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Plant-hummingbird interactions: natural history and ecological networks

Interações entre plantas e beija-flores: história natural e redes ecológicas

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Pietro Kiyoshi Maruyama Mendonça

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RESUMO

O entendimento sobre as interações mutualísticas entre plantas e animais, principalmente a nível de comunidade, tem avançado consideravelmente devido ao uso crescente da abordagem de redes complexas. Estes estudos têm revelado alguns padrões constantes na organização da "teia da vida", e as propriedades estruturais nas redes são sugeridas como tendo fortes implicações para a estabilidade e dinâmica das assembléias de espécies que interagem nas comunidades. Estudos mais recentes na área revelam a importância do acoplamento nos atributos das espécies na estruturação das redes. O crescente apreço dos atributos funcionais das espécies significa que o conhecimento acerca da história natural das espécies também terá importância crescente em estudos com redes de interações. Nesta tese, focamos especificamente na interação entre plantas e beija-flores, um grupo especializado de polinizadores vertebrados encontrados nas Américas, como modelo de estudo. Os estudos individuais encontrados nessa tese incluem a consideração de diferentes tipos de comportamentos exibidos pelos polinizadores ao visitarem uma flor (mutualismo vs. antagonismo), investigação de como diferentes atributos das espécies determinam a organização das redes de interações e também de como os atributos das espécies podem estar associados a incorporação de espécies exóticas de plantas nas redes de polinização. Assim, utilizamos abordagens que vão desde o estudo focal de uma espécie de planta e/ou polinizador à estudos em ampla escala geográfica englobando várias comunidades espalhadas pelas Américas. Todos os estudos apresentam um aspecto em comum: conduzimos estudos que combinam informações de história natural das espécies à abordagem das redes para reforçar como uma melhor compreensão básica das partes (i.e. espécies) pode permitir um melhor entendimento do conjunto (i.e. redes, ou comunidades). O uso de atributos funcionais relevantes (e.g. comportamento, morfologia, distribuição espaço-temporal, etc.) associado à abordagem de redes é promissor para avaliar a associação entre a estrutura das interações em comunidades e o funcionamento destas. Além disso, a consideração dos atributos das espécies pode ser útil no cenário de mudanças ambientais globais, podendo auxiliar nas previsões de como as espécies rearranjarão suas interações em ambientes cambiáveis. Dessa forma, compreender a associação entre os atributos das espécies e a estrutura das interações poderá ser uma estratégia interessante para entender, prever e mitigar os efeitos das mudanças ambientais em curso no planeta sobre os sistemas ecológicos e suas funções.

ABSTRACT

The comprehension of plant-animal mutualistic interactions, especially at community level, has advanced greatly due increasing appreciation of complex network approaches. These studies have revealed consistent patterns on the organization of the "web of life", and the structural properties of networks are regarded as having strong implications for the stability and dynamics of assemblages of species interacting in communities. In this context, recent studies in the field have revealed the importance of trait matching on network structure. The recognition of species functional traits as having a major role means that knowledge on natural history of species will have increasing importance in interaction network studies. Here, we focus on the interaction among plants and hummingbirds, a group of specialized vertebrate pollinators found across the Americas, as a model of study. Studies included in this thesis take different approaches such as consideration of distinct type of pollinator's behavior when visiting flowers (mutualism vs. antagonism); investigation on how distinct species traits determine the structure of the interaction networks and also on how species traits are associated to the incorporation of alien plant species in the pollination networks. In this sense, we used approaches encompassing case studies of a plant and/or animal species as well as a study with wide geographical scale, considering multiple communities across the Americas. All of these studies have one aspect in common: we conducted studies which combined information on natural history of species and network approaches in order to emphasize how better understanding of components (i.e. species) allow a better understanding of the whole (i.e. networks, or communities). The use of relevant functional traits (e.g. behavior, morphology, spatio-temporal distribution, etc.) allied to the network approach is promising in order to evaluate the association between the structure of the interactions in the communities and the functioning of these. Besides, it could be useful to consider species traits in the scenario of ongoing global changes, allowing projections of potential rewiring of the interactions in the changing world. In this sense, better comprehension of the association between traits and network structure may be an interesting strategy to understand, forecast and mitigate possible effects of current environmental changes on the ecological systems and their functioning.

SUMÁRIO

INTRODUÇÃO GERAL	11
CAPÍTULO 1: Nectar robbery by a hermit hummingbird: association to floral phenotype and its influence on flowers and network structure	15
CAPÍTULO 2: Pollination and breeding system of <i>Canna paniculata</i> (Cannaceae) in a montane Atlantic Rainforest: asymmetric dependence on a hermit hummingbird	39
CAPÍTULO 3: Morphological and spatio-temporal mismatches shape a neotropical savanna plant-hummingbird network	48
CAPÍTULO 4: The integration of alien plants in plant-hummingbird networks across the Americas: the importance of plant trait, pollinator generalization and insularity	67
CONSIDERAÇÕES FINAIS	129
REFERÊNCIAS	132
ANEXOS	148

INTRODUÇÃO GERAL

O entendimento sobre as interações mutualísticas entre plantas e animais, especialmente no nível de comunidade, tem avançado consideravelmente devido ao uso crescente da abordagem de redes complexas (Bascompte 2009). Após quase três décadas desde o artigo pioneiro de Jordano (1987), os estudos envolvendo redes revelaram alguns padrões consistentes recorrentes em diferentes sistemas mutualistas. Por exemplo, frequentemente apenas uma proporção pequena das interações possíveis entre espécies na rede é realizada, o que resulta numa conectância baixa ou moderada, ou seja, muitas espécies são ligadas apenas a alguns parceiros específicos (Jordano 1987). Mais além, redes mutualísticas possuem estrutura aninhada, na qual há um núcleo de espécies com muitas conexões, i.e., generalistas, interligadas e espécies pouco conectadas, i.e., especialistas, ligando-se geralmente a generalistas (Bascompte et al. 2003). Ao mesmo tempo, essas redes são comumente organizadas em módulos, caracterizados pelos sub-conjuntos de espécies interagindo preferencialmente entre si em relação a interações com espécies de outros sub-conjuntos na rede (Olesen et al. 2007). No nível de espécies, a distribuição do grau, i.e. número de parceiros de uma espécie, mostra a maioria das espécies tendo poucos parceiros e poucas espécies tendo muitos parceiros (Jordano et al. 2003). Além disso, existe forte assimetria na dependência entre espécies, o que significa que as espécies realizam a maioria das suas interações com parceiros que, por outro lado, dependem pouco das suas interações (Vázquez & Aizen 2004). Essas propriedades estruturais são sugeridas como tendo fortes implicações para a estabilidade e dinâmica das assembléias de espécies que interagem nas comunidades (Bascompte et al. 2006, Bastolla et al. 2009, Thébault & Fontaine 2010).

Esses padrões estruturais das redes são provavelmente gerados por diversos processos (Vázquez et al. 2009a), entretanto evidências empíricas sobre quais são estes processos e quais são suas importâncias relativas permanecem escassas. Nesse sentido, estudos recentes

com redes ecológicas tem demonstrado que o acoplamento nos atributos das espécies são determinantes cruciais da estrutura das redes, influenciando especialmente as interações entre pares de espécies, o que às vezes é referida como a micro-estrutura das redes (e.g. Junker et al. 2014, Vizentin-Bugoni et al. 2014). Esses estudos seguem uma tendência mais difundida recentemente em ecologia de comunidades, que adota uma abordagem baseada em atributos funcionais com intuito de permitir melhores generalizações (McGill et al. 2006). Que os atributos funcionais das espécies têm papel importante significa que o conhecimento acerca da história natural das espécies terá importância crescente em estudos com redes de interações. Neste contexto, esta tese representa uma contribuição à área da ecologia que se dedica ao entendimento das interações entre espécies nas comunidades ecológicas.

Aqui, focamos especificamente na interação entre plantas e beija-flores como modelo de estudo. Esses polinizadores chegaram ao continente sul americano aproximadamente 22 milhões de anos atrás (McGuire et al. 2014) e desde então se tornaram o grupo mais importante de polinizadores entre os vertebrados na região Neotropical (Stiles 1981, Bawa 1990, Cronk & Ojeda 2008). Inclusive, a associação mutualística especializada com plantas nectaríferas foi provavelmente responsável pela diversificação de alguns grupos de plantas (e.g. Bromeliaceae, Schmidt-Lebuhn et al. 2007). No primeiro e segundo capítulos, focamos principalmente na interação entre plantas e beija-flores da Floresta Atlântica do sudeste do Brasil (Maruyama et al. 2015a, b). Embora a maioria das angiospermas dependa de vetores bióticos para a sua polinização (Ollerton et al. 2011), nem todos os visitantes florais são polinizadores efetivos e alguns até agem como exploradores, roubando e pilhando os recursos florais (Inouye 1980, Irwin et al. 2010). Usando múltiplas abordagens incluindo a de redes, investigamos as interações envolvendo o beija-flor *Phaethornis ruber*, um pilhador comum e amplamente distribuído nas florestas tropicais da América do Sul, no sentido de contribuir para o conhecimento sobre os exploradores de mutualismos (Bronstein 2001). Seria esperado

que diferentes tipos de interações, i.e. mutualismo vs. antagonismo, influenciassem distintamente as propriedades de redes (Thébault & Fontaine 2010, Suave et al. 2014). Assim, ao considerar simultaneamente diferentes tipos de interações, poderiam ser revelados novos padrões e suas implicações para as dinâmicas eco-evolutivas que moldam as comunidades (Fontaine et al. 2011). Apesar de promissora, esta abordagem tem sido empregada por poucos estudos de redes que consideraram simultaneamente a interação das plantas tanto com polinizadores quanto exploradores (e.g. Genini et al. 2010, Yoshikawa & Isagi 2013) necessitando de mais investigações. Adicionalmente, o capítulo dois (Maruyama et al. 2015b) complementa o primeiro capítulo descrevendo a biologia da polinização da *Canna paniculata* (Cannaceae) com a qual realizamos um experimento de campo de pilhagem por *P. ruber*.

No terceiro capítulo, investigamos a importância relativa dos processos determinantes da ocorrência e frequência das interações entre plantas e polinizadores em comunidades. Estudos anteriores sugerem que interações em redes mutualísticas podem ser preditas principalmente pela abundância das espécies, com os atributos funcionais das espécies sendo menos importantes, entretanto recentemente mostramos que isso nem sempre é o caso (Vizentin-Bugoni et al. 2014). Em contraste a este estudo anterior que considerou uma rede de plantas e beija-flores da Floresta Atlântica, aqui estendemos esta conclusão para uma comunidade no Cerrado brasileiro (Maruyama et al. 2014). Além disso, avaliamos como os atributos das espécies se relacionam a formação de módulos na rede.

Finalmente, no quarto capítulo, utilizamos novamente a abordagem de redes para investigar o papel das plantas exóticas em redes de plantas e beija-flores nas Américas. Espécies exóticas invasoras são consideradas uma ameaça aos serviços ecossistêmicos cruciais como a polinização (Bjerknes et al. 2007, Morales & Traveset 2009). Contudo, estudos que avaliam a incorporação de espécies exóticas são, em sua maioria, focados em sistemas dominados por insetos polinizadores ou sistemas insulares (e.g. Olesen et al. 2002,

Stouffer et al. 2014). Aqui, compilamos 21 redes quantitativas de plantas e beija-flores distribuídas nas Américas Central e do Sul para avaliar como espécies de plantas exóticas estão incorporadas nas comunidades e como os atributos fenotípicos das espécies de plantas e beija-flores polinizadores contribuem para a integração das plantas exóticas.

CAPÍTULO 1

Nectar robbery by a hermit hummingbird: association to floral phenotype and its influence on flowers and network structure

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Abstract

Interactions between flowers and their visitors span from mutualism to antagonism. Although the literature is rich in studies focusing on mutualism, nectar robbery has mostly been investigated with phytocentric approaches and often focused on few plant species. To fill this gap, we focus on the interactions between a nectar-robbing hermit hummingbird, *Phaethornis ruber*, and its flowers. First, based on a literature review across the entire range of *P. ruber*, we characterized the association of floral larceny to floral phenotype. Then we examined the effects of robbing on nectar standing crop and pollinator visits of *Canna paniculata*, and, finally, we asked whether the incorporation of illegitimate interactions affects the plant-hummingbird network structure. We identified 97 plant species visited by *P. ruber*, which engaged in floral larceny in almost 30% of these flowers. Nectar robbery was especially common on flowers with long corollas. For *C. paniculata*, the depletion of nectar robbed by *P. ruber* was associated with decreased visitation rates of legitimate pollinators. At the community level, including illegitimate visits of *P. ruber* modified how modules within the network were organized, notably giving rise to a new module comprised by *P. ruber* and mostly robbed flowers. However, although illegitimate visits constituted ~ 9% of all interactions in the network, changes in nestedness, modularity and network level specialization were slight. Our results indicate that a flower robber may have strong effect on the pollination of plant species, yet including records of its illegitimate interactions has limited capacity to change overall network structure.

Key-words: antagonism, Atlantic rainforest, modularity, mutualism, *Phaethornis ruber*, plant-pollinator interactions

Introduction

Mutualism, defined as an interaction in which both partner species experience net positive effects, is one of the major interaction types in nature (Bronstein 2001). Nevertheless, organisms are entangled in multiple interactions that vary in type and strength. For instance, most flowering plants rely on animals for pollination (Ollerton et al. 2011), but not all flower visitors are effective pollinators (Irwin et al. 2010). Floral visitors even engage in floral larceny, i.e. robbing or thieving of floral rewards (Inouye 1980, Irwin et al. 2010). Some floral phenotypes might be especially associated with occurrence of floral larceny, such as longer and more enclosed corollas (Lara and Ornelas 2001, Irwin et al. 2010), but investigations encompassing large datasets are still lacking. Additionally, in a comprehensive review, Irwin et al. (2010) pointed out some little explored and fruitful avenues for future research in nectar robbery, notably overcoming the limitations caused by predominance of a phytocentric approach and lack of community-wide studies.

The same network structural property may have different consequences for network dynamics depending on whether the interaction is mutualistic or antagonistic (Thébault and Fontaine 2010). Therefore, simultaneously considering and merging these two types of interactions could reveal new eco-evolutionary patterns and dynamics shaping ecological communities (Fontaine et al. 2011). For instance, theoretical simulations with tripartite networks merging antagonistic and mutualistic sub-networks show that whereas greater connectance of antagonistic interactions lower the resilience of the community, connectance of the mutualistic interactions had an opposite effect (Sauve et al. 2014). If, by including illegitimate interactions structural properties of networks change drastically, in theory the dynamics and stability of the system should also change. This means that merging the interactions of both pollinators and floral larcenists may provide insightful results. For instance, inclusion of floral larcenists may change the structure of plants and flower-visitors

networks (Genini et al. 2010, Fontaine et al. 2011, Yoshikawa and Isagi 2013). Despite its potential importance, only few community-wide studies have simultaneously considered mutualistic and antagonistic flower visitors. Moreover, the simple addition of antagonistic interactions had drastic effects on the overall network structure (Genini et al. 2010, Yoshikawa and Isagi 2013). Specifically, these studies showed that addition of nectar robbers and flower-eaters increases the modularity of the network, i.e. sub-community structure seems more distinct when adding floral larcenists (Genini et al. 2010, Yoshikawa and Isagi 2013). Since pollination network structure has been suggested to have important eco-evolutionary consequences, these studies may point the necessity to consider floral larcenists when evaluating the ecological dynamics of plant-animal communities (Olesen et al. 2007, Thébault and Fontaine 2010, Sauve et al. 2014).

Here, we focus on a hummingbird nectar robber, the Reddish Hermit (*Phaethornis ruber*) as a model organism. This species belongs to the clade of Hermit hummingbirds, which are regarded as specialized and core-pollinators in Neotropical forests (Feinsinger and Colwell 1978, Sazima et al. 1995, Maruyama et al. 2014). However, the small Reddish Hermit is often recorded as a nectar robber in the lowland Atlantic Rainforest where it is common (Buzato et al. 2000). This makes it an ideal model organism to study possible species-species and community-wide effects of nectar robbery. First, we conducted a literature survey of all documented interaction records between *P. ruber* and plants, to ask whether particular floral traits were associated with the behavior of the hummingbird, i.e. whether the hummingbird acted as a pollinator, nectar robber, or nectar thief. In other words, we use an extensive database comprising a large number of plant species from several families to investigate the association between floral traits and hummingbird behavior. Second, we conducted a case study focusing on the interaction of *P. ruber* with *Canna paniculata* Ruiz & Pav. (Cannaceae), a plant species with intense robber activity by *P. ruber*,

to examine potential effects of *P. ruber* on plant reproduction. Finally, we collected data on a plant-hummingbird interaction network in a lowland Atlantic Rainforest community to explore whether the inclusion of floral larceny interactions influences how we characterize the network structure.

Material and methods

Literature survey

The literature survey on records of *Phaethornis ruber* interacting with plants was conducted using ISI Web of Science ® and Google Scholar®, using "*Phaethornis ruber*" as a search term. For each of the resulting references reporting observations of *P. ruber* visiting a plant, we extracted the following data whenever available: plant species and family; the hummingbird behavior while interacting with the plant, i.e. whether pollinating, robbing or thieving; flower corolla length; flower color (including secondary attractants such as bracts when present); nectar volume and concentration; and pollinator species visiting the plant. The difference between nectar robber and thief is whether the floral larcenist damages the flower when accessing the nectar: nectar robbers cause damages such as piercing the corolla, whereas nectar thieves illegitimately access the nectar without damaging the flower (Inouye 1980). Missing floral trait data were whenever possible complemented with an additional search specific for each plant species, e.g. using studies with the same plant at another location. For species with more than one study, data were averaged, i.e. for each plant species we use one value for each variable. Plant names were checked for their validity in the Plant List database (<http://www.theplantlist.org/>) and updated/corrected whenever necessary. Similar data for one community in the lowland Atlantic Rainforest (see below) were also

included in the survey. Following Wilson et al. (2004) and Dalsgaard et al. (2009), flower color visible to the human eye was coded from 1 to 4, ranging from short-wave length Hymenoptera syndrome colors (i.e. blue, violet flowers = 1) to increasing association to specialized hummingbird-pollinated syndromes (i.e. red flowers = 4), with 2 and 3 representing intermediate syndrome colors (see Online Resource 1 for details). We also coded the spectrum of legitimate flower visitors other than *P. ruber* according to increasing specialization to hummingbird pollination, using a 1-4 scale: 1) only insect pollinators, 2) insects and hummingbirds, 3) only hummingbirds, and 4) only large hermit hummingbirds (see Online Resource 1 for details).

To assess the relationship between floral phenotype and *P. ruber* behavior, we analyzed the floral variables using Nonmetric Multidimensional Scaling (NMDS), following previous studies that dealt with similar kind of data (e.g. Wilson et al. 2004, Dalsgaard et al. 2009, Ollerton et al. 2009). For the analysis, each floral variable was standardized by subtracting the minimum and dividing by the range, so that each variable had the same weight in the analysis. From the standardized data we calculated the Euclidian distance between species. The resulting dissimilarity matrix was used for computing the NMDS ordination with the function *metaMDSiter* in the *vegan* package in R, which identify a stable solution using several random starts with smaller stress values (Borcard et al. 2011, Oksanen et al. 2013). In our analysis, we set the number of random starts as 200, and examined whether solutions with two or three dimensions best describe the data. The optimal number of dimensions was three as the solution with two dimensions increased the stress level considerably, from *ca.* 10 to *ca.* 17 (Borcard et al. 2011). After identifying the preferred three-dimensional solution, we rotated the axis 1 according to floral corolla length, which best separated *P. ruber* behavior. We then used the function *envfit* to fit the pollinator visitor score and floral trait variables (as vectors), as well as the *P. ruber* behavior, i.e. pollinator, nectar robber, or nectar thief, (as factor -

centroid) into the ordination space. In this sense, we graphically illustrate how floral traits, pollinators and the behavior of our target hummingbird associate to the dimensions (axes) of the generated NMDS ordination (Borcard et al. 2011). In the case of the hummingbird behavior, the centroids show the averages of different behaviors in relation to the axes, i.e. to the dimensions representing the traits. The significance of the association between hummingbird behavior and the ordination axes was tested by 999 permutations (Borcard et al. 2011, Oksanen et al. 2013). Finally, we calculated the Pearson's correlation of each floral variable and the pollinator visitor score to the resulting three NMDS axes.

Case study

To assess how nectar robbing behavior of *P. ruber* may affect the availability of floral nectar, we conducted a case study with *Canna paniculata* in the Atlantic Rainforest at Núcleo Picinguaba - Cambucá. The study site is located in the Serra do Mar State Park in Ubatuba, São Paulo, Brazil (23°19'30"S; 44°56'24"W, ~50 m a.s.l.). The mean annual temperature in Picinguaba is 22°C and annual precipitation is 2200 mm, and never below 80 mm per month (Joly et al. 2012). *Canna paniculata* is a shrub common in the southeast Atlantic Rainforest, including the Serra do Mar State Park, occurring from lowland areas such as Picinguaba to higher areas up to 1000 m a.s.l. (Maruyama et al. 2015b). Data collection was conducted from February to July in 2012 and 2013, during the main flowering period of *C. paniculata*. We conducted focal observations (60 hours) in which we quantified the number of legitimate as well as illegitimate visits. Data collected at Picinguaba were compared to data from Santa Virgínia Field station (23°20'11"S, 45°8'45"W) a locality also within the Serra do Mar State Park but at ~900 m a.s.l., 21 km distant from Picinguaba (Maruyama et al. 2015b, See Online Resources 1). In Santa Virgínia *P. ruber* is absent, but otherwise the hummingbird-plant

communities are structured similarly (Buzato et al. 2000, Vizentin-Bugoni et al. 2014). Sampling in Santa Virgínia followed similar procedure and effort as in Picinguaba (Maruyama et al. 2015b).

We also conducted an experiment to assess the impact of nectar robbing on the floral nectar availability, using two treatments: 1) pollinator exclusion - legitimate access was prevented by putting a transparent plastic enclosure of *ca.* 2 cm on the tip of the flower; 2) robber exclusion - robbing was prevented by a "straw" made of the same plastic material with the same dimensions and put at the base of the corolla, allowing only legitimate visitors (see Online Resource 2 video file); and two controls: 3) bagged flowers - flowers isolated from all visitors with nylon mesh bags; 4) natural - open flowers in which all visits were allowed (n=30 for each category). All flowers were kept isolated with nylon mesh bags prior to the experiments. Treatments and controls were set before dawn, i.e. before the beginning of visitor activity and at the beginning of floral anthesis, which lasts one day. Treatments were as much as possible divided between plant individuals (n=12 clumps), and we always tried to set different treatments on the same individuals at the same time. After the previously mentioned focal observations, we also noted the presence of stingless bees (*Trigona* sp.) acting as nectar robbers, especially after the first hours in the morning ~09:30. Considering this, all our treatments were also divided in two time intervals, measuring the remaining amount of nectar in the flowers at 09:00-10:00 and 16:00-17:00 (n=15 for each time interval and each category). The remaining nectar volume in the flowers was compared using a linear mixed-effects model using the package *lme4* in R (Bates et al. 2014). We assumed different random intercepts for each individual clumps and first computed the full model with treatment and time interval with an interaction term as fixed effects. Afterwards we used the likelihood ratio test to attain p-values for these factors (e.g. comparing two models, one with and without the factor "Treatment" to assess its significance). Nectar volume was $\log_{10}$ transformed to fulfill

the assumptions of normal distribution of data and variance homoscedasticity. For the experimental categories in which we found a significant result, we also conducted a post hoc Tukey test. Since the “robber marks” left on the flowers differ between *P. ruber* and *Trigona* sp., it was possible to quantify the frequency of nectar robbing by each party, which was assessed in randomly collected flowers throughout the flowering season (n=180 flowers).

Community wide study

The hummingbird-plant interaction network data were collected in the coastal lowland Atlantic Rainforest at Picinguaba between January 2012 and June 2013. Interactions were recorded on focal plants either by an observer or by video cameras put in front of the plant, with 15 to 45 hours of observation for each plant species (sampling depended on plant abundance). During each observation session, we recorded all visits by hummingbirds as well as their behavior, i.e. whether they were visiting legitimately (potential pollination) or illegitimately. To evaluate how the inclusion of nectar larceny by *P. ruber* changes the network structure, we constructed two quantitative plant-floral visitor interaction networks. The first network was constructed considering only legitimate plant-hummingbird visits (hereafter Pollination network), whereas in the second matrix we also included instances in which hummingbirds acted as nectar robbers and thieves (hereafter Visitation network; all but one recorded nectar robbing involved *P. ruber*). For each of the two networks, we calculated distinct metrics illustrating different structural properties of the network:

- 1) Nestedness quantifies the degree on which interactions of specialized species are subsets of interactions of the more generalist species in the networks. Nestedness is one of the most recurrent patterns in ecological networks (Bascompte et al. 2003). We calculated the binary and weighted nestedness using the most conceptually consistent metric in the literature

(NODF and WNODF respectively; Almeida-Neto and Ulrich 2011). While binary nestedness accounts for the "plausibility of interaction" (i.e. forbidden links), adding quantitative measures of interactions might further reflect species preferences and illustrate whether the core of the network also contain the highest frequencies (Almeida-Neto and Ulrich 2011, Staniczenko et al. 2013).

