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COMMUNITY ASSEMBLY AND POTENTIAL FOR INDIRECT EFFECTS OF HUMMINGBIRD-POLLINATED PLANTS IN THE ATLANTIC FOREST

ESTRUTURAÇÃO DE COMUNIDADES E POTENCIAL PARA INTERAÇÕES INDIRETAS DE PLANTAS POLINIZADAS POR BEIJA-FLORES NA FLORESTA ATLÂNTICA

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RESUMO

A interação entre plantas e polinizadores influencia a estruturação das comunidades de plantas. Espécies de plantas que compartilham polinizadores podem competir ou se facilitar por sua polinização, impactando as populações de plantas e por consequência, suas ocorrências nas comunidades. Porém, ainda são poucos os estudos que investigam a influência da polinização na estruturação das comunidades e por quais mecanismos as plantas compartilham polinizadores e potencialmente exercem efeitos indiretos entre si. Nesta dissertação, enfocamos comunidades de plantas polinizadas por beija-flores na Floresta Atlântica como modelo de estudo. Utilizando uma abordagem filogenética e funcional, investigamos como o parentesco evolutivo, diferentes atributos florais e abundâncias determinam a estruturação espacial e temporal destas comunidades (Capítulo 1) e a partilha de polinizadores entre as espécies de plantas (Capítulo 2). Encontramos estrutura filogenética aleatória e estrutura funcional e temporal agregadas, indicando que processos relacionados ao atributo das espécies são importantes na escala espacial avaliada. Plantas com atributos florais semelhantes e espécies mais abundantes tem maior potencial para efeitos indiretos por compartilharem mais beija-flores. O primeiro resultado reforça o acoplamento fenotípico como um mecanismo estruturando as interações entre plantas e beija-flores, enquanto o segundo mostra que abundâncias podem se tornar importantes ao avaliar efeitos indiretos entre plantas nas comunidades. Em geral, padrões em ecologia de comunidades são contingentes à história evolutiva e atributos das espécies. Neste estudo, demonstramos que comunidades de plantas polinizadas por beija-flores podem exibir uma estrutura nos atributos florais, possivelmente devido a interações indiretas entre plantas compartilhando beija-flores. Além disso, esta estrutura também pode levar a um maior potencial para efeitos indiretos entre estas plantas.

ABSTRACT

Plant-pollinator interactions influence the assembly of plant communities. Plant species sharing pollinators engage on competitive or facilitative interactions for pollination, impacting plant populations and consequently, their occurrences in communities. However, there are few studies investigating how pollination influence community assembly and by which mechanisms plants have indirect effects when sharing pollinators. Here, we focused on hummingbird-pollinated plant communities of the Atlantic forest as study model. Using a phylogenetic and functional approach, we investigate how evolutionary relatedness, floral traits and abundances determine the spatial and temporal community assembly (Chapter 1) and pollinator-sharing among plant species (Chapter 2). We found random phylogenetic structure and clustered functional and temporal structure, indicating that trait-based processes increase in importance at the spatial scale evaluated. Plants with similar floral traits and abundant species have higher potential for indirect effects by sharing more hummingbird pollinators. The first result reinforces phenotypic match as a structuring mechanism of plant-hummingbird interactions, while the latter shows that abundance increases in importance when evaluating the indirect effects among plants in communities. In general, patterns in community ecology are contingent to the evolutionary history and traits of the species. Here we found that hummingbird-pollinated plant communities can exhibit a floral trait structure, possibly caused by indirect interactions between plants sharing pollinators. Moreover, these community structure can also lead to a higher potential for indirect effects between these plants.

SUMÁRIO

INTRODUÇÃO GERAL

POLINIZAÇÃO E A ESTRUTURAÇÃO DE COMUNIDADE DE PLANTAS

Entender os processos e mecanismos pelos quais as espécies coexistem em comunidades é um dos principais objetivos em ecologia (Diamond 1975, Chesson 2000, HilleRisLambers et al. 2012). Desta maneira, a composição de espécies das comunidades pode ser resultado de três principais conjuntos de processos: 1) processos estocásticos de extinção e recrutamento, ou qualquer evento aleatório que influencie a morte de indivíduos e entrada de novos indivíduos nas comunidades (Volkov et al. 2003), 2) processos históricos como eventos de especiação e dispersão a longa distância, que vão determinar padrões perceptíveis em escalas maiores de tempo e espaço (Ricklefs 2004) e 3) processos baseados no nicho das espécies, que irão determinar a ocorrência de cada espécie nas comunidades a partir de suas tolerâncias ao meio abiótico e interações com outros organismos (HilleRisLambers et al. 2012).

Para as comunidades de plantas, a maior parte dos estudos enfocou em como a montagem destas comunidades responde a diferentes condições abióticas (Götzenbergeret al. 2012). Ao abordar interações com outros organismos, estes estudos estiveram mais restritos à competição entre plantas por recursos providos pelo meio abiótico (Cavender-Bares et al. 2009). Porém, interações planta-animal possuem uma forte influência na ecologia e evolução das espécies de planta e, portanto, em processos que atuam em suas comunidades (Strauss & Irwin 2004). Dentre as interações planta-animal, podem-se destacar as interações entre plantas e polinizadores, por influenciar a permanência de espécies em uma comunidade ao impactar a reprodução das plantas (Sargent & Ackerly 2008, Freitas et al. 2015). Apesar disso, ainda existe pouca

evidência do papel da polinização na estruturação destas comunidades. Desta maneira, estudos de montagem de comunidades enfocando atributos florais e reprodutivos ou a história evolutiva de espécies de plantas que compartilham polinizadores contribuem ao avaliar como as plantas competem ou se facilitam através dos polinizadores (Gumbert et al. 1999, McEwen & Vamosi 2010, de Jager et al. 2011, Eaton et al. 2012, Muchhala et al. 2014, Shrestha et al. 2014).

São reconhecidos três principais processos pelos quais os polinizadores podem mediar interações entre plantas e influenciar sua permanência em comunidades: 1) filtragem biótica; 2) facilitação mediada pelos polinizadores e 3) competição mediada pelos polinizadores (Sargent & Ackerly 2008). A fauna local de polinizadores pode atuar como um filtro biótico, se uma espécie de planta depende de polinizadores para sua reprodução. Assim, a ausência de polinizadores adequados impossibilita o estabelecimento de populações viáveis de plantas em uma comunidade (Chalcoff et al. 2012). Quando os polinizadores são um filtro biótico importante, espera-se que as espécies de plantas em uma comunidade apresentem maior similaridade em seus atributos florais (estrutura funcional agregada), refletindo restrições impostas pela interação com a fauna de polinizadores disponível na comunidade (Shrestha et al. 2014). Espécies de polinizadores podem interagir preferencialmente com certas linhagens de plantas em uma comunidade (sinal filogenético das interações) e também se espera que as comunidades de plantas apresentem uma estrutura filogenética agregada (Sargent & Ackerly 2008). Por outro lado, as interações podem não ser restringidas pela história evolutiva (Danieli-Silva et al. 2012), o que levaria a uma convergência nos atributos florais e uma estrutura filogenética segregada ou aleatória (Sargent & Ackerly 2008).

A estrutura funcional agregada também pode ser resultado de interações de facilitação entre as plantas que compartilham polinizadores (Sargent & Ackerly 2008).

Neste caso, atributos florais similares podem aumentar a atratividade do conjunto total das espécies de planta aos polinizadores (Moeller 2004, de Jager et al. 2011). Esta convergência aumentaria o número de associações cognitivas (aprendizado) entre o mesmo tipo de flor e o recurso, resultando em maior taxa de visitação pelos polinizadores (Gumbert et al. 1999). Por outro lado, espécies com diferentes atributos florais (estrutura funcional segregada), porém equivalentes em sua oferta de recursos também leva a facilitação ao aumentar a atratividade aos polinizadores sem necessariamente competir por suas visitas (Ghazoul 2006). Além disso, poderia ocorrer facilitação através do suporte de polinizadores nas comunidades, quando plantas se beneficiam dos polinizadores que foram mantidos na área devido às espécies que floriram anteriormente na estação (Rathcke 1983). Neste último caso, a facilitação se daria através de uma fenologia também em estrutura segregada. De forma similar, a estrutura filogenética pode revelar processos similares à estrutura funcional caso os atributos florais sejam evolutivamente conservados (estrutura filogenética agregada) ou processos diferentes caso os atributos sejam convergentes (estrutura filogenética segregada ou aleatória, Sargent & Ackerly 2008).

Por último, competição entre plantas pode ocorrer quando polinizadores depositam pólen heteroespecífico, resultando em desperdício de pólen pela espécie doadora, bloqueio do estigma da espécie receptora e consequente diminuição do sucesso reprodutivo (Morales & Traveset 2008). Plantas também podem competir pela atração dos mesmos polinizadores, diminuindo suas taxas de visitação e, por consequência, o sucesso reprodutivo (Mitchell et al. 2009). Desta maneira, espera-se que as plantas segreguem o uso dos polinizadores, resultando em atributos florais divergentes (estrutura funcional segregada, Sargent & Ackerly 2008, Eaton et al. 2012, Muchhala et al. 2014). Plantas podem evitar a interferência do pólen heterospecífico ao depositar

pólen em partes distintas do corpo dos polinizadores (Muchhala & Potts 2007). Além disso, a sinalização floral é importante para o reconhecimento das diferentes espécies de plantas pelos polinizadores, e flores com sinalização divergente podem evitar movimentos interespecíficos dos polinizadores e evitar competir por sua atração (Chittka et al. 1997). Além destes mecanismos, uma estrutura segregada da fenologia de floração pode diminuir a competição tanto por deposição heteroespecífica de pólen como pela atração de polinizadores (Aizen & Vázquez 2006). Similar aos outros processos mediados pelos polinizadores, a estrutura filogenética das plantas pode seguir os padrões funcionais caso os atributos sejam filogeneticamente conservados (Sargent & Ackerly 2008).

Este quadro conceitual funciona como um guia geral para os possíveis processos atuando na estruturação das comunidades de plantas. Ainda, a ocorrência destes processos presume que as espécies de planta dependam de polinizadores para sua reprodução e que os polinizadores sejam um recurso escasso nas comunidades. Além disto, diferentes processos podem gerar os mesmos padrões (e.g. competição e facilitação gerando floração segregada) ou um mesmo processo levar a padrões distintos (e. g. facilitação através de similaridade floral ou de diversidade floral). Portanto, faz-se necessária uma avaliação crítica dos padrões de diversidade funcional e filogenética nas comunidades (Freitas et al. 2015). Abordagens que utilizem o *fitness* como um atributo funcional das plantas são promissoras para entender quais processos estão atuando nas comunidades. Desta maneira, é possível relacionar a estrutura da comunidade com um aumento (ou seja, resultado de facilitação) ou diminuição (competição) do sucesso reprodutivo das plantas em decorrência da interação com os polinizadores (Freitas et al. 2015, Lázaro et al. 2014, Wolowski et al. *em revisão*). Além disso, os processos estruturadores das comunidades frequentemente são contingentes a diferentes escalas

temporais e espaciais (HilleRisLambers et al. 2012). Em relação à polinização, a escala é especialmente importante pois plantas podem interagir de diferentes maneiras quando florescem juntas ou quando exibem floração sequencial (de competição a facilitação, Stiles 1977), ou ainda, podem compartilhar polinizadores de diferentes maneiras dependendo da escala espacial (Nottebrock et al. 2015). Portanto, estudos que abordem explicitamente diferentes escalas podem revelar os mecanismos pelos quais a interação com polinizadores estruturam as comunidades de plantas (Nottebrock et al. 2015).

A maioria dos estudos investigou a estrutura funcional e filogenética das comunidades de plantas utilizando apenas um atributo floral (e.g. Gumbert et al. 1999, Muchhala & Potts 2007, McEwen & Vamosi 2010, de Jager et al. 2011, Shrestha et al. 2014). Porém, plantas que compartilham polinizadores podem estabelecer interações entre si a partir de diversos mecanismos: sobreposição fenológica levando a facilitação ou competição (Stiles 1977), alteração nas visitas dos polinizadores devido a diferenças na sinalização floral (Chittka et al. 1997, Moeller 2004, Ghazoul 2006), ou devido a diferenças na abundância de recursos oferecidos (Carvalheiro et al. 2014) e através da deposição heteroespecífica de pólen (Morales & Traveset 2008). Cada um destes mecanismos é mediado por diferentes atributos florais, que por sua vez, estão sob diferentes pressões ecológicas (Eaton et al. 2012). Desta maneira, a avaliação de diversos atributos (e. g. comprimento da corola, cor floral, néctar) gera um quadro mais completo da influência da polinização na estruturação das comunidades de plantas.

ESTRUTURAÇÃO DE COMUNIDADES DE PLANTAS POLINIZADAS POR BEIJA-FLORES

Espécies polinizadas por beija-flores fornecem evidências mistas do papel dos polinizadores na estruturação das comunidades de plantas. Estudos enfocando a fenologia demonstram uma prevalência de floração segregada entre as espécies, gerando recursos para os beija-flores durante toda a estação favorável (Stiles 1977, Waser & Real 1979, Araujo et al. 1994, Kaehler et al. 2005, Aizen & Vázquez 2006, Aizen & Rovere 2010). Porém, estes estudos divergem na interpretação dos processos levando a floração segregada: nas montanhas rochosas do Colorado, foi demonstrado que este padrão leva a facilitação entre as espécies de plantas pela manutenção de populações de beija-flores migratórios nestas áreas (Waser & Real 1979). Para a floresta tropical da Costa Rica, interações competitivas foram mais importantes e a floração segregada evitaria custos com a deposição de pólen heterospecífico e a perda de recursos maternos na produção de híbridos inviáveis (Stiles 1977). Fenologias segregadas como resultado de competição também foram encontradas em comunidades temperadas da Argentina, dominadas pela espécie de beija-flor *Sephanoides sephaniodes* (Aizen & Vázquez 2006, Aizen & Rovere 2010).

Ao enfocar em grupos mais especializados (plantas de corola longa polinizadas apenas por beija-flores da subfamília Phaethornithinae (hermitões) e de corola curta polinizadas por beija-flores não-hermitões), Murray et al. (1987) encontraram evidências de deslocamento de caráter na fenologia e no local de deposição de pólen no corpo dos beija-flores, e portanto, processos competitivos. Estruturas similares também foram reportadas em outras comunidades de florestas tropicais, dividindo as plantas entre polinizadas por beija-flores hermitões e não-hermitões (Wolf et al. 1976, Feinsinger 1978, Buzato et al. 2000). Para o grupo de plantas polinizadas apenas por hermitões, espécies de plantas de uma comunidade de Cerrado também depositaram pólen em diferentes locais do corpo do beija-flor *Phaethornis pretrei* (Araújo et al.

2013). Portanto, há indícios de uma prevalência da competição como um processo estruturador das comunidades de plantas polinizadas por beija-flores.

