between partners (Blüthgen and Klein 2011). Although we did not have access to plant traits to perform analyses of trait complementarity with their bird partners, empirical networks have shown that complementarity is recurrent in plant-pollinators (Maglianesi et al. 2014) and plant-frugivore networks (Herrera and Pellmyr 2002). Moreover, trait matching between fruit size and beak gape is determinant in the composition and structure of frugivory by birds (Eklöf et al. 2013).

The negative correlation between connectance and number of species in the network is well known; in large networks, there are fewer mean links per species (Vazquez et al. 2009). Despite the fact that the model containing only bird species richness had a good fit, the model with functional diversity explained the connectance variance better. Just the increase of species richness may lead to a higher interaction redundancy due to the presence of species with a very similar trait set (Blüthgen and Klein 2011). On the other hand, the increase in the range of traits led to a higher number of mismatching interactions, which reduced the number of realised links between potential partners, generating fewer connected networks (Olesen et al. 2010).

The presence of modules in a mutualistic network is a recurrent pattern in distinct types of interaction networks (Olesen et al. 2007; Krasnov et al. 2012; Schleuning et al. 2014). Module formation is associated with the functional traits of the species (Maruyama et al. 2014), since species within the same module tend to have similar traits (Minoarivelo and Hui 2016). Nonetheless, modules can also keep closely related species in separate modules to avoid competition and maintain their coexistence (Silva et al. 2016). Thus, a higher variety of traits in the community contributes to generating a higher number of functional groups (Dupont and Olesen 2009), increasing the modular structure of the network.

Trait diversity is known to enhance the maintenance of biodiversity and ecosystem functions (Cardinale et al. 2012). Modularity is also positive for conservation because it is expected to promote community stability, as it minimises the spread of perturbations through the network (Tylianakis et al. 2010; Stouffer and Bascompte 2011). However, connectance, which is negatively related to trait diversity and modularity, also has a positive effect on the stability of the network (Dunne et al. 2002; Thebault and Fontaine 2010; Heleno et al. 2012). Conservation ecologists are interested in preserving the characteristics that promote system stability in ecological networks (Tylianakis et al. 2010); however, determining the important parameters that respond in antagonism make biodiversity conservation a very complex challenge.

### (b) Bird traits on species roles

The relationship between bird traits and species level metrics supported the hypothesis that gape width and frugivory level were the trait variables that best explained the variation in specialisation and species strength, respectively. The importance of specific traits in species roles is more common in communities with an unevenness trait distribution (Saavedra et al. 2014). In communities with trait-similar species, no trait was more relevant to explain species roles (Silva et al. 2016).

Gape width can be an essential factor in fruit choice (Lord 2004), being large-gaped bird able to ingest larger fruits that cannot be eaten by narrow-gaped birds (Wheelwright 1985). The concept of complementary specialisation considers a specialist species that interacts with partners that most other species do not (Blüthgen et al. 2006). In this way, larger the gape, wider the possibility of consuming fruits that are not consumed by other species, increasing the possibility of interacting with rarely visited partners, resulting in higher complementary specialisation.

As obligate frugivorous birds relied mostly on fruits, they needed to feed on a higher number of plant species and realise several feeding events to supply their nutritional needs (Fleming and Kress 2011), making the relevance of frugivorous birds across all partners closely related to their dependence on fruits. Our results corroborated with (Schleuning et al. 2011), who also found a higher species strength in obligate frugivorous birds. The frugivory level also influenced other species level parameters of birds, as obligate and partial frugivorous birds presented within and among-module connectivity values higher than opportunistic ones (Schleuning et al. 2014). The frugivory level also was relevant when explaining the position of birds and bats within frugivore-plant networks (Mello et al. 2015). In the tropics, a large part of angiosperm species produce fleshy fruits (Howe and Smallwood 1982; Fleming and Kress 2011), allowing a year-round offer of resources that maintains several birds that rely mostly on fruits (Snow 1981). In this situation, obligate and partial frugivores are very important to seed dispersal in tropical regions (Kissling et al. 2009); however, in tropical seasonal regions, like savannas, where highly frugivorous species are mostly absent, partial and opportunistic species can also play important roles in seed dispersal (Silva and Melo 2013).

We found a negative relation between body mass and species strength, but the tendency of small-bodied species to have a higher influence over their partners possibly happened not due to the influence of body mass over feeding behaviour, but due to their high abundance. Large frugivorous birds naturally occurred at low densities (Peres and Palacios 2007) and were very sensible to habitat alteration, being the most susceptible group to local extinction after a disturbance (Markl et al. 2012). In altered sites, the large-bodied frugivores were extinct or occurred in low densities, being functionally extinct (Galetti et al. 2013). As abundance had a great influence on the number of feeding events of a species (Vázquez et al.

2005), species more resistant to habitat alterations, mostly small and medium-bodied (Gomes et al. 2008), occurred in higher abundance, being more likely to impact the seed dispersion of the plant community. In this way, the model that contained frugivory level and body mass predicted that small-bodied obligate frugivores had higher species strength due to their higher need of fruit sources and their higher abundance.

Results partially corroborated our initial hypothesis that functional diversity of birds had a greater influence on the architecture of plant-frugivore networks than other diversity metrics. We also detected that specific bird traits, such as gape width and the dependence on fruits, were very important in mediating the function of bird species within the network. Further studies involving the importance of plant traits will be important to increase the knowledge about the relationship of diversity and network structure in plant-frugivore bird networks.

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# Anexo I

**Table S1.** Information’s about the plant-frugivores birds networks considered in the analyses.

| Site | Data collection | Bird species | Plant species | Coordinates | Reference |
|---|---|---|---|---|---|
| 1 | Fecal sample | 12 | 22 | 18°29’S;<br>48°23’W | Own data |
| 2 | Fecal sample | 4 | 17 | 18°57’S;<br>48°12’W | Own data |
| 3 | Fecal sample | 8 | 16 | 19º14’S;<br>47º08’W | Own data |
| 4 | Fecal sample | 4 | 12 | 18º51’S;<br>48º13’W | Own data |
| 5 | Direct Obs. | 18 | 27 | 12°56’S;<br>38°24’W | Andrade et al. 2011 |
| 6 | Direct Obs. | 9 | 10 | 12º59’S;<br>41º20’W | Faustino & Machado 2006 |
| 7 | Direct Obs. | 29 | 25 | 20º45’S;<br>42º52’W | Fadini & Marco Jr 2004 |
| 8 | Direct Obs. | 31 | 13 | 22º29’S;<br>47º36’W | Athiê & Dias 2012 |
| 9 | Direct Obs. | 30 | 21 | 18°59’S;<br>48°18’W | Silva & Pedroni 2014 |
| 10 | Direct Obs. | 29 | 35 | 22°49’S;<br>47°06’W | Galetti & Pizo 1996 |

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# Capítulo III

## HABITAT AND DIETARY SPECIALIZED BIRDS ARE THE MAIN SEED DISPERSERS IN FOREST UNDERSTORY

## PRINCIPAIS DISPERSORES DE SEMENTES EM SUB-BOSQUE SÃO AVES COM HABITAT E DIETA ESPECIALIZADOS

Formatação de acordo com o periódico: Biodiversity and Conservation

## Abstract

Each species in a plant-bird seed dispersal network plays different roles in network structure, the bird species being more topologically important, but not necessarily the most resistant to habitat disturbance. As a result, we aim to identify the extinction proneness traits that most effect the centrality metrics and determine the complementary specialization in the networks. We utilized four plant-bird networks from understory forest fragments in the Brazilian Cerrado, and for each species we applied three metrics: normalized degree, closeness centrality and betweenness centrality. Using a PCA analyses we unified all indices as the first principal component (PC1) and measure the extinction proneness traits (frugivory level, forest dependence and disturbance sensibility) with a GLM to best explain the variance in PC1. We also measure the complementary specialization in seed dispersal services on the four networks. The model containing frugivory level and forest dependence clearly explains the variance in PC1 (AICcw= 0.938). Three networks presented high specialization and low redundancy. In the understory of forest fragments in Cerrado, obligate frugivores and forest dependent species are the main seed dispersers, but ecologically specialized species tend to be more vulnerable to alterations in the environment. The seed dispersal services in these habitats are also very dependent on dispersal agent diversity, presenting a low redundancy, as the seed dispersal is dependent on species with low ecologically equivalent pairs.

**Key words:** Brazilian Cerrado, extinction proneness, centrality, frugivory, mutualistic networks.

## Resumo

Cada espécie em uma rede de interação desempenha papéis diferentes na estrutura da rede, sendo que as aves mais topologicamente importantes, não necessariamente são as mais resistentes a distúrbios. Os objetivos foram determinar os atributos de propensão à extinção que mais influencia na centralidade e determinar a especialização complementar nas redes. Foram utilizados quatro redes de frugivoria entre planta-avesno sub-bosque de fragmentos florestais no Cerrado. Para cada espécie foram aplicadas três métricas: grau normalizado, centralidade de proximidade e centralidade por intermédio. Através de análises de PCA, foram unificados todos os índices como o primeiro componente principal (PC1) e foi medido com um GLM, os atributos de extinção propensão (nívelde frugivoria, dependência de floresta e sensibilidade à perturbação) melhor explicam a variação no PC1. Também medimos a especialização complementares nas quatro redes. O modelo contendo nível de frugivoria e dependência de floresta melhor explicou a variação de PC1 (AICcw = 0,938). Três redes apresentaram alta especialização e baixa redundância. No sub-bosque de florestas no Cerrado, frugívoros obrigatórios e dependentes de florestas são os principais dispersores de sementes, mas espécies ecologicamente especializadas tendem a ser mais vulneráveis a alterações no ambiente. O serviço de dispersão de sementes é dependente da diversidade de agentes dispersores, apresentando baixa redundância, sendo a dispersão de sementes dependente de espécies pares equivalentes ecológicos.