2) Network wide specialization can be estimated both in binary and weighted networks. Binary specialization was quantified as "connectance", i.e. the ratio between the number of realized and possible links in the network. Quantitative specialization was estimated by the H_2' index, which describes how species restrict their interactions from those randomly expected based on partner's availability (Blüthgen et al. 2006).

3) Modularity indices quantify the prevalence of interactions within modules, i.e. subunits in the community, in relation to among module interactions (Q ; binary - Marquitti et al. 2014, weighted - Dormann and Strauss 2014). Olesen et al. (2007) showed that smaller plant-floral visitor networks with less than ~50 species are rarely modular. However, recent studies show that when incorporating quantitative information, i.e. the strength of interactions, functional specialization become more evident and modules are detected even in smaller networks (Dormann and Strauss 2014, Maruyama et al. 2014, Schleuning et al. 2014).

Modularity algorithms used here built on optimization procedures that iteratively try to maximize the modularity index of the final solution (Marquitti et al. 2014, Dormann and Strauss 2014). Importantly, as the algorithm is stochastic, module arrangement as well as the value of Q might vary slightly between runs (Marquitti et al. 2014, Maruyama et al. 2014, Dormann and Strauss 2014). However, since the objective of the procedure is to find the solution with the highest value of modularity, this shortcoming can be minimized by repeating the analysis multiple times and retaining the module conformation which yields the highest Q value (e.g. Schleuning et al. 2014, Maruyama et al. 2014). Here, we ran the analysis 30 times

for each network and kept the module conformation which yields the highest Q value. Additionally, although the Q value quantifies the support of the modular organization of a network, the information it gives is related to overall structure of the network and does not reflect more detailed organization of subunits, e.g. the actual species composition of the different modules. Nevertheless, the detailed organization of species into modules carries important information, since it might reflect functional specialization within communities (e.g. Maruyama et al. 2014) and is regarded as potential co-evolutionary units (Olesen et al. 2007). In this sense, it also illustrates the grouping of species with highest potential to affect each other within the network of interactions. The evaluation on the detailed organization of modules in networks was done only for quantitative networks, as binary networks did not have a modular organization different than expected by random (see Results).

Besides reflecting different properties, calculating both binary and weighted versions of the metrics allow us to better compare our results with two previous studies investigating the effect of merging illegitimate interactions within plant-floral visitor networks (binary nestedness and modularity in Genini et al. 2010, and binary modularity in Yoshikawa and Isagi 2013). All network metrics were calculated using the package *bipartite* in R (Dormann et al. 2008) with the exception of binary nestedness and modularity, for which we used ANINHADO (Guimarães Jr and Guimarães 2006) and the MODULAR software (Marquitti et al. 2014), respectively, and following their default recommendations. Network metrics can be affected by network size, and thus the significance of metrics has to be assessed by comparison with null model networks. For quantitative networks, we used the function *vaznull* in *bipartite* package, which generates simulated matrices with the same marginal totals and connectance as the original network. We estimated the 95% Confidence Interval (CI) for each metric from the simulated values, and a metric value was considered significant if it did not overlap with the CI. The comparison of the Pollination and Visitation networks is

first done by evaluating whether the incorporation of illegitimate interactions change the performance of the metrics in relation to the null model, i.e. their significance. Secondly, we compare the magnitude to which metric values changed after incorporation of illegitimate visits. Although no formal tests are conducted for the metric values, which were impaired by lack of replicates, these procedures are consistent with the two previous studies which evaluated similar questions and to which our results are compared (Genini et al. 2010, Yoshikawa and Isagi 2013).

Finally, in order to link the modularity results to floral traits, we conducted a NMDS for the plant species found in the lowland Atlantic Rainforest similarly to the analysis we did for the literature survey data. Traits used in this second ordination were: floral corolla length, color score, nectar volume and concentration. As in the first NMDS, we kept the three dimensional solution based on the stress value. Additionally, we used the function *envfit* to fit the module identity as a factor into the ordination space. First, we fit the module identity of Pollination network and assessed whether modules can be separated by traits. Afterwards, the same procedure was conducted for the same ordination, but then using the module identity defined by the Visitation network.

Results

Literature survey

We found 114 case studies reporting visits of *P. ruber* to flowers, comprising 100 plant species. From these, three species were excluded as we did not find any information on floral phenotype. From the remaining 97 species, in 16 (16.5%) we lacked some data on nectar, which were treated as missing values in the analysis. In the final dataset, we had species from

27 plant families, with Bromeliaceae (24 species), Rubiaceae (11) and Acanthaceae (10) being the most common families (see Online Resource 1 for details). Of these, 70 (72.2%) species are pollinated, 16 (16.5%) are robbed, and in six (6.2%) species *P. ruber* acts both as pollinator and robber. Additionally, in five (5.1%) species *P. ruber* was reported as nectar thief. The NMDS ordination resulted in a solution with stress of 10.19 ($r^2=0.93$), with axis 1 associated mainly to floral corolla length and nectar volume, axis 2 to color and visitor score, and axis 3 to nectar volume and concentration (Fig. 1). Distinct roles of *P. ruber* (pollinator, robber, and thief) in relation to flowers had better fit to the two dimensional plot of axis 1 and axis 3, in which robbing behavior's centroid was clearly separated from other behavior's centroids along axis 1 (goodness of fit, $r^2=0.22$, $p<0.001$). Since axis 1 is best correlated to corolla length and nectar volume (Pearson's $r>0.66$; Fig. 1), especially the former, nectar robbing associates best to long corolla flowers.

Case study

Our experiment showed that *P. ruber* had a dramatic effect on the availability of nectar in *C. paniculata* flowers (Fig. 2a-2b). It depleted almost all nectar available in the flowers in the early morning (Treatments: $\chi^2=205.22$; $df=2$; $p<0.001$), even before the activity of the other nectar robber, the stingless bee (Time interval: $\chi^2=0.5952$; $df=1$; $p=0.4404$). No interaction between the factors was observed (Treatment*Time interval: $\chi^2=0.092$; $df=3$; $p=0.9928$). Consequently, legitimate visits by hummingbirds to *C. paniculata* were extremely rare, being recorded only four times during our observations (two visits by the Hermit *Ramphodon naevius* and two visits by the Emerald *Thalurania glaucopis*). Of *C. paniculata* flowers sampled throughout the flowering season, 48.9% had robber marks left by *P. ruber*

only, 8.3% had robber marks left by *Trigona* sp. only, and 42.8% had marks left by both *P. ruber* and *Trigona* sp., and we had no records of intact flowers.

Community wide study

The hummingbird-plant network from the lowland Atlantic Rainforest in Picinguaba comprised 15 hummingbird and 44 plant species (Fig. 3). In the Pollination network, *P. ruber* was the species visiting the fifth most number of plant species (degree of 14) and third most in number of individual visits (180) in the network, totaling 1225 records/visits. On the other hand, in the Visitation network *P. ruber* became the hummingbird with third highest degree (23) and second most number of visits (300) in a total of 1346 interaction records. Although illegitimate visits constitute ~ 9% of all interactions, the addition of these had only small effects on network metrics (Table 1). Whether or not metrics depart from randomly obtained values did not change from Pollination to Visitation network. Within metrics with significant values, binary nestedness had an increase of 10.4%, while specialization (H_2') and quantitative modularity increased by 2.0 and 2.2%, respectively (Table 1). The small increase in weighted modularity was associated to the increase in the number of modules, from five to six (Fig. 3). The major change in the module conformation was the emergence of a module containing *P. ruber* as the only hummingbird species, separating it from other hermit hummingbirds with which it composed a single module in Pollination network (Fig. 3).

The NMDS of the floral traits from the lowland Atlantic Rainforest plant community had a stress value of 5.95 ($r^2=0.98$) with axis 1 associated to corolla length and axis 2 to color score and nectar concentration (Fig. 4). Module identities as factors in the multidimensional ordination can be statistically separated when considering the Pollination network (axes 1 and 2: $r^2=0.24$, $p=0.007$; axes 1 and 3: $r^2=0.20$, $p=0.027$). However, modules are not distinct in the

ordination when illegitimate interactions are included (axes 1 and 2: $r^2=0.19$, $p=0.077$; axes 1 and 3: $r^2=0.17$, $p=0.109$).

Discussion

We show that nectar robbing by *P. ruber* is common, especially in long corolla flowers, and has a strong effect on individual plants and their associations with pollinating hummingbirds. Nevertheless, incorporation of illegitimate interactions has small effects on the network metrics. In total, our literature survey - identifying 97 plant species visited by *P. ruber* - shows that in *ca.* 28% of the plants this hummingbird engages in nectar robbery or theft, i.e. illegitimate interactions. This shows that although legitimate and a mutualistic association with plants is the main strategy of *P. ruber*, exploitation is an important strategy to obtain nectar. Floral larceny in hummingbirds has commonly been reported for species of Mangos, Coquettes and Emeralds (Lara and Ornelas 2001 and references therein). The high proportion of plant species in which *P. ruber* acts as an exploiter is surprising for a hummingbird belonging to the clade of Hermits, which is often considered the most specialized group of pollinators within hummingbirds (Feinsinger and Colwell 1978, Sazima et al. 1995, Vizentin-Bugoni et al. 2014, Maruyama et al. 2014). In this sense, we reinforce the notion that nectar use by hummingbirds is more flexible and opportunistic than previously appreciated (e.g. Maruyama et al. 2013a).

This illegitimate strategy adopted by *P. ruber* has the potential to greatly affect the reproduction of plants in which it acts frequently, as we show for *C. paniculata*. Nectar robbers may influence plant reproduction negatively by reducing floral attractiveness to pollinators, but may also have a positive influence by either increasing the number of flowers the pollinators must visit or by increasing travelling distances to obtain their daily energy

requirements (Maloof and Inouye 2000, Irwin et al. 2010). The outcome depends among other factors on the identity of the legitimate pollinators and their ability to discern and avoid robbed flowers, the amount of nectar removed by the robbers and the floral neighborhood, i.e. the availability and attractiveness of other floral resources in the surrounding environment of the robbed species (McDade and Kinsman 1980, Maloof and Inouye 2000). Moreover, the dependence of plants on biotic vectors for reproduction likely plays an important role on the influence of floral larcenists, with pollinator-dependent and self-incompatible species being most negatively affected by nectar robbery (Burkle et al. 2007). At Picinguaba, *P. ruber* depleted almost completely the nectar of *C. paniculata*, which most likely explains the few legitimate visits to these flowers (McDade and Kinsman 1980, Justino et al. 2012). The low frequency of legitimate visits is even more striking when compared to Santa Virgínia, where *P. ruber* is absent and nectar robbers very infrequent (Maruyama et al. 2015b). With the same sampling effort and procedures, there we observed 84 legitimate visits by the Scale-throated Hermit, *Phaethornis eurynome* (Maruyama et al. 2015b), compared to only four legitimate visits observed at Picinguaba. Hummingbirds use several cues to avoid less rewarding robbed flowers (Irwin 2000), and almost complete depletion of nectar by *P. ruber*, combined with the high availability of other flower resources in Picinguaba (Fig. 3), makes *C. paniculata* less attractive to legitimate pollinators. Since *C. paniculata* is a self-compatible but pollinator-dependent species (Maruyama et al. 2015b), an expected outcome is that decreased visitation rates caused by nectar robbing would decrease plant reproduction (Burkle et al. 2007).

In contrast to the strong effect at individual plant species, the incorporation of illegitimate interactions had overall small effect on network structure (Table 1). Previous studies which contrasted networks with and without flower exploiters found more striking differences than in our case (Genini et al. 2010, Yoshikawa and Isagi 2013). This may be related to the relative proportion of exploiters in the networks, as one of the two systems

evaluated by Genini et al. (2010) also had few exploiters and less changes in the network structure. Previously reported increase in modularity and specialization when merging mutualistic and antagonistic interactions is attributed to higher specialization of antagonistic interactions, which may contribute to overall increase in network level functional specialization (Genini et al. 2010, Fontaine et al. 2011, Yoshikawa and Isagi 2013). In our study, binary nestedness increased the most and likely reflects the increased level of generalization of *P. ruber*, making it one of the "core generalist" species in the Visitation network. Our results indicate that one species, even though common and interacting frequently and widely with the plant assemblage, has limited influence on network metrics, i.e. how we characterize the overall structural properties of a network. This might be the case especially if the floral visitor has a dual role as both pollinator and an exploiter.

Although the overall network structural changes were small, the incorporation of illegitimate visits by *P. ruber* nevertheless changed the conformation of modules in the network (Fig. 3) and the trait distribution within modules (Fig. 4). Modules are regarded as "subcommunities within communities", in which tightly linked species have stronger influence among them than with species in other modules (Olesen et al. 2007). Hence, how modules are characterized in the network incorporating illegitimate visits can present complementary information on how species affect each other. For instance, it is reasonable to conclude that *P. ruber* has a strong influence on plant species that are "pulled away" from other modules into the new module with *P. ruber* in the Visitation network. For instance, our case-study species *C. paniculata* was included in module B in the Pollination network, but as interaction frequency with *P. ruber* is much higher than with the legitimate pollinators, in the Visitation network it is assigned to module A. To show this change may contribute to better represent the influence of the floral visitors and potentially of other plant species to our focal species. This interpretation is strengthened by the strong effect on the nectar standing crop

caused by *P. ruber*. We might expect similar effects for other plant species in which robbing is much more frequent than legitimate interactions (e.g. *Ruellia elegans* Poir, Acanthaceae). Finally, the separation of modules in the ordination space by considering the Pollination network but not the Visitation network reflects different rules by which specific pair-wise interactions occur. While the legitimate pair-wise interactions in plant-hummingbird networks are strongly influenced by morphological matching (Maruyama et al. 2014, Vizentin-Bugoni et al. 2014), by definition floral larcenists ignore the barriers imposed by plants to exploiters. Probably, this is the reason why floral traits explain modules less well in the Visitation network including illegitimate interactions.

Conclusion

We conclude that floral larcenists may have strong effects on nectar availability and pollination of particular plants and often are associated with long corolla flowers. Since species from several hummingbird clades switch between pollination and nectar robbing, hummingbirds may offer an interesting system for studying the evolutionary correlates of mutualism exploitation (see Bronstein 2001, Irwin et al. 2010). In contrast to previous studies, we show that network metrics are not strongly affected when including illegitimate interactions. Nevertheless, if detailed outcome for specific interactions or within module organization are considered, floral larcenists have the potential to affect the functioning of communities (e.g. community level seed production). To better understand the functioning of flower-floral visitor networks including floral larcenists, future studies could employ experimental manipulations at community level. Although it is prohibitive to actually manipulate an entire community of pollinators and plants, such studies could employ a subset of species and manipulate the presence of floral larcenists. In such a framework it would be

possible to evaluate how larcenists affect the interaction of other species as well as their functional outcome, for example on the fruit set. Only few recent studies had taken such an experimental approach (e.g. Brosi & Briggs 2013, Fründ et al. 2013), but whether or not floral larcenists affect other species' foraging behavior, as likely they do, and consequently the network structure remains to be investigated.

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Table 1. Network metrics for the Pollination network (PN) in which only legitimate hummingbird visits were considered and for the Floral Visitation network (VN) in which illegitimate visits, including nectar robbery and theft, were also included. The third column shows the proportional increase of the network metrics (from PN to VN) in relation to values observed for PN. The asterisk indicates significant network metrics, i.e. metrics that did not overlap to null model expectations (95% CI).

Network metrics	PN	VN	Inc. (%)
NODF	29.88*	32.98*	10.4
WNODF	30.86	32.90	6.6
Connectance	0.21	0.22	4.8
H ₂ '	0.49*	0.50*	2.0
Modularity (binary)	0.30	0.30	0.0
Modularity (weighted)	0.46*	0.47*	2.2

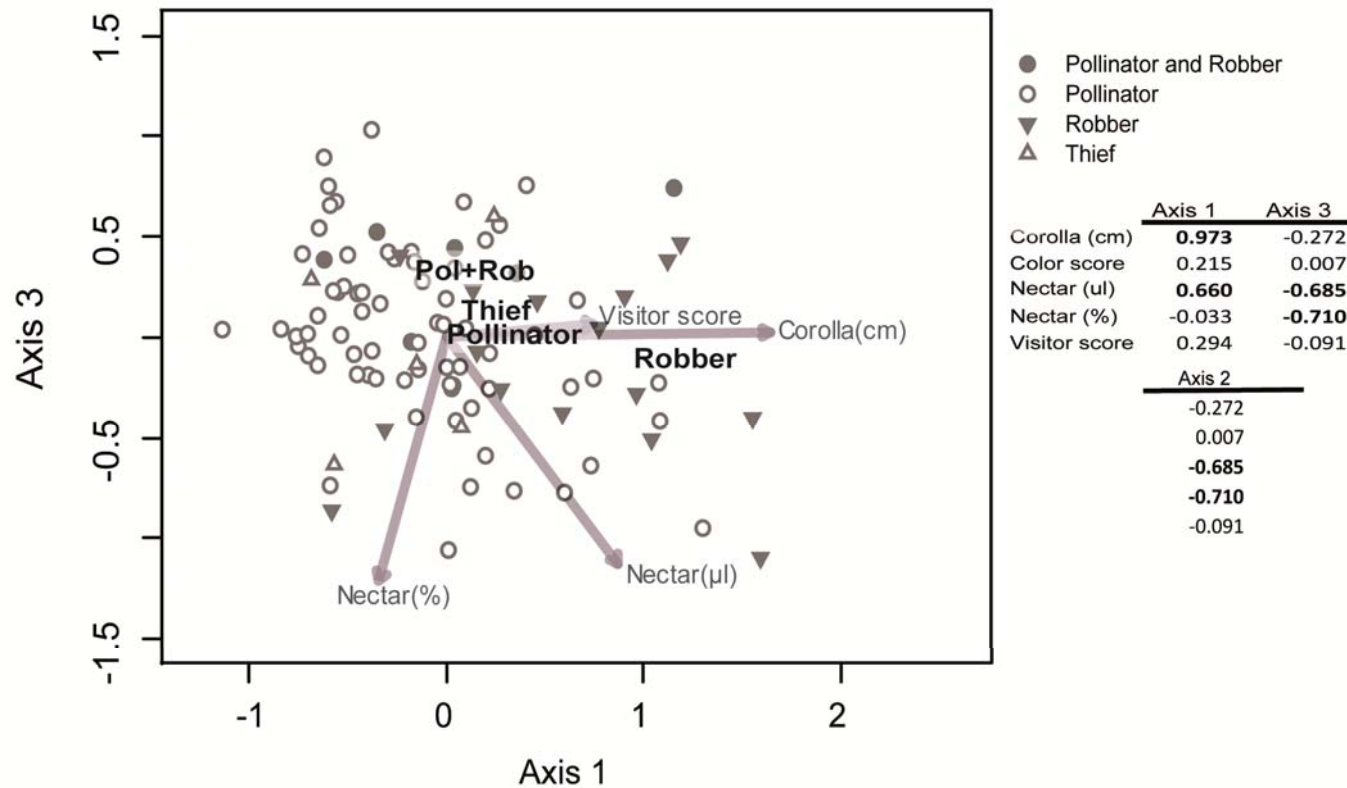


Fig. 1 Nonmetric Multidimensional Scaling of 97 plant species for which interaction records with *Phaethornis ruber* were obtained in our literature survey (stress = 10.19 and $r^2=0.93$). Axis 1 was rotated according to floral corolla length, and is shown together with axis 3, which better separated *P. ruber* behaviour. At right, the Pearson's correlation coefficient of the floral traits and visitor scores in relations to all three axes, with values in bold indicating significant and strong correlations ($|r|>0.65$). The plot with axes 1 and 3 is shown since it better illustrates the separation of *P. ruber* behaviors

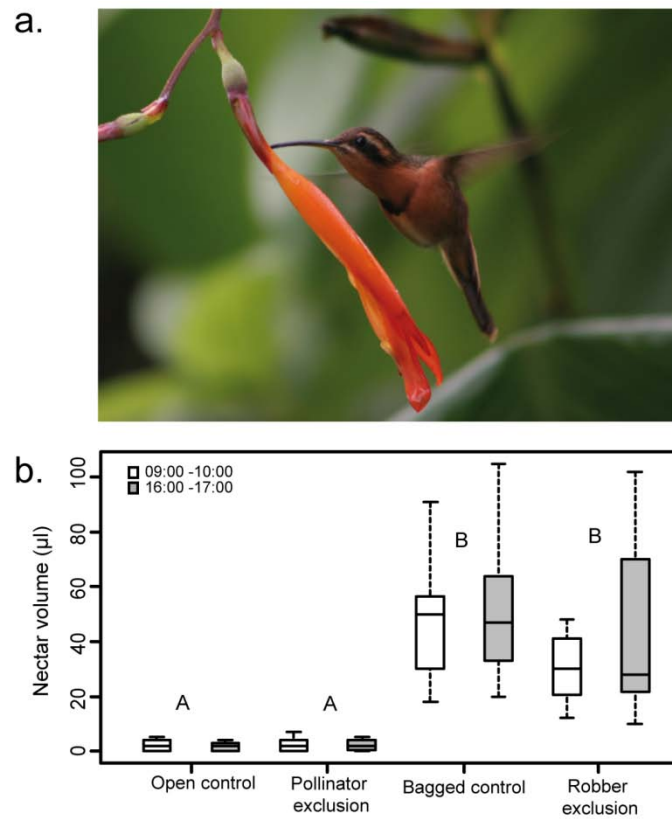


Fig. 2 a) Nectar robbing by *Phaethornis ruber* in *Canna paniculata*. b) Results from nectar robber exclusion experiments in *C. paniculata* which show the intensity of nectar volume depletion. Different letters indicate significant differences by *post hoc* Tukey test. The horizontal line in the boxes indicate the median for each treatment with upper and lower limits of the boxes indicating the lower and upper quartiles (25 % and 75 % respectively)

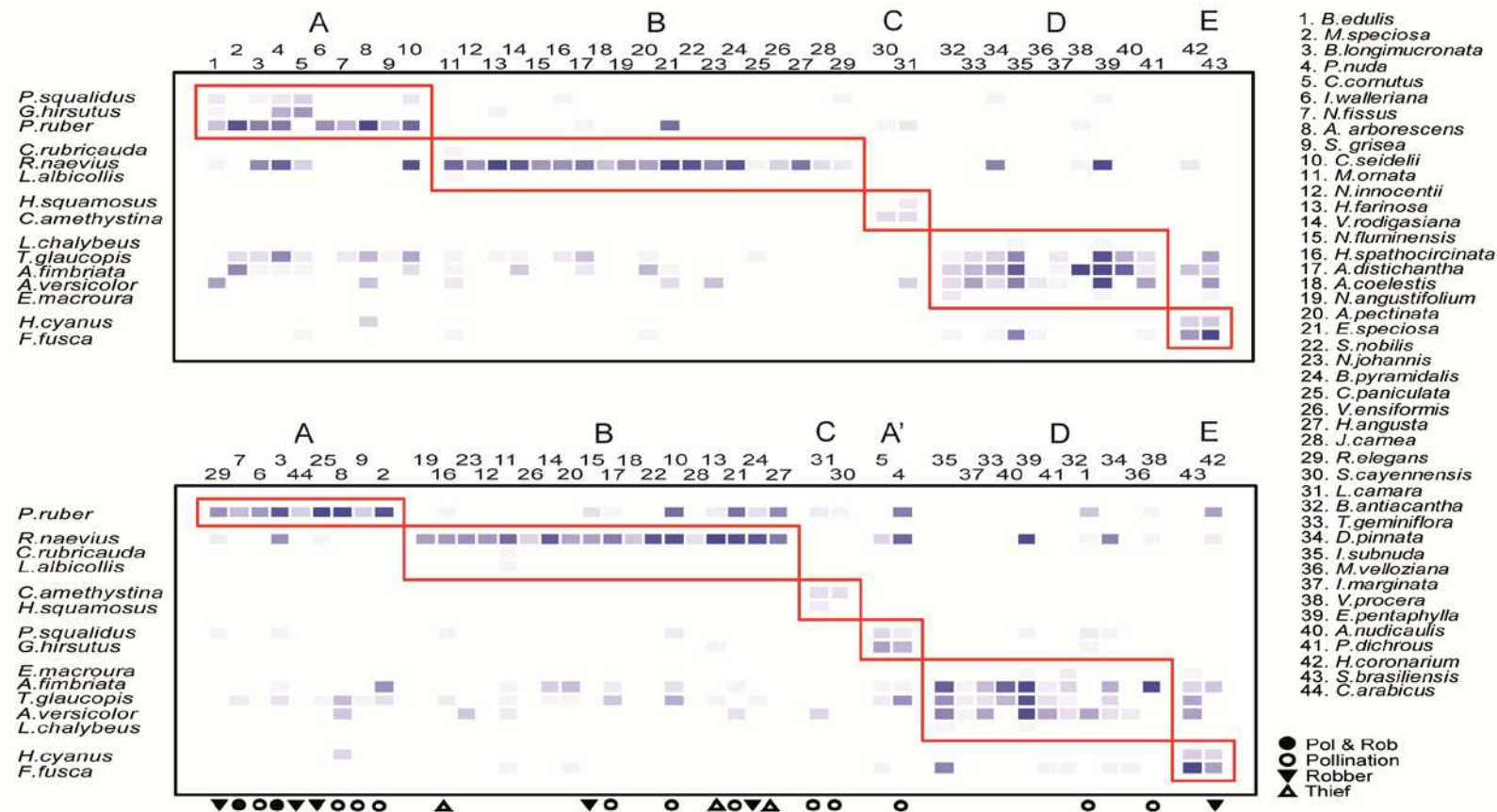


Fig. 3 Modules in the plant-hummingbird visitor network from Picinguaba, southeastern Brazil. Top matrix - Pollination network (PN) with only legitimate interactions. Bottom matrix - Visitation network (VN) also incorporated illegitimate interactions (nectar robbing and thieving). The capital letters above the matrices denote identities of modules in the networks. Note that the original module A is separated into two modules (A and A') when illegitimate visits are included. The module A in the bottom matrix has only *P. ruber* as floral visitor. In this new module (A') *P. ruber* is associated to several plants which in the top matrix belonged to modules with other hummingbird species