Estudos em comunidades de plantas polinizadas por beija-flores da Floresta Atlântica reportam convergência nos atributos florais e evidências de floração sequencial (Araujo et al. 1994, Araujo 1996, Buzato et al. 2000, Lopes 2002, Canela 2006, Rocca-de-Andrade 2006, Fonseca 2007). Ao enfocar a estruturação destas comunidades, encontrou-se estrutura filogenética segregada em comunidades montanas e estrutura agregada em comunidades de baixada (Wolowski et al. *em revisão*). Além disso, a estrutura funcional, medida pelo comprimento efetivo da corola, foi aleatória para todas as comunidades (Wolowski et al. *em revisão*). Desta maneira, a redução da escala de estudo e o enfoque em outros atributos florais pode revelar por quais mecanismos os beija-flores podem estruturar as comunidades de plantas na Floresta Atlântica.

INTERAÇÕES ENTRE PLANTAS MEDIADAS PELOS BEIJA-FLORES

Plantas podem interagir indiretamente entre si ao compartilhar os mesmos beija-flores em uma comunidade. Beija-flores incluem diferentes espécies de planta em suas rotas de visitas (Sazima et al. 1995), o que pode promover competição entre as plantas. Em uma série de experimentos, foi demonstrado que beija-flores promovem prejuízos via perda de pólen coespecífico ao visitar diferentes espécies de plantas em sequência (Feinsinger et al. 1991, Feinsinger & Tiebout 1991). Além disso, espécies de plantas podem competir pela atração de beija-flores, e os custos reprodutivos da menor taxa de visitação caracterizam uma pressão para maior divergência floral quando em simpatria (Caruso 2000). Por fim, evidências recentes mostraram deposição de pólen

heterospecífico entre plantas compartilhando beija-flores na Floresta Atlântica, podendo acarretar em custos para a produção de sementes (Fonseca et al. *aceito*).

Por outro lado, ao avaliar contextos temporais e espaciais maiores, plantas poderiam promover facilitação ao compartilhar os beija-flores. Em uma escala temporal maior, houve facilitação entre plantas florindo sequencialmente através da manutenção de populações viáveis de beija-flores na comunidade (Waser & Real 1979). Para uma comunidade da Floresta Atlântica, espécies de plantas polinizadas por beija-flores que possuíram uma floração mais sincrônica em relação à comunidade sofreram menor limitação polínica (Wolowski et al. *submetido*). Este resultado pode indicar uma facilitação entre estas espécies ao aumentarem a atratividade da comunidade para os beija-flores. Desta maneira uma maior taxa de visitação para as plantas poderia compensar os prejuízos da deposição de pólen heterospecífico (Wolowski et al. *submetido*). Além disso, ajustes finos através de divergência no local de deposição de pólen no corpo dos beija-flores podem levar a vantagens para plantas que compartilham os mesmos polinizadores.

Apesar dos beija-flores promoverem diversos tipos de interações entre as plantas, faltam estudos que determinem quais características das espécies de plantas e da interação com os beija-flores influenciam estes efeitos indiretos. Recentemente, foi demonstrado que espécies de plantas mais aparentadas e com atributos florais semelhantes, tem maior chance de causarem efeitos indiretos ao compartilhar insetos como polinizadores (Carvalheiro et al. 2014). Como as interações entre plantas e beija-flores são restritas por seus fenótipos (Maglianesi et al. 2014, Maruyama et al. 2014, Vizentin-Bugoni et al. 2014), os efeitos indiretos entre plantas que compartilham beija-flores também podem ser estruturados por mecanismos relacionados a seus atributos.

ESCOPO DA DISSERTAÇÃO

Aqui, enfocamos as plantas polinizadas por beija-flores na Floresta Atlântica como modelo de estudo. No primeiro capítulo, investigamos os padrões de diversidade filogenética e funcional (a partir de atributos florais) e a estrutura temporal (a partir da fenologia de floração) de quatro comunidades de plantas polinizadas por beija-flores (Parque Nacional do Itatiaia - Canela 2006, Wolowski 2013; Parque Estadual da Serra do Mar, Núcleo Santa Virgínia - Vizentin-Bugoni et al. 2014 e Núcleo Picinguaba (Casa da Farinha e Praia da Fazenda) - Maruyama et al. 2015). Utilizamos uma abordagem enfocando a diversidade filogenética e funcional destas comunidades em diferentes escalas espaciais e temporais. Além disso, avaliamos diversos atributos florais para obter um quadro mais completo da montagem destas comunidades. Por fim, investigamos como a sobreposição de floração entre as espécies pode estar relacionada aos seus atributos florais e parentesco evolutivo.

No segundo capítulo, utilizamos as redes de interação entre plantas e beija-flores das mesmas comunidades para investigar o potencial de efeitos indiretos entre as espécies de plantas. Como restrições fenotípicas são mais importantes que a abundância das espécies em determinar as interações diretas entre plantas e beija-flores (Maglianesi et al. 2014, Maruyama et al. 2014, Vizentin-Bugoni et al. 2014), espera-se que mecanismos relacionados aos atributos das espécies de plantas sejam importantes no potencial para efeitos indiretos. Aqui, avaliamos como a similaridade em diferentes atributos florais, parentesco evolutivo, fenologia de floração e abundância de flores das espécies de plantas influenciam o quanto elas compartilham as espécies de beija-flores nestas comunidades e, portanto, o potencial para efeitos indiretos entre as plantas.

CAPÍTULO 1

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Spatial and temporal assembly of hummingbird-pollinated plant communities: a multi-trait approach

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Abstract

Pollinators may structure plant communities via community filtering or indirect plant-plant interactions. Hummingbirds are known to promote indirect interactions between plants, with a prevalence of competition among hermit-pollinated plants. Despite this, recent evidence suggests that flowering overlap can increase hummingbird-pollinated plants' fitness through facilitation. Here we evaluated the spatial and temporal assembly of hummingbird-pollinated plant communities using phylogenetic and multi-trait (corolla lenght, anther and stigma height, flower color and nectar) approaches for four hummingbird-pollinated plant communities in the Brazilian Atlantic forest. We also investigated the temporal assembly of hermit- and mixed-pollination (including non-hermits) assemblages. We expect that facilitation prevails over broader scales reflected by trait or temporal similarity, while competition increases at local scales, with more niche divergence especially for the hermit-pollinated plant assemblages. Functional structure showed a clustered pattern for flowering phenology and floral traits in all commnuties, however, no significant phylogenetic structure was detected. This is consistent to patterns expected under a similar resource use and facilitative interactions for the attraction and maintenance of hummingbirds in these communities. Evidence for this is supported by similar corolla length of co-flowering hermit- and mixed-pollinated plant species. Specially, staggered flowering and anther height dissimilarity for mixed-pollinated plant species suggests pressure for divergence possibly to avoid competition for pollination. Hummingbird-plant interactions seem to play an important role in structuring these plant communities. Thus, studies of community assembly should take into account several traits realted to plant-pollinators interactions since multiple mechanisms may simultaneously structure communties.

Key words

Competition, community ecology, facilitation, floral diversity, phylogenetic diversity, pollination biology, plant-plant interactions, niche theory

Introduction

The causes determining species occurrences in communities still remain a question in ecology (HilleRisLambers *et al.* 2012), and trait-based approaches have helped to understand the mechanisms influencing species co-occurrence in communities (Díaz and Cabido 2001). According to this framework, the degree of trait similarity would determine the niche overlap and reveal processes related to similar resource use through abiotic or biotic pressures (Kraft *et al.* 2015) or related to divergent resource use as a result of competitive interactions (stabilizing niche differences *sensu* Chesson 2000). Community phylogenetic patterns can follow the same logic, if relatedness implies a similar resource use by the species in a community (Webb *et al.* 2002). In this sense, species interactions can also represent a niche space where the degree of partner similarity influences species occurrence in a community.

For plant communities, interactions with animals such as pollination may have a major role in determining species composition (Strauss and Irwin 2004, Sargent and Ackerly 2008). Many plant species depend on pollinators for their reproduction, and can only persist in a community in the presence of such mutualists (Chalcoff *et al*. 2012). In this scenario, only the plant species with reproductive traits suitable to interact with local pollinators will persist, implying that pollinators act as an ecological filter in such cases (Shrestha *et al.* 2016). The degree of similarity in niche use, including pollinator-sharing, also influences their fitness (Sargent and Ackerly 2008). Species sharing

pollinators can benefit each other if trait convergence promotes higher attractiveness for the whole community, increasing overall visitation rates (Moeller 2004). On the other hand, trait convergence can lead to inter-species visits and improper pollen transfer between plants (Chittka *et al.* 1997, Morales and Traveset 2008).Thus, plant communities may exhibit fine adjustments through divergence of floral traits to avoid competition for pollinator attraction or heterospecific pollen deposition (Muchhala and Potts 2007, de Jager *et al.* 2011, Muchhala *et al.* 2014).

Although trait and phylogenetic patterns are useful to study community assembly, the use of such patterns to infer ecological processes has been controversial (Gerhold *et al.* 2015). Multiple processes can simultaneously shape species composition, and their relative importance change with scale, which may hinder detection of niche-use patterns (Emerson and Gillespie 2008, Chase and Myers 2011). Scale is specially important for plant-pollinator systems because plants can interact in different temporal ranges: when flowering synchronically (via pollinator attraction, for example) but also when there is staggered flowering, via maintenance of pollinators in the area (Stiles 1977). Another issue is that many different floral traits are involved in the interaction with pollinators (Gegear and Laverty 2001). For example, resource accessibility is restricted by corolla length, which determines the potential pollinator assemblage of a flower and thus the degree of pollinator-sharing between species and its potential for competition or facilitation (Carvalheiro *et al.* 2014). Meanwhile, flower signals such as color influence pollinator movement between species and signal dissimilarity promotes flower constancy, reducing competition (Chittka *et al.* 1997), while signal similarity enhances pollinator attraction (Moeller 2004). Finally, if plants overlap in the position of reproductive structures, it can lead to heterospecific pollen

deposition between flowers (Morales and Traveset 2008). In this sense, a multi-trait approach is necessary to cover distinct aspects of the plant-pollinator systems.

Here, we aimed to overcome some of these limitations associated to community assembly studies by explicitly accounting for different spatial and temporal scales and using a multi-trait approach for hummingbird-pollinated plant communities. Hummingbird pollination evolved repeatedly in several Neotropical lineages, promoting speciation on many groups (e.g. Serrano-Serrano et al. 2015) and impacting species co-occurrence in communities (Perret *et al*. 2007). Interactions with hummingbirds, thus, can shape species composition within each community over large scales. At the local scale, i.e., within communities, many hummingbird species can promote indirect interactions among plant species. For instance, there is evidence of hummingbirds causing pollen loss on heterospecific stigmas (Feinsinger and Tiebout 1991) and for competition between plants for their attraction (Caruso 2000). At the same time, hummingbird-pollinated plant communities exhbit an year-round flowering in the tropics, keeping hummingbird populations in the area and causing an indirect facilitation via pollinator maintenance (Stiles 1977, Moeller 2004). Moreover, hummingbirds are often divided into trapliners (most of the hermits) and territorial foragers (most of the non-hermits). Trapliners tend to perform several switches between species in a foraging bout (Sazima *et al.* 1995) and thus one may expect divergence in some morphological traits such as the height of the reproductive structures between hermit-pollinated species in a community, in order to avoid heterospecific pollen transfer (Stiles 1977).

In the Atlantic forest, hummingbird-pollinated plant communities have been studied regarding flowering phenology, species composition, floral traits, pollinator behaviour and pollination networks (Sazima *et al.* 1995, Buzato *et al.* 2000, Vizentin-

Bugoni *et al.* 2014, Maruyama *et al.* 2015). Moreover, a recent study showed that plant assemblages sharing hummingbird pollinators present clear phylogenetic structure in some communities and species showing higher sychrony in flowering are engaged in facilitative interactions (Wolowski *et al. in review*). However, when investigating indirect interactions at fine scales, heterospecific pollen deposition seem to often occur in species pairs sharing the same hummingbird-pollinators (Fonseca *et al. in press*). In this sense, one can expect that co-flowering plant species pairs could diverge in its floral traits. Thus, distinct processes apparently act at different hierarchical scales in mediating indirect interactions between hummingbird-pollinated plants.

Here we assessed the phylogenetic and trait distribution patterns for four hummingbird-pollinated plant communities in the Atlantic forest across spatial (among communities) and temporal scales (within each community), using traits related to nectar accessibility (corolla length) and quality (sugar content), flower color and anther and stigma height. We addressed the following questions contrasting our community data against distinct null-models: (1) at the spatial scale, is there a phylogenetic or trait structure (i.e. overdispersed or clustered)? (2) within communities, is there a temporal structure in the flowering phenology (i.e. staggered or aggregated)? (3) does this temporal structure differ when evaluating hermit- and mixed-pollinated plant subgroups within the communities? (4) does pair wise phenological overlap (of the whole group of species and within hermit- and mixed-pollinated subgroups) depend on species relatedness or trait similarity? We expect: (1) clustered phylogenetic and functional structure associated to hummingbird attraction (color and nectar) at the broad spatial scale (i.e. within each community in relation to the regional species pool), reflecting pollinator filtering or facilitative processes mediated by the local hummingbird fauna, and (2) aggregated flowering also reflecting pressures to enhance hummingbird

attraction. Within subgroups, we expect that (3) hermit-pollinated assemblages exhibit staggered flowering more than mixed-pollinated assemblages, as an outcome of competitive interactions since hermits were shown to more commonly promote inter species visits. When evaluating pair wise phenological overlap, we expect (4) higher trait divergence among species with overlapped flowering, specially on traits related to avoid pair wise competitive interactions (corolla length, anther and stigma height) as well as higherpair wise divergence within hermit- than mixed-pollinated species pairs.

Methods

Study system

We evaluated four hummingbird-pollinated plant communities in the Brazilian Atlantic forest for which we have extensive knowledgment on the plant-pollinators interactions and species biology (Itatiaia - ITA, Canela 2006, Wolowski *et al*. 2013a, Wolowski *et al*. 2013b); Santa Virgínia - SVG, Vizentin-Bugoni *et al.* 2014, Casa da Farinha - FAR- and Praia da Fazenda - FAZ, Maruyama *et al.* 2015). All communities belong to the Mantiqueira and Serra do Mar mountain ranges with a distance of ca. 100km between the farthest areas. Two communities are located on montane (ITA and SVG) and two at lowland habitat (FAR and FAZ, Table S1). These communities share most of its hummingbird species and are composed by plant species mostly from Acanthaceae, Bromeliaceae, Campanulaceae, Fabaceae, Gesneriaceae and Malvaceae families (81.31% of total species). Thus, these communities form a regional species pool where it would be possible to detect if ecological interactions such as hummingbird-pollination have influenced local species composition.