**Palavras-chave:** Cerrado brasileiro, centralidade, frugivoria, redes mutualísticas, propensão à extinção.

## INTRODUCTION

The interactions between plants and animals in an ecological community can be interpreted as a complex network pattern where several species interact to obtain benefits (Bascompte and Jordano 2007). In the last decade, network theory has been a useful tool to visualize the complexity of mutualistic interactions (Heleno et al. 2014), examine their structure, test hypotheses (Bascompte and Jordano 2014) and distinguish the role that each species plays in the community (Dormann 2011). Among the mutualistic plant-animal interactions, frugivory and seed dispersal by animals are essential processes in the life cycle of several plant groups (Wang and Smith 2002) and thus for the maintenance of vegetation and animal diversity (Fleming 2005), especially in tropical ecosystems, where a large proportion of angiosperm produce fleshy fruits (Kissling et al. 2009). Within the bird phylogeny, consumption of flesh fruit is widespread, having evolved independently several times (Fleming and Kress 2013). Due to its high species diversity and wide morphological range, birds are the most important vectors in zoochoric seed dispersal (Fleming et al. 1987; Fleming and Kress 2013).

Highly redundant seed dispersal communities are more stable under species extinction scenarios due to the presence of more species that are functionally similar, providing the same ecological service (Hooper et al. 2005), but some habitat disturbances may reduce the functional trait pool of dispersal agents, meaning that this ecological service depends on an impoverished subset of dispersal vectors (Flynn et al. 2009; Albrecht et al. 2013). Since the extinction proneness of a bird species is mediated by their response traits (Luck et al. 2012), the fruit-eating avifauna composition in a certain area is not randomly determined, because historical factors and anthropogenic disturbance pressures select the species that are currently present (Gray et al. 2007; Gomes et al. 2008). Birds species that are highly dependent on fruit or have a large body mass tend to be functionally extinct in degraded areas (Sekercioğlu et al. 2004; Galetti et al. 2013) or in highly seasonal regions (Silva and Melo 2013). Species with important habitat requirements, or more susceptible to habitat alterations, also tend to be locally extinct in degraded habitats (Purvis et al. 2000). In the absence of these species, seed dispersal becomes dependent on opportunistic and small size fruit-eating birds (Markl et al. 2012), which may have a long-term and strong effect on vegetation structure and composition (Silva and Tabarelli 2000).

Seed dispersal interactions in species-rich environments usually involve several birds species, each one with different functions and contributions to the structure of interaction network (Moran et al. 2004; Jordano et al. 2007).The network structure of mutualistic interactions is asymmetric, which can be demonstrated by recurrent patterns, such as nestedness and modularity (Bascompte et al. 2003; Bascompte and Jordano 2007; Olesen et al. 2007; Fortuna et al. 2010). These patterns emerge due to the heterogeneous contribution of each species to the network, resulting in a combination of generalists (species that interact with a great part of the available partners and tend to have little effect on the dynamic of the whole network and over their partners) and specialist species (species that interact with few of the available partners and have little effect on the whole network). Although the overall properties of a mutualistic network tend to remain spatially and temporally constant (Plein et al. 2013), factors such as local abundance variation, trait distribution or environmental effect lead to temporal and spatial changes in the relative importance of each species to the network (Poisot et al. 2015).

Theoretical and empirical studies have shown that species more important to network structure and cohesion are not necessarily the most able to resist extinction (Loreau et al. 2001; Amatuzzi 2009; Saavedra et al. 2011; Vidal et al. 2014). The loss of functionally important species has a disproportional effect on a community (Carlo et al. 2007), which arouses great conservationist interest in determining the relative importance of a species to the network structure (Memmott et al. 2007; Tylianakis et al. 2010). Factors such as diet (Mello et al. 2015) or morphological traits (Silva & Melo in press) may indicate species that are more prone to playing certain roles in a network. Identifying these species is a great challenge, however, because their relative topological importance can be interpreted in different ways. One way is through the number of partners or through centrality indices (Martín González et al. 2010), which can be used to measure the relative importance of each node, determining those with the potential to affect more species and of greater importance in the cohesion of the network (Freeman 1979; Martín González et al. 2010).

As the bird species that contribute more to seed dispersal services are not necessarily the most persistent in the habitat, we aim to identify the bird traits that influence extinction proneness, and are related to bird species roles in the network topology. To do this we studied the plant-frugivore bird interactions network in the understory of forest areas in the Brazilian Cerrado and test two hypotheses: (1) birds species that are strongly dependent on fruits are the most important to the structure of the networks studied, since dietary specialization is an determinant factor in seed dispersal interactions (Moran and Catterall 2010; Mello et al. 2015); (2) The networks analyzed are highly redundant, the overall pattern of the network being less specialized than expected due the high overlap and resource sharing of frugivore birds in Cerrado (Silva and Melo 2013).

## METHODS

### Study site and dataset

Our dataset is comprised of plant-frugivore birds networks in the understories of four semi-deciduous forests in Central Brazil (Table 1), that are similar in phytophysiognomy and in potential avifauna composition. Although the Cerrado Biome is mostly highly seasonal (Gottsberger and Silberbauer-Gottsberger 2006), in forest understory there is fruit available all year around (Melo et al. 2013). We conducted captures of birds using mist nets spread along trails. In each area between 18 to 24 mist nets (12m x 3m, 32mm mesh) were set up, which were opened at sunrise and closed near sunset. The captures occurred over four or five day campaigns, with four campaigns per area (with 4-month intervals in the same area), between January 2013 and February 2014. The capture sampling effort conducted in each area was similar in order to minimize biases in the data collection. Each bird captured in the mist nets was identified to the species level (following Remsen et al. 2015), individually marked, and then fecal samples were collected from the fruit-eating birds.

In laboratory, the samples were analyzed in stereomicroscope, and the seeds found were considered evidence of a seed-dispersal interaction. Four weighted matrices were generated, one for each area. The rows and lines were filled with the plants and animals species and cells filled with interactions. We used frequency of occurrence, the number of fecal samples of birdi with seeds of plantj as the quantitative factor in the network. We could not identify the species of each seed, but we separated them into morphospecies, what did not analytically interfere in network analyses.

**Table 1.**Characterization of the four study networks of plant-frugivore bird interactions in the understory of semi-deciduous forest in the Brazilian Cerrado.

| **Network** | **Bird species** | **Plant species** | **Latitude (S)** | **Longitude (W)** | **Area (ha)** | **Altitude** |
|---|---|---|---|---|---|---|
| Galheiro | 12 | 22 | 18°29’ | 48°23’ | 120 | 880 |
| Água Fria | 4 | 17 | 18°57’ | 48°12’ | 200 | 670 |
| Glória | 8 | 16 | 19°14’ | 47°08’ | 30 | 910 |
| São José | 4 | 12 | 18°51’ | 48°13’ | 20 | 890 |

### Bird extinction proneness traits

All the fruit-eating birds registered in the networks were classified according to traits that may influence the endurance of a species in the environment: degree of frugivory, dependence on forest environment and sensibility to habitat disturbance. Although body mass is an important factor in species endurance (Vidal et al. 2013), most of the bird species in our dataset were small or medium-size passerines, so this trait was not taken in consideration. Demographic factors are also very important to extinction proneness, but they were not considered, as it is not intrinsic to the species, but to each population (Bennett and Owens 1997).

The degree of frugivory describes the importance of fruits in the diet of a species, and species with a wider diet are more prone to under changing condition (Clavel et al. 2011). The species were classified as obligate frugivores, for whom fruits are the main component in the diet; partial frugivores, species that utilize several types of resources in the diet; and opportunistic frugivores, that consumed fruits only as a complementary diet (according to del Hoyo et al. 2015; Sick 1997). Our dataset involved interactions in the understory, but not all the bird species that forage in this layer are totally dependent on forest habitats. We classified the bird species as forest-dependent, a species that breeds and obtains most of its resources in forests and are not able to persist in other kinds of habits; and forest-semi-dependent, species that make some opportunistic visits to the understory to obtain resources, but are able to survive in non-forest habits (according to Silva 1995). In relation to sensibility to habitat disturbance, we classified species as low-sensitive, a species that is slightly affected by disturbance in the habitat; and medium-sensitive, a species that resists minor disturbance, but doesn’t persist in places that are greatly disturbed (according to Stotz et al. 1996).

**Network analyses**

To describe the role that each species plays in the topology of the networks studied we utilized three species level metrics: normalized degree (ND), closeness centrality (CC) and betweenness centrality (BC). NDs were obtained by dividing the degree (number of interacting partners – i.e. plant species dispersed by each bird species) by the number of plant species in the networks, thus ranging from 0 to 1. The CC measures how close a species is to all other specie:

$$CC_i = \sum_{j=1;i\neq j}^{n} \frac{d_{ij}}{n-1}$$

n being the number of species in the network, and $dij$ the shortest distance between species $i$ and $j$ measured in the number of connections (Martín González et al. 2010). When a frugivore species feeds on plants that are largely consumed by the other species in a network, it will have a high closeness centrality, and when the frugivore feeds on more exclusive plant species, it will have a low closeness centrality (Mello et al. 2015). The BC measures the fraction of the shortest paths between all pairs of species in the network which pass through the focal species:

$$BC_i = 2 \sum_{j<k;i\neq j} \frac{g_{jk}(i)/g_{jk}}{(n-1)(n-2)}$$

n being the number of species in the network, $gjk$ the number of shortest paths linking any two species, and $gjk(i)$ the number of the shortest paths among $gjk$, that pass through I (Martín González et al. 2010). A frugivore species with high betweenness centrality is a connector in the guilds within the mutualistic network (Mello et al. 2015).