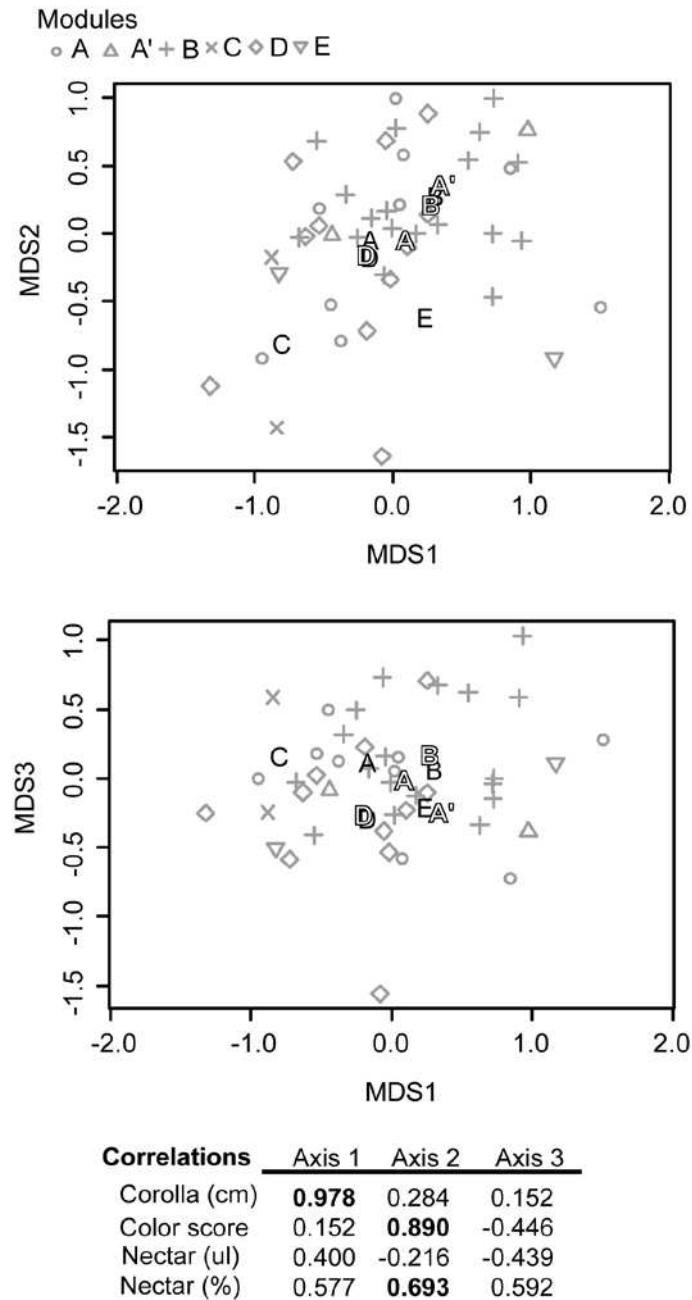


Fig. 4 Nonmetric Multidimensional Scaling of floral traits of plants from Picinguaba, southeastern Brazil (stress = 5.95 and $r^2=0.93$). Points represent plant species, while the letters indicate the floral phenotypic mean of each module. Module identities were fitted as factors in the multidimensional ordination (capital letters). Black letters indicate modules in Pollination networks (PN) while unfilled letters show module identities in the Visitation networks (VN), whenever species composition changes. Modules in PN can be statistically separated (axes 1 and 2: $r^2=0.24$, $p=0.007$; axes 1 and 3: $r^2=0.20$, $p=0.027$) but not in VN (axes 1 and 2: $r^2=0.19$, $p=0.077$; axes 1 and 3: $r^2=0.17$, $p=0.109$). Pearson's correlation coefficient of the floral traits and three axes are shown below the plots, with values in bold indicating significant and strong correlations ($|r|>0.65$)

CAPÍTULO 2

Pollination and breeding system of *Canna paniculata* (Cannaceae) in a montane Atlantic Rainforest: asymmetric dependence on a hermit hummingbird

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Abstract

We studied the pollination biology of *Canna paniculata* (Cannaceae), a common plant species in the Atlantic Rainforest of southeastern Brazil. The species presents specialized ornithophilous flowers, which in our study area are solely pollinated by the hermit hummingbird *Phaethornis eurynome*. Although *C. paniculata* is capable of bearing fruit after self-pollination, it requires pollinators for reproduction. We discuss the importance of hermit hummingbirds for the reproduction of specialized ornithophilous plants such as *C. paniculata*, including their asymmetric dependence on hermit hummingbirds - core pollinators in Neotropical forest ecosystems.

Keywords: hummingbirds, ornithophily, *Phaethornis eurynome*, Serra do Mar, Zingiberales

Hummingbirds arrived in South America some 22 million years ago (McGuire *et al.* 2014) and have since become the most important avian pollinator group in the Neotropics (Cronk & Ojeda 2008). As a result of this strong mutualistic association between hummingbirds and plants, numerous plant groups have achieved remarkable diversity (e.g., Schmidt-Lebuhn *et al.* 2007). More comprehensive information on pollination and reproductive biology for plants belonging to some of these groups are now available, such as the study by Matallana *et al.* (2010) for Bromeliaceae. Zingiberales is another monocot plant clade in which bird pollination is common (Cronk & Ojeda 2008), and although the pollination systems for some of the families within this group have been thoroughly studied (e.g., Costaceae, Kay & Schemske 2003; Heliconiaceae, Stiles 1975; Zingiberaceae, Sakai *et al.* 1999) data are still lacking for other groups. *Canna* L. is the only genus in Cannaceae and constitutes a conspicuous element in forests of the New World, where it is native, and in the Asian Paleotropics, where it has been introduced by humans (Prince 2010). The center of diversity of the family is South America (Prince 2010), and the species exhibit highly modified flowers, with the development of a colorful androecium and gynoecium with petaloid structures (Glinos & Cocucci 2011). Through a process known as “secondary pollen presentation”, the region below the apical and at the side of the lateral portion of the stigma acts as the pollen-dispensing structure, which demonstrates the unusual mechanism by which plants of the family achieve pollination (for details see Glinos & Cocucci 2011). Nevertheless, besides the aforementioned study, which detailed the functional adaption of this unusual floral morphology for *Canna indica* L. (Glinos & Cocucci 2011), we are unaware of other detailed studies on the pollination and reproduction for other species in the *Canna* family. Here, we report the pollination biology of *Canna paniculata* Ruiz & Pav. from a montane Atlantic Rainforest area in southeastern Brazil. This species occurs in scattered localities at low to mid elevation (<2,000 m) throughout the wetter areas of the Neotropics, ranging from Panama in the north to southeastern Argentina (Prince 2010).

We studied *C. paniculata* at the Santa Virgínia Field Station (23°20'10"S and 45°8'46"W, 916–950 m above sea level), located in Serra do Mar State Park in the state of São Paulo, Brazil, where *C. paniculata* is particularly common. Fieldwork was conducted during the flowering season of *C. paniculata* (June–September) in 2012 and 2013. Flowers were accompanied during anthesis and collected for morphological measurements (n = 10, one for each individual). Individuals were defined as clumps at least 5 m apart as the plant presents clonal growth. For all floral measurements, we used a digital caliper (error = 0.01

mm). In order to characterize the breeding system of *C. paniculata*, we conducted controlled pollination experiments with the following treatments: 1) manual “cross-pollination” (crossing between flowers from different individuals); 2) manual “self-pollination” (pollination within the same flower); 3) “spontaneous self-pollination” (flowers kept isolated in nylon mesh bags); 4) “agamospermy” (flowers emasculated before opening and kept isolated); and 5) marked control flowers open to visitation to estimate “natural pollination”. All treatments were distributed as much as possible among 22 individuals within the study area, and only flowers at the first day of opening were used in the treatments. The fruit set was evaluated two months after the experiments. In order to quantify the volume of nectar produced and its concentration at the end of the day (~17:00), flowers were bagged before opening with nylon mesh bags and nectar was measured using a microsyringe and a pocket refractometer (Eclipse ® 0–50 brix; $n = 17$ flowers from 12 individuals). We also conducted 60 hours of plant focal observations in eight individuals from 06:00 to 18:00 to identify the pollinators of *C. paniculata*.

C. paniculata presents red-orange flowers with traces of yellow (Fig. 1A) and individual clumps offer 4.3 ± 3.9 (range of 1–20) flowers per day during the flowering period. The opening of flowers started early in the morning before sunrise (~06:00) and lasted until the afternoon of the second day (~16:00), i.e., flowers lasted roughly 1½ days. As reported for other members of the family (Glinos & Cocucci 2011), *C. paniculata* showed secondary pollen deposition at the side of the flattened style, where pollen is deposited by the single theca in an elliptical clump. Flowers measure *ca.* 6 cm in total length, but the actual restriction to the pollinator, i.e., the corolla tube, amounts to 4.07 ± 1.03 cm in length with 0.51 ± 0.12 cm of opening. Controlled pollination experiments showed that *C. paniculata* is able to produce fruits after self-pollination, although the fruit set is less than half in comparison to cross-pollinated flowers (Table 1). Moreover, this species requires pollinators to bear seeds, as no fruit was set after spontaneous self-pollination or agamospermy. Flowers exposed to natural pollination had two times more fruit set than self-pollinated flowers, but 13.8% less than cross-pollinated flowers (Table 1). Nectar production amounted to 45.0 ± 34.5 µl, with sugar concentration of $23.4\% \pm 3.11\%$. During focal observations, the only pollinator observed was the Scale-throated hermit, *Phaethornis eurynome* (Lesson 1832), which visited individuals of *C. paniculata* 84 times (1.40 ± 0.94 visits/hour). This species seemingly acted as a “trapliner”, returning at the same clump of flowers at roughly regular intervals (see Stiles 1975). When approaching the flower, the hummingbird first touched the tip of the stigma (i.e.,

the receptive region, see Fig. 1A, marked with an arrow) with its head, and subsequently, the clump of pollen deposited in the flattened style was pressed against the head of the pollinator (Fig. 1B, marked with an arrow). During our fieldwork, we also noted that stingless bees, *Trigona* sp., robbed nectar from approximately 20.8% (n = 250) of flowers.

Despite being a widespread group in the tropics, this is only the second detailed report on pollination and breeding biology for a *Canna* species. Hummingbird pollination seems to be common for species in the genus, but presumably the one species occurring in North America, *C. flaccida* Salisb., is pollinated by nocturnal moths (Prince 2010). *C. indica* is also pollinated by a single species of hummingbird in Argentina, the Blue-tufted starthroat, *Heliomaster furcifer* (Shaw 1812), from the Mountain gems clade (Glinos & Cocucci 2011). The prevalence of hummingbird pollination (or other birds in introduced areas) in Cannaceae requires further investigation. The identity of *C. paniculata*'s sole pollinator and external morphological characteristics of the flowers conform to the classical notion of ornithophily, and this is reinforced by the presence of abundant and diluted nectar similar to other ornithophilous species (Cronk & Ojeda 2008). Moreover, bird pollination in other groups within Zingiberales resembles the adaptations found in *C. paniculata*. For instance, in *Costus* L. (Costaceae), adaptation to hummingbird pollination is achieved by narrow, long tubular flowers with brightly colored bracts (yellow, orange, or red), which present copious amounts of nectar (Kay & Schemske 2003). Similar traits are found for hummingbird pollinated Heliconiaceae in wet forests of Costa Rica (Stiles 1975). In the Bornean Zingiberaceae, sunbird-pollinated species also presented long tubular corollas with conspicuous colors (often red), and with copious production of more diluted nectar in relation to insect pollinated species (Sakai *et al.* 1999). Altogether, these parallels reinforce the association of some prominent floral traits to specialized bird pollination within Zingiberales.

Although both *C. indica* and *C. paniculata* have similarly elongated corolla flowers, differences in pollinating hummingbird species imply distinct areas of pollen deposition. For a non-hermit species, *H. furcifer* has a long bill of 2.8 ± 0.2 cm in length, enabling it to access the nectar in the flower. However, because its bill is straight (Glinos & Cocucci 2011), during its visits the bill is tightly encased in the slightly curved floral tube, and pollen is deposited on the hummingbird's bill when it forces its way out of this "entrapment" (Glinos & Cocucci 2011). In *C. paniculata*, pollination is carried out by the hermit *P. eurynome* with a curved bill of 3.4 ± 0.1 cm (Vizentin-Bugoni *et al.* 2014; Fig. 1C), which promotes a good fit to the long, slightly curved corolla of the flower.. While visiting the flower, the head of the

hummingbird often touches the receptive part of the stigma first, and thereafter it comes into contact with the pollen (Fig. 1A, C). Although this does not ensure cross-pollination, since an individual plant can present more than one open flower at a time, chances of self-pollination are at least diminished.

Considering the breeding system, *C. paniculata* can be regarded as self-compatible (with an Index of Self-Incompatibility of 0.36—estimated as the division of the fruit set through self-pollination by cross-pollination, as in Wolowski *et al.* 2013), similar to other groups of monocots strongly associated to hummingbird pollination such as the bromeliads (Matallana *et al.* 2010) and hummingbird pollinated plants in general (Wolowski *et al.* 2013). Nevertheless, *C. paniculata* requires pollinators to set fruits, characterizing its dependence on pollen vectors. Naturally pollinated (i.e., control) flowers show *P. eurynome* as a relatively good pollinator, being able to set more fruits than when self-pollinated, even though pollination success is not as high as hand cross-pollination. The distinctive traplining behavior of hermit hummingbirds, as we may also infer for *P. eurynome*, is expected to increase the rates of outcrossing (Stiles 1975), which also characterizes hermit hummingbirds as relatively efficient pollinators. This is further supported if one considers that for *C. indica* pollinated by *H. furcifer*, a presumably territorial hummingbird, fruit set in control flowers was only 20% in comparison to 86% in hand crossed flowers (Glinos & Cocucci 2011). These results illustrate the link between distinct hummingbird behaviors (e.g., territorialism) and pollination success (Justino *et al.* 2012).

At the community level, in the studied montane Atlantic Rainforest site, *P. eurynome* is a “core” hummingbird pollinator, interacting with more plant species than any other hummingbird species, and being the sole pollinator of many long-tubed flowers; at least 24 other plant species, 15 of which have overlapping flowering with *C. paniculata* (Vizentin-Bugoni *et al.* 2014). Similar community organization is found in lowland Atlantic Forest areas, where the Saw-billed hermit *Ramphodon naevius* (Dumont 1818) is solely responsible for the pollination of the more specialized long-tubed flowers (Sazima *et al.* 1995). Also in the Neotropical savanna, where patches of forest habitats are found embedded in the landscape, similar organization can be seen, where the Planalto hermit *P. pretrei* (Lesson & Delattre 1839) interact with the more specialized flowers (Maruyama *et al.* 2014). In summary, this suggests that there is an asymmetrical interaction among hermit hummingbirds and the plant species they pollinate. While many plant species (such as *C. paniculata*) depend on only one hermit hummingbird species for their reproduction, each plant species alone

potentially has less importance for the hermit hummingbirds that pollinate them. Although this asymmetry between interacting plants and hummingbirds might vary between communities (see Maruyama *et al.* 2013a), it should have strong implications for the structure and dynamics of the entire plant-hummingbird community, and hence, deserves further investigations.

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Table 1. Fruit set after controlled pollination experiments and natural pollination in *Canna paniculata* Ruiz & Pav. (Cannaceae) at the Santa Virgínia Field Station, Serra do Mar State Park, São Paulo, Brazil.

Pollination treatment	% (Flowers)
Cross-pollination	53.8 (n = 52)
Self-pollination	19.2 (n = 52)
Spontaneous self-pollination	0.0 (n = 65)
Agamospermy	0.0 (n = 58)
Natural pollination	40.0 (n = 70)



Figure 1. A, *Phaethornis eurynome* (Lesson 1832), visiting the flower of *Canna paniculata* Ruiz & Pav. Note the head of hummingbird contacting the apical receptive part of the stigma (arrow) when approaching the flower. B, When the bill is completely inserted in the corolla, the hummingbird's head makes contact with the flattened part of the style (arrow), which acts as secondary pollen presenter. C, In detail, the long and curved bill of *P. eurynome*.

CAPÍTULO 3

Morphological and spatio-temporal mismatches shape a neotropical savanna plant-hummingbird network†

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ABSTRACT

Complex networks of species interactions might be determined by species traits but also by simple chance meetings governed by species abundances. Although the idea that species traits structure mutualistic networks is appealing, most studies have found abundance to be a major structuring mechanism underlying interaction frequencies. With a well-resolved plant-hummingbird interaction network from the Neotropical savanna in Brazil, we asked whether species morphology, phenology, nectar availability and habitat occupancy and/or abundance best predicted the frequency of interactions. For this, we constructed interaction probability matrices and compared them to the observed plant-hummingbird matrix through a likelihood approach. Furthermore, a recently proposed modularity algorithm for weighted bipartite networks was employed to evaluate whether these factors also scale-up to the formation of modules in the network. Interaction frequencies were best predicted by species morphology, phenology and habitat occupancy, while species abundances and nectar availability performed poorly. The plant-hummingbird network was modular, and modules were associated to morphological specialization and habitat occupancy. Our findings highlight the importance of traits as determinants of interaction frequencies and network structure, corroborating the results of a previous study on a plant-hummingbird network from the Brazilian Atlantic Forest. Thus, we propose that traits matter more in tropical plant-hummingbird networks than in less specialized systems. To test the generality of this hypothesis, future research could employ geographic or taxonomic cross-system comparisons contrasting networks with known differences in level of specialization.

Key words: Cerrado; forbidden links; habitats; modules; phenology; pollination; QuanBiMo.

SPECIES ARE PART OF COMPLEX NETWORKS OF INTERACTIONS THAT STRUCTURE ECOLOGICAL COMMUNITIES. However, the mechanisms determining the occurrence and strength of species interactions in local communities remain debated (Vázquez *et al.* 2009b, Olesen *et al.* 2011, Junker *et al.* 2013, Vizentin-Bugoni *et al.* 2014). Much of this debate has been centered on the importance of species traits, such as floral corolla and pollinator mouthpart length or fruit and the bill gape size of frugivore birds (Olesen *et al.* 2011, Vizentin-Bugoni *et al.* 2014). Furthermore, because species should occur in the same location and at the same time to interact, spatio-temporal mismatches among species may also determine the structure and dynamics of ecological networks (Morales & Vázquez 2008, Vázquez *et al.* 2009a, b, Olesen *et al.* 2011, Vizentin-Bugoni *et al.* 2014). In ecological networks, species traits constraining interactions are often referred to as ‘forbidden links’ (Olesen *et al.* 2011), although this term may better relate to the incidence of interactions (binary networks), and not necessarily their strength (weighted networks). Several recent studies, however, have shown that species abundances can be as important, or even more important, than species traits in structuring ecological interaction networks, including plant-frugivore (Krishna *et al.* 2008), plant-pollinator (Vázquez *et al.* 2009b), host plant-epiphyte (Sáyago *et al.* 2013) and plant-ant interaction networks (Dáttilo *et al.* 2014).

Although current evidence supports a large importance of abundance in shaping interaction networks, it is noteworthy that a recent study of a specialized plant-hummingbird network in the Brazilian Atlantic Forest showed mismatches in species morphology and phenology as the major factors structuring interactions (Vizentin-Bugoni *et al.* 2014). It remains to be investigated if this unique result is due to the intrinsic nature of the system considered. However, the result is consistent with natural history knowledge that interactions between tropical plants and hummingbirds are indeed determined by species traits, including

plant and hummingbird morphology, nectar availability, and hummingbird foraging behavior (Stiles 1975, Feinsinger & Colwell 1978, Dalsgaard *et al.* 2009). Here we use a plant-hummingbird network to further understand the factors shaping plant-pollinator interaction networks. Besides species morphology and phenology, we also evaluated the effect of floral nectar availability, which commonly affects hummingbird visitation pattern (*e.g.*, Justino *et al.* 2012) and spatial co-occurrence via habitat occupancy (see also Jordano *et al.* 2006, Morales & Vázquez 2008, Vázquez *et al.* 2009a).

By limiting the occurrence of pairwise interactions, morphological traits, as well as phenological and spatial constraints might also ‘scale-up’ to the formation of sub-community structure within an ecological network, *i.e.*, modules characterized by high within-module prevalence over between-module interactions (Dormann & Strauss 2014). Modules in pollination networks are proposed to reflect specialized functional groups of pollinators and floral traits, which may determine the subset of preferentially interacting species (Olesen *et al.* 2007, Danieli-Silva *et al.* 2012) or seasonality in floral and pollinator appearance, *i.e.*, phenological matching (Martín González *et al.* 2012). Although modularity is common in plant-pollinator networks, we know surprisingly little about the role of species traits and spatio-temporal occurrence as determinants of modules. Furthermore, virtually all information is based upon binary networks (*e.g.*, Olesen *et al.* 2007, Martín González *et al.* 2012, Danieli-Silva *et al.* 2012, Dalsgaard *et al.* 2013).

In this study we used data on the interactions between hummingbirds and their flowers from one locality in the Cerrado, the Neotropical savanna ecosystem in the central portion of Brazil. The Cerrado is a clear example of a complex and patchy ecosystem (Silva & Bates 2002), in which the mosaic of distinct habitats is connected by the movement of species, especially highly mobile avian species (Tubelis *et al.* 2004, Maruyama *et al.* 2013b). In this sense, it provides a good model system to test if species’ spatial distribution is an important

factor in determining patterns of species interactions in ecological communities in addition to species traits, phenology and abundance. We use the recently proposed QuanBiMo algorithm to compute and define modules in weighted bipartite networks (Dormann & Strauss 2014) and probability matrices to predict the important factors influencing interaction frequencies (Vázquez *et al.* 2009b). We addressed two questions: (1) what is the relative importance of species abundance, morphological matching, phenological overlap, habitat occupancy, and floral energy/nectar production in determining interaction frequencies? (2) Do the observed modules associate to the same properties relevant for predicting interaction frequencies?

METHODS

STUDY SITE.—We collected data at Panga Ecological Station (hereafter ‘Panga’; 19°10'27"S, 48°23'51"W) in Brazil. Panga covers approximately 400 ha and includes many plant formations that characterize the Cerrado ecosystem, from grasslands and open savannas to dense forest formations. The climate is seasonal, characterized by a warm rainy season from October to March and a cooler dry season from April to September. The mean monthly temperature is 22.8 °C and mean annual precipitation is 1482 mm (Cardoso *et al.* 2009).