Functional traits

Phenological data were collected monthly in all communities (Wolowski 2013, Vizentin-Bugoni *et al*. 2014, Maruyama *et al*. 2015). The number of flowers per species was recorded along pre-existing trails. To avoid differences caused by species richness and/or sampling design, we used the relative number of flowers produced per species per community along 12 months as a proxy for flower abundance (Carvalheiro *et al.* 2014). All communities showed a full year-round flowering. For communities with more than one-year survey (ITA and SVG), we selected the year with most of the flowering species were recorded. In spite of this, interannual variation in flowering of a given species flowering was small (phenological overlap tested with Mantel tests; ITA: $r = 0.65$, $p = 0.001$; SVG: $r = 0.42$, $p = 0.001$).

Floral traits data were collected in all communities from July/2014 to September/2015. We measured directly in the field all morphological features using a digital caliper: effective corolla length (CL), i.e. the measure from the base of the nectary to the flower tube opening (*sensu* Wolf *et al.* 1976) as a proxy of resource accessibility; and stigma and anther height (SH and AH, respectively), measured from the base of the nectary to the top of each structure as the estimate of the position of placement and transfer on the hummingbird body. Flower color was measured by the spectral reflectance of the petals using a USB4000 spectrophotometer (OceanOptics, Inc., Dunedin, FL, USA) coupled with a deuterium-halogen light source (DH-2000; OceanOptics, Inc., Ostfildern, Germany), with a light emission range between 215 nm and 1700 nm. We took all reflectance measurements at a 45° angle, using barium sulphate and a black chamber as the white and a black standard, respectively. To

analyse the color in the hummingbird subjective view, we modeled hummingbird vision

based on the photoreceptor sensitivities and noise values of *Sephanoides sephaniodes*

(Herrera *et al.* 2008) and adopted the oil droplet parameters from Hart and Vorobyev

(2005). Information on nectar production was collected in the field for most species, and

completed with information from the literature. Missing information of floral

morphology was also gathered from the the literature, whenever possible. We only

considered the measures of nectar production when nectar was collected in flowers

bagged before the anthesis and kept isolated from visitors for at least 12h. We

calculated nectar sugar content (SC) as the product of volume and concentration. Some

of the floral traits owere not possible to collect in the field and not available in the

literature (8.59%), leading to distinct subsets of species for each floral trait (see

Suporting Information; Tables S2-S4 summarizes species' floral traits and source of the

data).

Plant phylogeny

The plant phylogenetic hypothesis for the regional species pool was built based

on the consensus supertree of the APG III (Tree R20091100) in Phylomatic (Webb and

Donoghue 2005). We calibrated branch lengths using the BLADJ function in Phylocom

(Webb *et al.* 2008), based on the Angiosperm lineages divergence times proposed by

Bell *et al.* (2010). Because the relationships within Bromeliaceae familiy were

assembled as a polytomy after Phylomatic procedures, we resolved the relationships at

the subfamily level following Givnish *et al.* 2011 (see Figure S1).

Data analyses

Spatial assembly

To evaluate the phylogenetic structure, we included all species reported to be
hummingbird-pollinated on each community (Table S3). We calculated abundance-
weighted mean pairwise distance (MPD) between all species for each community as an
index for phylogenetic structure (Webb *et al.* 2002). We compared the observed indices
with a null distribution generated with the abundance-weighted version of the
independent-swap algorithm (10,000 times, Gotelli 2000). Assessment of functional
structure followed the same procedure described above, considereing the floral traits
(color, corolla length, anther and stigma position, nectar sugar content, Table S3-S4). A
MPD significantly higher than the null distribution indicates overdispersion while a
lower MPD indicates clustering. We calculated distances between species as the
Euclidian distance for each of the reproductive traits. Except for flower color, we
calculated perceptual distances using the logarithm version of the receptor noise-limited
model (Vorobyev and Osorio 1998).

Communities may exhibit trait structure because there is a strong phylogenetic
signal in the evolution of specific traits, regardless of the influence of an ecological
process (Eaton *et al.* 2012). In order to assess these potential influences, we calculated
the phylogenetic signal for each trait. For the quantitative traits (morphological features
and nectar sugar content) phylogenetic signal was measured by the Blomberg's *K*
statistic (Blomberg *et al.* 2003). The *K* statistic assess whether the species traits follow a
divergence pattern different from what is expected under Brownian motion evolution. A
K higher than one means that closely related species are more similar than expected by
Brownian motion evolution and less than one indicates that closely related species are

less similar than this same expectation (Blomberg *et al.* 2003). To assess its

significance, we calculated phylogenetic independent contrasts (PIC, Felsenstein 1985)

for each trait and compared it to a null distribution generated by 10,000 random trees

assembled by reshuffling species into the null phylogenies. For floral color, for which

we had a perceptual distance matrix, we calculated the phylogenetic signal as the

correlation between color and phylogenetic distances using Mantel test (Shrestha *et al.*

2014).

Temporal assembly

We quantified temporal niche overlap among all pairwise species combinations

for each community to assess the temporal structure, using the Czechanowksi index,

based on the overlap of the histograms representing two temporal distributions

(Feinsinger *et al.* 1981). This is a more adequate index for quantitative phenological

data, since it accounts for the flowering intensity at each temporal unity evaluated

(Castro-Arellano *et al*. 2010). We calculated the mean pairwise phenological overlap

(MPO, hereafter) for each community and the significance was assessed by comparing

the mean to the null distribution generated by 10,000 random phenological

combinations generated with the ROSARIO algorithm (Castro-Arellano *et al.* 2010)

using the software TimeOverlap. This algorithm preserves the entire phenological

interval for each species, controlling for temporal autocorrelation and offering a more

conservative evaluation of the temporal structure (Castro-Arellano *et al.* 2010). A

higher mean overlap than the null distribution indicates aggregated flowering while a

lower mean overlap means a staggered flowering.

We performed the temporal assembly analysis for the subset of hermit- and

mixed-pollinated (hermits and non-hermits) species that we had data on hummingbird

visitation frequency in each community (Canela 2006, Vizentin-Bugoni *et al.* 2014,

Maruyama *et al.* 2015, Table S3). There were only few plant species predominantly

pollinated by non-hermits that would justify a separate category for them (~13% of the

species), so we kept only the above mentioned two. The hermit-pollinated assemblages

were composed by plant species with at least 80% of the flower visits performed by a

trap liner hermit hummingbird. We selected this threshold since it included ~53% of the

species, which is consistent with the number of interaction partners of hermits in most

Atlantic forest communities (Buzato *et al*. 2000, Canela 2006, Vizentin-Bugoni *et al*.

2014). The hermit category included all *Phaethornithinae* species except *Phaethornis*

ruber, since this hummingbird usually has very opportunistic foraging strategy, relying

heavily in nectar robbing and often acting in the community as a non-hermit (Maruyama

et al. 2015). The mixed-pollinated assemblages were composed by species pollinated by

both hermits and non-hermits at similar frequencies (when at least 21% of the total

visits to the plant were performed by a hummingbird of each category).

Determinants of pairwise phenological overlap

We assessed whether temporal overlap among species of each community was

explained by the phylogenetic relatedness or trait similarity by fitting the species

pairwise temporal overlap with the phylogenetic and trait distances as fixed variables in

mixed-models. We used the species pair and community as random factors, to account

for the dependency related to species identities and local composition. To deal with

zero-inflation, we converted the response variable into a binomial variable to investigate

which factors influence the probability of flowering overlap. We assigned 0 when there was no temporal overlap and 1 to all positive values, assuming a binomial-distribution error structure. The variability in the phenological overlap was tested using the subset of positive values and assuming Gaussian-distribution error structure (Carvalheiro *et al.* 2014). We run mixed models with combinations between all fixed variables and the null model with only the response variable and the random factors. Best models were selected based on the values of ΔAIC, assuming models with ΔAIC<2 as equivalents. We included in these analysis species for which we had information for all floral traits (90.65% of all species). We tested three sets of models: the first including all hummingbird-pollinated species ("Whole community"), a second including only hermit-pollinated species ("Hermit assemblage") and a third including only mixed-pollinated species ("Mixed assemblage"). For all models we rescaled the phylogenetic distances to meet statistical assumptions.

Results

Spatial assembly

None of the communities presented a phylogenetic structure that differed from random (Fig. 1A, Table S1). Nevertheless, for some traits in two communities showed a significant clustered pattern: anther height, stigma height and flower color in SVG and nectar sugar content in ITA (Fig. 1, Table S1). For other traits in other communities, no clear pattern was observed (Fig. 1, Table S1). All traits had a phylogenetic signal with K less than one, meaning that closely related species were less similar than expected by Browniam motion evolution (corolla length (CL): 0.23; anther height (AH): 0.18; stigma height (SH): 0.20; nectar sugar content (SC): 0.18). Moreover, we found

significative PICs for all these traits (CL: 4.94 ± 6.86, p = 0.001; AH: 6.62 ± 8.54, p = 0.002; SH: 6.83 ± 9.81, p = 0.001; SC: 0.87 ± 1.23, p = 0.012). These two analyses suggest a weak phylogenetic signal, i.e., ~20% of the variance was explained by phylogenetic relationship, *sensu* Blomberg *et al*. 2003) for these floral traits. Flower color did not show a phylogenetic signal by Mantel test (r = -0.077, p = 0.999).

Temporal assembly

We found a prevalence of random flowering temporal structure, followed by aggregated and staggered structures. When considering all hummingbird-pollinated plant species, we found two communities with temporal structure that did not differed from rando, while flowering was more overlapped than expected by chance in two other communities, indicating an aggregated temporal structure (Fig. 2A, Table S2). For the assemblages of only hermit-pollinated plants, temporal structure did not differ from random in all communities (Fig. 2B, Table S2). For the mixed-pollinated plant assemblages, temporal structure also did not differ from random with the exception of ITA (Fig. 2C, Table S2). ITA had less flowering overlap than expected by chance, producing a staggered flowering pattern (Fig. 2C). Accordingly, the mixed-pollinated plant assemblage in FAR had an extremely low mean flowering overlap, showing a tendency to staggered flowering (MPO = 0.002, p = 0.075, Fig. 2C, Table 2).

Determinants of pairwise flowering overlap

Trait similarity and phylogenetic relatedness did not explain the probability (Binomial model), nor the variability (Gaussian model) in pairwise flowering overlap

among all hummingbird-pollinated plants (Table 1). Within, subgroups, hermit-
pollinated species with similar corolla length had higher probability of flowering
together (Binomial model, Table 1). Mixed-pollinated plants with similar corolla length,
but with different anther height and phylogenetic distantly related had more chance of
flowering together (Binomial model, Table 1). Reproductive traits and phylogenetic
relatedness did not explain the variability of the pairwise flowering overlap between
hermit- and mixed-pollinated plants (Gaussian model, Table 1).

Discussion

Spatial assembly

Communities of hummingbird-pollinated plants represented random samples of
the regional species pool. Lack of overdispersed or clustered phylogenetic structure may
be explained by the spatial scale considered in the study (Emmerson and Gillespie
2008). In a previous study, which included a broader spatial range and more
hummingbird-pollinated plant communities from the Atlantic forest (n=seven),
overdispersed phylogenetic structure was associated with montane communities while
clustered phylogenetic structure was associated with lowland communities (Wolowski
et al. in review). This suggests that mechanisms acting on a broader spatial scale, such
as habitat filtering are more likely to operate structuring the composition of these
communities than mechanisms related to hummingbird pollination. This is consistent
with the hypothesis that phylogenetic structure is a product of long spatial and temporal
process acting on ecological systems (Ricklefs 2004, Chase and Myers 2011). Thus, at
the spatial scale evaluated here, it seems that the regional species pool is composed by

hummingbird-pollinated plant lineages that are able to disperse and persist at distinct communities leading to the random pattern of phylogenetic structure observed.

On the other hand, functional structure indicate clustering of some traits in the two montane communities (40% of the traits evaluated). In these communities, hermit specialized plants are more prevalent than in lowland communities (~57% vs. ~46% Canela 2006, Vizentin-Bugoni *et al.* 2014, Maruyama *et al.* 2015). Moreover, in the montane communities, hermit specialized plants are pollinated almost exclusively by only one hummingbird species (*Phaethornis eurynome*), in contrast with lowland communities. This may narrow the niche space of the hermit specialized plants in the montane communities, reflecting a biotic filter played by these hummingbirds. For instance, floral traits providing a mechanical fit for the pollen transport are expected to be under stronger selection (Eaton *et al.* 2012). Thus, species with similar anther and stigma height might be expected because hummingbird-pollinated plants can maximize pollen export when it is deposited on the hummingbird forehead or throat, due to higher surface area and less probability of losing pollen to the environment (Rocca and Sazima 2013). Furthermore, hermits behave as trapliners, flying over high rewarding routs which could favor plants with high nectar sugar content (Feinsinger and Colwell 1978, Sazima *et al.* 1995). Lastly, color similarity can lead to higher flower visitation rates, which could increase in montane communities due to the lower irradiance of this type of forest and consequently less detectability of low-waveband colours (Altshuler 2003). Therefore, our results suggest that hermit hummingbirds can act as an biotic filter leading to clustered functional assembly, a role that was previously reported only for insect pollinators (de Jager *et al.* 2011, Shrestha *et al.* 2016).

When considering the broader scale in Wolowski et al. (*in review*) study, the corolla length (the floral trait evaluated) did not show a significant distribution pattern in

hummingbird-pollinated plant communities. This suggests that the importance of trait-based processes increases at smaller spatial scale, which is consistent with general theory of community assembly and species coexistence (HilleRisLambers *et al.* 2012). Moreover, we found a significant structure for other floral traits than corolla length, making a multi-trait approach necessary to cover more aspects of the pollination niche of the plant species. Nevertheless, we found no functional structure for any trait at the lowland communities. These communities have more hummingbird species with diverse foraging behaviors, from trapliners to territorials and intermediate behaviors (Sazima *et al*. 1995, Buzato *et al*. 2000). A possibility is that both competition and facilitation for pollination are acting in these communities, since both processes were already reported for hummingbird-pollinated plants e can occur simoutaneously in the same community (Hegland *et al*. 2009, Tur *et al*. 2016). In this scenario, floral traits could be under distinct ecological pressures leading to the overall lack of functional structure in lowland communities.

Temporal assembly

Flowering overlap varied from random to cluster among hummingbird-pollinated plant communities. Though all communities offered nectar resources for hummingbirds during all year. This feature is especially important for plant communities pollinated by long-living animals since plants can benefit each other by the local maintenance of pollinators (Stiles 1977). Thus, the year-round flowering is consistent with the hypothesis of facilitation through pollinator maintenance (Ratchke 1983, Moeller 2004). It is also important to mention that the abiotic conditions of the Atlantic forest, with no strong seasonallity, are favorable for a year-round flowering

community (Staggemeier *et al*. 2010). Besides, staggered flowering was not observed as we expected. Instead, the aggregated flowering in two communities fit the expectation that plants synchronize its flowering with the period that hummingbirds are more available in these communities (Maruyama *et al.* 2014, Vizentin-Bugoni *et al*. 2014). Moreover, a community of plants sharing hummingbird pollinators had less pollen limitation when flowering in synchrony (Wolowski *et al*. *in review*). This suggests that aggregated flowering can benefit plants via facilitation through pollinator attraction. Therefore, both temporal structures observed could reflect positive plant-plant interactions mediated by temporal pollinator availability in these areas.