We used the H2’ metric to detect complementarity patterns in the networks (Blüthgen et al. 2006), which measures the degree of redundancy and complementarity in the network (Blüthgen and Klein 2011). This metric compares the frequency distribution of interactions with a neutral expected probability distribution across the entire community, quantifying the overlap in frugivore species among plant species and vice-versa (Blüthgen et al. 2006). To test the significance, we compared the observed values of each network with 1000 null models generated with the Patefield algorithm (r2d; Patefield 1981), which uses fixed marginal totals to distribute the interactions and produce a set of networks where all species are randomly associated (Blüthgen et al. 2008). Network metrics were carried out with R 3.1.2 and package Bipartite (Dormann et al. 2009).

### Statistical analyses

As centrality metrics are usually strongly correlated in complex networks (Wuchty and Stadler 2003; Martín González et al. 2010), we performed a principal component analysis (PCA) on the three metrics, ND, CC and BC, seeking to synthesize a one-dimensional index of the topological importance of each node. We submitted all variables to a box-cox transformation to correct each variable for skewness, center and scale (Cox and Box 1964). The values of Principal Component 1 (PC1) were then utilized as a unified topological metric, since it retained most of the information of the centrality measure (Estrada 2007; Sazima et al. 2010).

To determine which bird resistance traits most effect species level metrics, we used a generalized linear model (GLM). We included frugivory level, dependence on forest habitats and sensibility to habitat disturbance as predictor variables. We used PC1 scores as response variables. We calculated linear models for all possible combinations of predictor variables, including a null model. Models were compared according to Akaike's information criterion, corrected for small sample sizes (Bolker et al. 2009). Statistical analyses were carried out with R 3.1.2, using the lme4 package for linear regression, MuMIn for model testing and caret for data transformation.

## RESULTS

The four networks registered a total of 16 bird species (7+3.83 per network), 16.75+4.11 plant species per network, and 261 interactions (Fig. 1). Frugivory levels of the registered birds comprised four obligate frugivores, nine partial and three opportunistic. Ten species were forest dependent, five semi-dependent and only one was independent. The family with most species registered (n=6) was Thraupidae, followed by Pipridae and Turdidade (n=3), however, Pipridae was the bird family with more interactions recorded (n=111), followed by Tyrannidae (n=41). The Band-tailed Manakin (*Pipra fasciicauda*) and Helmeted Manakin (*Antilophia galeata*) were the bird species more important to the network topology (PC1= 4.068 and 3.339, respectively; Fig. 2) and both are obligate frugivores, dependent on forest environments and medium-sensible to habitat disturbance. The Helmeted Manakin had the highest species degree in three networks (75%) and were responsible for 42.5% (n=111) of the total interactions recorded.

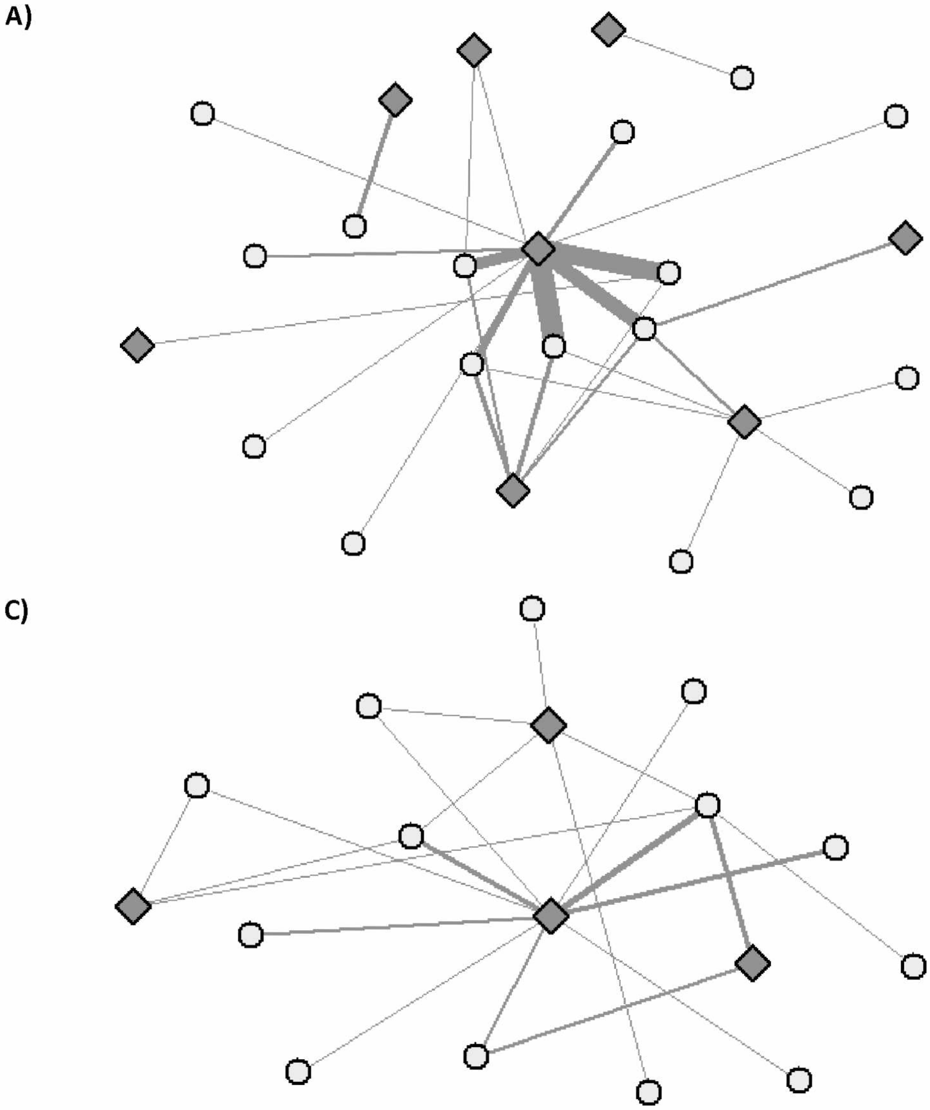
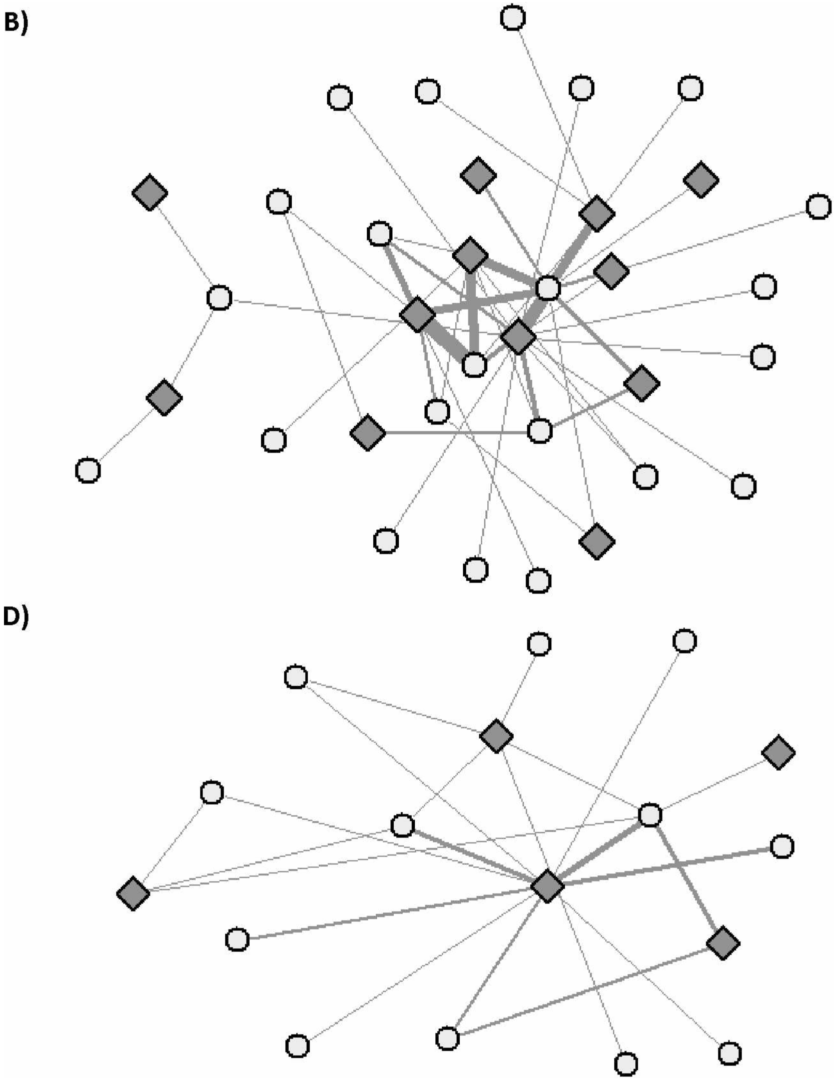


**Figure 1.** Graph representation of the four networks from forest and circles represent plants. **A)** Glória; **B)** Galheiro; **C)** Água Fri



understory in the Brazilian Cerrado. Diamonds represent birds
a; **D)** São José.