PLANT-HUMMINGBIRD INTERACTIONS AND ABUNDANCE.—Sampling took place every other week from November 1996 to November 1997, mostly from 0600–1200 h. The overall flower availability, hummingbird abundance, and all plant-hummingbird interactions were quantified. We collected data on flower-hummingbird interactions along transects separated from each other by at least 25 m. We placed these transects in open savanna (11 transects of 50 m × 8 m) and in forest formations (10 transects of 50 m × 8 m). In addition, we placed two transects at the forest edge, one in the forest-savanna transition (165 m × 8 m), and another (200 m × 8 m) along the stream bordering the reserve. Sampled area varied between habitats

according to their relative area: a total of 4400 m² in open savanna, 4000 m² inside the forest, and 2920 m² on the forest edge. We defined a visit by a hummingbird to a plant as the moment the hummingbird started probing the flowers until the moment it left the plant. Plant species were included in the network as long as they received legitimate visits by hummingbirds, regardless of whether they conformed to the classical ornithophilous syndrome (Maruyama *et al.* 2013a). To ensure that our sampling was sufficient, we performed an individual-based rarefaction analysis, replacing the number of individuals and species by the number of interactions and each pairwise combination of species (Gotelli & Colwell 2001).

We quantified plant abundance as the total number of flowers produced by each plant species over the study period in the same transects interaction data were collected. We estimated hummingbird abundance visually while walking along transects and following the ‘line transect count’ method (Bibby *et al.* 2000). Counting was mostly restricted to records obtained within the transect width, ensuring comparability among habitats. More details on the sampling procedures, including morphological traits assessments and total focal hours spent on each plant species, can be found in Maruyama *et al.* (2013a).

CONSTRUCTING AND CONTRASTING PROBABILITY MATRICES OF INTERACTIONS.—We evaluated which factors contributed in structuring the observed interactions between flowers and hummingbirds by constructing interaction probability matrices and comparing those with the observed interaction matrix through a likelihood approach, as proposed by Vázquez *et al.* (2009b) and following the modifications in Vizentin-Bugoni *et al.* (2014). The observed matrix (O) is a quantitative plant-pollinator interaction matrix with rows corresponding to plant species (*i*) and columns to pollinators (*j*). Each cell entry is the number of interactions (visits) recorded between a given hummingbird and plant species (*o_{ij}*). The probability matrix based on abundance (A) was constructed as the product of flower abundance per plant species

by the abundance of each hummingbird species. The cell values in this matrix are the pairwise product of each plant-hummingbird pair.

To determine the role of temporal match, we constructed the probability matrix based on phenological overlap (F) with cell entries expressing the number of months a plant and a hummingbird co-occurred over the sampling period. Hummingbird bill length and flower corolla length were used to construct the probability matrix based on morphological match (M). An interaction was considered as possible, and the corresponding cell filled with one, if a given hummingbird species have a bill equal or longer than the flower corolla length. To account for hummingbird tongue extension capacity, we calibrated this measure by adding a conservative value of one third to the actual bill length (as in Vizentin-Bugoni *et al.* 2014). Data on hummingbird bill length and floral corolla length were extracted from previous studies from the same region (Grantsau 1989, Justino *et al.* 2012, Araújo *et al.* 2013, Maruyama *et al.* 2013a). Two species of plants (*Heliconia psittacorum* L.f. and *Ruellia brevifolia* (Pohl) C. Ezcurra) had longer corollas than the bill length of one of the hummingbird species they interacted with (*Thalurania furcata* [Gmelin, 1788]). In these two cases we believe that the broader corolla opening in the flowers allows visits of hummingbirds with shorter bills than the corolla length (see also Araújo *et al.* 2013). Therefore, in the matrix M, interaction of these two plant species with all other non-hermit hummingbirds were allowed, since they all have similar bill length as *T. furcata*. The sole hermit hummingbird in our study, *Phaethornis pretrei* (Lesson & Delattre, 1839), has a longer bill length and also visited these two species.

In addition to the above-mentioned parameters previously evaluated by Vizentin-Bugoni *et al.* (2014) for another plant-hummingbird network, we also considered the potential role of floral nectar production and habitat (spatial) overlap on species interactions. The effect of nectar availability on hummingbird behavior can be complex, with unique responses of

each hummingbird species at different scales (Dalsgaard *et al.* 2009, Justino *et al.* 2012, Maruyama *et al.* 2013a). Thus, we constructed several different probability matrices to evaluate the role of nectar availability (N1-N4). Data on nectar and flower production for the plant assemblage can be found elsewhere (Maruyama *et al.* 2013a) and sugar content was estimated from these nectar parameters following Galetto and Bernaderllo (2005). The first nectar availability probability matrix (N1) was constructed based on the average amount of sugar a single flower of each plant species produced, while for the second matrix (N2) we multiplied this value by the number of flowers produced per day for an average plant individual during flowering peak. In these two matrices all plant species have a unique value corresponding to their resource availability, *i.e.*, all hummingbird species have the same probability to interact with a given plant species. The more resource a plant produce, the higher the probability of interaction, which is consistent with empirical data for hummingbird-flower relationships (*e.g.*, Justino *et al.* 2012).

We also constructed two more matrices (N3, N4) combining the hummingbird weight to nectar availability in an attempt to incorporate species-specific differences among hummingbird species in the probability of the interactions. For this, we took the two previously mentioned nectar matrices and multiplied their cell entries by the corresponding hummingbird species' weight. Larger hummingbirds therefore had higher probability of interacting with plants, especially those with flowers providing greater rewards. Smaller hummingbirds had lower probability of interaction, but interacted more frequently with more rewarding flowers. The underlying assumption here is that larger hummingbirds requires more energy and are also able to exclude, through aggressive behavior, smaller hummingbirds from more rewarding plants (*e.g.*, Feinsinger & Colwell 1978, Justino *et al.* 2012). Thus, we had four probability matrices considering nectar production, two considering only plant nectar production data (N1, N2) and two incorporating hummingbird weight (N3, N4) that differed

in the scale of the nectar availability considered: at flower (N1, N3) or plant individual level (N2, N4). The habitat/spatial overlap matrix (H) was constructed by calculating the relative abundance of each species in the three habitats (savanna, forest interior and forest edge) from the species total abundances (Table S1). Then, for each hummingbird-plant species pair, we calculated the Pianka's index of niche overlap using the package *spaa* (Zhang 2013) for the R programming language (R Development Core Team 2012). The entry in each cell in the matrix is the pairwise value of Pianka's index, with 0 indicating no overlap and 1 expressing total overlap in habitat use.

All matrices (A, F, M, N, H) were normalized by dividing each cell by the matrix sum so as to minimize the difference in the variation on the cell entries among different matrices. Based on above-mentioned matrices, we also constructed probability matrices using combinations among them by the Hadamard (element-wise) product, which were likewise normalized after the multiplication. Finally, a null matrix (NULL) in which all plant and hummingbird species have the same probability of interaction was considered as a benchmark for comparison with all other probability matrices. The ability of individual parameters and parameter combinations to predict the observed interaction frequencies was evaluated through a likelihood approach with calculation of Akaike Information Criteria (AIC) and Δ AIC, assuming that the probability of interaction between a given plant and hummingbird species followed a multinomial distribution (Vázquez *et al.* 2009b). The likelihood was calculated using the function *dmultinom* in the *stats* package of R (R Development Core Team 2012). For nectar matrices (N1-N4) the AIC values were first calculated separately, and the model that performed best was used for subsequent analysis. Following Vizentin-Bugoni *et al.* (2014), the number of parameters used to weight different model complexities was defined as the sum of the number of species of each probability matrix included in the given model, with the exception of the 'NULL' matrix, which was assigned with one parameter since it was not

properly based on a matrix. A model matrix was considered to better predict the observed matrix when having a smaller value of AIC, and models with $\Delta\text{AIC} < 14$ as equivalents (Burnham *et al.* 2011).

SPECIALIZATION AND MODULES IN THE NETWORK.—To calculate the network level specialization we calculated the index H_2' , which characterizes the degree of specialization among species in the entire network (Blüthgen *et al.* 2006). The observed H_2' value was contrasted to 10000 randomized networks to assess its significance, using the null models generated by functions *r2dtable* and *vaznull* in R-package bipartite (Dormann *et al.* 2008). In the first model, which uses the Patefield's algorithm, the marginal totals are constrained in the randomizations. The second is more "conservative" by also keeping the connectance constant, thus keeping the proportion of unrealized interactions, which might represent forbidden links (Dormann *et al.* 2008).

We next sought to evaluate if the factors that determine interaction frequencies also scaled-up to determine modules within the network. To examine this, we first evaluated if the studied hummingbird-plant interaction network was organized into modules. To test for modularity we used the QuanBiMo algorithm, which was specifically developed for weighted (quantitative) bipartite networks (Dormann & Strauss 2014) and is implemented in the R package bipartite (Dormann *et al.* 2008). The QuanBiMo algorithm computes modules based on a hierarchical representation of species link weight and optimal allocation to modules through swapping in a Simulated Annealing-Monte Carlo approach (Dormann & Strauss 2014). The level of modularity (Q) measures the extent to which species interact mainly within their module, ranging from 0 to 1. The higher the Q value, the stronger the data support the division of a network into modules. Modularity was calculated with the function *computeModules*, setting the number of Markov Chain Monte Carlo (MCMC) moves to yield no improvement before the algorithm stops to 10^6 steps, which is the default option adequate

for our network size (Dormann & Strauss 2014). Since the algorithm is stochastic, module arrangement can vary between each run, thus we retained the module conformation with the highest Q value as the optimum after 50 independent runs. To assess the significance of Q of the observed network, null model expectations from 100 randomized networks were computed using the functions *r2dtable* and *vaznull* in bipartite package. Values of Q in the randomizations were then used to calculate the z-score, which is the number of standard deviations a datum is above the mean of the 100 randomized networks. Z-score values of ≥ 2 are considered significantly modular (Dormann & Strauss 2014). Having identified how species separate into modules, we examined if modules associate with species abundance, morphology, nectar availability, phenology and spatial co-occupancy (habitat occupancy). Floral traits such as flower corolla length, nectar volume, concentration and sugar content of plants belonging to different modules were compared with ANOVA and post-hoc Tukey tests. We also tested this for flower abundance per plant species using a Kruskal-Wallis rank sum test. As each module consisted of only one or two hummingbird species (see RESULTS), formal tests associating modules with hummingbird traits were not conducted.

RESULTS

The savanna hummingbird-plant network was formed by six hummingbird and 18 plant species that interacted 554 times in total through 34 pairwise combinations (Fig. 1, also see Maruyama *et al.* 2013a). Rarefaction indicated our sampling was sufficient for detection of most pairwise interaction in the community (Fig. S1). The best predictor model for the interactions, *i.e.*, the model with lower AIC, was the one combining the matrices M (morphology), F (phenology) and H (habitat), followed by the pairwise combinations among

them and then each of these single matrices (Fig. 2). In contrast, all models incorporating species abundances performed poorly, with worse fit than the benchmark NULL matrix (Fig. 2). Likewise, none of the matrices based on nectar availability (N1-N4) performed better than the NULL matrix (Fig. S2); not even the best performing N3 matrix, which was used in all trait combining analyse.

Network level specialization was considerable ($H_2'=0.598$), and higher than the values observed in the randomized networks ($\pm SE$; $r2dtable$: 0.045 ± 0.001 ; $vaznull$: 0.372 ± 0.001). The plant-hummingbird network had a modularity value of $Q=0.484 \pm 0.001$ ($\pm SE$) and high Z-score ($r2dtable$ - 35.14; $vaznull$ - 5.54), which indicate significant modularity. Four modules were detected, which were overall consistent across the 50 runs (Fig. 1; Table S2): Module A was formed by the sole hermit hummingbird *Phaethornis pretrei* and the four flowers with the longest corollas that occurred mostly in the forest habitats, including interior and edge (Fig. 1, Table 1). Module B comprised the other hummingbird species that was mostly found in forest habitats, *Thalurania furcata*, and shorter corolla flowers, also for the most part found in this habitat. Modules C and D included plant and hummingbird species mostly occurring in the open savanna habitat but which also occurred at the edge. The flowers in module C and D did not differ significantly in traits from those in module B. The identity of species composing modules A and B were consistent across all 50 runs, whereas modules C and D changed in 14 of the 50 runs (Table S2). Module C was in 14 runs formed only by the hummingbird *A. fimbriata* (Gmelin, 1788) and the plant *Stachytarpheta gesnerioides* Cham. contrasting to the most common module conformation, in which module C consisted of two hummingbird and six plant species (Fig. 1).

DISCUSSION

We have shown that spatio-temporal overlap and species morphology, but not species abundance and floral energy, predict interaction frequencies in a plant-hummingbird network from the Brazilian Cerrado; morphology and spatial distribution are also related to the formation of modules. Our results are similar to those observed in the Atlantic Forest (Vizentin-Bugoni *et al.* 2014), even though floral traits suggest plant communities in the Cerrado are less specialized for hummingbird pollination (Maruyama *et al.* 2013a). Furthermore, the transect method we used should increase the influence of abundance on the interaction records compared to the timed observations carried out by Vizentin-Bugoni *et al.* (2014) in the Atlantic Forest, since it samples the interactions per plant species relative to their abundances (see Gibson *et al.* 2011). Taken together, this suggests species morphology and spatio-temporal mismatches are relatively more important than abundance in organizing plant-hummingbird interactions.

The role of species morphology in structuring the interactions and therefore forming modules is supported by the separation of the long-billed hermit hummingbird *Phaethornis pretrei* from the other hummingbird species (Fig. 1). Hermit hummingbirds are often associated with morphologically specialized flowers (Feinsinger & Colwell 1978, Sazima *et al.* 1995, Maruyama *et al.* 2015a), which may lead to the formation of distinct sub-units in plant-hummingbird networks. Moreover, plant and pollinator distribution over time and space can be important drivers of network structure by constraining species interactions (Vázquez *et al.* 2009a,b, Martín González *et al.* 2012, Vizentin-Bugoni *et al.* 2014). In our network there is an example of the lack of phenological overlap creating forbidden links — the hummingbird *Amazilia fimbriata* (Gmelin, 1788) and the few plant species it visits. Although

this is one of the most common hummingbird pollinators in the open habitats of the Cerrado (Araújo *et al.* 2013), it was recorded only for three months during our study period (Fig. S3). This “forbid” many of the morphologically possible pairwise interaction between this hummingbird and local plant species. Yet, although seasonality may be an important driver of modularity for some ecological networks (Martín González *et al.* 2012, Schleuning *et al.* 2014), we did not observe an association between modules and the seasonality (i.e., dry and wet seasons) that is so characteristic of the Cerrado (Fig. S3). Hence, even though phenological overlap is important in determining interaction frequency between species of hummingbirds and plants, it did not scale-up to also determine modules within the network. Most hummingbirds, in contrast to plants, were distributed through the year and this inhibited the formation of seasonal modules. This suggests that seasonality is a more important driver of modularity for plants interacting with mutualists with high within-year turnover, e.g., insects with shorter life or activity spans (Martín González *et al.* 2012) or migrant frugivorous birds (Schleuning *et al.* 2014).

In contrast to seasonality, the spatial distribution into forest and savanna habitats clearly delimited some of the modules we identified (Fig. 1). Species interactions are inherently spatial, since individuals must meet in space to interact (Morales & Vázquez 2008). For example, in the forests of Trinidad, a major generator of forbidden links in a plant-hummingbird network is the vertical decoupling of habitat, *i.e.*, canopy vs. understory (Snow & Snow 1972, Jordano *et al.* 2006). In the Cerrado, the patchy distribution of habitats creates a spatially heterogeneous landscape, and plant-animal interactions are probably constrained by species preferences for one of these habitats. Specifically, two species of hummingbirds are more associated with forest — *P. pretrei* and *Thalurania furcata* (Araújo *et al.* 2013) — and each belonged to separate modules from the hummingbirds primarily found in open habitats. While the module for the hermit *P. pretrei* can be easily explained by morphological

specialization (*i.e.*, longer bill and corolla length), *T. furcata* is very similar to other hummingbirds occurring in the savanna. The formation of its own module is therefore best explained by its preference for forest. Our results suggest that in addition to morphological traits and phenology, habitat preference is an additional form of spatial complexity that can constrain interactions (Morales & Vázquez 2008, Vázquez *et al.* 2009b) and determine network structure.

Although in general species morphology and spatio-temporal mismatches performed well in determining interactions and network structure, we were surprised to find that nectar performed poorly (Fig. 2; Table 1). The inability of nectar-based matrices in predicting interaction frequencies might indicate a need to incorporate a threshold at which larger hummingbirds do not interact with flowers producing less rewards (Dalsgaard *et al.* 2009, Justino *et al.* 2012). To do so, though, would require more detailed information on the energetic requirements of each hummingbird species (Feinsinger & Colwell 1978, Altshuler *et al.* 2004). Of course, it could also be possible that nectar availability is indeed less important than other traits in determining interaction frequencies. This seems especially likely if traits operate in a hierarchical manner such that one (*e.g.*, nectar) becomes relevant only if others (*e.g.*, corolla length) have already permitted a given pairwise interaction to occur (Junker *et al.* 2013).

Recent studies have provided additional evidence that species traits play a relatively more important role than abundance in structuring interaction networks (Junker *et al.* 2013, Vizentin-Bugoni *et al.* 2014, and this study). Interestingly, these studies were all characterized by networks with relatively higher levels of specialization, *i.e.*, $H_2' > 0.51$ (Blüthgen *et al.* 2007). Furthermore, some of the studies showing higher importance of abundance have been conducted using more generalized systems, such as plant-frugivorous bird and plant-ant networks (Blüthgen *et al.* 2007, Krishna *et al.* 2008, Dáttilo *et al.* 2014). We propose that

future research would benefit of cross-network comparisons testing the hypothesis that traits have greater effects in specialized than in generalized systems. This could be tested across large spatial gradients with a single system, for instance by contrasting more specialized tropical hummingbird-plant networks with more generalized temperate ones (Dalsgaard *et al.* 2011). Alternatively, one could compare the performance of traits and abundance in structuring different types of mutualistic systems in the same location, *e.g.*, by comparing more generalized tropical plant-frugivorous bird networks with more specialized plant-pollinator ones.

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TABLE 1. *Floral traits and flower abundance of plants from the four modules found in the savanna plant-hummingbird network. Differences were tested with ANOVA and post-hoc Tukey test, but Kruskal-Wallis test for flower abundance. Values express the mean $\pm$ standard error. * Significantly different from other modules.*

Traits	Modules				F _{3,14} / K	p-value
	A	B	C	D		
Corolla (mm)	35.0 $\pm$ 1.6*	19.7 $\pm$ 2.1	15.2 $\pm$ 1.8	12.5 $\pm$ 0.89	9.33	0.001
Nectar volume (μ l)	14.4 $\pm$ 1.6	20.5 $\pm$ 2.9	34.1 $\pm$ 6.4	12.2 $\pm$ 2.2	1.67	0.220
Nectar concentration (%)	22.3 $\pm$ 0.6	16.9 $\pm$ 1.5	20.2 $\pm$ 1.3	22.6 $\pm$ 1.2	0.92	0.456
Nectar sugar (mg)	3.4 $\pm$ 0.4	3.7 $\pm$ 0.7	7.6 $\pm$ 1.5	3.1 $\pm$ 0.7	1.28	0.319
Flower abundance	755.2 $\pm$ 84.1	442.0 $\pm$ 113.8	387.8 $\pm$ 70.3	5839.2 $\pm$ 1216.3	3.28	0.350

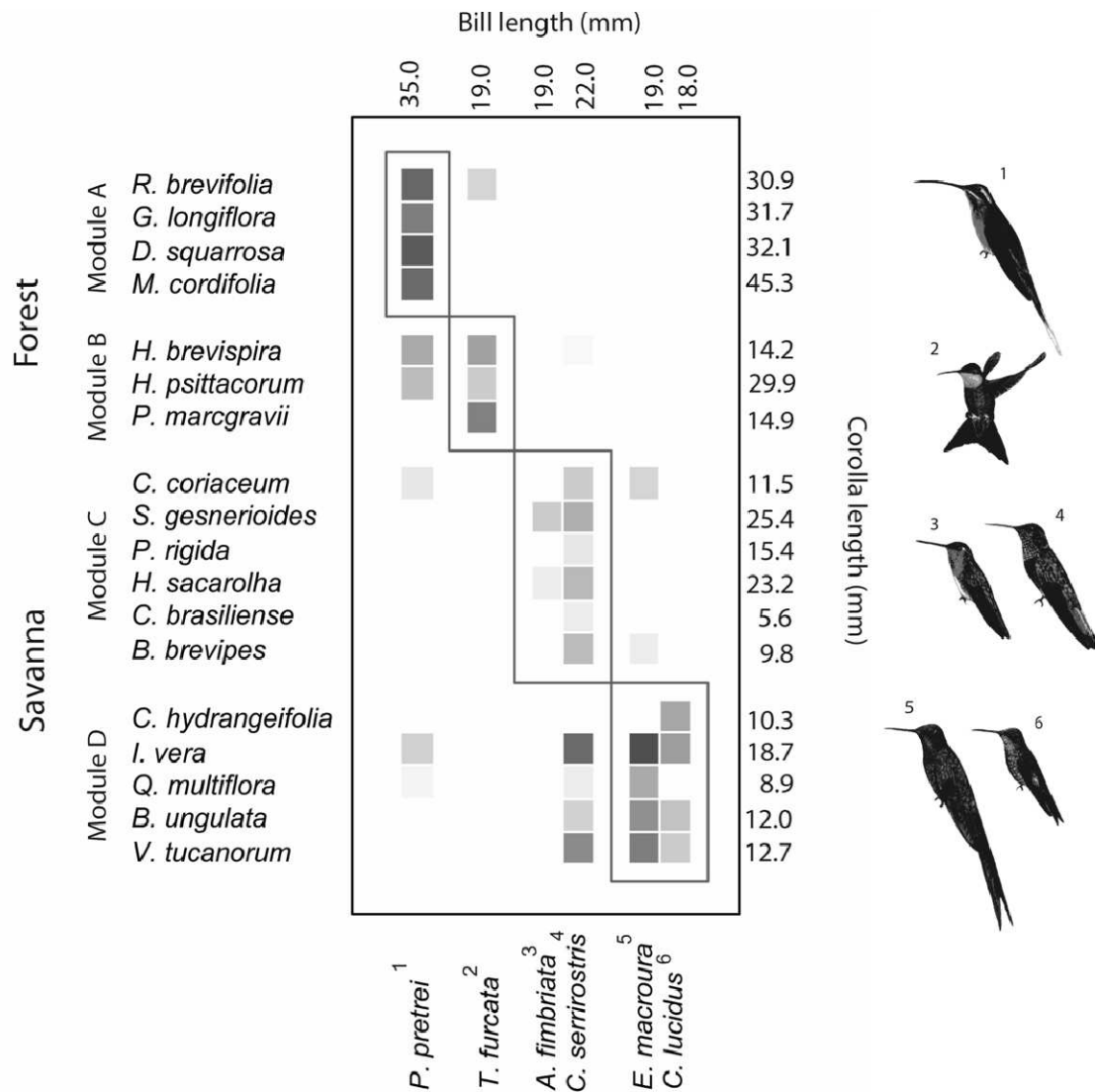


FIGURE 1. Plant-hummingbird interaction matrix from Panga Ecological Station in Brazil's Cerrado. The matrix shows the most common module conformation through 50 runs, using the algorithm QuanBiMo. Intensity of grey-shading represents the interaction frequency. Corolla and bill length for each plant and hummingbird species are shown opposite to their names. For corolla length we show the effective measurement of flower restriction to hummingbird visitors. The silhouette of hummingbirds shows their relative size (adapted from Grantsau 1989).