Contrary to our expectation, flowering of hermit-pollinated plants within communities was not staggered. Instead, one mixed-pollinated assemblage exhibited staggered flowering. Staggered flowering was found in a temperate community composed by few plant species and one hummingbird species, leading to strong pollinator-sharing and competition for pollination (Aizen and Vázquez 2006). Therefore, more diverse hummingbird assemblages may not impose enough pressure towards flowering divergence due to reduced pollinator-sharing among plant species. Moreover, our results do not fit the presumed temporal divergence of tropical hermit-pollinated species in response to competition mediated by hermit hummingbirds (Stiles 1977). In the studied plant communities, the mixed assemblages were composed by fewer plant species, which could lead to stronger pairwise pollinator-sharing than on hermit assemblages. Thereby, our results suggest that non-hermits may impose higher pressure towards flowering divergence than hermits.

Determinants of pairwise flowering overlap

At the whole-community level trait similarity and phylogenetic relatedness did not influence the probability flowering overlap,besides the expected flowering divergence at this reduced scale. A possible explanation is that tropical plant-hummingbird networks are trait-structured according to two distinct hummingbird groups, with long- and short- corolla flowers being visited preferentially by long- (hermits) and short-billed (non-hermits) hummingbirds, respectively (Maruyama *et al.* 2014, Vizentin-Bugoni *et al.* 2014). Following this network structure, phylogeny and trait-based processes mediated by the pollinators would be important only when evaluating these subgroups of plants. Thus, we only found trait and relatedness determining patterns of flowering overlap when separating these communities based on their pollinator assemblage.

Contrary to the expected trait divergence, hermit-pollinated flowers with similar corolla length had higher probability of flowering together. Since corolla length is positively correlated with nectar production on hummingbird-pollinated flowers (Ornelas *et al.* 2007), species flowering together had higher probability of offering similar amounts of resources to hermit hummingbirds. Similar resource levels enhance the overall attractiveness of the community if different plant species provide complementary resources to their pollinators, and enhanced attractiveness translates into higher fitness for the plants (Moeller 2004, Ghazoul 2006, Lázaro *et al.* 2014). In this way, plants with similar nectar resources can attract and support more hermits in a community without implying in hummingbird-choices based on reward quality. Plant-plant facilitation through complementary resources is expected when pollinators are less abundant in the community (Ratchke 1983). We postulate that besides pollinator abundance, facilitation via enhanced attractiveness is also expected when pollinators have high energetic demands, such as hermit hummingbirds.

Besides the expectation of flower divergence only among hermit-pollinated pairs, we found more divergence between mixed-pollinated species. Although co-flowering mixed hummingbird-pollinated plant species showed similar corolla length, they also had distinct anther height. In this scenario, plant species can benefit from the facilitation of flowering together and avoid heterospecific pollen deposition through fine adjustments on pollen placement (Sargent and Ackerly 2008). Heterospecific pollen mixtures on stigmas have strong detrimental effects when heterospecific loads are more intense (Ashman and Arceo-Gómez 2013). Even tough non-hermits visit few plants in a foraging bout, these hummingbirds could promote several switches and intense heterospecific pollen loads among species pairs included in a territory (Fonseca *et al*. *in press*). Our results suggest that plants sharing non-hermits may experienced stronger pairwise competition than plants sharing hermit pollinators.

There is growing evidence that plant communities are organized through floral trait similarity (Gumbert *et al.* 1999, de Jager *et al.* 2011, Shrestha *et al*. 2016). In fact, floral trait similarity seems to be more prevalent than floral divergence when analyzing large plant communities with different lineages such as the hummingbird-pollinated plant communities evaluated here. Moreover, facilitation for pollination might play an important role among distantly related species (e.g. Ghazoul 2006, Lázaro *et al.* 2014, Wolowski *et al. in review*). On the other hand, competition may play a role in more specific cases when phylogenetic relatedness imply higher cost via heterospecific pollen interference and waste of maternal resources to produce unviable fruits or hybrids (Kay and Schemske 2008). Nevertheless, competitive interactions among hummingbird-pollinated plants exist (Feinsinger and Tiebout 1991, Caruso 2000, Fonseca *et al*. *in press*), but our results suggest that competition for pollination may only structure hummingbird-pollinated plant communities at a more local spatial and temporal scale,

when considering few plants that share the same pollinator species (e.g. Aizen and Vázquez 2006). In the evaluated scale, our results indicate a biotic filter role played by hummingbirds and an overall facilitation through increased hummingbird maintenance and attraction.

We found that hummingbird-pollinated plant communities show a functional organization, which was lacking when these communities were evaluated at a higher spatial scale (Wolowski *et al*. *in review*). Trait-based process increasing in importance at smaller scales is a pervasive pattern along a broad range of ecological systems, including plants, animals and their interactions (Ricklefs 2004, Emmerson and Gillespie 2008, Chase and Myers 2011). In this sense, our results showed that floral traits influence the organization of the pollination niche, which in turn is an important driver of plant community organization (Sargent and Ackerly 2008). Floral traits mediate the degree of hummingbird-sharing among plants, which may lead to plant-plant interactions and an effect on community assembly (Chapter 2). The assembly of these communities points out to both facilitative and competitive interactions, despite the common claim that only competition is a major process driving species distributions (HilleRisLambers *et al.* 2012). Our results demonstrated that pollination structure plant communities through distinct mechanisms and we argue that studies should use a multi-trait approach to account for the complexity of plant-pollinator interactions.

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Table 1. Model parameters for the probability (Binomial model) and variability of phenological overlap (Gaussian model) for the hummingbird-pollinated plant communities ("Whole community") and the hermit and mixed plant assemblages. Fixed effects: phylogenetic (P); corolla length (CL); anther height (AH); stigma height (SH); color (C) distances. All models included the random effects (species pair and community) (community. Estimates of the factors in the best models (in bold) are given in parenthesis. Explained deviance = difference between the deviance of the models and of a model including only the intercept. ΔAIC = Akaike Information Criteria value after selection including models with all possible combinations among fixed effects.

Whole community (Binomial)	d.f.	Explained deviance	ΔAIC
P+CL+AH+SH+C	9	33.40%	7.91
Null	4	32.08%	0.0
Whole community (Gaussian)			
P+CL+AH+SH+C	10	19.50%	7.03
Null	5	19.69%	0.0
Hermit assemblage (Binomial)			
CL(-0.03)	5	44.00%	0.0
Null	4	29.56%	2.31
Hermit assemblage (Gaussian)			
P+CL+AH+SH+C	5	28.73%	7.79
Null	4	28.16%	0.0
Mixed assemblage (Binomial)			
CL(-0.05)+AH(0.03)+P(0.02)	7	8.10%	0.0
Null	4	27.19%	4.98

Mixed assemblage (Gaussian)			
P+CL+AH+SH+C	5	37.47%	8.34
Null	4	36.40%	0.0

Figure legends

Figure 1. Phylogenetic and functional structure of hummingbird-pollinated communities in Atlantic forest, Southeastern Brazil. Phylogenetic and functional structure were evaluated at a spatial scale encompassing all communities (ITA = Itatiaia; SVG = Santa Virgínia; FAR = Casa da Farinha; FAZ = Praia da Fazenda). Grey triangle = Mean pairwise distance (MPD) observed for each community. Empty circle = mean MPD of 10000 null assembled communities, with bars representing 95% confidence interval. "A" letter represents an aggregated structure at $p < 0.05$ level.

Figure 2. Temporal structure of hummingbird-pollinated plant communities in the Atlantic forest, Southeastern Brazil. Temporal structure was evaluated for all hummingbird-pollinated plant species ("Whole community"), for the subset of hermit-pollinated plants ("Hermit assemblage") and for the subset of mixed-pollinated plant species ("Mixed assemblage") in each community (ITA = Itatiaia; SVG = Santa Virgínia; FAR = Casa da Farinha; FAZ = Praia da Fazenda). Grey triangle = Mean phenological overlap (MPO) observed for each community. Empty circle = mean MPD of 10,000 null assembled communities, with bars representing 95% confidence interval. "A" letter represent an aggregated and "S" a staggered flowering at $p < 0.05$ level.

Figure 1.

Figure 2.

Whole community

Hermit assemblage

Mixed assemblage
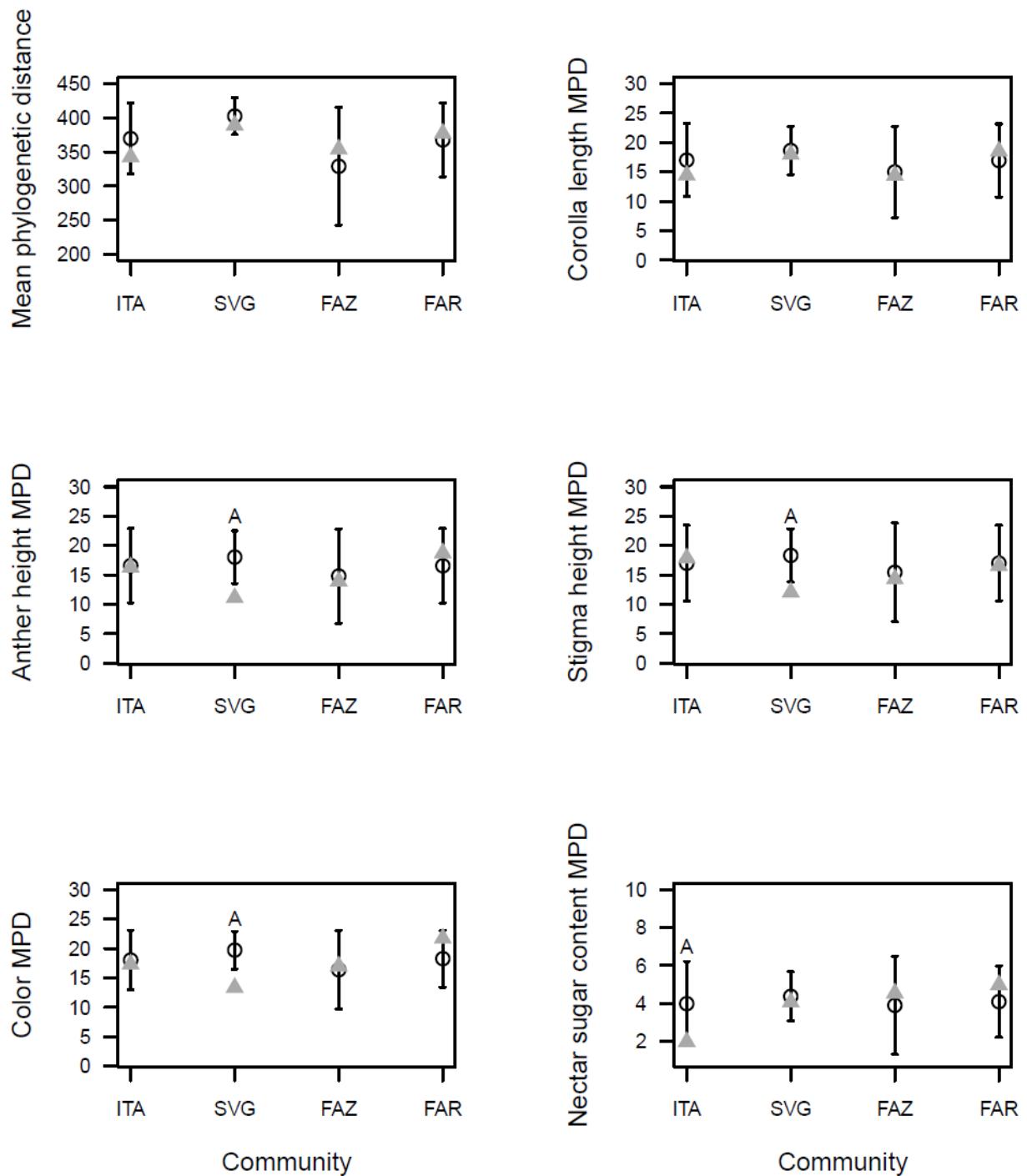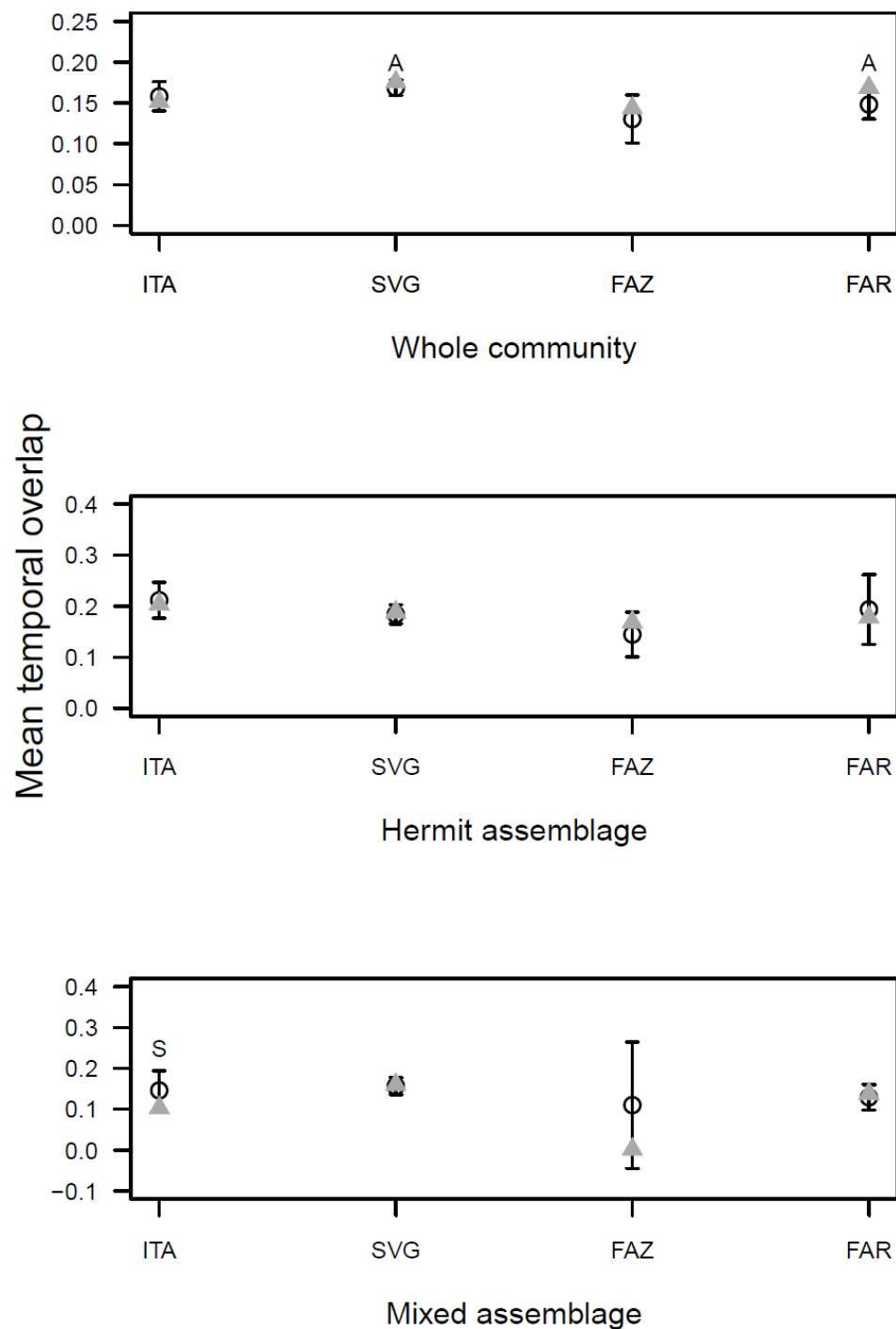
Supplementary material

Table S1. Characteristics and localization of the four hummingbird-pollinated communities studied at the Brazilian Atlantic forest. ITA = Itatiaia; SVG = Santa Virgínia; FAR = Casa da Farinha; FAZ = Praia da Fazenda.