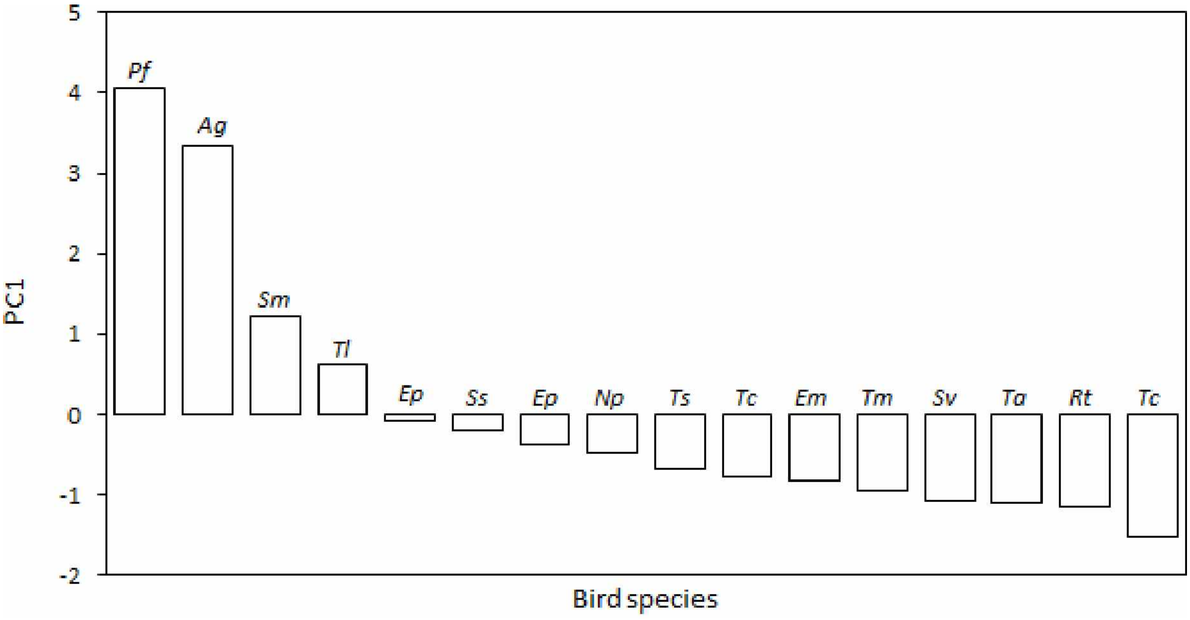
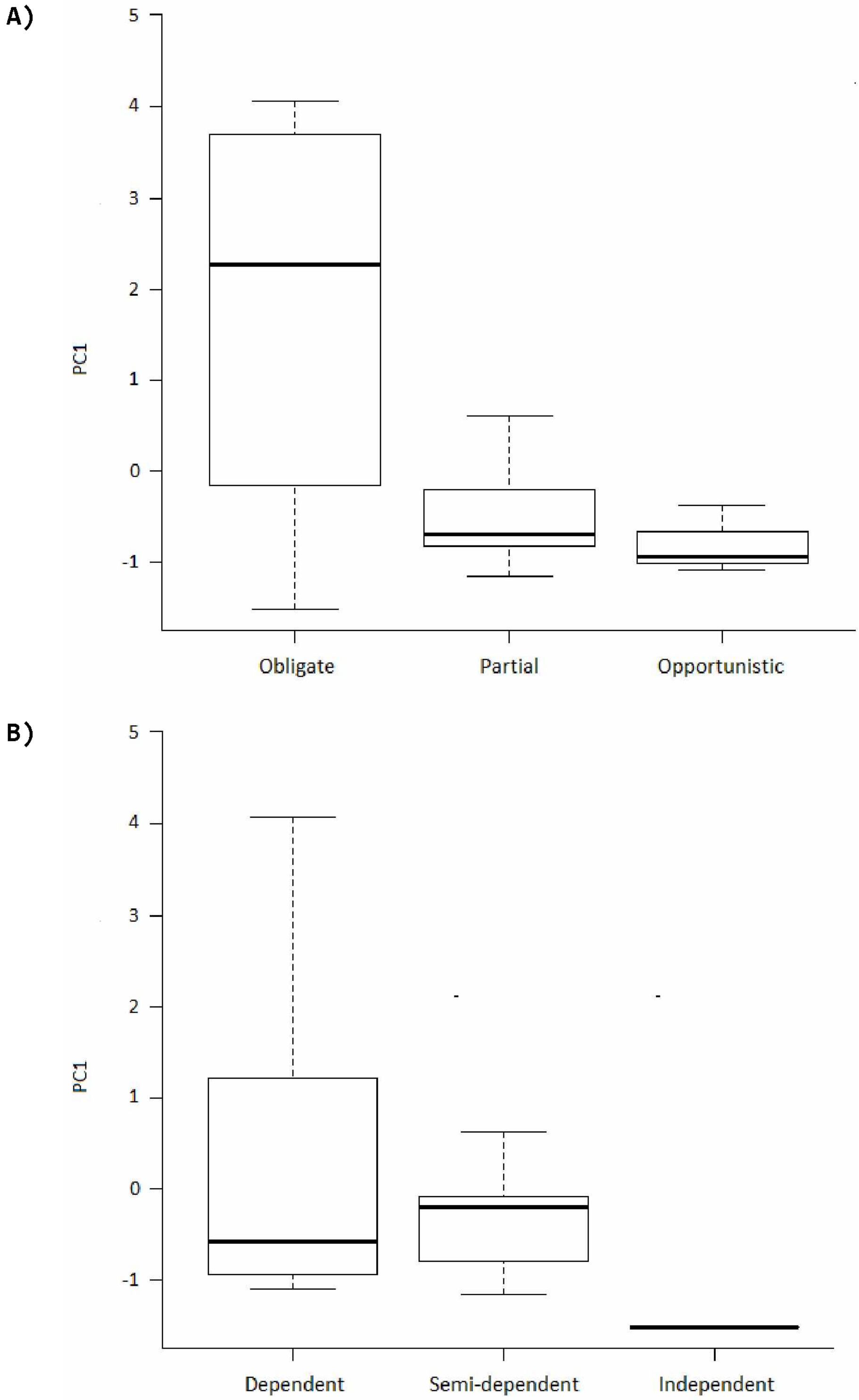


**Figure 2.** Unified centrality index (PC1) of bird species registered in the four plant-frugivores bird networks in the Brazilian Cerrado. *Pp = Pipra fasciicauda; Ag = Antilophia galeata, Sm = Saltator maximus; Tl = Turdus leucomelas; Ep = Elaenia parvirostris; Ss = Saltator similis; Ep = Eucometis penicillata; Np = Neopelma pallescens; Ts = Turdus subalaris; Tc = Tachyphonus coronatus; Em = Elaenia mesoleuca; Tm = Trichothraupis melanops; Sv = Schiffornis virescens; Ta = Turdus albicollis; Rt = Ramphastos toco; Tc = Tangara cayana.*

The first component of the PCA explained 86% of the variance in the centrality metrics, so it was used as the centrality metrics index (PC1). This unified index was clearly explained by the model containing frugivory level and forest dependence (AICc= 0.00; AICcw= 0.938), the most topologically important to network structure being obligate frugivores and species dependent and semi-dependent on forest environments (Fig. 3). No other model with a combinations of predictor variables showed even minimum explanatory power (AICc ≤ 2). As opposed to our hypothesis, three networks (75%) were more complementarily specialized than randomly, and one was less specialized (Table 2), indicating a general low niche overlap and a certain degree of specialization for each species.



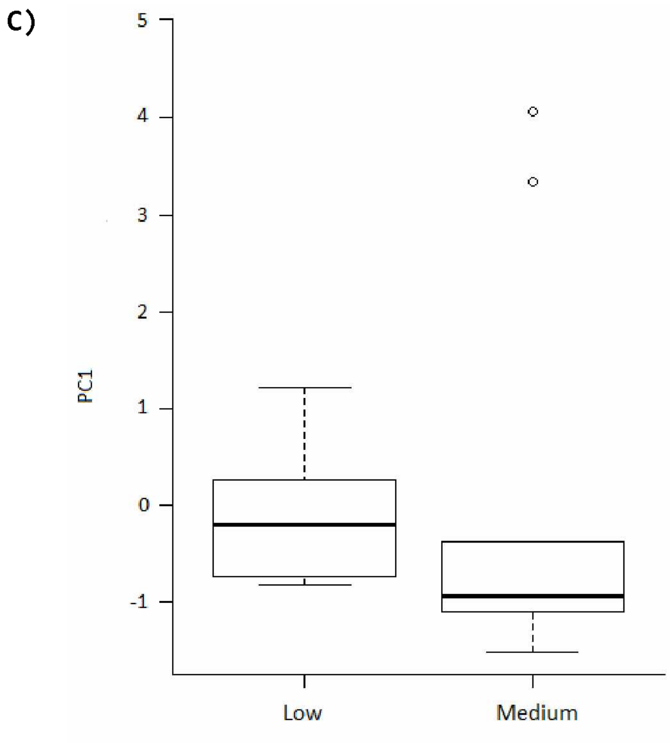


**Figure 3.** Boxplot of unified centrality index (PC1) of bird species registered in the four plant-frugivores birds networks in the Brazilian Cerrado according to extinction proneness traits. A) Frugivory level: dependent, semi-dependent and independent. B) Forest dependence: dependent, semi-dependent and independent; C) Habitat sensibility: low and medium.