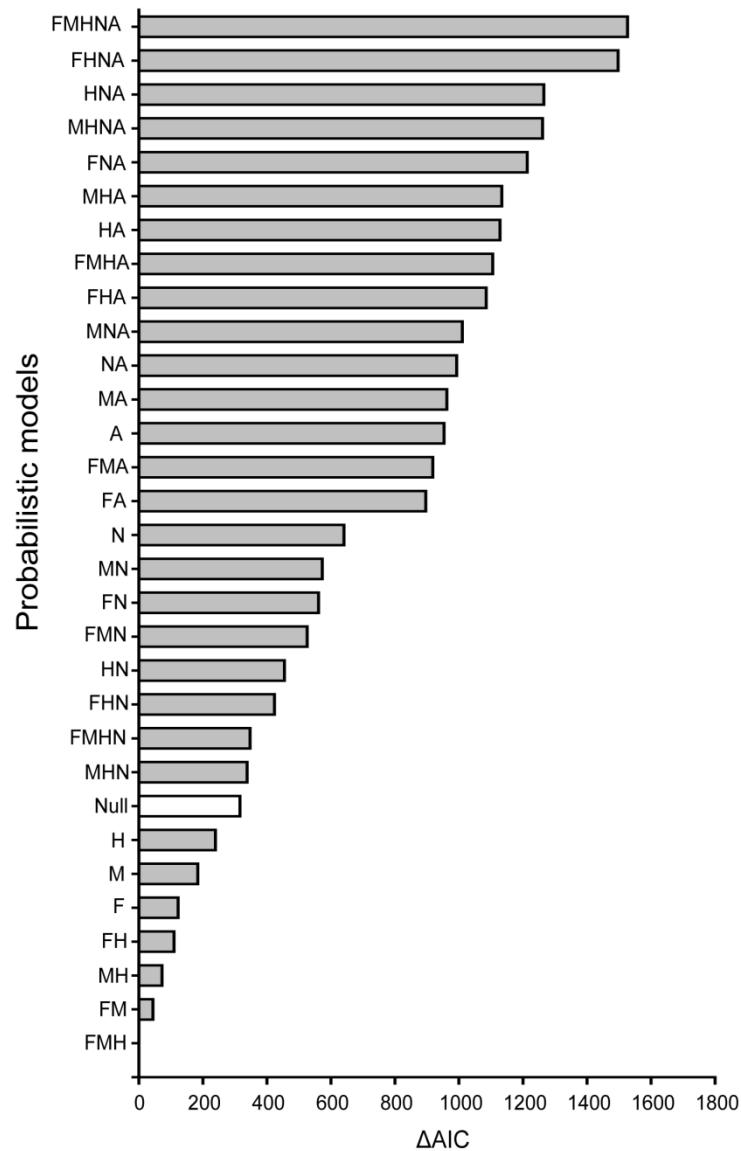


FIGURE 2. ΔAIC values of the probabilistic models (matrices) constructed incorporating species abundance (A), phenology (F), morphology (M), nectar (N) and habitat occupancy (H), and all possible combinations among them in relation to the best model (FMH) fitted to the observed matrix; NULL is the model in which all pairwise interactions have the same probability (white bar). Shorter bars indicate better fit of a given model in relation to model FMH, which presented the best fit to the observed network (*i.e.*, lowest AIC value).

CAPÍTULO 4

The integration of alien plants in plant-hummingbird networks across the Americas: the importance of plant trait, pollinator generalization and insularity*



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*Formatado para *Diversity and Distributions*

ABSTRACT

Aim Alien plants are often integrated as core generalists into plant-pollinator networks. However, this finding is mostly based on analyses of networks from generalised temperate or insular ecosystems. Here, we investigated the role of alien plants in tropical and more specialized plant-hummingbird networks, assessing the importance of species traits and insularity on alien plant integration.

Location Mainland and insular Americas.

Methods We used species-level network indices to quantitatively assess the role of alien plants in 21 quantitative plant-hummingbird networks where alien plants occur. We then evaluated whether plant traits, including previous adaptations to bird-pollination, and insularity associate to these network indices. Finally, we tested the association between hummingbird bill length, a proxy for functional generalization, and the probability of interaction with alien plants across the networks.

Results Within the 21 networks, we identified 32 alien plant species and 352 native plant species. On average, alien plant species attracted more hummingbird species than native species, but alien plants were visited more exclusively by some hummingbird species, thus reaching higher levels of complementary specialization. Additionally, an average alien species was more important for the cohesion of plant-hummingbird networks than native plant species. Large alien plants and those occurring on islands distributed more evenly their interactions across the networks, thereby acting as network connectors. Hummingbird morphology also related with the incorporation of alien plants in the networks, as short-billed hummingbirds had a higher probability of including alien plants within their array of interactions.

Main conclusions Where plant introductions have occurred, alien plants appear strongly integrated into plant-hummingbird networks. Plant traits, however, explained little how alien species are integrated. Short-billed hummingbirds, often characterized as functionally generalized pollinators, act as facilitators of alien integration. Our results show that plant-hummingbird networks are dynamic and open for invasion.

Key-words

Exotic plants, invasion biology, ornithophily, plant-pollinator interactions, specialization, species traits, species-level network indices

INTRODUCTION

Alien species may become invasive and are a major threat to biodiversity and ecosystem functioning, including key ecosystem services such as pollination (Colautti & MacIsaac 2004, Gurevitch & Padilla 2004, Pyšek et al. 2004, Morales & Traveset 2009, Simberloff et al. 2013). The successful establishment of alien plant species might be contingent on the acquisition of mutualistic partners, e.g. pollinators, outside their native range (Richardson et al. 2000, Bufford & Daehler 2014, Traveset & Richardson 2014). Under such a scenario, alien plants may compete for pollinators and decrease the fitness of native plants, for instance by offering greater quantities of floral rewards and thereby decreasing the attractiveness of native flowers (Chittka & Schürkens 2001, Morales & Traveset 2009). Conversely, alien plants could also benefit native plants by increasing the overall availability of floral resources, thereby increasing pollinator abundance and activity on native plants (Bjerknes et al. 2007, Lopezaraiza-Mikel et al. 2007, Bartomeus et al. 2008). Thus, alien plants' ability to establish, and their effect on the pollination of native plants, may depend on their floral traits and the community context (Bjerknes et al. 2007, Morales & Traveset 2009, Gibson et al. 2012, Simberloff et al. 2013).

Hence, in order to understand the potential impacts of alien species on ecosystems, it is important to characterize the community-wide roles of these plants (Davis et al. 2011). One approach to do this is to use ecological interaction network analyses to conduct community-wide studies identifying and describing the interactions between organisms. Several studies have used such approach to investigate the role of alien plants on plant-pollinator communities (Memmott & Waser 2002, Olesen et al. 2002, Aizen et al. 2008, Vilà et al. 2009, Albrecht et al. 2014, Stouffer et al. 2014, Traveset & Richardson 2014). However, most of these studies have considered either

temperate systems, which predominantly consist of generalized insect pollinators (e.g. Aizen et al. 2008, Bartomeus et al. 2008), or focus on generalized island communities where the impact of invasive species might be most severe (e.g. Olesen et al. 2002, Traveset et al. 2013, Traveset & Richardson 2014, but see Kaiser-Bunbury et al. 2011). As interaction network's stability may be more sensitive to the integration of alien species in specialized than in generalized systems (Kaiser-Bunbury et al. 2011), studies on specialized systems and over large geographical scales can contribute to our understanding of the general effects of alien species.

One such model system are the interaction networks between plants and hummingbirds, across the Americas ranging from relatively specialized to generalized networks, and which includes mainland and insular environments (Stiles 1981, Martín González et al. 2015). Hummingbirds are the most specialized group of nectar-feeding birds and the most important vertebrate pollinators in the Americas (Stiles 1981, Bawa 1990, Cronk & Ojeda 2008). As specific floral phenotypes are associated with hummingbird pollination (Cronk & Ojeda 2008), it could be expected that alien plants lacking a shared evolutionary history with hummingbirds would not be readily incorporated as important species in those networks (Richardson et al. 2000; Aizen et al. 2008). At the same time, Old World plants with convergent adaptation to bird pollination, notably to sunbirds and honeyeaters in Africa and South-east Asia (Cronk & Ojeda 2008, Fleming & Muchhala 2008, Geerts & Pauw 2009, Janeček et al. 2015), could be well-integrated in novel plant-hummingbird communities in the Americas – at least more than alien plant species not previously pollinated by birds.

Given the increasing concerns over the effects of alien species on ecosystems (Davis et al. 2011, Richardson & Ricciardi 2013, Simberloff et al. 2013), community-wide studies on the role of alien plants across large geographic gradients could provide

new insights into their potential threats to biodiversity. Here, we characterize the role of alien plants in 21 quantitative plant-hummingbird pollination networks distributed broadly across the Neotropics, including both mainland and island environments (Fig. 1). We asked: 1) whether an average alien plant is topologically more important than a native species, i.e. whether alien plants have a disproportionately large effect on plant-hummingbird networks; 2) whether alien plant traits, such as pre-adaptation to bird pollination, as well as insularity relate to the integration of plants into networks; and 3) whether hummingbirds with short-bills, often characterized as functionally generalized, facilitate the integration of alien plant species into networks.

MATERIAL & METHODS

Plant-hummingbird networks and alien plants classification

In order to investigate the role of alien plant species in pollination networks, we compiled plant-hummingbird networks in which exotic plant species could be confidently identified (Figure 1). For this, we used an established database on quantitative plant-hummingbird interaction networks (see Dalsgaard et al. 2011 and Martín González et al. 2015 for previous versions of the database, updated details in Table S1-S3). We only considered legitimate interactions here, in which a hummingbird was observed contacting the reproductive structures of the flowers and with potential for pollination. For each network, plants were classified as either native or alien - taking into account the locality of a given network and the plant distribution range according to openly available databases, notably: Tropicos (<http://www.tropicos.org/>), GRIN Taxonomy for Plants for North America (<http://www.ars-grin.gov/>), Flora of the West Indies for the Caribbean (<http://botany.si.edu/antilles/WestIndies/query.cfm>), Brazilian Flora Checklist for networks from Brazil (<http://floradobrasil.jbrj.gov.br/>) and The Plant

List (<http://www.theplantlist.org/>). Plant names used here followed The Plant List database. A total of 75 (19%) plant occurrences in the networks were not identified to species level, but to genus or family level only (Table S2); for these we adopted a conservative approach of only attributing "alien" status if the genus/family at the given locality was identified as alien in the databases. Because the geographical origin of some plants is poorly known, the classification of these can be imprecise (Pyšek et al. 2004), and the use of a single general database has been argued for to standardize possible bias (Stouffer et al. 2014). However, our dataset is composed primarily of networks from the Neotropical region, which has relatively poor historical species records compared to North America and Europe (Pyšek et al. 2004). Since even for well recorded regions these general databases can fail to successfully classify species (see Stouffer et al. 2014), we preferred to use regional databases, which rely on local plant specialists, e.g. the Brazilian Flora Checklist. Whenever conflicts among databases appeared, or we were unsure of the classification, we contacted experts with working experience on the flora of the specific region (listed in the Acknowledgments).

Species-level network metrics

For each plant-hummingbird community, interactions were summarized as a bipartite matrix, with each cell filled with the frequency of the pairwise interaction between a plant and a hummingbird species. The role of each plant and hummingbird species within the networks were described by five distinct species-level indices, capturing distinct topological properties of a species: 1) the degree of a species (k_i) is computed as the number of partners a given species i is linked to in the network; 2) species strength (s_i) is the sum of the proportions of interactions performed by a given species i across all its interaction partners, i.e., it measures how the assemblage of hummingbirds

depend on a specific plant species or *vice versa* (Bascompte et al. 2006); 3) complementary specialization, (d'_i) quantifies how interaction frequencies of a given species deviate in relation to the availability of interaction partners in the network, defined by their marginal totals; the higher the value of d' , the more exclusive are the interactions of the species in relation to the other species in the network (Blüthgen et al. 2006). In addition, we calculated the level of quantitative modularity of each network, i.e. formation of distinct sub-communities within an ecological network characterized by high within-module prevalence over between-module interactions (Dormann & Strauss 2014). For each network, we estimated the module conformation using the QuanBiMo algorithm with the number of Markov Chain Monte Carlo (MCMC) moves to yield no improvement before the algorithm stops set to 10^7 steps (Dormann & Strauss 2014). From the module conformation with the highest modularity after 20 independent runs for each network (as in Maruyama et al. 2014), we calculated two species-level network indices: 4) between-module connectivity c and 5) within-module connectivity z . Whereas c_i describes how evenly the interactions of species i are distributed across modules in the network, z_i quantifies the importance of a given species i within its module (Dormann & Strauss 2014). Species-level network indices showed a positive correlation in some cases, indicating that species with high values for a given index tended to also have high values for another index (Table S4). The correlation was especially high between degree and species strength (Pearson's $r = 0.68$ for plants, and $r = 0.92$ for hummingbirds; Table S4), and between species strength and within module connectivity for plants, i.e. z (Pearson's $r = 0.70$; Table S4). However, these indices complement each other and we therefore used all five indices when comparing alien vs. native plants. In order to compare the five species-level network indices across different networks, we transformed all network indices to z-scores, i.e., indices were standardized

within each network by subtracting the mean value of each group (plants or hummingbirds) and dividing the results by its standard deviation (as in Vidal et al. 2014). Calculations of species-level network indices were conducted with *bipartite* package (Dormann et al. 2008) in R (R Development Core Team 2014).

To test whether alien plant species differed from native species, we used a null model to contrast the observed difference of means of the species-level indices between native and alien plants to the differences of the means calculated from randomizations shuffling the alien or native status of the plants (Vidal et al. 2014). The significance (*p*-values) was obtained by dividing the number of times the absolute differences generated from 10,000 randomizations were equal or larger than the observed difference of the means (Manly 1997). Whenever a plant species occurred in more than a single network (74 species, 19.3% of all plants), the average for each of the standardized indices was calculated and used for the null model analysis. We note that with the exception of the degree which becomes non-significant, results were qualitatively similar if we consider the instances in which the same species occurred in different networks as distinct samples. To quantify the magnitude of the difference between native and alien plant species, we calculated Cohen's *d* effect size as the standardized mean difference between the indices of each group, i.e. the difference between means divided by the standard deviation of the respective index for all plants (Nakagawa & Cuthill 2007, Sullivan & Feinn 2012). For example, an effect size of around 0.5 is considered a medium effect, meaning that an average alien plant species have a higher index value than 69% of the natives (Nakagawa & Cuthill 2007, Sullivan & Feinn 2012).

Species traits, network roles and insularity

For all alien plants identified in the 21 networks, we classified the species according to traits we hypothesized as relevant for their role in the networks. Trait information was gathered from the original sources of the network data (Table S1), as well as by a follow-up literature search using Google Scholar® with the species name as the search term. All alien plants were classified according to (a) the size of the plant, which potentially reflect their floral display (i.e. large or small, the former including trees and large herbs such as bananas, and the latter including shrubs, climbers and small herbs); (b) flower type (tubular, brush or other), (c) the length of the flowers (mm), and (d) whether or not they were bird-pollinated (Table S5). To determine the latter, we used references from the plant-hummingbird network database as well as field based studies on the floral morphology and pollination biology of the plants, including information on the associated floral visitors and pollinators (Table S5-S6). Additionally, we classified whether an alien plant occurred on an island or on mainland communities. As we were only able to evaluate alien plant traits, and not the traits of the native plants, we asked whether particular characteristics of the aliens influence its integration into the networks.

We evaluated how plant traits and insularity related to plant species-level network indices with linear mixed effects models (LMM) using the *lme4* package (Bates 2014) in R (R Development Core Team. 2014). We used the plant traits (i.e. size, flower type, flower length and previous association to bird pollination) and insularity of the network as fixed factors. Alien plant species identity was included as a random effect to account for non-independence of the observations of the same species in different networks (Bolker et al. 2009, Zuur et al. 2009). We ran models separately for each of the five distinct species-level network indices. The full models included all predictors and were compared to reduced models using the function "dredge" in R

package *MuMIn* (Barton 2014), according to their values of Akaike information criteria corrected for small sample sizes (Bolker *et al.* 2009, Zuur *et al.* 2009). Models with $\Delta AICc \leq 2$ were considered to be equivalent. We also estimated the proportion of variance explained by the fixed factors in the selected best model as marginal R^2 , and the proportion of variance explained by fixed and random factors as conditional R^2 (Nakagawa & Schielzeth 2013, Barton 2014).

Finally, we asked whether hummingbird bill length, a functional bird trait associated to flower choice (Dalsgaard *et al.* 2009, Maruyama *et al.* 2014, Maglianesi *et al.* 2014), was related to the probability of hummingbirds including alien plants in their array of interactions. Longer billed-hummingbirds are considered functionally more specialized (Dalsgaard *et al.* 2009, Maruyama *et al.* 2014, Maglianesi *et al.* 2014). For this, we compiled information on hummingbird's bill length (Table S3) and assessed whether a given hummingbird species interacted with an alien plant across the networks. Then, we fitted a generalized linear model with binomial error distribution containing hummingbird bill length as predictor of the probability that a hummingbird species interacted with alien plant species (Zuur *et al.* 2009). This analysis was conducted at species level, contrasting each species' bill length to the presence of interaction with alien plants across all the networks in which a given hummingbird species occurred. We also conducted a similar analysis excluding hummingbird species occurring on Caribbean islands, as well as using the body mass instead of the bill length.

RESULTS

The 21 plant-hummingbird networks include a total of 74 hummingbird and 384 plant species, of which 32 plants were classified as being alien to the networks in which they

occurred. Individual networks had between seven and 65 plant species, with on average $10.8 \pm 8.2\%$ ($\pm$ sd) and up to 28.6% of alien plant species (Figure 1, Table S7). Alien plants belonged to 16 plant families, with Musaceae and Myrtaceae constituting the most frequent families (Table S5-S6). Most alien plant species (~63%) had tubular flowers, and about half of them (~47%) had previous association with bird pollinators (Table S5-S6). Around 50% of alien species originated are from Asia, about 19% originated from Africa and 19% from other regions of the Americas (Table S5).

Overall, alien plant species had higher values of species strength than native species (effect size, k : Cohen's $d = 0.56$; 95% Confidence Interval = 0.36-0.77; null model $p = 0.003$; Figure 2). Likewise, alien plants also had higher values of within module connectivity (z : Cohen's $d = 0.49$; 95% CI = 0.29-0.69; $p = 0.006$; Figure 2). For degree (k) and complementary specialization (d'), 95% CI of effect sizes did also not overlap zero and null models were marginally significant (k : Cohen's $d = 0.35$; 95% CI = 0.15-0.56; $p = 0.049$; d' : Cohen's $d = 0.35$, 95% CI = 0.15-0.55; $p = 0.050$; Figure 2). However, alien plants did not differ from native species in connecting distinct modules (c : Cohen's $d = 0.07$; 95% CI = -0.12-0.27; $p = 0.662$). Hence, an average alien plant is more important for hummingbirds in terms of relative interaction frequency. There is also a tendency for alien plant species to have more partners and for some hummingbird species to interact more exclusively with alien plants.

Alien plant traits did not relate to species-level network indices, except for between-module connectivity (c), since the model containing only the intercept was always included within the best models (Table S8). For c , the best two models included insularity and size of the alien plants; the model containing both terms had R^2 marginal = 0.22 and R^2 conditional = 0.33. Specifically, aliens on islands (estimate = 0.35, SE = 0.30) and larger alien plants (estimate = 0.75, SE = 0.27) had higher values for

connectivity, i.e. were more important for interconnecting modules. Finally, we found that short-billed hummingbirds were more likely to interact with alien plants than were long-billed hummingbirds (slope: -0.10; $p < 0.01$; Figure 3). Excluding the hummingbird species occurring in the Caribbean islands did not change our results (slope: -0.08; $p = 0.036$; Figure S1) and body mass was found unrelated to the probability of using alien plants ($p = 0.091$)

DISCUSSION

We show that alien plants have strongly integrated into plant-hummingbird networks, playing key roles in the networks where they occur. Alien plants have more partners (higher degree) and hummingbirds show higher dependency on them than on an average native plant, both across the entire network and within their modules. Although we note that the networks contained many more native than alien plant species (352 versus 32 species), these results suggest that alien plants are important and act as core generalists in these networks (Aizen et al. 2008, Bartomeus et al. 2008, Vilà et al. 2009, Stouffer et al. 2014, Traveset & Richardson 2014). Moreover, some alien plants may function as "private" floral resources for some hummingbird species, as revealed by their high degree of complementary specialization (Blüthgen et al. 2006, Stouffer et al. 2014).

The traits we hypothesized a priori to determine how alien plants would integrate into the networks showed little importance. For instance, convergent evolution to bird pollination has been suggested as an example of previous adaptation to specific pollinator types aiding the incorporation of aliens to novel plant-pollinator networks (Richardson et al. 2000, Geerts & Pauw 2009). However, this pre-adaptation did not apply to network roles of alien plants in plant-hummingbird networks. Hummingbirds may favour specific floral traits (Cronk & Ojeda 2008), but they may also show

opportunism in flower use by visiting and pollinating non-ornithophilous plants (e.g. Dalsgaard et al. 2009, Maruyama et al. 2013). Due to this opportunism, specialized floral traits may not relate to plant species roles in plant-hummingbird networks (Maruyama et al. 2013).

Two points, however, should be considered. First, we could only consider those plant species recorded visited by hummingbirds, i.e., participating in the web of interactions. However, it is likely that other alien plants were present in the studied communities and that these were not visited by hummingbirds. If such non-participating alien species had been considered, it is possible that plant traits, including the previous adaptation to bird-pollination, could have emerged as important for alien integration. Additionally, quantitative network indices incorporating the frequency of the interaction in some cases work well to estimate the total effect of mutualists on their interaction partners (Vázquez et al. 2005). However, recent studies show that the set of floral traits associated with specific pollinator groups may be indicative of their efficiency in promoting pollen transfer (King et al. 2013, Rosas-Guerrero et al. 2014). Complementary data, such as interspecific pollen deposition or the contribution of hummingbirds to alien plants reproduction, are thus essential next steps to fully assess the impact of alien plants (Richardson et al. 2000, Lopezaraiza-Mikel et al. 2007, Bufford & Daehler 2014, Traveset & Richardson 2014).

It has been suggested that alien plants are core components of plant-insect pollinator networks, due to their high abundance in invaded communities (Lopezaraiza-Mikel et al. 2007, Aizen et al. 2008, Albrecht et al. 2014). We cannot test the possible effect of abundance, since we lack abundance data for our networks, and it is possible that abundance is an important factor. In spite of that, recent studies have shown that abundance is less important than traits in structuring interactions among plants and

hummingbirds, in contrast to more generalized insect pollination systems (Maruyama et al. 2014, Vizentin-Bugoni et al. 2014). Thus, for plant-hummingbird networks, abundance might be a less likely predictor of alien topological importance. Instead, we suggest that other plant traits, such as the temporal availability of alien flowers in relation to native plants, could be important for explaining the integration of alien species in these networks (see Godoy et al. 2009).

Although most plant traits evaluated here did not relate to the role of alien plants in the networks, we found that larger alien plants had higher values of between module connectivity than smaller alien plants. Thus, presumably those alien plants that offer more floral resources distribute their interactions more widely among modules in networks, acting as connectors in these networks. Connectors blur the boundaries between modules and contribute to the spread of perturbations throughout communities (Albrecht et al. 2014). Alien plants occurring in depauperate island networks were also better connectors than alien plants on the mainland, which indicates that they may have greater potential to affect insular than mainland communities (e.g. Traveset et al. 2013, but see Kaiser-Bunbury et al. 2011).

From the hummingbird perspective, we show that species with shorter bills, which are often characterized to be functionally more generalized (e.g. Dalsgaard et al. 2009, Maruyama et al. 2014, Maglianesi et al. 2014), show higher probabilities of incorporating alien plant species in their web of interactions. Previous studies have suggested that generalist insect pollinators facilitate alien plant establishment, since these often include alien plants in their interactions (Richardson et al. 2000, Memmott & Waser 2002, Olesen et al. 2002, Lopezaraiza-Mikel et al. 2007, Aizen et al. 2008, Bartomeus et al. 2008, Traveset et al. 2013, Stouffer et al. 2014). However, "generalists" in previous studies were defined based in their roles in networks, e.g.,

number of partners. Here, we show a direct link between integration of alien plants and a functional trait of the pollinators, i.e. hummingbirds.