Community	Coordinates	Altitude (m)	Mean annual precipitation (mm)	Richness
ITA	22º27' S, 44º36' W	900-1100	2400	32
SVG	23º17'S, 45º11'W	850-1000	2100	58
FAR	23°20', 44°50'W	150-200	2200	19
FAZ	23°21'S, 44°51'W	0-50	2200	31

Table S2. Hummingbird-pollinated species from the Brazilian Atlantic forest included in the study, respective botanical families and abbreviations. ITA = Itatiaia; SVG = Santa Virgínia; FAR = Casa da Farinha; FAZ = Praia da Fazenda

Family/Species	Abbreviation	Community
Acanthaceae		
Aphelandra colorata	Apco	SVG
Aphelandra longiflora	Aplo	SVG
Justicia carnea	Juca	FAR
Justicia sebastianopolitana	Juse	ITA
Justicia cf. parabolica	Jupa	SVG
Justicia sp	Jusp	SVG
Mendoncia velloziana	Meve	ITA, SVG
Odontonema barbelerioides	Odba	ITA
Staurogyne itatiaiae	Stit	ITA
Alstroemeriaceae		
Alstroemeria inodora	Alin	SVG
Bomarea edulis	Boed	FAZ
Asteraceae		
Mutisia speciosa	Musp	FAZ, SVG
Bignoniaceae		
Pyrostegia venusta	Pyve	ITA, SVG
Bromeliaceae		
Aechmea coelestis	Aeco	FAZ
Aechmea distichantha	Aedi	FAZ, SVG

Aechmea gamosepala	Aega	SVG
Aechmea cf. organensis	Aeor	SVG
Aechmea nudicaulis	Aenu	ITA, FAZ, SVG
Aechmea pectinata	Aepe	FAZ
Aechmea vanhoutteana	Aeva	ITA, SVG
Billbergia amoena	Biam	SVG
Billbergia distachia	Bidi	ITA
Billbergia pyramidalis	Bipy	FAR, FAZ, SVG
Billbergia vittata	Bivi	ITA
Bromelia antiacantha	Bran	FAZ
Canistropsis seidelii	Case	FAR, FAZ
Canistrum perplexum	Cape	SVG
Edmundoa lindenii	Edli	SVG
Neoregelia johannis	Nejo	FAR, FAZ
Nidularium angustifolium	Nian	FAR, FAZ
Nidularium bicolor	Nibi	ITA
Nidularium innocentii	Niin	FAR, FAZ, SVG
Nidularium itatiaiae	Niit	ITA
Nidularium longiflorum	Nilo	SVG
Nidularium procerum	Nipr	SVG
Nidularium rutilans	Niru	SVG
Pitcairnia flammea	Pifl	ITA

Quesnelia augusto-coburgii	Quau	ITA
Quesnelia arvensis	Quar	FAR
Tillandsia geminiflora	Tige	ITA, FAZ, SVG
Tillandsia stricta	Tist	ITA, SVG
Tillandsia tenuifolia	Tite	ITA, SVG
Tillandsia dura	Tidu	SVG
Vriesea carinata	Vrca	ITA, SVG
Vriesea ensiformis	Vren	FAR, FAZ
Vriesea erythrodactylon	Vrer	SVG
Vriesea gradata	Vrgr	ITA
Vriesea incurvata	Vrin	SVG
Vriesea inflata	Vrif	SVG
Vriesea longicaulis	Vrlo	ITA
Vriesea penduliflora	Vrpe	ITA
Vriesea philippocoburgii	Vrph	SVG
Vriesea procera	Vrpo	FAZ
Vriesea rodigasiana	Vrro	FAR
Vriesea simplex	Vrsi	SVG
Vriesea **sp.1**	Vrsp1	SVG
Vriesea **sp.2**	Vrsp2	SVG
Wittrockia superba	Wisu	SVG
Campanulaceae		
Centropogon cornutus	Ceco	FAZ, SVG

Siphocampylus convolvulaceus	Sicv	SVG
Siphocampylus longipedunculatus	Silo	ITA, SVG
Siphocampylus lauroanus	Sila	SVG
Cannaceae		
Canna paniculata	Capa	SVG
Costaceae		
Costus arabicus	Coar	FAR, FAZ
Fabaceae		
Dahsltedtia pinnata	Dapi	FAR, FAZ
Erythrina speciosa	Ersp	FAZ, SVG
Inga marginata	Inma	FAR
Inga sessilis	Inse	SVG
Inga subnuda	Insu	FAZ
Gentianaceae		
Macrocarpaea rubra	Maru	SVG
Gesneriaceae		
Besleria longimucronata	Belo	FAR, SVG
Nematanthus crassifolius	Necr	ITA
Nematanthus fissus	Nefi	FAR, FAZ
Nematanthus fluminensis	Nefl	FAR, FAZ, SVG
Nematanthus fornix	Nefo	ITA
Nematanthus fritschii	Nefr	SVG

Nematanthus gregarius	Negr	SVG
Nematanthus lanceolatus	Nela	ITA
Nematanthus **sp.**	Nesp	SVG
Nematanthus monanthos	Nemo	FAR
Nematanthus sericeus	Nese	SVG
Sinningia cooperi	Sico	ITA, SVG
Sinningia elatior	Siel	SVG
Sinningia gigantifolia	Sigi	ITA
Sinningia glazioviana	Sigl	SVG

Heliconiaceae

Heliconia angusta	Hean	FAR, FAZ
Heliconia farinosa	Hefa	FAR

Lamiaceae

Salvia sellowiana	Sase	ITA, SVG
Salvia cf. balaustina	Saba	SVG

Loranthaceae

Psittacanthus brasiliensis	Psbr	ITA
Psittacanthus dichroos	Psdi	FAR, SVG

Malvaceae

Callianthe bedforniana	Cabe	ITA
Callianthe rufinerva	Caru	SVG
Eriotheca gracilipes	Ergr	FAZ
Spirotheca rivieri	Spri	SVG

Marantaceae

Stromanthe thalia	Stth	ITA
Marcgraviaceae		
Schwartzia brasiliensis	Scbr	FAZ
Onagraceae		
Fuchsia regia	Fure	ITA, SVG
Orchidaceae		
Elleanthus brasiliensis	Elbr	ITA
Orobanchaceae		
Velloziela dracocephaloides	Vedr	ITA
Rubiaceae		
Manettia cordifolia	Maco	SVG
Manettia mitis	Mami	ITA
Psychotria nuda	Psnu	FAR, FAZ
Psychotria ruellifolia	Psru	ITA
Sabicea grisea	Sagr	FAZ
Verbenaceae		
Stachytarpheta cayennensis	Stca	FAZ
Zingiberaceae		
Renealmia petasites	Repe	SVG

Table S3. Floral traits and pollination type of the hummingbird-pollinated plant species of the Atlantic forest. Morphological data are given in milimeters. Color number indicate the number of flowers for each X indicates that we collected reflectance data. Source refers only to morphological data. CAN 2006 = Canela 2006 (PhD Thesis); VIZ 2014 = Vizentin-Bugoni *et al*. 2014; BER 2015 = Bergamo *et al*. 2015; MAR 2015 - Maruyama *et al*. 2015. Values represent mean ± standard-deviation (number of flowers sampled).

Family *Species*	Color	Corolla length	Anther height	Stigma height	Pollination type	Source
Acanthaceae						
Aphelandra colorata	5	39.37 ± 0.95 (4)	52.99 ± 2.08 (4)	52.28 ± 1.17 (4)	hermit	this study
A. longiflora	5	43.23 ± 2.58 (4)	40.23 ± 2.06 (4)	40.71 ± 2.11 (4)	hermit	this study
Justicia carnea	6	36.19 ± 0.75 (6)	59.50 ± 1.54 (6)	61.80 ± 1.79 (6)	hermit	this study
J. sebastianopolitana	5	29.49 ± 1.01 (4)	38.94 ± 0.34 (4)	39.49 ± 0.57 (4)	hermit	this study
J. parabolica	9	31.53 ± 1.28 (7)	39.74 ± 2.48 (7)	41.19 ± 1.21 (7)	hermit	this study
Justicia **sp.**	7	15.92 ± 1.37 (7)	20.97 ± 0.75 (7)	21.84 ± 1.09 (7)	hermit	this study
Mendocia velloziana	1	29.81 ±	24.98 ±	28.15 ±	mixed	this study

		0.36 (2)	3.13 (2)	4.07 (2)		
Odontonema barbelerioides	7	44.72 ± 3.11 (7)	43.60 ± 3.29 (7)	43.06 ± 3.29 (7)	hermit	this study
Staurogyne itatiaiae	8	17.12 ± 1.69 (6)	14.58 ± 1.14 (6)	15.79 ± 0.66 (6)	hermit	this study
Alstroemeriaceae						
Alstroemeria inodora	5	25.69 ± 4.50 (8)	36.86 ± 6.52 (6)	41.2 ± 3.17 (5)	mixed	this study
Bomarea edulis	6	22.79 ± 3.17 (6)	24.45 ± 2.29 (6)	22.13 ± 3.36 (6)	mixed	this study
Asteraceae						
Mutisia speciosa	4	23.81 ± 2.74 (6)	38.79 ± 4.69 (6)	38.79 ± 4.69 (6)	mixed	this study
Bignoniaceae						
Pyrostegia venusta	4	34.52 ± 2.99 (4)	43.75 ± 5.07 (4)	46.14 ± 4.64 (4)	hermit	this study
Bromeliaceae						
Aechmea coelestis	5	28.72 ± 1.88 (5)	26.60 ± 0.93 (5)	23.45 ± 0.51 (6)	mixed	this study
A. disthicantha	9	15.28 ± 1.66 (11)	13.41 (11)	12.54 (11)	mixed	this study
A. gamosepala	1	19.97 (1)	18.62 (1)	18.1 (1)	mixed	this study
A. organensis	-	12.1 (5)	-	-	mixed	VIZ 2014
A. nudicaulis	5	13.56 ± 0.94 (6)	12.28 ± 0.70 (6)	10.26 ± 1.36 (6)	mixed	this study

A. pectinata	-	30 (10)	-	-	mixed	MAR 2015
A. vanhoutteana	4	9.1 (4)	19.6 (4)	18.9 (4)	mixed	this study
Billbergia amoena	6	38.55 ± 2.08 (5)	49.31 ± 1.02 (5)	51.79 ± 0.44 (5)	hermit	this study
B. distachia	9	37.92 ± 3.41 (8)	50.41 ± 2.99 (8)	54.87 ± 3.48 (8)	hermit	this study
B. pyramidalis	4	37.83 ± 6.28 (4)	47.56 ± 5.27 (4)	50.78 ± 3.78 (4)	hermit	this study
B. vittata	1	26.97 (1)	43.42 (1)	46.77 (1)	mixed	this study
Bromelia antiacantha	2	18.61 ± 1.35 (2)	15.18 ± 1.12 (2)	12.17 ± 1.00 (2)	mixed	this study
Canistropsis seidelii	6	24.86 ± 1.87 (6)	21.20 ± 1.73 (6)	21.20 ± 1.73 (6)	mixed	this study
Canistrum perplexum	6	24.77 ± 2.13 (7)	23.03 ± 1.66 (7)	21.17 ± 1.49 (7)	mixed	this study
Edmundoa lindenii	-	17.10 (5)	-	-	mixed	VIZ 2014
Neoregelia johannis	5	33.60 ± 0.97 (5)	32.02 ± 2.08 (5)	30.89 ± 2.13 (5)	hermit	this study
Nidularium angustifolium	5	38.59 ± 1.76 (5)	35.73 ± 1.76 (5)	34.07 ± 1.55 (5)	hermit	this study
N. bicolor	4	43.19 ±1.47 (4)	40.75 ± 2.07 (4)	38.32 ± 2.57 (4)	hermit	this study
N. innocentii	25	51.21 ± 6.05 (23)	47.25 ± 6.38 (23)	47.66 ± 5.95 (23)	hermit	this study

N. itatiaiae	2	45.42 ± 8.40 (2)	39.91 ± 7.03 (2)	39.37 ± 7.80 (2)	hermit	this study
N. longiflorum	8	63.36 ± 5.17 (6)	59.92 ± 5.27 (6)	62.23 ± 5.41 (6)	hermit	this study
N. procerum	11	41.73 ±2.17 (7)	38.45 ± 1.16 (7)	37.43 ± 0.58 (7)	hermit	this study
N. rutilans	3	52.73 ± 2.43 (3)	47.94 ± 4.20 (3)	47.94 ± 4.20 (3)	hermit	this study
Pitcairnia flammea	9	36.56 ± 2.51 (9)	58.72 ± 2.38 (9)	63.47 ± 2.46 (9)	mixed	this study
Quesnelia augusto-coburgii	5	48.70 ± 1.13 (5)	47.43 ± 1.06 (5)	47.43 ± 1.06 (5)	hermit	this study
Q. arvensis	3	19.26 ± 0.31 (3)	17.21 ± 0.24 (3)	15.96 ± 0.21 (3)	hermit	this study
Tillandsia geminiflora	9	17.61 ± 1.48 (9)	13.93 ± 2.29 (9)	14.70 ± 2.29 (9)	mixed	this study
T. stricta	5	17.60 ± 2.42 (5)	13.79 ± 2.49 (5)	14.26 ± 2.24 (5)	mixed	this study
T. tenuifolia	-	-	-	-	mixed	-
T. dura	1	20.01 (1)	18.99 (1)	19.61 (1)	mixed	this study
Vriesea carinata	12	42.26 ± 3.28 (7)	54.41 ± 5.23 (7)	57.64 ± 5.11 (7)	hermit	this study
V. ensiformis	3	50.39 ± 2.15 (2)	55.67 ± 1.15 (2)	60.84 ± 0.08	hermit	this study
V. erythrodactylon	3	41.17 ±	49.11 ±	51.73 ±	hermit	this study