## DISCUSSION

The seed dispersal service in forest environments in the Brazilian Cerrado relies on a reduced set of bird species, and the species more important to the network structure are highly dependent on fruits and not able to live in non-forest habitats. The centrality metrics were high correlated, enabling unification into a single component. The bird species highly central in our network are close to many other species and also stay between many pairs of species, a pattern also found in pollination (Martín González et al. 2010), clean (Sazima et al. 2010) and trophic networks (Estrada 2007).

Each bird species responds differently to threats, according to their response traits set (Luck et al. 2012). Anthropogenic environmental changes filter the species that are able to survive within modified habitats and lead to nearly or even extinction the species that cannot hold out (Smart et al. 2006).The species that are ecologically specialized should have greater fitness in stable habitats, and ecological generalists can be favored in changeable conditions (Kassen 2002; Marvier et al. 2004). As neotropical landscapes are in the majority under human-made disturbance, what remains are fragments with homogeneous bird communities ruled by generalist species (Devictor et al. 2008). The Brazilian Cerrado has faced an increase in land-use change in recent decades, resulting in several small to medium-size forest fragments surrounded by crops and pastures (Klink and Machado 2005). The frugivore avifauna in our system of study reflects the actual stage of Cerrado avifauna where the more sensitive species, as the large-bodied ones (Gomes et al. 2008; Vidal et al. 2013)are absent or functionally extinct. As a result, there is a lack of species that are able to disperse large seeds, which may lead to major alterations in plant composition (Silva and Tabarelli 2000). The two more important contributors to network structure, the Band-tailed Manakin and Helmeted Manakin, are Pipridae, a highly diverse taxon in tropical forest biomes such as the Amazon and Atlantic forest (Snow 2004), but with a small pool of species available in the study region. Even being responsible for a great portion of the seed dispersers in the understory of Cerrado forests, manakins don’t replace large-bodied and high mobile frugivores, since their diet relies mainly on small juicy fruits rich in carbohydrates (Moermond and Denslow 1985).

As the diet of obligate frugivores is predominantly flesh fruits, they usually consume a large range of fruit species to fulfill their nutritional requirements (Fleming and Kress 2013). Excluding the abundance effect, this is a major determinant of network properties (Vázquez et al. 2005; Vázquez et al. 2007; Krishna et al. 2008; Vázquez et al. 2009): from a network point of view, these frugivore birds interact with a large part of the available plant partners, tending to be more topologically important to a network structure. Their importance has been demonstrated by several network studies using different network metrics (Schleuning et al. 2011, 2014; Mello et al. 2015; Silva and Melo in press). Despite usually representing a minor proportion of the total avifauna in a community, obligate frugivores are especially important for the functional maintenance of frugivory rates, and their loss has disproportional effects on the seed dispersal service (Ferger et al. 2015). Species that are specialized in a single resource type tend to be less resistant to habitat alterations, since it is difficult for them to use alternative resources in changeable scenarios (Sodhi et al. 2004) and frugivore birds are more affected by anthropogenic habitat degradation than usual (Sekercioğlu et al. 2004; Gray et al. 2007).

The two more important contributors to network structure are highly restricted to the forest, feeding predominantly on understory fruits (Silva and Melo 2011; Marini 1992) and nesting in this layer (Marini 1992). Forest tree species often rely on forest frugivore assemblages for dispersal of their seeds, since non-forest birds don’t usually forage in the forest understory interior (personal observation), and frugivore birds depend on these fruits for supply their energetic needs (Lehouck et al. 2009). In general, frugivore birds that are dependent on forest environments are more likely to be made extinct after local habitat disturbance, or in small fragments of habitat, than species with fewer habitat requirements (Sekercioğlu et al. 2004; Kirika et al. 2008; Lehouck et al. 2009). For example, up to a quarter of the bird species associated with forest environments in the Brazilian Cerrado may be made extinct as a result of only the disturbance of surrounding areas (Machado 2000). Several factors, such as a preference for closed-canopy, more restrictive habitat requirements (Bennun et al. 1996) and limited mobility in open habitats (Lens et al. 2002) affect the persistence of bird species in disturbed or fragmented places.

Silva and Melo (2013) found that frugivory interactions in the cerrado sensu stricto, the savanna vegetation that prevails in the Brazilian Cerrado, are redundant and the frugivore assemblage is dominated by partial and opportunistic frugivores. High seasonality leads to a very irregular spatial distribution of fruits, which precludes the occurrence of species high dependent on fruits in this environment, but in forests of the same region, we found a frugivore assemblage comprised of species specialized in fruit eating, which are very dependent on this resource. While ecological redundancy may enhance ecosystem resilience (Walker 1995), communities with high complementary specialization tend to be functionally fragile, since some functions depend on one or a few species, without ecologically equivalent (Bluthgen and Klein 2011). These communities are very dependent on a high diversity of frugivore species to don’t generate gaps in ecosystem services (Loreau et al. 2001; Garcia and Martinez

2012). In this way, events that lead to a species local extinction, such as habitat disturbance and fragmentation (Marini and Garcia 2005), may have a strong impact on the seed dispersal process of a forest, since small and disturbed forest fragments support depauperate avifauna (Luck and Daily 2003).

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# Capítulo IV

## MODULARITY IN ECOLOGICAL NETWORKS BETWEEN FRUGIVOROUS BIRDS AND CONGENERIC PLANT SPECIES

MODULARIDADE EM REDES ECOLÓGICAS ENTRE AVES FRUGÍVORAS E PLANTAS CONGÊNERES

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## Abstract

Ecological and evolutionary factors influence the presence of modules in species interaction networks, and these modules usually cluster functional similar species. But whether closely related species form modules is still unknown. We tested whether the interaction networks formed by frugivorous birds and *Miconia* plants are modular and evaluated how modules were divided. To do so, we gathered from the literature data concerning four networks of *Miconia* and their frugivorous birds. We quantified modularity using binary and weighted algorithms and also tested the relationship between bird traits (body mass, dietary specialization, migratory behaviour and phylogeny) in relation to within- and among-module connectivity indices (c and z values). If considering only binary information, networks did not present distinct modular structure. Nevertheless, by including interaction strength, modules can be detected in all four *Miconia*-bird networks. None of the bird traits, however, was related with the connectivity indices. The possible fluctuation of frugivorous bird abundance coupled with the asynchronic fruiting period of *Miconia* might favour the formation of temporal modules comprising birds and plant species with phenological overlap, ensuring seed dispersal and facilitating the coexistence in sympatry. Bird traits had little effect on the role that each species plays within the modular network, probably because the frugivorous assemblages were dominated by small-bodied and opportunistic species.

**Key words:** frugivory, *Miconia*, mutualistic networks, QuanBiMo, seed dispersal.

## Resumo

Fatores ecológicos e evolutivos influenciam na presença de módulos em uma rede de interações. Apesar de módulos serem esperados em diferentes escalas hierárquicas, ainda carecem evidências de modularidade em redes planta-frugívoros. Nós testamos se redes formadas por aves frugívoras e plantas do gênero *Miconia* são modulares e como esses módulos são divididos. Pra isso, usamos quatro redes de interações com *Miconia* e aves frugívoras. Nós quantificamos a modularidade com algoritmos binários e ponderados e testamos a relação entre atributos das aves (massa corporal, grau de frugivoria, comportamento migratório e família) e os índices de conectividades dentro e entre módulos (índices c e z). Considerando apenas dados binários, as redes não apresentaram estrutura modular. No entanto, utilizando a força de interação, módulos puderam ser detectados em todas as redes de interação *Miconia*-aves. Nenhuma dos atributos das aves foi relacionada com os índices de conectividade. A possível flutuação na abundância dos frugívoros somada à frutificação assincrônica de *Miconia* podem favorecer a formação de módulos temporais compostos por plantas e aves com sobreposição fenológica, garantindo a dispersão de sementes e facilitando a coexistência de espécies simpátricas. Como a assembléia de frugívoros é dominada por espécies de pequeno porte e com comportamento alimentar oportunista, os atributos das aves tiveram pouco efeito na função de cada espécie na formação dos módulos.

**Palavras chave:** frugivoria, dispersão de sementes, *Miconia*, QuanBiMo, redes mutualísticas.

## INTRODUCTION

Interactions among species are not randomly structured and numerous studies have shown that networks of species' interactions show some recurrent patterns (Bascompte 2009). One such pattern is the presence of modules, i.e. subunits or compartments, with within-group prevalence of interactions (Olesen *et al.* 2007, Vázquez *et al.* 2009a). Modules have been detected in distinct types of interaction networks, including plant-pollinator (Martín González *et al.* 2012, Maruyama *et al.* 2014, Olesen *et al.* 2007), prey-predator (Krause *et al.* 2003), host-parasite (Krasnov *et al.* 2012), plant-ant (Fonseca & Ganade 1996) and plant-frugivore networks (Donatti *et al.* 2011, Mello *et al.* 2011, Schleuning *et al.* 2014). Modular organization can also be found at different hierarchical levels; meaning that modules have been reported not only for communities, but also within population interactions performed by each individual of a species (Tur*et al.* 2015). Likewise, modules within modules are also expected in nature (Dormann & Strauss 2014). Organization of the interactions into distinct modules is theoretically expected to promote species coexistence and community stability as perturbations are unlikely to spread quickly across different modules in the network (Stouffer & Bascompte 2011, Tylianakis *et al.* 2010).