CONCLUSION

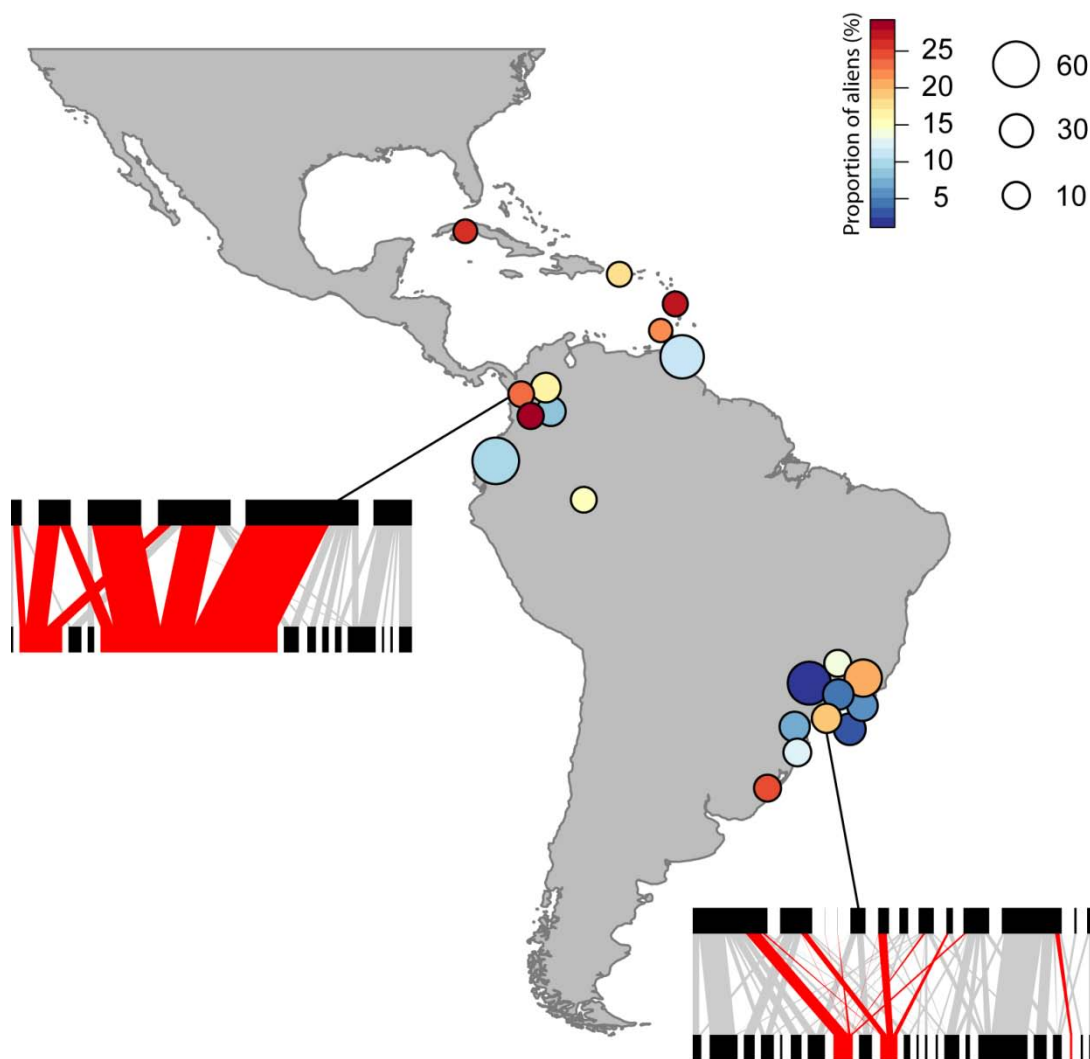
Invasive plants are regarded as one of the major current threats to biodiversity. One of the key components for alien plants to establish in novel ecosystems is their successful integration into mutualistic networks (Richardson et al. 2000, Traveset & Richardson 2014). Although examples of successful integration of alien species in temperate and insular insect-plant systems are common (e.g. Olesen et al. 2002, Aizen et al. 2008, Bartomeus et al. 2008, Vilà et al. 2009, Stouffer et al. 2014), here we show that alien plants are strongly integrated into the web of interactions even for more specialized tropical pollination systems, such as hummingbird pollination systems. By acting as core generalist species in the networks, these plants may impact the entire plant-pollinator network (Traveset et al. 2013) and even modify their eco-evolutionary dynamics (Guimarães et al. 2011). In sum, our results here show that plant-hummingbird networks are dynamic and open for invasion, emulating what happens in other plant-pollinator systems.

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Figure 1 Distribution of 21 Neotropical plant-hummingbird networks containing alien plant species. Circle size represents the total number of plant species in each network; colors indicate the proportion of alien plants in each network. Note that some points have been slightly moved to avoid overlap. Two network representations illustrate how alien plants are integrated into the networks (top network, Colombian Andes, Snow & Snow 1980; bottom network, Brazilian Atlantic Rainforest, Maruyama et al. 2015). Hummingbirds and native plants are represented as black and green rectangles respectively, with grey-shaded lines depicting interactions between them. Alien plants and their interactions are marked in red. Rectangle and line widths are proportional to the frequency of species and interactions, respectively.



1 **Figure 2** Species-level network indices for 352 native and 32 alien plant species across 21 plant-hummingbird networks. On the left, we show
 2 the effect sizes (Cohen's d) comparing alien and native plant species for various network indices; an effect size is considered significant if the
 3 95% CI of the mean differences do not overlap zero (Nakagawa & Cuthill 2007). On the right, box-plots illustrate the distribution of standardized
 4 index values along with their significance, as obtained from null model analysis. With the exception of c , both approaches found that an average
 5 alien plant have higher network index values than an average native plant.

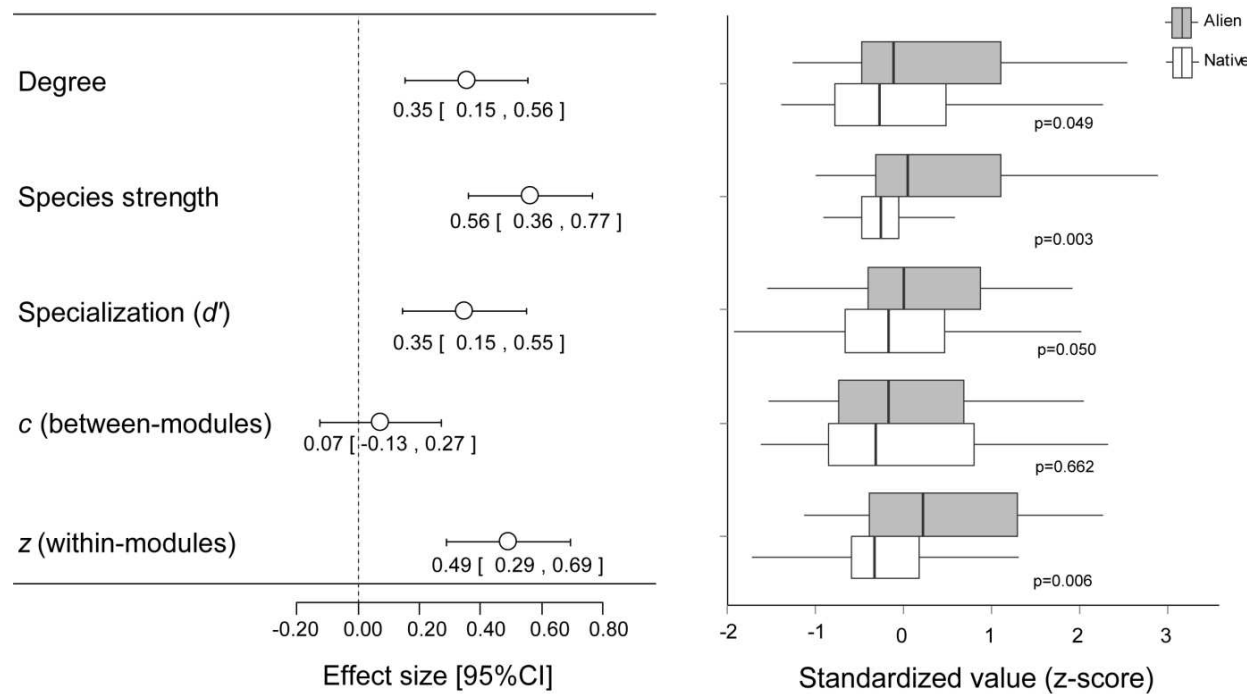


Figure 3 Probability of hummingbird species incorporating alien plant species into their interactions in relation to their bill length. Each circle illustrates whether a given hummingbird species incorporates alien plants (1), or not (0). The fitted line reflects the modelled probability of hummingbird species feeding on alien plants; showing that short-billed hummingbirds have a higher probability of feeding on alien plants than do long-billed hummingbird species. We used Generalized Linear Models with binomial error distribution to assess the significance of the relationships.

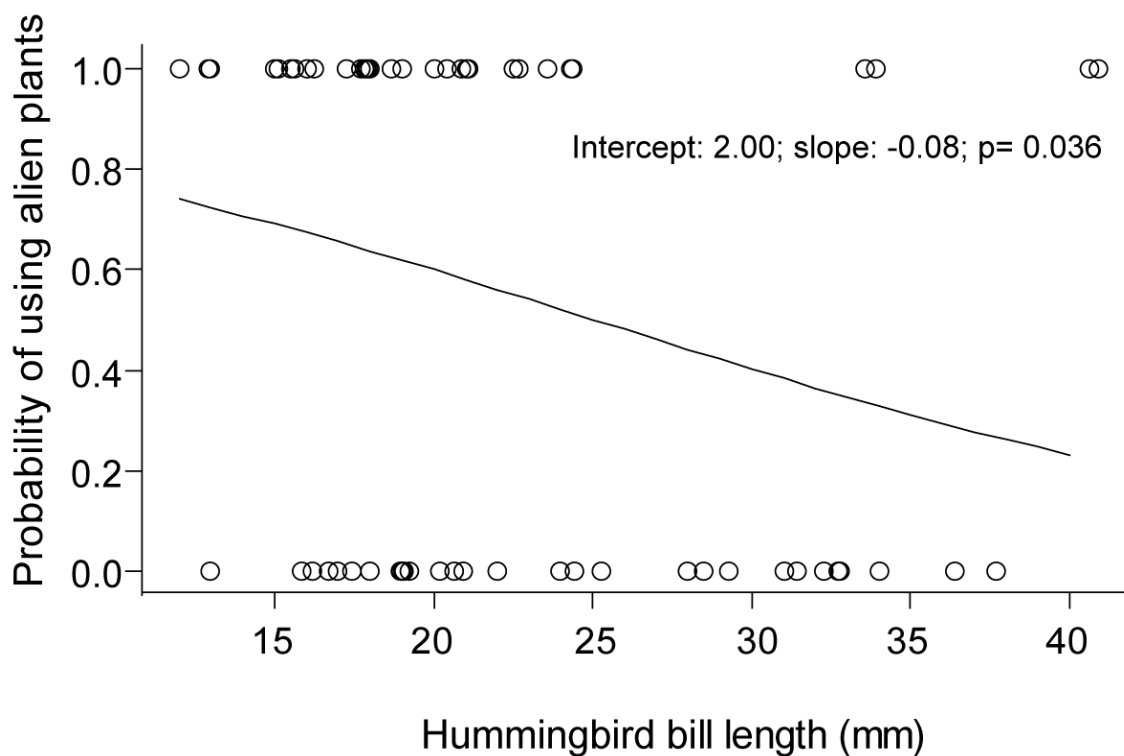


Figure S1. Probability of hummingbird species incorporating alien plant species into their interactions in relation to their bill length, here species occurring at Caribbean islands networks were excluded. Each circle illustrates whether a given hummingbird species incorporates alien plants (1), or not (0). The fitted line reflects the modelled probability of hummingbird species feeding on alien plants; showing that short-billed hummingbirds have a higher probability of feeding on alien plants than do long-billed hummingbird species. We used Generalized Linear Models with binomial error distribution to assess the significance of the relationships.

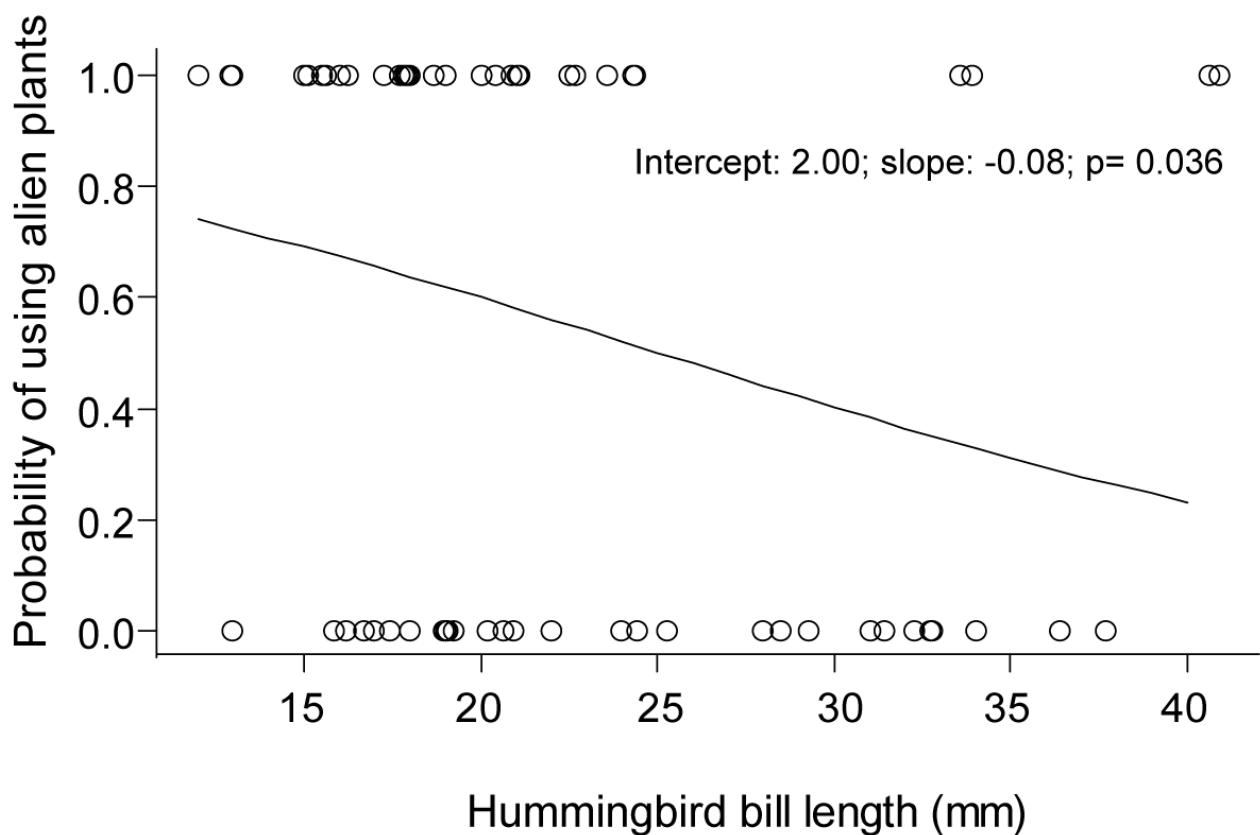


Table S1. Coordinates, description, location and data references for each studied plant-hummingbird network.

ID number	Latitude	Longitude	Site description and general location	Data Source Reference
1	22.28	-81.20	Swamp forest, Hurricane disturbed, Cuba	Baquero, A.C. (2014) Evolutionary and ecological insight into hummingbird-plant communities in the Caribbean. <i>MSc Thesis</i> . University of Copenhagen, Denmark.
2	18.13	-66.82	Elfin forest, Puerto Rico	Dalsgaard, B., Martín González, A.M., Olesen, J.M., Ollerton, J., Timmermann, A., Andersen, L.H. & Tossas, A.G. (2009) Plant–hummingbird interactions in the West Indies: floral specialisation gradients associated with environment and hummingbird size. <i>Oecologia</i> , 159 , 757–766.
3	15.25	-61.37	Coastal dry scrubland, Dominica	Dalsgaard, B., Martín González, A.M., Olesen, J.M., Ollerton, J., Timmermann, A., Andersen, L.H. & Tossas, A.G. (2009) Plant–hummingbird interactions in the West Indies: floral specialisation gradients associated with environment and hummingbird size. <i>Oecologia</i> , 159 , 757–766.
4	12.10	-61.68	Rainforest, Grenada	Dalsgaard, B., Martín González, A.M., Olesen, J.M., Ollerton, J., Timmermann, A., Andersen, L.H. & Tossas, A.G. (2009) Plant–hummingbird interactions in the West Indies: floral specialisation gradients associated with environment and hummingbird size. <i>Oecologia</i> , 159 , 757–766.
5	10.67	-61.28	Mixed forest, Trinidad	Snow, B.K. & Snow, D.W. (1972) Feeding niches of hummingbirds in a Trinidad Valley. <i>The Journal of Animal Ecology</i> , 41 , 471–485.
6	5.92	-73.53	Andean humid montane forest, Colombia	Snow, D.W. & Snow, B.K. (1980) Relationships between hummingbirds and flowers in the Andes of Colombia. <i>Bulletin of the British Museum of Natural History (Zoology)</i> , 38 , 105–139.
7	5.90	-73.42	Andean humid montane forest, Colombia	Snow, D.W. & Snow, B.K. (1980) Relationships between hummingbirds and flowers in the Andes of Colombia. <i>Bulletin of the British Museum of Natural History (Zoology)</i> , 38 , 105–139.
8	4.54	-75.77	Andean second growth humid forest, Colombia	Cardona, J., & Cardona P.A. (2011) Uso de recursos florales por el ensamble de aves nectarívoras en el campus de la Universidad del Quindío. <i>BSc Thesis</i> . Universidad del Quindío, Colombia.
9	4.50	-75.60	Andean second growth humid forest, Colombia	Marín-Gómez, O.H. <i>Unpublished data</i> .

ID number	Latitude	Longitude	Site description and general location	Data Source Reference
10	-0.02	-78.77	Andean rainforest, mid-elevation, Ecuador.	Walther, B.A. & Brieschke, H. (2001) Hummingbird-flower relationships in a mid-elevation rainforest near Mindo, northwestern Ecuador. <i>International Journal of Ornithology</i> , 4 , 115–135.
11	-3.82	-70.27	Amazonian rainforest, SE Colombia	Cotton, P.A. (1998) The hummingbird community of a lowland Amazonian rainforest. <i>Ibis</i> , 140 , 512–521.
12	-22.73	-45.58	Montane Forest, SE Brazil	Sazima, I., Buzato, S. & Sazima, M. (1996) An assemblage of hummingbird-pollinated flowers in a montane forest in southeastern Brazil. <i>Botanica Acta</i> , 109 , 149–160.
13	-23.28	-45.05	Montane Atlantic forest, SE Brazil	Vizentin–Bugoni, J., Maruyama, P.K. & Sazima, M. (2014) Processes entangling interactions in communities: forbidden links are more important than abundance in a hummingbird–plant network. <i>Proceedings of the Royal Society of London B</i> , 281 , 1–8.
14	-23.35	-44.83	Atlantic forest, SE Brazil	Araujo, A.C. (1996) Beija-flores e seus recursos florais numa área de planície costeira do litoral norte de São Paulo, sudeste do Brasil. <i>MSc. Thesis</i> . Universidade Estadual de Campinas, Brazil.
15	-23.37	-45.04	Secondary Atlantic forest, SE Brazil	Maruyama, P.K, Vizentin-Bugoni, J., Dalsgaard, B., Sazima, I. & Sazima, M. (2015) Nectar robbery by a hermit hummingbird: association to floral phenotype and its influence on flowers and network structure. <i>Oecologia</i> , 178,783–793.
16	-23.48	-44.87	Restinga, Atlantic forest, SE Brazil	Maruyama, P.K, Vizentin-Bugoni, J., Dalsgaard, B., Sazima, I. & Sazima, M. (2015) Nectar robbery by a hermit hummingbird: association to floral phenotype and its influence on flowers and network structure. <i>Oecologia</i> , 178,783–793.
17	-23.58	-45.07	Coastal Atlantic Forest, SE Brazil	Maruyama, P.K, Vizentin-Bugoni, J., Dalsgaard, B., Sazima, I. & Sazima, M. (2015) Nectar robbery by a hermit hummingbird: association to floral phenotype and its influence on flowers and network structure. <i>Oecologia</i> , 178,783–793.
18	-23.63	-45.85	Coastal cloud Atlantic forest, SE Brazil	Snow D.W. & Snow, B.K. (1986) Feeding ecology of hummingbirds in the Serra do Mar, southeastern Brazil. <i>Hornero</i> , 12 , 286–296.
19	-25.32	-48.707	Atlantic Forest, S Brazil	Malucelli, T. S. (2014) Fatores envolvidos na estruturação das redes de polinização beija-flor-planta em um gradiente sucessional. <i>MSc. Thesis</i> . Universidade Federal do Paraná, Brazil.

ID number	Latitude	Longitude	Site description and general location	Data Source Reference
20	-27.27	-49.01	Atlantic Forest, S Brazil	Kohler, G. (2011) Redes de interação planta-beija-flor em um gradiente altitudinal de Floresta Atlântica no Sul do Brasil. <i>MSc. Thesis</i> . Universidade Federal do Paraná, Brazil.
21	-31.80	-52.42	Pampa, S Brazil	Vizentin-Bugoni, J. & Rui, A.M. <i>Unpublished data</i> .

Table S2. List of plant species found across 21 plant-hummingbird networks.

Family	Plant species	Author	Network ID
Acanthaceae	<i>Aphelandra colorata</i>	(Vell. Conc.) Wass.	13
Acanthaceae	<i>Aphelandra</i> sp.		6
Acanthaceae	<i>Dicliptera pohliana</i>	Ness	21
Acanthaceae	<i>Dicliptera squarrosa</i>	Ness	8
Acanthaceae	<i>Geissomeria</i> sp.		13
Acanthaceae	<i>Justicia brasiliana</i>	Roth	20,21
Acanthaceae	<i>Justicia carnea</i>	Lindl.	17,18,20
Acanthaceae	<i>Justicia secunda</i>	Vahl	4
Acanthaceae	<i>Justicia</i> sp.1		13
Acanthaceae	<i>Justicia</i> sp.2		13
Acanthaceae	<i>Justicia</i> sp.3		5
Acanthaceae	<i>Mendoncia</i> sp.		13
Acanthaceae	<i>Mendoncia velloziana</i>	(Mart.) Nees	15,18,19
Acanthaceae	<i>Pachystachys coccinea</i>	Nees	5,19
Acanthaceae	<i>Ruellia elegans</i>	Poir.	15
Acanthaceae	<i>Sanchezia munita</i>	Ruiz & Pav./Ruiz & Pav.	11
Acanthaceae	<i>Sanchezia nobilis</i>	Hook.f.	17
Acanthaceae	<i>Sanchezia putumayensis</i>	Leonard	11
Acanthaceae	<i>Trichanthera gigantea</i>	(Humb. & Bonpl.) Nees	9

Family	Plant species	Author	Network ID
Adoxaceae	<i>Sambucus</i> sp.		10
Alstromeriaceae	<i>Alstroemeria inodora</i>	Herb.	12,13,18
Alstromeriaceae	<i>Alstroemeria isabellana</i>	Herb.	18
Alstromeriaceae	<i>Bomarea carderi</i>	Mast.	6,9
Alstromeriaceae	<i>Bomarea edulis</i>	(Tussac) Herb.	15,16
Alstromeriaceae	<i>Bomarea pardina</i>	Herb.	10
Alstromeriaceae	<i>Bomarea</i> sp.		9
Amaryllidaceae	<i>Hippeastrum aulicum</i>	(Ker Gwal.) Herb.	20
Amaryllidaceae	<i>Hippeastrum aviflorum</i>	(Ravenna) Dutilh	12
Apocynaceae	<i>Mandevilla</i> aff. <i>mollissima</i>	(Kunth) K. Schum.	7
Apocynaceae	<i>Mandevilla funiformis</i>	(Vell.) K. Schum.	18
Apocynaceae	<i>Mandevilla hirsuta</i>	(Rich.) K. Schum.	5
Apocynaceae	<i>Pentalinon luteum</i>	(L.) B.F. Hansen & Wunderlin	1
Apocynaceae	<i>Tabernaemontana alba</i>	Mill.	1
Apocynaceae	<i>Tabernaemontana cymosa</i>	Jacq.	5
Asparagaceae	<i>Furcraea</i> sp.		10
Balsaminaceae	<i>Impatiens</i> sp.		10
Balsaminaceae	<i>Impatiens walleriana</i>	Hook. f.	2,15,16
Bignoniaceae	<i>Arrabidaea</i> sp.		14
Bignoniaceae	<i>Campsis grandiflora</i>	(Thunb.) K.Schum.	21

Family	Plant species	Author	Network ID
Bignoniaceae	<i>Cuspidaria inaequalis</i>	(DC. ex Splitg.) L.G.Lohmann	5
Bignoniaceae	<i>Dolichandra unguis.cati</i>	(L.) L.G.Lohmann	5
Bignoniaceae	<i>Handroanthus chrysanthus</i>	(Jacq.) S.O.Grose	8
Bignoniaceae	<i>Handroanthus umbellatus</i>	(Sond.) Mattos	19
Bignoniaceae	<i>Jacaranda mimosifolia</i>	D.Don	21
Bignoniaceae	<i>Jacaranda puberula</i>	Cham.	14
Bignoniaceae	<i>Lundia cordata</i>	(Vell.) DC.	14
Bignoniaceae	<i>Pyrostegia venusta</i>	(Ker Gwal.) Miers	13
Bignoniaceae	<i>Spathodea campanulata</i>	P.Beauv.	8
Bignoniaceae	<i>Tabebuia cassinoides</i>	(Lam.) DC.	14
Bignoniaceae	<i>Tabebuia heterophylla</i>	(DC.) Britton	3
Bignoniaceae	<i>Tabebuia stenocalyx</i>	Sprague & Stapf	5
Bignoniaceae	<i>Tecoma stans</i>	(L.) Juss. ex Kunth	3
Boraginaceae	<i>Cordia bicolor</i>	A.DC. ex DC.	5
Boraginaceae	<i>Cordia bullata</i>	(L.) Roem. & Schult.	3
Boraginaceae	<i>Cordia curassavica</i>	(Jacq.) Roem. & Schult.	5
Boraginaceae	<i>Cordia multispicata</i>	Cham.	14
Bromeliaceae	<i>Aechmea aquilega</i>	(Salisb.) Griseb.	5
Bromeliaceae	<i>Aechmea blumenavii</i>	Reitz	20
Bromeliaceae	<i>Aechmea coelestis</i>	(K.Koch) E.Morren	16