		0.56 (3)	2.28 (3)	2.37 (3)		
V. gradata	5	44.43 ± 3.23 (5)	56.28 ± 4.21 (5)	58.97± 3.57 (5)	hermit	this study
V. incurvata	9	48.59 ± 3.84 (10)	56.96 ± 3.59 (10)	60.04 ± 4.61 (10)	hermit	this study
V. inflata	4	47.01 ± 2.11 (6)	54.60 ± 3.77 (6)	57.37 ± 2.49 (6)	hermit	this study
V. longicaulis	2	35.63 ± 1.30 (2)	40.39 ± 2.38 (2)	42.78 ± 1.90 (2)	mixed	this study
V. penduliflora	-	35.8 (3)	33.95 (3)	36.1 (3)	mixed	CAN 2006
V. phillipocoburgii	-	27.1 (5)	-	-	mixed	VIZ 2014
V. procera	2	33.97 ± 0.93 (2)	31.67 ± 0.62 (2)	29.1 ± 1.00 (2)	mixed	this study
V. rodigasiana	5	26.91 ± 1.37 (5)	32.79 ± 2.32 (5)	37.13 ± 2.47 (5)	hermit	this study
V. simplex	6	51.56 ± 3.68 (5)	60.21 ± 5.90 (5)	62.45 ± 6.74 (5)	hermit	this study
Vriesea **sp.1**	5	44.08 ± 0.64 (2)	49.91 ± 0.17 (2)	52.27 ± 0.76 (2)	hermit	this study
Vriesea **sp.2**	5	31.72 ± 2.59 (5)	42.37 ± 3.09 (5)	48.91 ± 1.92 (5)	mixed	this study
W. superba	-	18.5 (5)	-	-	mixed	VIZ 2014
Campanulaceae						
Centropogon cornutus	7	46.63 ± 2.79 (7)	61.58 ± 4.00 (7)	65.52 ± 5.34 (7)	hermit	this study

Siphocampylus convolvulaceus	6	43.39 ± 2.64 (6)	52.81 ± 4.46 (6)	55.05 ± 5.03 (6)	hermit	this study
S. longipedunculatus	7	42.01 ± 3.26 (10)	48.57 ± 3.67 (10)	50.18 ± 3.24 (10)	hermit	this study
S. lauroanus	6	42.03± 5.47 (6)	47.46 ± 3.80 (6)	49.72 ± 4.59 (6)	hermit	this study
Cannaceae						
Canna paniculata	12	56.15 ± 8.73 (12)	69.59 ± 9.26 (12)	76.62 ± 10.14(12)	hermit	this study
Costaceae						
Costus arabicus	13	48.30 ± 2.68 (7)	40.40 ± 6.22 (7)	42.96 ± 6.78 (7)	mixed	BER 2015
Fabaceae						
Dahlstedtia pinnata	5	41.45 ± 1.53 (5)	37.48 ± 0.63 (5)	38.82 ± 1.49 (5)	mixed	this study
Erythrina speciosa	10	51.15 ± 3.67 (10)	44.04 ± 3.63 (10)	37.27 ± 4.29 (10)	mixed	this study
Inga marginata	-	14.6 (10)	-	-	mixed	MAR 2015
I. sessillis	-	12.92 (10)	-	-	mixed	VIZ 2014
I. subnuda	2	12.92 ± 2.55 (2)	48.36 ± 3.80 (2)	44.17 ± 1.69 (2)	mixed	this study
Gentianaceae						
Macrocarpaea rubra	5	28.50 ± 2.83 (5)	27.47 ± 3.57 (2)	23.43 ± 2.53 (5)	mixed	this study

Gesneriaceae

Besleria longimucronata	12	23.57 ± 2.89 (11)	18.38 ± 2.41 (11)	16.79 ± 1.44 (11)	mixed	this study
Nematanthus crassifolius	8	50.31 ± 4.87 (7)	48.84 ± 2.93 (4)	49.39 ± 2.77 (5)	hermit	this study
N. fissus	9	27.51 ± 3.35 (9)	22.19 ± 5.23 (5)	23.34 ± 3.84 (5)	mixed	this study
N. fluminensis	13	53.30 ± 3.90 (14)	49.16 ± 5.02 (7)	51.62 ± 5.68 (11)	hermit	this study
N. fornix	5	26.5 ± 0.18 (10)	22.7 ± 0.30 (10)	22.9 ± 0.20 (10)	mixed	CAN 2006
N. fritschii	10	45.34 ± 4.34 (6)	42.82 ± 2.41 (4)	36.14 ± 0.30 (2)	hermit	this study
N. gregarius	5	24.85 ± 1.36 (5)	18.57 ± 3.48 (4)	19.78 ± 1.77 (4)	mixed	this study
N. lanceolatus	4	26.10 ± 1.58 (2)	22.38 ± 1.75 (2)	23.63 (1)	hermit	this study
Nematanthus **sp**	10	50.52 ± 1.77 (6)	47.04 ± 4.14 (5)	49.65 ± 3.21 (6)	hermit	this study
N. monanthus	3	32.09 (1)	29.64 (1)	29.64 (1)	-	this study
N. sericeus	5	36.45 ± 2.18 (5)	30.66 ± 1.84 (5)	31.73 ± 5.45 (3)	mixed	this study
Sinningia cooperi	6	38.92 ± 1.78 (9)	59.68 ± 2.77 (5)	65.94 ± 2.45 (4)	hermit	this study
S. elatior	-	30.4 ±	-	-	mixed	this study

		0.28 (8)				
S. gigantifolia	1	37.76 (1)	32.22 (1)	37.60 (1)	hermit	this study
S. glazioviana	10	42.50 ± 1.64 (7)	47.75 ± 3.32 (7)	51.80 ± 1.99 (7)	hermit	this study
Heliconiaceae						
Heliconia angusta	7	30.97 ± 1.02 (3)	53.36 ± 1.71 (3)	46.90 ± 0.81 (3)	hermit	this study
H. farinosa	6	36.74 ± 5.84 (6)	49.85 ± 3.24 (6)	46.12 ± 1.58 (6)	hermit	this study
Lamiaceae						
Salvia sellowiana	9	40.86 ± 9.29 (9)	50.11 ± 5.80 (9)	55.05 ± 5.13 (9)	hermit	this study
S. balaustina	3	41.34 ± 2.12 (3)	56.87 ± 3.56 (3)	64.31 ± 2.30 (3)	-	this study
Loranthaceae						
Psittacanthus brasiliensis	-	29.4 (10)	-	-	mixed	CAN 2006
P. dichroos	5	28.69 ± 1.24 (5)	44.47 ± 1.17 (5)	47.88 ± 0.76 (5)	mixed	this study
Malvaceae						
Callianthe bedfordiana	7	27.03 ± 4.16 (5)	24.82 ± 1.35 (5)	25.96 ± 2.88 (5)	mixed	this study
C. rufinerva	9	16.74 ± 3.70 (6)	13.72 ± 4.08 (6)	13.85 ± 5.11 (6)	mixed	this study
Eriotheca gracilpes	2	0 (1)	15.76 (1)	15.76 (1)	mixed	this study

Species	N				Type	Source
Spirotheca rivieri	1	5.91 (1)	28.12 (1)	32.32 (1)	mixed	this study
Marantaceae						
Stromanthe thalia	4	7.42 ± 0.74 (3)	6.41 ± 0.66 (3)	6.73 ± 0.96 (3)	mixed	this study
Marcgraviaceae						
Schwartzia brasiliensis	5	7.28 ± 1.08	7.28 ± 1.08	7.28 ± 1.08	mixed	this study
Onagraceae						
Fuchsia regia	5	25.24 ± 3.08 (10)	52.77 ± 4.74 (4)	51.42 ± 5.88 (6)	mixed	this study
Orchidaceae						
Elleanthus brasiliensis	3	8.12 ± 0.78 (3)	6.45 ± 0.97 (3)	5.41 ± 0.87 (3)	hermit	this study
Orobanchaceae						
Velloziela dracocephaloides	5	73.72 ± 2.64 (5)	52.11 ± 1.45 (5)	63.64 ± 1.65 (5)	hermit	this study
Rubiaceae						
Mannetia cordifolia	5	49.17 ± 3.67 (5)	48.10 ± 3.89 (5)	45.50 ± 1.65 (5)	hermit	this study
M. mitis	5	25.41 ± 0.73 (5)	31.29 ± 1.98 (5)	34.34 ± 2.33 (5)	hermit	this study
Psychotria nuda (brev/long)	8	19.88 ± 1.75 (10)	18.34 ± 0.43 (5) / 16.29 ± 1.71 (5)	12.42 ± 2.30 (5) / 19.53 ± 1.91 (5)	mixed	this study

P. ruellifolia	1	20.7 (1)	20.2 (1)	14.1 (1)	mixed	this study
Sabicea grisea	2	15.7 ± 0.61 (2)	12.64 ± 0.13 (2)	14.38 ± 0.49 (2)	mixed	this study
Verbenaceae						
Stachytarpheta cayennensis	5	8.58 ± 0.97 (5)	8.58 ± 0.97 (5)	8.58 ± 0.97 (5)	mixed	this study
Zingiberaceae						
Renealmia petasites	4	29.36 ± 2.82 (4)	24.61 ± 2.03 (4)	23.37 ± 1.85 (4)	-	this study

Table S4. Species nectar attributes. Volume refers to nectar accumulated on flowers previously bagged bud for at least 12h. Concentration refers to sugar concentration on the accumulated nectar. Sugar content was calculated as the product of volume and nectar. BUZ 2000 = Buzato *et al*. 2000; SAN 2005 = SanMartinGajardo and Sazima 2005; CAN 2006 = Canela 2006 (PhD Thesis); MAC 2006 = Machado and Semir 2006; ROC 2006 = Rocca-de-Andrade 2006 (PhD Thesis); FON 2012 = Fonseca 2012 (PhD Thesis); AMO 2013 = Amorim *et al*. 2013; BER 2015 = Bergamo *et al*. 2015; MAR 2015 = Maruyama *et al*. 2015; NUN 2015 = Nunes *et al*. 2015;

Family *Species*	Volume (μl)	Concentration (% Brix)	Sugar content (mg/μl)	Number of flowers	Source
Acanthaceae					
Aphelandra colorata	22.91	22.5	5.18	11	this study
A. longiflora	7.93	15.57	1.23	7	this study
Justicia carnea	24.2	20.4	4.97	10	MAR 2015
J. sebastianopolitana	11.5	22	2.53	10	CAN 2006
J. parabolica	6.58	15.83	1.21	6	this study
Justicia sp	4.67	14.04	0.69	12	this study
Mendocia velloziana	47.67	27.67	13.52	3	MAR 2015
Odontonema barbelerioides	15	17.4	2.61	10	CAN 2006
Staurogyne itatiaiae	2	15	0.3	8	CAN 2006
Alstroemeriaceae					
Alstroemeria inodora	17.57	16.21	2.91	7	this study
Bomarea edulis	33	21.2	6.93	10	MAR 2015
Asteraceae					

Mutisia speciosa	9.2	24.25	2.27	10	MAR 2015
Bignoniaceae					
Pyrostegia venusta	10.29	17.64	1.94	7	this study
Bromeliaceae	11.25	24.25	2.75	4	MAR 2015
Aechmea coelestis	27.9	26.6	7.34	10	MAR 2015
A. disthicantha	9.22	22	2.03	9	this study
A. gamosepala	10.9	17.75	2.02	10	MAR 2015
A. organensis	66.33	29.83	19.90	3	MAR 2015
A. nudicaulis	26.21	22.79	5.88	14	this study
A. pectinata	63	20.22	10.79	9	this study
A. vanhoutteana	20.1	16.5	3.32	10	BUZ 2000
Billbergia amoena	50.4	25.05	13.15	10	MAR 2015
B. distachia	-	-	-	-	-
B. pyramidalis	39.6	30.2	12.08	5	MAR 2015
B. vittata	28.65	26.3	7.68	10	MAR 2015
Bromelia antiacantha	34.25	23.63	8.18	8	this study
Canistropsis seidelii	-	-	-	-	-
Canistrum perplexum	34.3	26.05	9.14	10	MAR 2015
Edmundoa lindenii	21.5	32.05	6.97	10	MAR 2015
Neoregelia johannis	-	-	-	-	-
Nidularium angustifolium	41.63	32.38	13.55	8	MAR 2015
N. bicolor	-	-	-	-	-
N. innocentii	11.8	26.9	3.22	5	this study
N. itatiaiae	11.93	26.25	2.86	14	this study
N. longiflorum	-	-	-	-	-

N. procerum	34	13.8	4.69	10	CAN 2006
N. rutilans	6.5	22.2	1.44	2	BUZ 2000
Pitcairnia flammea	35	24	8.4	10	CAN 2006
Quesnelia augusto-coburgii	7.6	18.85	1.40	10	MAR 2015
Q. arvensis	4	10.9	0.49	5	this study
Tillandsia geminiflora	2.75	13.38	2.21	4	this study
T. stricta	3.22	14.78	0.48	9	this study
T. tenuifolia	8.53	19.8	1.85	15	this study
T. dura	67	30.5	20.43	5	MAR 2015
Vriesea carinata	26	27	7.02	1	this study
V. ensiformis	12.13	25.5	3.32	4	this study
V. erythrodactylon	55.33	24.33	15.01	3	this study
V. gradata	16.5	11.25	1.88	2	this study
V. incurvata	-	-	-	-	-
V. inflata	-	-	-	-	-
V. longicaulis	26.8	22.2	5.95	10	MAC 2006
V. penduliflora	35.5	18.85	6.88	10	MAR 2015
V. phillipocoburgii	30.6	21.55	6.70	10	MAR 2015
V. procera	37	25.83	9.38	4	this study
V. rodigasiana	3	21	0.63	1	this study
V. simplex	-	-	-	-	-
Vriesea **sp.1**	63.82	26.41	16.66	11	this study
Vriesea **sp.2**					
W. superba	12.8	25.3	3.24	10	BUZ 2000

Campanulaceae

Centropogon cornutus	110.7	26.3	29.11	10	MAR 2015
Siphocampylus convolvulaceus	32.67	11.67	2.53	3	this study
S. longipedunculatus	11	15	1.65	1	this study
S. lauroanus	28.4	29.9	5.96	5	this study
Cannaceae					
Canna paniculata	59.1	20	11.81	10	MAR 2015
Costaceae					
Costus arabicus	37.37	35.98	13.48	30	BER 2015
Fabaceae					
Dahlstedtia pinnata	77.2	14.95	11.49	10	MAR 2015
Erythrina speciosa	13.1	21.4	3.07	10	MAR 2015
Inga marginata	1.1	6.2	0.07	10	MAR 2015
I. sessillis	148	9.3	13.76	5	AMO 2013
I. subnuda	63.4	19.05	11.79	10	MAR 2015
Gentianaceae					
Macrocarpaea rubra	32.78	10.89	3.89	9	this study
Gesneriaceae					
Besleria longimucronata	14	16	2.24	5	MAR 2015
Nematanthus crassifolius	12.5	26.5	3.31	4	CAN 2006
N. fissus	15.33	29	4.45	3	MAR 2015
N. fluminensis	31.6	32.3	10.33	5	MAR 2015
N. fornix	3	21.9	0.66	4	BUZ 2000
N. fritschii	28.5	28.7	8.37	5	this study
N. gregarius	10.7	20.6	2.69	5	this study
N. lanceolatus	-	-	-	-	-