Once modules are identified, species in the network can also be classified according to distinct roles, whether they are important connectors of different modules and/or act as central components within a module (Olesen *et al.* 2007, Schleuning *et al.* 2014). Although modular structure is frequent in nature, this pattern might be less pronounced when analyzing some subgroups within communities. For instance, plant-frugivore networks seem to be less modular than other types of interaction (Rezende *et al.* 2007), but this trend might reflect the overrepresentation of plant-bird networks in the available datasets which in fact comprise only one taxonomic and presumably few functional groups of seed dispersers (Donatti *et al.* 2011, Mello *et al.* 2011). Furthermore, most of the studies conducted so far are based on binary interaction data which might overestimate the role of rare and singleton species and/or underestimate highly interactive species (Dormann & Strauss 2014).

Plant-frugivore interactions are marked by large overlaps and resource share (Silva & Melo 2013, Terborgh & Diamond 1970), which ultimately lead to low levels of complementary specialization in relation to other types of interaction (Blüthgen *et al.* 2007). In spite of this, some assemblages of closely related animal-dispersed plants show apparent pattern of sequential fruiting, which might minimize the competition for seed dispersers and finally benefit the entire community of frugivores by providing constant supply of food resources (Maruyama *et al.* 2013, Poulin *et al.* 1999). In this sense, closely related plants which present similar fruits, thus impairing formation of morphology related modules, yet temporally segregating their fruiting phenology could be a good system to test whether temporal distribution of interactions drives formation of modules in small networks. By contrasting binary and weighted modularity algorithms, we can also demonstrate the importance of considering the strength of the interactions to detect subtle structural patterns in ecological networks (Dormann & Strauss 2014). Here we use data on interaction of four assemblages of *Miconia* (Melastomataceae) and their frugivorous birds from Neotropical habitats to test the following hypotheses: (1) networks centre on *Miconia* are modular and each module is composed of a *Miconia* species and their main partners; (2)modules in these networks can be efficiently detected by weighted algorithms and (3) dietary specialization is the bird trait that best explains species roles in the modular networks

## METHODS

### Plant species

*Miconia* (Melastomataceae) with approximately 1100 described species is one of the richest genera among Neotropical angiosperms. *Miconia* species can present many habits including shrubs, herbs, epiphytes, treelets and trees, and are usually associated with edges and natural gaps in the vegetation (Ellison *et al.* 1993). Plants from this group can be found in a range of environments, from open habitats as grasslands to savannas and extremely humid tropical rain forests (Romero & Martins 2002). One important characteristic of *Miconia* is a tight association to frugivorous animals for seed dispersal. The small carbohydrate-rich fruits contain numerous tiny seeds and are eaten and dispersed by several species of bird, including many generalist species (Maruyama *et al.* 2013, Snow 1981). Furthermore, species of *Miconia* are among the most important resources for fruit-eating birds in Neotropical environments (Maruyama *et al.* 2013, Stiles & Rosselli 1993). Commonly, assemblages of *Miconia* species show asynchronous and complementary fruiting period (Maruyama *et al.* 2013, Poulin *et al.* 1999) which is believed to reduce interspecific competition for dispersal agents (Wheelwright 1985) and might contribute to the high number of species of this genus occurring in sympatry.

### Interaction data

Data on interaction of *Miconia* and frugivorous birds came from four distinct communities, three from the Neotropical savannas in Brazil and one from the rain forest of Panama. Savanna networks were collected at Caça e Pesca (18°55' S, 48°17' W, Maruyama *et al.* 2013), Panga (19°10' S, 48°23' W, Borges 2010, Appendix 1) and Duratex (18°50' S, 47°49' W, Paniago 2014, Appendix 2), all areas with remnants of native vegetation in the region. In each of these sites, interactions among species of *Miconia* and frugivore birds were recorded through focal observations, where the observers remained about 10 m distant from the focal tree and recorded the fruit-eating interactions. From these records, we constructed bipartite interaction matrices with each cell representing the number of interaction events, i.e. instances in which a bird visited a plant individual, of the corresponding plant-bird pair. For the Panamanian network, data were collected at Soberania National Park (09°10' N, 79°07' W, Poulin *et al.* 1999) and instead of visits, interaction strength among a pair of species is represented by the number of fruit records in regurgitation or faecal samples collected from mist-netted birds (Poulin *et al.* 1999). Although differences in the methods to record the interaction exist, this should not affect our overall interpretation of the results as we are characterizing the networks pattern within each of the communities. After constructing these matrices considering the frequency - strength of the interaction, we also constructed for each of the matrices a binary version, representing the presence or absence of interaction among a pair of plant and bird. Networks used in our study were the only ones in literature that are collected specifically for *Miconia* assemblages which ensured an equivalent sampling for each plant species. Hence, although some broader community-wide networks containing *Miconia* species are available in the literature, we did not include those here.

## Network analysis

To measure the binary modularity in the networks, we used the software MODULAR (Marquitti *et al.* 2014), quantifying the modularity using the metric proposed by Barber (2007) for bipartite networks:

$$Q_B = \sum_{i=1}^{N_M} \left[ \frac{E_i}{E} - \left( \frac{k_i^C . k_i^R}{E^2} \right) \right],$$

where $N_M$ is the number of modules, $E_i$ is the number of links in module $i$, $E$ is the number of links in the complete network, $k_i^C$ is the sum of the degrees of the nodes within module $i$ that belong to set $C$ and $k_i^R$ is the sum of the degrees of the nodes within module $i$ that belong to set $R$. The significance of the bipartite modularity was compared against 1000 random networks, generated by two null models. The first one is Erdős-Rényi model (Erdős & Rényi 1959), where each pair of nodes has the same probability of being connected by a link and the second is null model 2 (Bascompte *et al.* 2003), where the probability of a pair being connected by an edge is proportional to the number of edges that the nodes have.

To quantify the modularity in the weighted networks, we used the algorithm QuanBiMo (Dormann & Strauss 2014). This algorithm detects the presence of modules in weighted bipartite networks based on a hierarchical representation of species link weights and optimal allocation to modules (Dormann & Strauss 2014). The algorithm is a modification of the Newman's quantity of modularity $Q$ (Barber 2007):

$$Q = \frac{1}{2N} \sum_{ij} (A_{ij} - K_{ij}) \delta(m_i, m_j),$$

where $N$ is the total number of interactions in the network; $A_{ij}$ is the number of interactions between frugivorous species $i$ and plant species $j$; $K_{ij}$ represents the random expected probability of interactions within a module; the function $(m_i, m_j)$ is 1 when species $i$ and $j$ are in the same module ($m_i = m_j$) and 0 if they are in different modules ($m_i \neq m_j$). The modularity $Q$ ranges from 0 (no support for division of modules) to 1 (maximum degree of modularity). The QuanBiMo algorithm was run with the function computeModules in R-package bipartite (Dormann*et al.* 2009).

The absolute value of $Q$ is dependent on network size and number of links (Dormann & Strauss 2014), so we tested the estimates of modularity $Q$ with 1000 randomizations generated by two null models: Patefield null model (*r2dtable*) – which uses fixed marginal totals to distribute the interactions and produce a set of networks in which all species are randomly associated (Blüthgen *et al.* 2008); and the null model propose by (Vázquez *et al.* 2007), which retain the number of interactions per species and the network connectance (*vaznull*).

To identify species roles in modular network we estimated for each species the within-module degree *z* and the among-module connectivity *c*-scores (Guimerà & Amaral 2005, Olesen *et al.* 2007):

$$c = 1 - \sum_{t=1}^{N_M} \left(\frac{k_{it}}{k_i}\right)^2, \qquad z = \frac{k_{is} - k_s}{SD_{ks}},$$

where, $k_{is}$ is number of links of $i$ to other species in its own module $s$; $k_s$ and $SD_{ks}$ are average and standard deviation of within module $k$ of all species in $s$; $k_i$ is degree of species $i$; $k_{it}$ is number of links from $i$ to species in module $t$. As binary networks did not show significant modularity, we only calculated the weighted version of these indices, which are computed based on species strength instead of number of links (Dormann & Strauss 2014). For calculations of weighted *c* and *z*-scores, we used the function czvalues in bipartite.

### Bird traits

In order to relate network role of birds to their ecological traits, we gathered data on bird body mass, migration behaviour, dietary specialization and taxonomic family. As the morphology of the *Miconia* berries in this study is very similar (Maruyama *et al.* 2007), bill gape width should not constrain the interaction, therefore, it was not considered here. The fruit-eating birds were classified into three dietary categories following Kissling *et al.* (2007) as (1) obligate frugivores – species that have fruits as the major food items in their diet; (2) partial frugivores – species that include other major food items in diet; and (3) opportunistic fruit-eaters – species that only occasionally eat fruits as supplementary food resource. Data on the diet of birds were gathered from published studies, and for savanna areas also included personal observations in the areas of studies (del Hoyo *et al.* 2015, Sick 1997). Bird body mass influences in food choices and in the number of fruits consumed (Wotton & Kelly 2012), thus it might be related to the network role. For each bird species we obtained data on average body mass of adult specimens from the literature (Dunning 2008). As temporal distribution of species in a community might constrain the partners to interact with (Vázquez *et al.* 2009b, Vizentin-Bugoni *et al.* 2014), we classified the migratory behaviour of the bird species as: (1) resident – sedentary species that remain year-round in the area stay; (2) nomad – a species that perform irregular moments in response to resource availability and (3) migratory – species that make short or long and well-defined seasonal movements. Movement information was gathered from Loiselle & Blake (1991), Nunes & Tomas (2008), del Hoyo *et al.* (2015), and personal observations. Finally, as many traits in birds are phylogenetically conserved (Losos 2008), we also included the family of birds as a category in our analysis to reflect species relatedness. Classification and nomenclature of birds followed South American Classification Committee (Remsen *et al.* 2015).