Family	Plant species	Author	Network ID
Bromeliaceae	<i>Aechmea contracta</i>	(Mart. ex Schult. & Schult.f.) Baker	11
Bromeliaceae	<i>Aechmea dichlamydea</i>	Baker	5
Bromeliaceae	<i>Aechmea distichantha</i>	Lem,	12,13,14,16
Bromeliaceae	<i>Aechmea fendleri</i>	André ex Mez	5
Bromeliaceae	<i>Aechmea gamosepala</i>	Wittm.	13
Bromeliaceae	<i>Aechmea nudicaulis</i>	(L.) Griseb.	5,12,13,14,16,19,21
Bromeliaceae	<i>Aechmea organensis</i>	Wawra	13
Bromeliaceae	<i>Aechmea pectinata</i>	Baker	14,16,18
Bromeliaceae	<i>Aechmea recurvata</i>	(Klotzsch) L.B.Sm.	21
Bromeliaceae	<i>Aechmea williamsii</i>	(L.B.Sm.) L.B.Sm. & M.A.Spencer	11
Bromeliaceae	<i>Billbergia amoena</i>	(Lodd.) Lindl.	13,20
Bromeliaceae	<i>Billbergia distachya</i>	(Vell.) Mez	12
Bromeliaceae	<i>Billbergia pyramidalis</i>	(Sims) Lindl.	5,14,16,17
Bromeliaceae	<i>Bromelia antiacantha</i>	Bertol.	16,21
Bromeliaceae	<i>Canistropsis seidelii</i>	(L.B.Sm. & Reitz) Leme	14,16,17
Bromeliaceae	<i>Canistrum cf. fragrans</i>	(Linden) Mabb.	13
Bromeliaceae	<i>Canistrum cyathiforme</i>	(Vell.) Mez	12
Bromeliaceae	<i>Canistrum giganteum</i>	(Baker) L.B.Sm.	18
Bromeliaceae	<i>Canistrum perplexum</i>	L.B.Sm.	13
Bromeliaceae	<i>Guzmania berteroniana</i>	(Schult. & Schult.f.) Mez	2

Family	Plant species	Author	Network ID
Bromeliaceae	<i>Guzmania danielii</i>	L.B.Sm.	10
Bromeliaceae	<i>Guzmania jaramilloi</i>	H.E.Luther	10
Bromeliaceae	<i>Guzmania monostachia</i>	(L.) Rusby ex Mez	5
Bromeliaceae	<i>Guzmania</i> sp. 1		10
Bromeliaceae	<i>Guzmania</i> sp.2		10
Bromeliaceae	<i>Guzmania</i> sp.3		9
Bromeliaceae	<i>Guzmania</i> sp.4		7
Bromeliaceae	<i>Guzmania squarrosa</i>	(Mez & Sodiro) L.B.Sm. & Pittendr.	6
Bromeliaceae	<i>Guzmania teuscheri</i>	L.B.Sm.	10
Bromeliaceae	<i>Mezobromelia</i> sp.		9
Bromeliaceae	<i>Neoregelia johannis</i>	(Carrière) L.B.Sm.	15,17
Bromeliaceae	<i>Nidularium angustifolium</i>	Ule	17
Bromeliaceae	<i>Nidularium innocentii</i>	Lem.	13,14,16,17,18,19,20
Bromeliaceae	<i>Nidularium longiflorum</i>	Ule	13
Bromeliaceae	<i>Nidularium marigoii</i>	Leme	12
Bromeliaceae	<i>Nidularium procerum</i>	Lindm.	13,14,19
Bromeliaceae	<i>Nidularium rutilans</i>	E.Morren	13
Bromeliaceae	<i>Pitcairnia nigra</i>	(Carrière) André	10
Bromeliaceae	<i>Pitcairnia</i> sp.		6
Bromeliaceae	<i>Quesnelia</i> sp.		13

Family	Plant species	Author	Network ID
Bromeliaceae	<i>Tillandsia aeranthos</i>	(Loisel.) L.B.Sm.	21
Bromeliaceae	<i>Tillandsia aff.turneri</i>	Baker	6
Bromeliaceae	<i>Tillandsia fasciculata</i>	Sw.	5
Bromeliaceae	<i>Tillandsia geminiflora</i>	Brongn.	13,15,16
Bromeliaceae	<i>Tillandsia sp. 1</i>		13
Bromeliaceae	<i>Tillandsia sp.2</i>		13
Bromeliaceae	<i>Tillandsia sp.3</i>		20
Bromeliaceae	<i>Tillandsia stricta</i>	Sol.	12,13,18
Bromeliaceae	<i>Tillandsia utriculata</i>	L.	5
Bromeliaceae	<i>Vriesea carinata</i>	Wawra	13,19,20
Bromeliaceae	<i>Vriesea ensiformis</i>	(Vell.) Beer	14,16,17,19
Bromeliaceae	<i>Vriesea erythrodactylon</i>	E.Morren ex Mez	13,20
Bromeliaceae	<i>Vriesea incurvata</i>	Gaudich.	13,18,19,20
Bromeliaceae	<i>Vriesea inflata</i>	(Wawra) Wawra	13
Bromeliaceae	<i>Vriesea jonghei</i>	(K. Koch) E.Morren	18
Bromeliaceae	<i>Vriesea procera</i>	(Mart. ex Schult. & Schult.f.) Wittm.	5,14,15,16
Bromeliaceae	<i>Vriesea rodigasiana</i>	E.Morren	14,15,17
Bromeliaceae	<i>Vriesea sceptrum</i>	Mez	12
Bromeliaceae	<i>Vriesea simplex</i>	(Vell.) Beer	13
Bromeliaceae	<i>Vriesea sp.</i>		13

Family	Plant species	Author	Network ID
Bromeliaceae	<i>Vriesea vagans</i>	(L.B.Sm.) L.B.Sm.	20
Bromeliaceae	<i>Wittrockia superba</i>	Lindm.	13
Campanulaceae	<i>Burmeistera cyclostigmata</i>	Donn. Sm.	10
Campanulaceae	<i>Burmeistera globosa</i>	E. Wimm.	6
Campanulaceae	<i>Burmeistera</i> sp.		10
Campanulaceae	<i>Centropogon cornutus</i>	(L.) Druce	4,5,8,9,13,14,15,16
Campanulaceae	<i>Centropogon latisepalus</i>	Gleason	9
Campanulaceae	<i>Centropogon</i> sp.		10
Campanulaceae	<i>Siphocampylus convolvulaceus</i>	(Cham.) G.Don	13
Campanulaceae	<i>Siphocampylus longipedunculatus</i>	Pohl	13
Campanulaceae	<i>Siphocampylus</i> sp.		13
Campanulaceae	<i>Siphocampylus sulfureus</i>	E.Wimm.	12
Campanulaceae	<i>Siphocampylus westinianus</i>	(Thunb.) Pohl	12
Cannaceae	<i>Canna indica</i>	L.	7, 8
Cannaceae	<i>Canna panniculata</i>	Ruiz & Pav.	13,15
Cannaceae	<i>Canna</i> sp.		10
Caprifoliaceae	<i>Lonicera japonica</i>	Thunb.	12
Chrysobalanaceae	<i>Couepia schottii</i>	Fritsch	14
Clusiaceae	<i>Clusia</i> sp.1		6
Clusiaceae	<i>Clusia</i> sp.2		10

Family	Plant species	Author	Network ID
Clusiaceae	<i>Symphonia globulifera</i>	L.f.	5
Combretaceae	<i>Combretum llewelynii</i>	Macbride	11
Compositae	<i>Mutisia speciosa</i>	Aiton ex Hook.	12,13,14,16
Compositae	<i>Piptocarpha notata</i>	(Less.) Baker	18
Convolvulaceae	<i>Ipomoea</i> sp.1		7
Convolvulaceae	<i>Ipomoea</i> sp.2		20
Convolvulaceae	<i>Jacquemontia sphaerostigma</i>	(Cav.) Rusby	14
Costaceae	<i>Costus scaber</i>	Ruiz & Pav.	4,11
Costaceae	<i>Costus</i> sp.1		5
Costaceae	<i>Costus</i> sp.2		9
Costaceae	<i>Costus spiralis</i>	(Jacq.) Roscoe	5,11,14,19
Crassulaceae	<i>Kalanchoe</i> sp.	Adans.	10
Cucurbitaceae	<i>Gurania lobata</i>	(L.) J.F. Pruski	5,11
Cucurbitaceae	<i>Gurania rhizantha</i>	(Poepp. & Endl.) C.Jeffrey	11
Ericaceae	<i>Agarista</i> sp.		12
Ericaceae	<i>Cavendishia bracteata</i>	(Ruiz & Pav. ex A. St. Hilaire) Horold	6,9
Ericaceae	<i>Cavendishia grandifolia</i>	Herold	10
Ericaceae	<i>Cavendishia guatapeensis</i>	Mansfeld	6
Ericaceae	<i>Cavendishia pubescens</i>	(Kunth) Hemsl.	6,7
Ericaceae	<i>Cavendishia tarapotana</i>	(Meissner) Bentham & Hooker f.	10

Family	Plant species	Author	Network ID
Ericaceae	<i>Disterigma</i> sp.		6
Ericaceae	<i>Ericaceae</i> sp.		10
Ericaceae	<i>Macleania pentaptera</i>	Horold	10
Ericaceae	<i>Macleania recumbens</i>	Horold	10
Ericaceae	<i>Psammisia aberrans</i>	A.C. Smith	10
Ericaceae	<i>Psammisia ecuadorensis</i>	Horold	10
Ericaceae	<i>Psammisia falcata</i>	(Kunth) Klotzsch	6
Ericaceae	<i>Psammisia oreogenes</i>	Sleum.	10
Ericaceae	<i>Psammisia pauciflora</i>	Griseb	10
Ericaceae	<i>Psammisia penduliflor</i>	(Dunal) Klotzsch	7
Ericaceae	<i>Psammisia sodiroi</i>	Horold	10
Ericaceae	<i>Psammisia ulbrichiana</i>	Horold	10
Ericaceae	<i>Thibaudia rigidiflora</i>	A.C. Smith	6
Gentianaceae	<i>Chelonanthus alatus</i>	(Aubl.) Pulle	5
Gentianaceae	<i>Macrocarpaea</i> sp.		6
Gentianaceae	<i>Macrocarpea rubra</i>	Malme	13
Gesneriaceae	<i>Alloplectus</i> sp.		10
Gesneriaceae	<i>Besleria longimucronata</i>	Hoehne	13,15,17
Gesneriaceae	<i>Besleria solanoides</i>	C.V. Morton	9,10
Gesneriaceae	<i>Columnea ciliata</i>	(Wiehler) L.P. Kvist & L.E. Skog	10

Family	Plant species	Author	Network ID
Gesneriaceae	<i>Columnnea dimidiata</i>	(Benth.) Kuntze	9
Gesneriaceae	<i>Columnnea medicinalis</i>	(Wiehler) L.P. Kvist & L.E. Skog	10
Gesneriaceae	<i>Columnnea strigos</i>	Benth.	10
Gesneriaceae	<i>Gasteranthus</i> sp.		10
Gesneriaceae	<i>Gesneriaceae</i> sp.1		10
Gesneriaceae	<i>Gesneriaceae</i> sp.2		10
Gesneriaceae	<i>Gesneriaceae</i> sp.3		10
Gesneriaceae	<i>Gesneriaceae</i> sp.4		11
Gesneriaceae	<i>Glossoloma bolivianum</i>	(Britton ex Rusby) J.L. Clark	10
Gesneriaceae	<i>Huilaea minor</i>	(L.Uribe) Lozano & N.Ruiz-R.	6
Gesneriaceae	<i>Kohleria affinis</i>	(Fritsch) Roalson & Boggan	9
Gesneriaceae	<i>Kohleria inaequalis</i>	(Benth.) Wiehler	9
Gesneriaceae	<i>Kohleria spicata</i>	(Kunth) Oerst.	10
Gesneriaceae	<i>Nematanthus australis</i>	Chautems	20
Gesneriaceae	<i>Nematanthus fissus</i>	(Vell.) L.E. Skog	16
Gesneriaceae	<i>Nematanthus fluminensis</i>	(Vell.) Fristch	13,14,16,17
Gesneriaceae	<i>Nematanthus fornix</i>	(Vell.) Chautems	12
Gesneriaceae	<i>Nematanthus fritschii</i>	Hoehne	13,18
Gesneriaceae	<i>Nematanthus gregarius</i>	D.L. Denham	13,18
Gesneriaceae	<i>Nematanthus maculatus</i>	(Fritsch) Wiehler	13

Family	Plant species	Author	Network ID
Gesneriaceae	<i>Nematanthus</i> sp. 1		13
Gesneriaceae	<i>Nematanthus tessmannii</i>	(Hoehne) Chautems	19
Gesneriaceae	<i>Sinningia cooperi</i>	(Paxton) Wiehler	13
Gesneriaceae	<i>Sinningia douglasii</i>	(Lindl.) Chautems	12,20
Gesneriaceae	<i>Sinningia elatior</i>	(Kunth) Chautems	13
Gesneriaceae	<i>Sinningia glazioviana</i>	(Fritsch) Chautems	13
Heliconiaceae	<i>Heliconia angusta</i>	Vell.	14,16,17
Heliconiaceae	<i>Heliconia bihai</i>	(L.) L.	4,5
Heliconiaceae	<i>Heliconia burleana</i>	Abalo & G. Morales	10
Heliconiaceae	<i>Heliconia farinosa</i>	Raddi	15,17,18,19,20
Heliconiaceae	<i>Heliconia griggsiana</i>	L.B.Sm.	8,9
Heliconiaceae	<i>Heliconia hirsuta</i>	L.f.	5
Heliconiaceae	<i>Heliconia juruana</i>	Loes.	11
Heliconiaceae	<i>Heliconia latispatha</i>	Benth.	8,9
Heliconiaceae	<i>Heliconia psittacorum</i>	L.f.	5
Heliconiaceae	<i>Heliconia schumanniana</i>	Loes.	11
Heliconiaceae	<i>Heliconia</i> sp.		5
Heliconiaceae	<i>Heliconia</i> sp. 1		7
Heliconiaceae	<i>Heliconia</i> sp. 2		10
Heliconiaceae	<i>Heliconia spathocircinata</i>	Aristeg.	14,15

Family	Plant species	Author	Network ID
Heliconiaceae	<i>Heliconia stricta</i>	Huber	11
Heliconiaceae	<i>Heliconia venusta</i>	Abalo & G.Morales	9
Iridaceae	<i>Crocasmia</i> × <i>crocosmiiflora</i>	(Lemoine) N.E.Br.	13
Iridaceae	<i>Iridaceae</i> sp.		10
Lamiaceae	<i>Aegiphila perplexa</i>	Moldenke	5
Lamiaceae	<i>Clerodendrum aculeatum</i>	L.	1
Lamiaceae	<i>Lamiaceae</i> sp.		10
Lamiaceae	<i>Leonotis nepetifolia</i>	(L.) R. Br.	3
Lamiaceae	<i>Salvia arenaria</i>	Willd. ex Schult.	12
Lamiaceae	<i>salvia articulata</i>	A.St.-Hil. ex Benth.	18
Lamiaceae	<i>Salvia</i> sp.		10
Lamiaceae	<i>Vitex divaricata</i>	Sw.	5
Lecythidaceae	<i>Lecythidoideae</i> sp.		10
Leguminosae	<i>Abarema brachystachya</i>	Barneby & J.W. Grimes	14
Leguminosae	<i>Albizia pedicellaris</i>	(Dc.) L.Rico	14
Leguminosae	<i>Albizia saman</i>	(Jacq.) Merr.	1,5
Leguminosae	<i>Brownea coccinea</i> subsp. <i>capitella</i>	(Jacq.) D. Velásquez & G. Agostini	5
Leguminosae	<i>Calliandra brevipes</i>	Benth.	21
Leguminosae	<i>Calliandra guildingii</i>	Benth.	5
Leguminosae	<i>Calliandra purdiaei</i>	Benth.	7

Family	Plant species	Author	Network ID
Leguminosae	<i>Calliandra tweediei</i>	Benth.	21
Leguminosae	<i>Camptosema scarlatinum</i>	(Mart. Ex Benth.) Bukart	12
Leguminosae	<i>Clathrotropis brachypetala</i>	(Tul.) Kleinhoonte	5
Leguminosae	<i>Collaea speciosa</i>	(Loisel.) DC.	12
Leguminosae	<i>Dahlstedtia pentaphylla</i>	(Taub.) Burkart	19
Leguminosae	<i>Dahlstedtia pinnata</i>	(Benth.) Malme	15,16,17,18,19
Leguminosae	<i>Dioclea</i> sp.		18
Leguminosae	<i>Erythrina corallodendron</i>	L.	5
Leguminosae	<i>Erythrina crista-galli</i>	L.	21
Leguminosae	<i>Erythrina edulis</i>	Micheli	8
Leguminosae	<i>Erythrina fusca</i>	Lour.	5,11
Leguminosae	<i>Erythrina poeppigiana</i>	(Walp.) O.F. Cook	5
Leguminosae	<i>Erythrina rubrinervia</i>	Kunth	9
Leguminosae	<i>Erythrina</i> sp.		10
Leguminosae	<i>Erythrina speciosa</i>	Andrews	8,13,14,16,19,21
Leguminosae	<i>Inga densiflora</i>	Benth.	8
Leguminosae	<i>Inga edulis</i>	Mart.	14,19
Leguminosae	<i>Inga ingoides</i>	(Rich.) Willd.	5
Leguminosae	<i>Inga ingoides</i>	(Rich.) Willd.	8,9
Leguminosae	<i>Inga leiocalycina</i>	Benth.	11

Family	Plant species	Author	Network ID
Leguminosae	<i>Inga semialata</i>	(Vell.) C.Mart.	15,17
Leguminosae	<i>Inga sessilis</i>	(Vell.) Mart.	13
Leguminosae	<i>Inga sp.1</i>		18
Leguminosae	<i>Inga sp.2</i>		10
Leguminosae	<i>Inga sp.3</i>		5
Leguminosae	<i>Inga subnuda</i>	Benth.	14,16
Leguminosae	<i>Inga venosa</i>	Griseb.	5
Leguminosae	<i>Leguminosae sp.</i>		10
Leguminosae	<i>Lonchocarpus benthamianus</i>	Pittier	3
Leguminosae	<i>Lysiloma latisiliquum</i>	(L.) Benth.	1
Leguminosae	<i>Neorudolphia volubilis</i>	(Willd.) Britton	2
Leguminosae	<i>Phaseolus coccineus</i>	L.	6
Leguminosae	<i>Pithecellobium jupunba</i>	(Willd.) Urb.	5
Leguminosae	<i>Schizolobium parahyba</i>	(Vell.) S.F.Blake	19
Leguminosae	<i>Tachigalia paniculata</i>	Aubl.	11
Leguminosae	<i>Tephrosia noctiflora</i>	Bojer ex Baker	3
Loranthaceae	<i>Loranthaceae sp.</i>		18
Loranthaceae	<i>Psittacanthus cucularis</i>	(Lam.) G. Don	11
Loranthaceae	<i>Psittacanthus dichrous</i>	(Mart.) Mart.	13,14,16
Lythraceae	<i>Cuphea melvilla</i>	Lindl.	11

Family	Plant species	Author	Network ID
Malvaceae	<i>Abutilon</i> aff. <i>regnellii</i>	Miq.	12
Malvaceae	<i>Abutilon darwinii</i>	Hook.f.	10
Malvaceae	<i>Abutilon</i> sp. 1		13
Malvaceae	<i>Dombeya wallichii</i>	(Lindl.) Benth. & Hook.f.	14
Malvaceae	<i>Eriotheca pentaphylla</i>	(Vell. & K.Schum.) A.Robyns	14,16
Malvaceae	<i>Guazuma ulmifolia</i>	Lam.	1
Malvaceae	<i>Hibiscus rosa.sinensis</i>	L.	10,14
Malvaceae	<i>Luehea divaricata</i>	Mart. & Zucc.	21
Malvaceae	<i>Malvaviscus arboreus</i>	Cav.	10
Malvaceae	<i>Quararibea lasiocalyx</i>	K.Schum.	11
Malvaceae	<i>Spirotheca rivieri</i>	(Decne.) Ulbr.	13
Malvaceae	<i>Talipariti tiliaceum</i>	(L.) Fryxell	14
Malvaceae	<i>Urena lobata</i>	L.	2
Marantaceae	<i>Calathea capitata</i>	(Ruiz & Pav.) Lindl.	11
Marantaceae	<i>Ischnosiphon arouma</i>	(Aubl.) Korn.	5
Marantaceae	<i>Maranta furcata</i>	Nees & Mart.	14
Marcgraviaceae	<i>Marcgravia myriostigma</i>	Triana & Planch.	14
Marcgraviaceae	<i>Marcgravia polyantha</i>	Delpino	18
Marcgraviaceae	<i>Marcgravia</i> sp.		5
Marcgraviaceae	<i>Norantea guianensis</i>	Aubl.	5

Family	Plant species	Author	Network ID
Marcgraviaceae	<i>Sarcopera</i> sp.		10
Marcgraviaceae	<i>Schwartzia brasiliensis</i>	(Choisy) Bedell ex Gir.-Cañas	14,16,19
Melastomataceae	<i>Acinodendron sintenisii</i>	(Cogn.) Kuntze	2
Melastomataceae	<i>Melastomataceae</i> sp.		10
Musaceae	<i>Musa balbisiana</i>	Colla	19
Musaceae	<i>Musa ornata</i>	Roxb.	15
Musaceae	<i>Musa</i> sp. 1		7
Musaceae	<i>Musa</i> sp.2		10
Musaceae	<i>Musa velutina</i>	H.Wendl. & Drude	8,9
Musaceae	<i>Musa x paradisiaca</i>	L.	8
Myrtaceae	<i>Callistemon speciosus</i>	(Sims) Sweet	21
Myrtaceae	<i>Eucalyptus globulus</i>	Labill.	9
Myrtaceae	<i>Melaleuca leucadendra</i>	(L.) L.	21
Myrtaceae	<i>Syzigium malaccense</i>	(L.) Merr. & L.M.Perry	11
Myrtaceae	<i>Syzygium jambos</i>	(L.) Alston	4,5,7,14
Nyctaginaceae	<i>Bougainvillea</i> sp.		10
Onagraceae	<i>Fuchsia macrostigma</i>	Benth.	10
Onagraceae	<i>Fuchsia regia</i>	(Vell.) Munz	12,13,18,20
Orchidaceae	<i>Elleanthus aurantiacus</i>	(Lindl.) Rchb.f.	9
Orchidaceae	<i>Elleanthus smithii</i>	Schltr.	6

Family	Plant species	Author	Network ID
Orchidaceae	<i>Orchidaceae</i> sp.		10
Orobanchaceae	<i>Esterhazyia splendida</i>	J.C.Mikan	12
Passifloraceae	<i>Passiflora aff involucrata</i>	(Masters) A.Gentry	11
Passifloraceae	<i>Passiflora quadriglandulosa</i>	Rodschied	11
Passifloraceae	<i>Passiflora spinosa</i>	(Poeppig&Endlicher) Masters	11
Passifloraceae	<i>Passifloraceae</i> sp.		10
Passifloraceae	<i>Turnera ulmifolia</i>	L.	1,3
Polygonaceae	<i>Antigonon leptopus</i>	Hook. & Arn.	1
Rosaceae	<i>Rubus rosifolius</i>	Sm.	19
Rubiaceae	<i>Erithalis fruticosa</i>	L.	3
Rubiaceae	<i>Genipa americana</i>	L.	11
Rubiaceae	<i>Gonzalagunia hirsuta</i>	K.Schum.	4,5
Rubiaceae	<i>Hamelia patens</i>	Jacq.	5,7,8,9
Rubiaceae	<i>Isertia parviflora</i>	Vahl	5
Rubiaceae	<i>Manettia aff.sabiceoides</i>	Wernham	6,7
Rubiaceae	<i>Manettia cordifolia</i>	Mart.	13,18
Rubiaceae	<i>Manettia luteorubra</i>	(Vell.) Benth.	19
Rubiaceae	<i>Manettia pubescens</i>	Cham. & Schltdl.	12
Rubiaceae	<i>Morinda citrifolia</i>	L.	3
Rubiaceae	<i>Palicourea acetosoides</i>	Wernham	9