Nematanthus **sp**	-	-	-	-	-
N. monanthus	34.5	30	10.35	1	FON 2012
N. sericeus	6	23	1.38	1	this study
Sinningia cooperi	5	20.8	1	5	this study
S. elatior	14	26.75	3.75	2	this study
S. gigantifolia	10.1	22.4	2.5	27	SAN 2005
S. glazioviana	11.5	25.4	3.01	10	this study
Heliconiaceae					
Heliconia angusta	44.67	23.25	10.43	6	MAR 2015
H. farinosa	51.7	24.9	12.35	10	MAR 2015
Lamiaceae					
Salvia sellowiana	20.5	27.5	5.64	10	CAN 2006
S. balaustina	4.4	22.5	0.99	7	BUZ 2000
Loranthaceae					
Psittacanthus brasiliensis	-	-	-	-
P. dichroos	28.0	22.8	5.68	2	MAR 2015
Malvaceae					
Callianthe bedfordiana	150	15	22.5	-	this study
C. rufinerva	172.6	14.1	24.42	5	this study
Eriotheca gracilpes	248.2	8.65	21.02	10	MAR 2015
Spirotheca rivieri	141.9	6	8.51	-	ROC 2006
Marantaceae					
Stromanthe thalia	-	-	-	-
Marcgraviaceae					
Schwartzia brasiliensis	62	14.85	8.64	10	MAR 2015

Onagraceae

| *Fuchsia regia* | 32.17 | 13.25 | 3.93 | 6 | this study |

Orchidaceae

| *Elleanthus brasiliensis* | 4.15 | 21.11 | 0.88 | 66 | NUN 2015 |

Orobanchaceae

| *Velloziela dracocephaloides* | 10 | 12.5 | 1.25 | 2 | CAN 2006 |

Rubiaceae

Mannetia cordifolia	18.14	14.21	2.53	7	this study
M. mitis	25.5	17.2	4.386	10	CAN 2006
Psychotria nuda (**brev/long**)	18.45	19.6	3.70	10	MAR 2015
P. ruellifolia	2.96	16.76	0.45	27	this study
Sabicea grisea	16.7	21.55	3.67	10	MAR 2015

Verbenaceae

| *Stachytarpheta cayennensis* | 1.3 | 14.4 | 0.18 | 10 | MAR 2015 |

Zingiberaceae

| *Renealmia petasites* | - | - | - | - |

Table S5. Phylogenetic and functional structure of hummingbird-pollinated plant communities in the Brazilian Atlantic forest. We obtained each structure by comparing phylogenetic and functional distances (MPD indexes) of each community with a null distribution formed by the regional species pool. Communities: ITA = Itatiaia, SVG = Santa Virgínia, FAR = Casa da Farinha, FAZ = Praia da Fazenda. MPDobs = Mean pairwise distance of the observed community. MPDnull = Mean pair wise distance of the 10000 null random assembled communities for the factor evaluated. Bold values indicate significance at $p < 0.05$ level.

		Phylogenetic and functional structure		
	Community	MPDobs	MPDnull (mean ± SD)	p
Phylogenetic distance	ITA	342.775	369.694 ± 26.603	0.146
	SVG	389.309	402.655 ± 13.85	0.156
	FAR	354.095	329.04 ± 44.00	0.688
	FAZ	377.261	367.778 ± 27.584	0.597
Corolla length	ITA	14.452	17.012 ± 3.169	0.222
	SVG	17.986	18.655 ± 2.095	0.350
	FAR	14.393	15.009 ± 3.963	0.4459
	FAZ	18.54	16.941 ± 3.179	0.690
Anther height	ITA	16.310	16.590 ± 3.222	0.4388
	SVG	**11.131**	**18.036 ± 2.283**	**0.004**
	FAR	13.936	14.819 ± 4.093	0.397

	FAZ	18.733	16.562 ± 3.222	0.715
Stigma height	ITA	17.885	16.996 ± 3.27	0.587
	SVG	**12.067**	**18.322 ± 2.320**	**0.008**
	FAR	14.312	15.448 ± 4.277	0.394
	FAZ	16.560	17.013 ± 3.281	0.429
Color	ITA	17.339	18.038 ± 2.593	0.337
	SVG	**13.371**	**19.734 ± 1.635**	**0.001**
	FAR	17.008	16.394 ± 3.418	0.562
	FAZ	21.741	18.278 ± 2.463	0.429
Nectar sugar content	**ITA**	**1.978**	**3.987 ± 1.141**	**0.025**
	SVG	4.065	4.374 ± 0.664	0.316
	FAR	4.541	3.900 ± 1.319	0.707
	FAZ	4.979	4.092 ± 0.964	0.829

Table S6. Temporal structure of flowering phenology of all hummingbird-pollinated species studied ("Whole community") and for the hermit and mixed-pollinated plant assemblages. We obtained each structure by comparing phenological overlap (MPO indexes) of each community with a null distribituion formed by the ROSARIO algorithm. MPOobs = Mean phenological overlap of the observed community/assemblage. MPOnull = Mean phenological overlap of the 10000 null random communities or assemblages evaluated. Bold values indicate significance at $p < 0.05$ level.

		Phenological structure		
	Local	MPOobs	MPOnull (mean ± SD)	p
Whole community	ITA	0.151	0.158 ± 0.009	0.258
	SVG	**0.176**	**0.169 ± 0.005**	**0.046**
	FAR	0.144	0.130 ± 0.015	0.837
	FAZ	**0.169**	**0.148 ± 0.009**	**0.027**
Hermit assemblage	ITA	0.204	0.212 ± 0.018	0.615
	SVG	0.188	0.184 ± 0.009	0.263
	FAR	0.169	0.144 ± 0.022	0.131
	FAZ	0.178	0.194 ± 0.035	0.630
Mixed assemblage	**ITA**	**0.103**	**0.146 ± 0.024**	**0.038**
	SVG	0.160	0.157 ± 0.011	0.695
	FAR	0.002	0.110 ± 0.079	0.075
	FAZ	0.138	0.129 ± 0.016	0.757
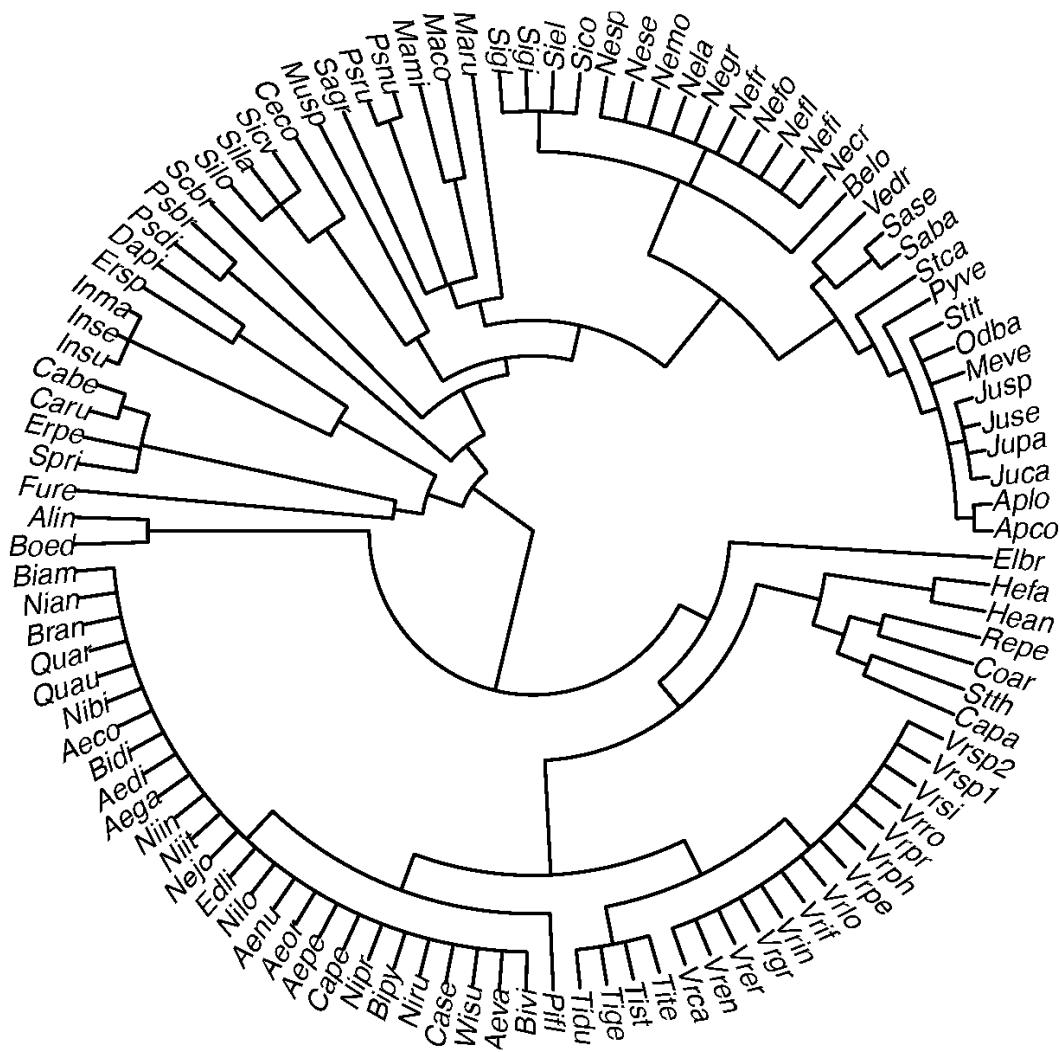
Figure S1. Phylogenetic hypothesis for hummingbird-pollinated plants. Tree topology

was based on the APG III tree R20091100 built in Phylomatic (Webb and Donoghue

2005), with modifications to resolve relationships among subfamilies of Bromeliaceae

(Givnish *et al*. 2011). Branch lengths indicate divergence times following Bell *et al*.

2010. Tip labels indicate species abbreviations given in Table S2.

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CAPÍTULO 2

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Floral traits and abundance influence the potential for indirect effects between plants sharing hummingbird pollinators

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Abstract

Plants engage on indirect interactions through shared pollinators. For instance, sympatric hummingbird-pollinated plants have been shown to be involved in interactions that vary from competition to facilitation. Since interaction with hummingbirds is strongly constrained by phenotypic-matching, indirect plant-plant interactions may also be restricted by trait-based mechanisms. In this context, we evaluated what mechanisms, including morphological trait similarity, phenological overlap, evolutionary relatedness and abundances, affect how hummingbird-pollinated plants engage in indirect interactions (measured as pollinator-sharing) within communities. We found that plants with similar corolla length and anther height had higher potential to indirectly affect each other while more abundant species had higher potential to indirectly affect other species. On the other hand, stigma height, flower colour, phenology and evolutionary relatedness had less influence on the potential for indirect interactions. By showing that traits matter for indirect interactions among plants sharing hummingbird pollinators, our results support the finding that phenotypic-matching has a major role in plant-hummingbird systems. Nevertheless, here we show that plant abundance, although not determining the interactions with hummingbirds, is important in structuring indirect interactions among plants within communities. Our study provides insights on the mechanisms ruling the indirect interaction among plants sharing the same specialized group of pollinators. Moreover, mechanisms that are not important when considering the direct interaction to pollinators may become relevant when considering the indirect interaction among plants. Since many plant-hummingbird communities, as well as other specialized systems show similar structural properties, the mechanisms found here may operate in similar ways in other communities.

Key words

Atlantic forest, competition, facilitation, ecological interactions, plant-pollinator networks, pollination ecology, reproductive interference

Introduction

Indirect effects through a third species are widespread across different interaction types and ecological communities (Wootton 1994). In this context, trait similarity between interacting species may indirectly determine how they overlap in the use of the resources provided by a third species leading to competition or facilitation (Beltrán et al. 2012). Accordingly, if evolutionary relatedness modulates resource use, phylogeny can determine the nature of the indirect effects (Morales & Traveset 2009). At the same time, abundant species generally interact with more partners directly, which can strengthen or dilute the indirect effects they have (Müller et al. 1999). In this sense, species traits, evolutionary relatedness and abundance influence the direct interactions across several interaction networks (Vázquez et al. 2009, Eklöf et al. 2013) and potentially also determine how species sharing interaction partners affect each other indirectly.

Plants sharing pollinators can facilitate or compete with each other by enhancing or reducing the spectra and frequency of pollinator visitation and the quality of pollen delivery (Ratchke 1983). Moreover, plants compete with each other via reproductive interference caused by heterospecific pollen deposition (Morales & Traveset 2008). These indirect effects may alter plant fitness, which can lead to selection of floral traits that promote facilitation (Moeller 2004) or character displacement in response to competition (Fishman & Wyatt 1999). If fitness differences affect the persistence of

plant populations, indirect effects can scale-up to the community level and influence plant diversity at communities (Sargent & Ackerly 2008, Lázaro et al. 2014). Trait-based mechanisms, evolutionary relatedness and abundance were reported to influence the potential for indirect effects between insect-pollinated plants (Morales & Traveset 2009, Carvalheiro et al. 2014). Nevertheless, the strength and direction of each factor depend on the considered pollinator group (Carvalheiro et al. 2014). Thus, it still worth to investigate what influences the potential for indirect effects between plants sharing highly specialized interactions, such as those among plants and hummingbirds in the Neotropics.

Hummingbird-pollinated plant species engage in plant-plant indirect interactions via pollinator sharing with evidence of facilitation (Wolowski et al. *submitted*) to competition (Feinsinger & Tiebout 1991, Aizen & Rovere 2010). Plant-hummingbird interactions form highly phenotypic-specialized networks in some communities, with a prevalence of morphological (corolla length-bill size) and spatio-temporal matching over abundance determining their interactions (Maglianesi et al. 2014, Maruyama et al. 2014, Vizentin-Bugoni et al. 2014). For instance, plant species with similar traits associated to nectar accessibility (in this case, corolla length) and with phenological overlap are expected to promote higher indirect effects on each other via shared hummingbird species (Aizen & Rovere 2010). Moreover, hummingbirds can carry heterospecific pollen mixtures on the same part of their body leading plant species with similar pollen placement more prone to reciprocal indirect effects (Feinsinger & Tiebout 1991). Finally, species with flowers having similar signals may attract the same pollinators, leading to potential indirect effects (Chittka et al. 1997), a topic that still scarcely evaluated at the community level (but see Renoult et al. 2015), including plant-hummingbird networks.