### Statistical analysis

The relationship between network roles, as represented by *c* and *z* scores, and bird traits was evaluated with linear mixed-effects models (Bolker *et al.* 2009). We used as fixed factors the body mass, dietary specialization, migratory behaviour and taxonomic family. Bird species identity was included as a random effect to account for non-independence within observations of the same species in different networks (Bolker *et al.* 2009). For each of the response variables, *c* and *z*-scores, we ran the models separately. The full model including all factors and reduced models were fitted using the function dredge in R package MuMln and compared by their values of the Akaike information criterion corrected for small sample sizes (Bolker *et al.* 2009). Models with ΔAICc ≤ 2 were considered as equivalent.

## RESULTS

Considering all networks, 66 species of bird, 12 *Miconia* species and 953 interactions were recorded. Thraupidae were the best-represented family with 24 species (36.4%), followed by Tyrannidae with 11 (16.7%). Seventeen (25.8%) species were classified as obligate frugivores, while 23 (34.8%) and 26 (39.4%) were classified as partial frugivores and opportunistic fruit-eaters, respectively. For migratory behaviour, 43 species (65.1%) are resident, 10 (15.2%) are nomad and 13 (19.7%) are migrant. Considering the body mass, most birds are small with 87.9% of the bird species weighing less than 100 g.

When considering binary matrices, none of the networks had values of modularity different from random, irrespective of the null models used. All quantitative versions of the networks, in contrast, were modular with each presenting three modules ($P < 0.01$ for both null models; Table 1). Each module within these networks contained one or two *Miconia* species associated with their most common frugivores

(Figure 1). Model selection showed that neither *c* nor *z*-scores can be associated to body mass, dietary specialization, migratory behaviour and bird family, as no model including fixed factors performed better than the model including only the intercept (Table 2).

**Table 1.** Values of modularity in binary and weighted versions of four *Miconia*-frugivore bird networks: Caça e Pesca (Maruyama *et al.* 2013), Panga (Borges 2010), Duratex (Paniago 2014) and Panama (Poulin *et al.* 1999); and the significance against the null models. Null 1 = Erdős and Rényi model (Erdős & Rényi 1959); Null 2 = “null model 2” of Bascompte *et al.* (2003); r2dtable= Null model Patefield (Patefield 1981); vaznull = Null model proposed by Vázquez*et al.* (2007); $Q_{obs}$ = value of modularity Q observed in the networks; $Q_{null}$ = value of mean modularity Q generated by 1000 null models.

| | Binary | | | | | Weighted | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Area | $Q_{obs}$ | Null1 | | Null2 | | $Q_{obs}$ | r2dtable | | vaznull | |
| | | $Q_{null}$ | p | $Q_{null}$ | p | | $Q_{null}$ | p | $Q_{null}$ | p |
| Caça e Pesca | 0.178 | 0.202 | 0.78 | 0.195 | 0.73 | 0.240 | 0.118 | <0.01* | 0.143 | <0.01 |
| Panga | 0.294 | 0.265 | 0.33 | 0.260 | 0.30 | 0.399 | 0.183 | <0.01* | 0.233 | <0.01 |
| Duratex | 0.376 | 0.364 | 0.39 | 0.351 | 0.31 | 0.240 | 0.096 | <0.01* | 0.1463 | <0.01 |
| Panama | 0.352 | 0.331 | 0.31 | 0.323 | 0.24 | 0.245 | 0.126 | <0.01* | 0.1697 | <0.01 |

**Table 2.** Comparisons of statistical models containing combinations of bird traits that explaining the within- and among-module connectivity indices (c and z scores) in four *Miconia*-frugivore bird networks (Borges 2010, Maruyama *et al.* 2013, Paniago 2014, Poulin *et al.* 1999). Models with ΔAICc< 2 were considered equivalent and include here in the table. None of the bird trait models has more explanatory power than the models containing only the intercept.

| Model | AICc | ΔAICc | AICcweight |
|---|---|---|---|
| **c-score** | | | |
| Intercept only | 691.1 | 0.00 | 0.288 |
| Dietary specialization | 692.0 | 0.88 | 0.185 |
| Body mass | 692.5 | 1.38 | 0.145 |
| Body mass + Dietary specialization | 692.7 | 1.58 | 0.131 |
| | | | |
| **z-score** | | | |
| Intercept only | 726.3 | 0.00 | 0.181 |
| Body mass | 726.7 | 0.34 | 0.153 |
| Body mass + Dietary specialization | 726.7 | 0.41 | 0.148 |
| Migratory behavior | 727.0 | 0.66 | 0.131 |
| Dietary specialization | 727.3 | 0.97 | 0.112 |
| Bodymass + Migratory behaviour | 727.3 | 1.00 | 0.110 |
| Body mass + Dietary specialization+ Migratory behaviour | 727.7 | 1.34 | 0.093 |
| Dietary specialization + Migratory behavior | 728.2 | 1.86 | 0.072 |

## DISCUSSION

Modules could only be found by incorporating the strength of the interactions in *Miconia*-bird networks. The importance of using weighted information, such as interaction strength in network analyses has been recognized as an important step in understanding the architecture of ecological communities (Gilarranz *et al.* 2012, Ings *et al.* 2009). Schleuning *et al.* (2014) in a study with 18 plant-frugivore networks, only one third presented significant modularity with binary data, while including information on the strength of interaction allowed the detection of modules in all but one of these networks. Similarly, although small binary pollination networks do not show distinct modular organization (Olesen *et al.* 2007), the inclusion of quantitative information led to the detection of modules even in species-poor hummingbird-plant pollination networks (Maruyama *et al.* 2014, 2015). Moreover, these modules are associated to the functional traits of the species (Maruyama *et al.* 2014, 2015). Overall, it seems that inclusion of quantitative information led to detection of finer partitioning in networks.

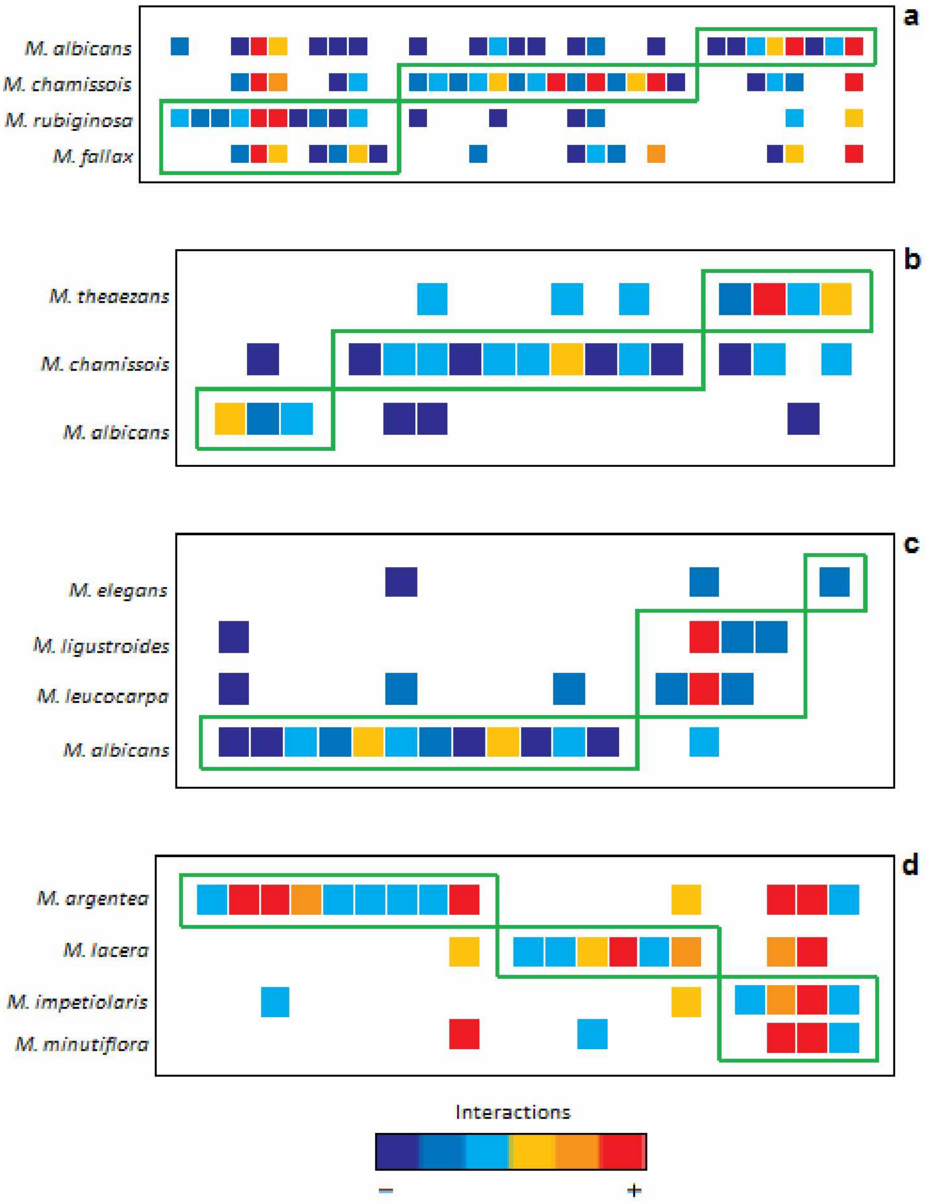

**Figure 1.** Modules identified by the QuanBiMo algorithm in four weighted *Miconia*-frugivore bird networks: Caça e Pesca (Maruyama *et al.* 2013) (a), Panga (Borges 2010) (b), Duratex (Paniago 2014) (c) and Panama (Poulin *et al.* 1999) (d). Warm tones represent a higher number of interactions and cool tones represent fewer interactions. The green boxes represent the modules identified and each row is a *Miconia* species.