Family	Plant species	Author	Network ID
Rubiaceae	<i>Palicourea aff lasiantha</i>	K.Krause	11
Rubiaceae	<i>Palicourea anderssoniana</i>	C.M.Taylor	10
Rubiaceae	<i>Palicourea cf. vagans</i>	Wernham	6
Rubiaceae	<i>Palicourea crocea</i>	(Sw.) Roem. & Schult.	2,4,5,11
Rubiaceae	<i>Palicourea demissa</i>	Standl.	6,10
Rubiaceae	<i>Palicourea fastigiata</i>	Kunth	11
Rubiaceae	<i>Palicourea sodiroi</i>	Standl.	10
Rubiaceae	<i>Palicourea</i> sp.1		6
Rubiaceae	<i>Palicourea</i> sp.2		11
Rubiaceae	<i>Posoqueria</i> sp.		6
Rubiaceae	<i>Psychotria berteriana</i>	DC.	2
Rubiaceae	<i>Psychotria leiocarpa</i>	Cham. & Schltdl.	13
Rubiaceae	<i>Psychotria mapouriioides</i>	DC.	5
Rubiaceae	<i>Psychotria muscosa</i>	(Jacq.) Steyerl.	5
Rubiaceae	<i>Psychotria nuda</i>	(Cham. & Schltdl.) Wawra	14,15,16,17,19
Rubiaceae	<i>Psychotria</i> sp.		5
Rubiaceae	<i>Psychotria suterella</i>	Mull. Arg.	19,20
Rubiaceae	<i>Rubiaceae</i> sp.		10
Rubiaceae	<i>Sabicea grisea</i>	Cham. & Schltdl.	14,15,16
Rubiaceae	<i>Schradera exotica</i>	(J.F.Gmel.) Standl.	2

Family	Plant species	Author	Network ID
Rubiaceae	<i>Warszewiczia coccinea</i>	(Vahl) Klotzsch	5
Rutaceae	<i>Citrus</i> sp.	L.	5
Rutaceae	<i>Rutaceae</i> sp.		10
Salicaceae	<i>Ryania speciosa</i>	M. Vahl	5
Schlegeliaceae	<i>Schlegelia brachyantha</i>	Griseb.	2
Scrophulariaceae	<i>Buddleja brasiliensis</i>	J.Jacq.	12,18
Scrophulariaceae	<i>Castilleja scorzonerifolia</i>	Kunth	7
Solanaceae	<i>Acnistus arborescens</i>	(L.) Schltdl.	15,19
Solanaceae	<i>Brugmansia arborea</i>	(L.) Steud.	10
Solanaceae	<i>Cestrum corymbosum</i>	Schltdl.	12
Solanaceae	<i>Cestrum macrophyllum</i>	Vent.	2
Solanaceae	<i>Cestrum</i> sp.		10
Tropaeolaceae	<i>Tropaeolum pentaphyllum</i>	Lam.	21
Verbenaceae	<i>Citharexylum spinosum</i>	L.	3
Verbenaceae	<i>Lantana camara</i>	L.	5,13,15
Verbenaceae	<i>Lantana nivea</i>	Vent.	14
Verbenaceae	<i>Stachytarpheta cayennensis</i>	(Rich.) Vahl	15,16
Verbenaceae	<i>Stachytarpheta jamaicensis</i>	(L.) Vahl	3
Verbenaceae	<i>Stachytarpheta maximiliani</i>	Schauer	19
Verbenaceae	<i>Stachytarpheta</i> sp.		14

Family	Plant species	Author	Network ID
Xanthorrhoeaceae	<i>Phormium tenax</i>	J.R.Forst. & G.Forst.	18
Zingiberaceae	<i>Hedychium coronarium</i>	J.Koenig	14,15,20
Zingiberaceae	<i>Renealmia alpinia</i>	(Rottb.) Maas	2
Zingiberaceae	<i>Renealmia sessilifolia</i>	Gagnep.	10
Zingiberaceae	<i>Renealmia</i> sp.		5

Table S3. List of hummingbird species found across 21 plant-hummingbird networks. References for hummingbird bill length data are also listed.

Species	Network ID	Bill length (mm)	Data sources
<i>Orthorhyncus cristatus</i>	3,4	10.72	Brown and Bowers 1985
<i>Mellisuga helenae</i>	1	10.76	Andrea Baquero, unpublished
<i>Lophornis chalybeus</i>	13,14,16,19	12.00	Vizentin-Bugoni et al. 2014
<i>Ocreatus underwoodii</i>	6,9,10	12.93	Graham et al. 2012
<i>Calliphlox amethystina</i>	15	13.00	Grantsau 1989
<i>Chrysolampis mosquitus</i>	5	13.00	Snow & Snow 1972
<i>Chlorostilbon maugaeus</i>	2	13.62	Brown and Bowers 1985
<i>Adelomyia melanogenys</i>	6,9,10	14.98	Graham et al. 2012
<i>Stephanoxis lalandi</i>	12,21	15.00	Vizentin-Bugoni et al. 2014
<i>Stephanoxis lodigessi</i>	13	15.86	Jeferson Vizentin-Bugoni, unpublished
<i>Chlorostilbon mellisugus</i>	8,11	15.14	Graham et al. 2012
<i>Agelaiocercus kingi</i>	6,9	15.53	Graham et al. 2012
<i>Amazilia versicolor</i>	13,15,16,17,18,19,20	15.60	Snow & Snow 1986
<i>Hylocharis cyanus</i>	14,15,16	16.00	Araujo 1996
<i>Chlorostilbon gibsoni</i>	7	16.20	Snow & Snow 1980
<i>Agelaiocercus coelestis</i>	10	16.25	Graham et al. 2012
<i>Chaetocercus mulsant</i>	6	16.70	Snow & Snow 1980
<i>Boissonneaua flavescens</i>	6,9,10	16.96	Graham et al. 2012

Species	Network ID	Bill length (mm)	Data sources
<i>Chlorostilbon ricordii</i>		1	17.20 Andrea Baquero
<i>Chlorostilbon poortmani</i>		6	17.26 Graham et al. 2012
<i>Colibri delphinae</i>		10	17.42 Graham et al. 2012
<i>Calliphlox mitchellii</i>		10	17.70 Walther & Brieschke 2001
<i>Amazilia cyanifrons</i>		7	17.80 Snow & Snow 1980
<i>Thalurania glaucopis</i>	13,14,15,16,17,18,19,20,21		17.90 Araujo 1996
<i>Amazilia saucerrottei</i>		8,9	17.92 Oscar Humberto Marin-Gomez, unpublished
<i>Amazilia tobaci</i>		5	18.00 Snow & Snow 1972
<i>Chlorestes notatus</i>		5,11	18.00 Snow & Snow 1972
<i>Chlorostilbon lucidus</i>		12,19,21	18.00 Grantsau 1989
<i>Heliangelus amethysticollis</i>		6	18.00 Snow & Snow 1980
<i>Amazilia chionopectus</i>		5,14	18.68 Araujo 1996
<i>Heliodoxa aurescens</i>		11	18.96 Graham et al. 2012
<i>Clytolaema rubricauda</i>	12,13,15,18,20		19.00 Vizentin-Bugoni et al. 2014
<i>Eupetomena macroura</i>		13,14,16	19.00 Grantsau 1989
<i>Florisuga mellivora</i>		5,9,10,11	19.00 Snow & Snow 1972
<i>Hylocharis chrysura</i>		21	19.00
<i>Urosticte benjamini</i>		10	19.06 Graham et al. 2012
<i>Thalurania fannyi</i>		10	19.21 Graham et al. 2012
<i>Leucochloris albicollis</i>	12,13,14,15,18,21		20.00 Vizentin-Bugoni et al. 2014

Species	Network ID	Bill length (mm)	Data sources
<i>Amazilia tzacatl</i>	7,8,9,10	20.02	Graham et al. 2012
<i>Aphantochroa cirrochloris</i>	19	20.17	Grantsau 1989
<i>Phaethornis ruber</i>	11,14,15,16	20.40	Araujo 1996
<i>Thalurania furcata</i>	11	20.65	Graham et al. 2012
<i>Chrysuronia oenone</i>	11	20.86	Graham 2012
<i>Amazilia fimbriata</i>	11,14,15,16,17,19,20	20.90	Araujo 1996
<i>Colibri thalassinus</i>	6,10	20.95	Graham et al. 2012
<i>Phaethornis longuemareus</i>	5	20.95	Graham et al. 2012
<i>Heliodoxa rubinoides</i>	10	21.06	Graham et al. 2012
<i>Florisuga fusca</i>	13,14,15,16,18,19,21	21.10	Snow & Snow 1986
<i>Colibri serrirostris</i>	12	22.00	Grantsau 1989
<i>Boissonneaua jardini</i>	10	22.50	Walther & Brieschke 2001
<i>Amazilia franciae</i>	7,9,10	22.67	Graham et al. 2012
<i>Eulampis holosericeus</i>	3,4	22.74	Brown and Bowers 1985
<i>Anthracothorax nigricollis</i>	5,7,8,9,11,14,21	23.59	Graham et al. 2012
<i>Phaethornis squalidus</i>	15,16,17,19	24.00	Grantsau 1989
<i>Heliodoxa imperatrix</i>	10	24.29	Graham et al. 2012
<i>Colibri coruscans</i>	6,9,10	24.35	Graham et al. 2012
<i>Anthracothorax viridis</i>	2	24.40	Kodric-Brown et al. 1984
<i>Campylopterus largipennis</i>	11	25.28	Graham et al. 2012

Species	Network ID	Bill length (mm)	Data sources
<i>Coeligena prunellei</i>		6	27.99 Graham et al. 2012
<i>Threnetes leucurus</i>		11	28.50 Cotton 1998
<i>Phaethornis bourcieri</i>		11	29.30 Graham et al. 2012
<i>Glaucis hirsutus</i>	4,5,11,14,15,16		31.00 Snow & Snow1972
<i>Heliomaster squamosus</i>		15	31.00 Grantsau 1989
<i>Coeligena coeligena</i>		9	31.40 Oscar Humberto Marin-Gomez, unpublished
<i>Coeligena torquata</i>		6	32.28 Graham et al. 2012
<i>Doryfera ludoviciae</i>		6,9,10	32.73 Graham et al. 2012
<i>Phaethornis hispidus</i>		11	32.76 Graham et al. 2012
<i>Coeligena wilsoni</i>		10	33.57 Graham et al. 2012
<i>Ramphodon naevius</i>	14,15,16,17,19,20		33.90 Araujo 1996
<i>Phaethornis eurynome</i>	12,13,18,19,20		34.00 Vizentin-Bugoni et al. 2014
<i>Heliomaster longirostris</i>		8	36.41 Oscar Humberto Marin-Gomez, unpublished
<i>Phaethornis superciliosus</i>		11	37.70 Cotton 1998
<i>Phaethornis syrmatophorus</i>		10	40.60 Graham et al. 2012
<i>Phaethornis guy</i>		5,7,8,9	40.88 Graham et al. 2012

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Table S4. Pearson correlation r among distinct species-level network indices calculated across 21 quantitative plant-hummingbird networks. For hummingbirds, indices related to species roles in modules were not included as many modules within networks contained only one hummingbird species, rendering these indices less meaningful. Moreover, the correlation of the indices in relation to hummingbird bill length is also shown. Strong correlations ($r > 0.6$) are in bold.

Plants	Strength	Specialization (d')	c	z
Degree	0.68	-0.01	0.62	0.53
Strength		0.30	0.23	0.70
Specialization (d')			-0.33	0.31
c				0.14
Hummingbirds	Strength	Specialization (d')	Bill length	
Degree	0.92	-0.05	0.17	
Strength		0.14	0.22	
Specialization (d')			0.38	

Table S5. List of the 32 alien plant species found across 21 plant-hummingbird networks. See Table S6 for references and details on the assessment of pollination systems for the plants.

Family	Plant species	Bird pollination	Country	Network ID	Origin	Size	Flower	
							Type	Length (mm)
Acanthaceae	<i>Dicliptera squarrosa</i>	Yes	Colombia	8	America	small	tube	27.90
Acanthaceae	<i>Sanchezia nobilis</i>	Yes	SE Brazil	17	America	small	tube	46.60
Balsaminaceae	<i>Impatiens</i> sp.	Unknown	Ecuador	10	Africa	small	tube	-
Balsaminaceae	<i>Impatiens walleriana</i>	No	Puerto Rico, SE Brazil	2,15,16	Africa	small	tube	14.30
Bignoniaceae	<i>Campsis grandiflora</i>	Yes	S Brazil	21	Asia	small	tube	32.10
Bignoniaceae	<i>Spathodea campanulata</i>	Yes	Colombia	8	Africa	large	other	102.90
Caprifoliaceae	<i>Lonicera japonica</i>	No	SE Brazil	12	Asia	small	tube	28.00
Iridaceae	<i>Crocasmia x crocosmiiflora</i>	Yes	SE Brazil	13	Africa	small	tube	14.10
Lamiaceae	<i>Leonotis nepetifolia</i>	Yes	Dominica	3	Africa	small	tube	11.09
Leguminosae	<i>Albizia saman</i>	No	Cuba	1,5	America	large	brush	9.95
Leguminosae	<i>Phaseolus coccineus</i>	No	Colombia	6	America	small	other	4.38
Leguminosae	<i>Tephrosia noctiflora</i>	No	Dominica	3	Africa	small	other	5.38
Malvaceae	<i>Dombeya wallichii</i>	No	SE Brazil	14	Asia/Africa?	small	other	10.00
Malvaceae	<i>Hibiscus rosa.sinensis</i>	Yes	Ecuador, SE Brazil	10,14	Asia	small	tube	24.50
Malvaceae	<i>Talipariti tiliaceum</i>	No	SE Brazil	14	Asia	small	tube	57.20

Family	Plant species	Bird pollination	Country	Network ID	Origin	Size	Flower	
							Type	Length (mm)
Musaceae	<i>Musa ornata</i>	Yes	SE Brazil	15	Asia	large	tube	39.50
Musaceae	<i>Musa rosacea</i>	Yes	S Brazil	19	Asia	large	tube	38.44
Musaceae	<i>Musa</i> sp.	Unknown	Colombia	7	Asia	large	tube	35.00
Musaceae	<i>Musa</i> sp.	Unknown	Ecuador	10	Asia	large	tube	-
Musaceae	<i>Musa velutina</i>	Yes	Colombia	8,9	Asia	large	tube	32.10
Musaceae	<i>Musa x paradisiaca</i>	No	Colombia	9	Asia	large	tube	31.80
Myrtaceae	<i>Callistemon speciosus</i>	Yes	S Brazil	21	Oceania	small	brush	3.10
Myrtaceae	<i>Eucalyptus globulus</i>	Yes	Colombia	9	Oceania	large	brush	13.20
Myrtaceae	<i>Melaleuca leucadendra</i>	No	S Brazil	21	Oceania	large	brush	2.90
Myrtaceae	<i>Syzygium jambos</i>	Yes	Colombia, Grenada, Trinidad, SE Brazil	4,5,7,14	Asia	large	brush	2.69
Myrtaceae	<i>Syzygium malaccens</i>	Yes	Colombia	11	Asia	large	brush	20.00
Polygonaceae	<i>Antigonon leptopus</i>	No	Cuba	1	America	small	other	3.11
Rubiaceae	<i>Morinda citrifolia</i>	No	Dominica	3	Asia	large	tube	9.29
Rutaceae	<i>Citrus</i> sp.	No	Trinidad	5	Asia	large	other	-
Verbenaceae	<i>Lantana nivea</i>	No	SE Brazil	14	America?	small	tube	11.60
Xanthorrhoeaceae	<i>Phormium tenax</i>	Yes	SE Brazil	18	Oceania	small	tube	29.00
Zingiberaceae	<i>Hedychium coronarium</i>	No	SE, S Brazil	14,15,20	Asia	small	tube	60.90

Table S6. Alien plant species across 21 plant-hummingbird networks and details on the assessment of their pollination system.

Plant species	Pollinators			Network ID
	Birds	Bats	Insects	
<i>Dicliptera squarrosa</i>	x			1
<i>Sanchezia nobilis</i>	x			2,*
<i>Impatiens walleriana</i>			x	3
<i>Campsis grandiflora</i>	x		x	4,5
<i>Spathodea campanulata</i>	x			6,7,8,9,10
<i>Lonicera japonica</i>			x	11
<i>Crocosmia x crocosmiiflora</i>	x		x	12
<i>Leonotis nepetifolia</i>	x		x	13,14
<i>Albizia saman</i>			x	15,16
<i>Phaseolus coccineus</i>			x	17,18
<i>Tephrosia noctiflora</i>			x	19,20
<i>Dombeya wallichii</i>			x	21,22
<i>Hibiscus rosa.sinensis</i>	x			23,24
<i>Talipariti tiliaceum</i>			x	25,26
<i>Musa ornata</i>	x		x	27,28,29,30
<i>Musa rosacea</i>		x		27,28,29,30

Plant species	Pollinators			Network ID
	Birds	Bats	Insects	
<i>Musa velutina</i>	x			27,28,29,30
<i>Musa x paradisiaca</i>	x	x	x	27,28,29,30
<i>Callistemon speciosus</i>	x		x	31,32,33
<i>Eucalyptus globulus</i>	x			34
<i>Melaleuca leucadendra</i>			x	31,35
<i>Syzygium jambos</i>	x	x		36,37,38
<i>Syzygium malaccens</i>	x	x	x	36,37,38
<i>Antigonon leptopus</i>			x	39
<i>Morinda citrifolia</i>			x	40, 41, 42
<i>Citrus</i> sp.			x	43
<i>Lantana nivea</i>			x	44
<i>Phormium tenax</i>	x		x	45
<i>Hedychium coronarium</i>			x	46

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* Personal observations

Table S7. Proportion of alien plant species and alien plant species interactions across 21 plant-hummingbird networks in Americas.

Network ID	Plant richness		Number of interactions	
	Total	Aliens (Prop.)	Total	Aliens (Prop.)
1	8	0.25	133	0.65
2	11	0.09	246	<0.01
3	11	0.27	1348	0.56
4	7	0.14	500	0.12
5	57	0.05	1417	0.07
6	13	0.15	257	0.68
7	22	0.05	343	0.05
8	14	0.29	1376	0.20
9	23	0.09	2957	0.03
10	65	0.05	2162	0.02
11	13	0.08	1203	0.14
12	25	0.04	482	0.01
13	56	0.02	2804	<0.01
14	42	0.14	8450	0.01
15	22	0.14	330	0.16
16	28	0.04	721	0.01
17	16	0.06	173	0.16
18	25	0.04	250	0.19
19	24	0.04	451	0.21
20	18	0.06	562	<0.01
21	16	0.19	481	0.23

Table S8. Comparison of linear mixed effect models explaining network indices of the alien plant species across 21 plant-hummingbird networks. We included plant traits (plant size, flower type, flower length and previous association to bird pollinators) as well as insularity of the network as fixed factors. Alien plant species identity was included as a random effect to account for plant species occurring in several networks. We only show the best models defined by $\Delta AICc < 2$. Note that with the exception of *c*, for all network indices the intercept only “model” was among the best models.

Network index	Model description	AICc	$\Delta AICc$	Weight
Degree	Size	116.9	-	0.173
	~intercept only	117.9	1.02	0.104
	Bird pollination+Size	118.2	1.33	0.089
	Bird pollination	118.6	1.71	0.074
	Insularity+Size	118.7	1.77	0.072
Species strength	~intercept only	127.3	-	0.268
	Bird pollination	129	1.72	0.114
	Size	129.1	1.75	0.112
	Insularity	129.2	1.89	0.104
d'	Size	119.7	-	0.262
	~intercept only	121.6	1.84	0.105
<i>c</i> (between module)	Size	105.3	-	0.305
	Size+Insularity	106.6	1.34	0.156
<i>z</i> (within module)	~intercept only	125.6	-	0.264
	Bird pollination	127.1	1.57	0.121
	Insularity	127.4	1.81	0.107

CONSIDERAÇÕES FINAIS

Espera-se que o crescente interesse dos ecólogos pela associação dos atributos funcionais e história natural das espécies às abordagens de redes de interações contribuirá para maiores avanços no entendimento das interações entre espécies em comunidades. Nesta tese, especificamente no primeiro capítulo, demonstramos que a consideração concomitante de diferentes tipos de interações, i.e. mutualísticas ou antagonísticas, muda a distribuição dos atributos florais entre módulos de interações numa rede de plantas e beija-flores da Floresta Atlântica (Maruyama et al. 2015a). Tendo em vista que módulos tem sido interpretados como potenciais "unidades coevolutivas" (Olesen et al. 2007), a caracterização de rede incorporando explicitamente as interações ilegítimas poderia aprimorar a compreensão de como as espécies se influenciam na comunidade. Neste sentido, sugerimos que estudos futuros considerem a investigação experimental de como redes são influenciadas por exploradores de mutualismos, e.g. pela mudança de comportamento dos polinizadores. Além disso, este estudo ilustra como a abordagem de redes pode ser utilizada em conjunto com outras abordagens para a investigação de um fenômeno ecológico de uma maneira compreensiva. Adicionalmente, o segundo capítulo oferece informações sobre a história natural de uma espécie que utilizamos como um estudo de caso no primeiro capítulo, o que possibilitou aprofundar a discussão sobre as possíveis consequências da interação de pilhagem que estudamos.

No terceiro capítulo, mostramos que sobreposição espaço-temporal e morfologia das espécies, mas não suas abundâncias ou a oferta de néctar, são os determinantes mais importantes da frequência das interações numa rede de plantas e beija-flores do Cerrado; complementarmente, demonstramos que o acoplamento morfológico de bicos e corolas e as diferenças na ocupação de habitats são importantes determinantes da formação de módulos de interação na rede (Maruyama et al. 2014). Em concordância com o nosso estudo anterior (Vizentin-Bugoni *et al.* 2014), reforçamos a importância dos atributos das espécies na

estruturação das redes de plantas e beija-flores. Neste contexto, sugerimos que estudos futuros investiguem a prevalência da importância dos atributos como estruturadores de interações dentro de dois contextos: 1) dentro de um mesmo sistema ao longo de escalas espaciais mais amplas; 2) estendendo a investigação a diferentes tipos de sistemas mutualísticos. Finalmente, no quarto capítulo, mostramos que espécies exóticas de plantas são geralmente bem integradas nas redes de interações com os beija-flores nas Américas. Nesse sentido, as interações entre plantas e beija-flores se assemelham àquelas entre insetos polinizadores e plantas e sistemas insulares. Entretanto, os atributos das plantas exóticas (tamanho, características da flor e adaptações prévias a polinização por aves) aparenta ser pouco relevante na determinação da integração da espécie na comunidade, mas pode influenciar a conectividade entre subconjuntos interativos de espécies na rede (módulos). Além disso, beija-flores mais generalistas - definidos funcionalmente por possuírem bicos mais curtos - agem como facilitadores da incorporação de espécies exóticas por incluir-las nas suas interações. Estudos futuros incluindo o efeito que essas plantas exóticas tem na reprodução de plantas nativas, assim como na atração e persistência de beija-flores são próximos passos que irão contribuir ainda mais para caracterizar melhor o impacto de plantas exóticas em comunidades Neotropicais.

Promessas associadas a uma abordagem mais baseada em atributos das espécies são muitas. O uso de atributos funcionais relevantes e associado à abordagem de redes são promissores para avaliar a associação entre a estrutura das interações em comunidades e o funcionamento ecossistêmico (Schluning et al. 2015). Neste sentido, a consideração dos atributos das espécies também pode ser útil no cenário de mudanças ambientais globais, podendo auxiliar nas predições de como as espécies rearranjarão suas interações em ambientes cambiáveis (e.g. Gravel et al. 2013). Adicionalmente, acredita-se que o emprego de abordagens mais baseada em atributos e história natural das espécies em estudos

macroecológicos de larga escala poderia permitir avanços significativos (Kissling & Schlueening 2015). Por exemplo, variáveis macro-climáticas atuais e históricas podem ser associadas a estrutura de redes ecológicas (e.g. Dalsgaard et al. 2013), entretanto a associação entre a estrutura das redes e clima passa pela influência desta na distribuição das espécies e seus atributos fenotípicos. Dessa forma, compreender a associação entre clima, atributos das espécies e a estrutura das interações é de suma importância para entender, prever e mitigar os efeitos das mudanças ambientais em curso no planeta sobre os sistemas ecológicos e suas funções (Kissling & Schlueening 2015, Schlueening et al. 2015).

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ANEXOS

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Declaro para os devidos fins que o conteúdo de minha dissertação de Mestrado/tese de Doutorado intitulada Interações entre plantas e beija-flores: história natural e redes ecológicas:

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