Interspecific competition among plants for dispersal agents is regarded as a force that can shape the structure of plant-frugivore interactions (Herrera 1981, Howe & Estabrook 1977, Howe & Smallwood

1982). As interaction pressures are expected to be stronger among closely related species due to similarity in niches (Webb *et al.* 2002), sympatric congeneric species tend to have mechanisms to ensure their co-existence (Beltrán *et al.* 2012). Berries of the 12 *Miconia* species analyzed are very similar in morphology and nutritional values (Maruyama *et al.* 2007), meaning that these traits play little role in selection of different dispersal agents, and hence in generating modules. However, the fruiting asynchrony observed, with no overlap in fruiting peak among the sympatric species (Maruyama *et al.* 2013, Poulin *et al.* 1999), potentially suffices to generate the modular structure and also facilitate the co-existence of species by promoting facilitation among plants (Poulin *et al.* 1999).

The abundance of bird populations fluctuates year-round, especially in seasonal environments, due to several factors, such as total or partial migration and dispersal (Loiselle & Blake 1991). Moreover, more than one third of the species associated with the *Miconia* species perform seasonal movements. Frugivorous birds are subject to high resource fluctuations (Loiselle & Blake 1991), having greater tendency to seasonal movement compared to insectivorous species (Levey & Stiles 1992). Nevertheless, bird migration behaviour did not strongly associate to species role in the networks. One important point that should be noticed, though, is that consumer species may seasonally switch their foraging behaviour according to resource variability (Carnicer *et al.* 2009), e.g. insectivorous and omnivorous birds can change the proportion of fruits in their diet according to the availability of their main resources (Borghesio &Laiolo 2004) or with the life stage (Robbins 1981). Even within more specialized frugivorous birds, the availability of fruiting plants other than *Miconia* might change the relative attractiveness of these less-rewarding carbohydrate-rich fruits (Maruyama *et al.* 2013). In this sense, this potential diet variation in frugivorous birds would function as a seasonal pattern in fruit consumption, which coupled with possible abundance fluctuation and asynchronic fruiting period in *Miconia* could favour the formation of modules comprising birds (or their seasonal diet preferences) and plant species with stronger phenological overlap.

None of the bird morphological traits or taxonomic relatedness affected the within- and among-module connectivity. In general, body mass has been shown to be an important driver in structuring ecological networks (Arim *et al.* 2011, Rezende *et al.* 2009), although it has been shown to have little explanatory power in the variation of centrality metrics in plant-frugivore networks (Mello *et al.* 2015). This lack of association might be especially likely if the assemblage of animals considered shows little variation in the trait. Birds associated with *Miconia* are mostly passerines, a group composed by small to medium-sized species. Fruit-eating bird assemblages dominated by small-bodied species tend to be less specialized (Menke *et al.* 2012), resulting in modularity roles more evenly distributed among bird species. Furthermore, Saavedra *et al.* (2014) found little effect of morphological traits in interaction strength in the forest-edge frugivore networks, where *Miconia* species are widespread and small-bodied birds are predominant. Considering the dietary specialization, obligate and partial frugivorous had within- and among-module connectivity values higher than opportunistic ones in most community-wide plant-frugivorous bird networks (Schleuning *et al.* 2014). Once again, the fact that most birds associated with *Miconia* are generalist, small-bodied birds is probably related to the lack between diet and network roles, since even generalist frugivores have important roles in dispersing the seed of these species (Howe 1993, Maruyama *et al.* 2013, Poulin *et al.* 1999, Snow 1981). Nevertheless, this independence from specific groups of dispersal agents may ensure the seed dispersal services from a variety of species (Jordano *et al.* 2007) which is especially important for high-fecundity pioneer species with small-seeded fruits (Howe 1993).

At what hierarchical level or with what kind of information, i.e. binary and weighted, modules can be detected in ecological systems is still only beginning to be addressed in the literature (Schleuning *et al.* 2014, Tur *et al.* 2015). We showed that modular structure can be detected within closely related sympatric species, but only when using weighted information incorporating the strength of the interactions. The use of quantitative information has been argued for in recent studies (Dormann & Strauss 2014, Schleuning *et al.* 2014) and we hope our study illustrated how finer partitioning of interactions can be detected by using it. Even when evaluating the role of species within networks, analyzing quantitative data may deeply affect how we quantify the importance of each species in a network (Scotti *et al.* 2007). The next question to answer is at what hierarchical level the detection of modular organization has real impact on how we assess the stability and dynamics of ecological systems. Modules have been detected for a myriad of ecological systems, from entire assemblage/community to within species/populations individual-based networks (Donatti *et al.* 2011, Tur *et al.* 2015). Closely related sympatric species also show modular interaction pattern, possibly related to asynchronous fruiting period, but not with morphological and behavioural traits of birds such as body mass, diet and migratory behaviour. How each of these modular patterns, present at distinct layers of hierarchy, can promote co-existence of species and hence the functioning of ecological systems, deserve further investigation in the future.

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# ANEXO 2

**Appendix 1.** Frugivory interaction matrix between three *Miconia* species and 17 bird species in a Neotropical savanna in Brazil (Panga; 19°10' S, 48°23' W). Frugivory interactions were recorded from April to November 2007 and in each *Miconia* species was performed from 30 to 42 h of focal-plant observation. Source: Borges (2010).

| | *Miconia theaezans* | *Miconia albicans* | *Miconia chamissois* | Total |
|---|---|---|---|---|
| *Tangara cayana* | 28 | 0 | 2 | 30 |
| *Dacnis cayana* | 6 | 0 | 4 | 10 |
| *Tachyponus rufus* | 4 | 1 | 3 | 8 |
| *Antilophia galeata* | 2 | 0 | 5 | 7 |
| *Elaenia* sp. | 4 | 1 | 0 | 5 |
| *Volatinia jacarina* | 0 | 5 | 0 | 5 |
| *Saltator similis* | 1 | 0 | 3 | 4 |
| *Turdus leucomelas* | 0 | 0 | 4 | 4 |
| *Ramphocelus carbo* | 0 | 0 | 4 | 4 |
| *Schystochlamys melanopis* | 2 | 0 | 1 | 3 |
| *Cyanocorax cyanopogon* | 0 | 2 | 1 | 3 |
| *Tangara palmarum* | 0 | 1 | 2 | 3 |
| *Sporophila nigricollis* | 0 | 3 | 0 | 3 |
| *Pipraeidea melanonota* | 0 | 0 | 1 | 1 |
| *Tersina viridis* | 0 | 0 | 1 | 1 |
| *Lanio cucullatus* | 0 | 0 | 1 | 1 |
| *Euphonia chlorotica* | 0 | 0 | 1 | 1 |
| Total | 47 | 13 | 33 | |

**Appendix 2.** Frugivory interaction matrix between four *Miconia* species and 17 bird species in a Neotropical savanna in Brazil (Duratex; 18°50' S, 47°49' W). Frugivory interactions were recorded from August 2012 to December 2013 and in each *Miconia* species was performed about 35 h of focal-plant observation. Source: Paniago (2014).

| | *Miconia albicans* | *Miconia elegans* | *Miconia leucocarpa* | *Miconia ligustroides* | Total |
|---|---|---|---|---|---|
| *Elaenia* sp. | 8 | 1 | 82 | 52 | 143 |
| *Piranga flava* | 14 | 0 | 0 | 0 | 14 |
| *Tangara cayana* | 8 | 0 | 4 | 0 | 12 |
| *Zonotrichia capensis* | 12 | 0 | 0 | 0 | 12 |
| *Tangara palmarum* | 7 | 1 | 3 | 0 | 11 |
| *Cyanocorax cristatellus* | 0 | 0 | 3 | 3 | 6 |
| *Hemithraupis guira* | 5 | 0 | 0 | 0 | 5 |
| *Turdus leucomelas* | 4 | 0 | 0 | 0 | 4 |
| *Sporophila* sp. | 2 | 0 | 1 | 1 | 4 |
| *Aratinga aurea* | 0 | 0 | 0 | 4 | 4 |
| *Saltator maximus* | 3 | 0 | 0 | 0 | 3 |
| *Antilophia galeata* | 0 | 3 | 0 | 0 | 3 |
| *Dacnis cayana* | 2 | 0 | 0 | 0 | 2 |
| *Euphonia chlorotica* | 2 | 0 | 0 | 0 | 2 |
| *Lanio cucullatus* | 1 | 0 | 0 | 0 | 1 |
| *Tangara sayaca* | 1 | 0 | 0 | 0 | 1 |
| *Volatinia jacarina* | 0 | 0 | 1 | 0 | 1 |
| Total | 69 | 5 | 94 | 60 | |