Although plant-hummingbird interactions are highly specialized due to phenotypic-match, few studies have employed a multi-trait approach to investigate what determines indirect interactions at community level (but see Maruyama et al. 2015). This leads to uncertainty about which floral traits or other potential mechanisms (e.g. density-dependent mechanisms such as flower abundance) have a relevant role on the potential for indirect effects when plants share hummingbird pollinators. Here, we used four hummingbird-pollinated plant communities for which we have extensive knowledge in the Brazilian Atlantic forest (Canela 2006, Wolowski 2013, Vizentin-Bugoni et al. 2014, Maruyama et al. 2015, Fig. 1) to ask how floral traits, evolutionary relatedness, flowering phenology and abundance (in terms of flower number) influence the potential for indirect effects among hummingbird-pollinated plant species. We expect that this potential increase with trait similarity and phenological overlap among species, following phenotypic-matching patterns and because flowering aggregation can lead to a higher attraction of hummingbirds (Maglianesi et al 2014, Maruyama et al. 2014, Vizentin-Bugoni et al. 2014, Chapter 1). Evolutionary relatedness among plant species may imply a similar use by pollinators and stronger effects of heterospecific pollen competition (Morales & Traveset 2008, Morales & Traveset 2009). However, hummingbird-pollinated plant species have weak phylogenetic signal for several floral traits (Wolowski et al. *submitted*, Chapter 1), thus we do not expect higher potential for indirect effects between closely related species. Lastly, plants with abundant flowers can attract more pollinators and impose stronger indirect effects (Rathcke 1983, Ye et al. 2014). However, since flower abundance was shown to matter little in structuring plant-hummingbird networks (Maruyama et al. 2014, Vizentin-Bugoni et al. 2014), we expect this to have a minor role on the potential for indirect effects among plants too.

Methods

Study system

We selected four plant-hummingbird communities previously studied in the Atlantic forest, Southeastern Brazil, with quantitative data of hummingbird visitation to flowering plant species. Two communities are located in montane Atlantic forests: Itatiaia (ITA) - 22º 27' S, 44º 36' W at 900-1,100 m of altitude above sea level (a.s.l.) in the Itatiaia National Park (Canela 2006) and Santa Virgínia (SVG) - 23º 17' S, 45º 11' W at 850-1100 m of altitude a.s.l. in the Serra do Mar State Park (Vizentin-Bugoni et al. 2014). The other two communities are located in lowland Atlantic forests: Casa da Farinha (FAR) - 23º20', 44º50'W at 150-200 m of altitude and Praia da Fazenda (FAZ) - 23º21'S, 44º51'W at 0-50 m of altitude a.s.l., both in the Serra do Mar State Park (Maruyama et al. 2015).

Hummingbird visitation data

These previous studies performed focal plant observations and camera video recording in order to collect data on hummingbird-visitation. The observation sessions were done at 5-6 h intervals at morning (starting around 0600 am) and afternoon (ending around 1800 pm). We only considered legitimate interactions with potential for pollination, i.e. when the hummingbird touched anthers and stigmas of the flowers. We included 86 plant species, with most representatives belonging to Bromeliaceae (39.53%), Gesneriaceae (15.12%), Acanthaceae (10.47%), Campanulaceae (4.65%), Malvaceae (4.65%) and Rubiaceae (4.65%) families (Table S1). For this study, we used 80% of the plant species, for which we had information on floral traits (see below) and quantitative hummingbird visitation (ITA: 28 spp; SVG: 47 spp; FAR: 15 spp; FAZ: 26 spp., Table S1). All communities had ~15h of observation per plant species, except for

SVG with ~50h of observation (Vizentin-Bugoni et al. 2015). Although differences in sampling effort exist, these are among communities and not within each community among plant species for which the potential for indirect interaction is calculated. Moreover, it was recently shown that ~15h of observation per plant species is sufficient in order to have a consistent description of a hummingbird-plant network properties (Vizentin-Bugoni et al. 2015).

Functional traits

Flowering phenology data was collected monthly in all communities (ITA: Wolowski 2013; SVG: Vizentin-Bugoni et al. 2014, FAR and FAZ: Maruyama et al. 2015). All hummingbird-visited plants in flower were recorded along pre-existing trails. Since communities differ on plant species richness and/or sampling design, we used the relative number of flowers produced per each species per community along 12 months as the measure of flower abundance to minimize sampling effects. For ITA and SVG, which had more than one year of survey, we selected the year when most of the species flowered. Interannual variation in flowering of a given species was small (phenological overlap tested with Mantel; ITA: r = 0.65, p = 0.001; SVG: r = 0.42, p = 0.001)

We collected floral trait data in all communities from July/2014 to September/2015. The morphological traits were measured directly in the field using a digital caliper. As a proxy for resource accessibility, we measured the effective corolla length, from the base of the nectary to the flower tube opening (*sensu* Wolf et al. 1976), hereafter corolla length. In order to estimate the position of pollen placement and transfer on the pollinator body, we measured anther and stigma height from the base of the nectary to the top of the respective reproductive structures. Flower colour was

measured as the spectral reflectance of the petals using a USB4000 spectrophotometer (OceanOptics, Inc., Dunedin, FL, USA) coupled with a deuterium-halogen light source (DH-2000; OceanOptics, Inc., Ostfildern, Germany), with a light emission range between 215 nm and 1700 nm. We took all reflectance measurements at a 45º angle, using barium sulphate and a black chamber as the white and black standards, respectively. Although some species exhibit other attractive coloured structures (e.g. flower bracts of Bromeliaceae), we measured the petals in order to have homologous structures measured for all species. For species with more than one petal colour, we measured the colour that occupied most of the petal area.

Plant phylogeny

We obtained the hummingbird-pollinated plant phylogenetic hypothesis from the topology of the consensus supertree of the APG III (Tree R20091100 in Phylomatic, Webb and Donoghue 2005). We calibrated branch lengths using the BLADJ function in Phylocom (Webb et al. 2008), with divergence times proposed by Bell et al. (2010). This consensus supertree lacks information about several clades at the subfamily level, rendering polytomies along our assembled tree. Since Bromeliaceae were overrepresented in all communities and the subfamilies were assembled as a large polytomy after Phylomatic procedures, we resolved the relationships at the subfamily level using the tree given on Givnish et al. (2011). Figure S1 of Chapter 1 summarizes the hummingbird-pollinated plant phylogeny.

Data analysis

To assess the potential of indirect effects between species, we calculated the degree of pollinator sharing between all pair of species using the Müller's index (Müller et al. 1999). This is a quantitative index based on the interaction frequency data of plant-hummingbird networks that varies from 0 (no pollinator sharing) to 1 (complete pollinator overlap). The index is a proxy on how much a plant species (acting plant) contributes to the diet (in terms of interaction frequency) of all pollinators shared with other plant species (receiving plant). It produces asymmetric effects among a pair of plant species because each plant species contributes differently to the diet of each pollinator. This is a reliable assumption because indirect effects are normally asymmetric among a species pair in nature (Wootton1993, Beltrán et al. 2012). The Müller's index has been used to quantify the indirect effects across several interaction types, from apparent competition (Müller et al. 1999) to the potential for competition or facilitation between species sharing pollinators (Carvalheiro et al. 2014).

We quantified acting plant species similarity in relation to all species in each community by calculating pairwise distances for each variable. Euclidian distance among plants was calculated based on each of the floral traits (corolla length, anther and stigma height). For colour, we calculated the perceptual distances using the logarithm version of the receptor noise-limited model (Vorobyev & Osorio 1998), based on a model of hummingbird vision with the photoreceptor sensitivities and noise values of *Sephanoides sephaniodes* (Herrera et al. 2008) and the oil droplet parameters of Hart &Vorobyev (2005). For flowering phenology, we calculated the phenological overlap using the Czechanowksi index, which is more appropriate for quantitative phenological data and also produces asymetric values between a pair of plant species (Feinsinger et al. 1981). Phylogenetic distances were calculated based on the divergence times along the phylogeny branches. Lastly, we calculated the abundance difference between a pair

of plant species as the log of the ratio between the relative abundance of the pair. Here, the expectation is that the asymmetric nature of the indirect effects can be generated by differences on the abundance of the species (Carvalheiro et al. 2014). Lastly, we also used the relative abundance of the acting plant species to investigate the role of abundance on the potential for indirect effects.

To test the influence of trait similarity, relatedness and abundance on the potential for indirect interactions, we used the Müller's index as a response variable in Linear Mixed Models, assuming a Gaussian error structure. Zero-inflation was not a problem, since only 6.3% of the pairs of plant species exhibited no pollinator-sharing (224 out of 3250 combinations) in our dataset. Floral traits, phylogenetic and abundance distances, phenological overlap and relative abundance of the acting plant were used as fixed variables. We checked multicolinearity between the fixed factors using a VIF test, assuming $VIF > 3$ as correlated variables (Zuur et al. 2009). Only anther and stigma height were correlated ($VIF > 11$). We chose to remove stigma height, because many of the flowers included in the study exhibit approach herkogamy (*sensu* Lloyd & Webb 1986). In this sense, when a hummingbird visit a flower, the stigma touches more regions of the pollinator body when compared to the anther. Then, anther height gives a more specific measurement of pollen placement and transfer on the hummingbird body. We accounted for the local species composition dependency by using the acting plant species identity and the communities as random variables. We tested models with all possible combinations between the fixed variables and a model with the response variable alone with the random effects ("Null model"). Best models were selected based on ΔAIC values, considering models with ΔAIC of 0 to 2 as equivalents (Burnham & Anderson 2002). For all models, we rescaled phylogenetic distances to meet model

assumptions. Then, we plotted the partial residuals of each significative fixed effect to investigate the strength and directionality of each variable.

Results

We evaluated 3520 pairs of co-occurring plant species pollinated by hummingbirds (650 pairs in ITA; 2162 in SVG; 552 in FAZ and 156 in FAR). From these, 93.6% pairs exhibited some degree of pollinator sharing (Müller's index values from $1x10^{-5}$ to 0.35, Fig. 1). Floral traits and abundance played an important role explaining the degree of potential indirect effects, since all the best selected models included corolla length, anther height, phylogenetic distance and the abundance of the acting plant (Table 1). As expected, species pairs with similar corolla length or anther height had a higher degree of pollinator sharing, leading to a higher potential of indirect effects of the acting plant species (Fig. 1, Fig. 2A-B). Although phylogeny was included in the best model, we found a weak effect of phylogenetic distance on the potential for indirect effects (Fig. 2C). Finally, contrary to our expectations, species abundance influenced indirect interactions among plants, as more abundant acting plant species also exhibited higher potential for indirect effects (Fig. 2D). Flower colour similarity, phenological overlap and abundance difference among the species pair had a minor role in explaining the degree of pollinator-sharing.

Discussion

Here we showed that several mechanisms affect how plant species share their hummingbird pollinators. Overall, our results showed that flower trait similarity

including corolla length and anther height, influence the potential for indirect effects among hummingbird-pollinated plant species. Moreover, abundant species also had a higher potential to affect others indirectly. Nevertheless, the strength of these effects was variable and some traits (flower colour) and factors (phylogenetic relatedness and flowering phenology overlap) did not have an influence on the degree of pollinator sharing. Below, we discuss each mechanism in detail.

As expected, our results reinforce that nectar accessibility is an important trait determining resource-sharing between hummingbirds by phenotypic matching patterns based on corolla length and bill size (Maglianesi et al. 2004, Maruyama et al. 2014, Vizentin-Bugoni et al. 2014). In this sense, short-billed hummingbirds can only access legitimately flowers with short-corollas, leaving long-corolla flowers to long-billed hummingbirds and generating resource partition through floral barriers (Rodríguéz-Gironés & Santamaría 2007). Our results for this phenotypic-specialized pollination system contrast with the results reported for insect-pollinated networks, on which corolla length similarity plays a minor role on the potential for indirect interactions (Carvalheiro et al. 2014). Insect-pollinated plants often exhibit other traits as floral barriers such as colour (Lunau et al. 2011, Bergamo et al. 2015), nectar splitting (how nectar is distributed among floral units, Carvalheiro et al. 2014) and/or flower orientation (Campbell et al. 2015). Therefore, corolla length similarity arises as an important mechanism that differentiates how pollinator sharing occurs among hummingbird-pollinated plant species in comparison with insect pollination.

Pollen placement on hummingbird's bodies measured by anther height also had an important role in determining the potential for indirect effects. This can be an outcome of the costs of pollen loss, because there are sites in hummingbird's body where pollen delivery is higher (e.g. the forehead, Rocca & Sazima 2013). Nevertheless,

a study in the Atlantic rainforest reported hummingbirds carrying heterospecific pollen mixtures on certain body parts like the forehead or the base of the upper bill (Fonseca et al. *in review*). Consequently, these hummingbird-pollinated plant species with similar anther height were also found to be in competitive interactions via heterospecific pollen deposition (Fonseca et al. *in review*). Our results reinforce that species sharing traits related to pollen movement and the same hummingbird pollinators engage in indirect interactions, and possibly interactions of antagonistic nature. Moreover, if competitive interactions mediated by pollen placement are important, it can have consequences for the assembly of these plant communities (Aizen & Rovere 2010, Araújo et al. 2013, Chapter 1).

Although kept in the best model, phylogenetic relatedness was a poor predictor of the potential for indirect effects, with only a weak trend of closely related species to be more likely to share hummingbird pollinators. We attribute this weak effect to two contrasting processes with likely opposite results: 1) in hummingbird-pollinated plant communities, sympatric speciation do not necessarily follow divergence of floral traits making closely related species similar in its pollination niches (niche conservatism, Perret et al. 2007, Serrano-Serrano et al. 2015). On the other hand, 2) convergent evolution is also an important process shaping flower traits in several communities of hummingbird-pollinated plant species (Ferreira et al. 2015, Wolowski et al. *submitted*) since this pollination system arised from pollinator shifts in several unrelated plant lineages, with similar directionality of its flower trait evolution (Fleming & Muchhala 2008). We suggest that both processes act together, making phylogenetic relatedness a good proxy for potential indirect effects only for specific lineages where hummingbirds acted as drivers of plant speciation (e.g. *Sinningiae* clade, Perret et al. 2007). Our results contrast with what was reported for insect-pollinated plants, specially with bee

pollination, that exhibited a strong phylogenetic signal (Carvalheiro et al. 2014). Thus, for specialized system, like hummingbird pollination, evolution affects plant resource use in a convergent way, while bees seem to include more closely related species in a community in their diet. The weak effect of phylogeny has an important implication regarding the use of phyogeny as a proxy of floral traits or pollination niche of the plants and suggests that this procedure may not be applied to communities composed by several lineages of hummingbird-pollinated plant species.

Abundance was important in determining the potential for indirect interactions among plants, although it was already shown to be less important for the interaction of plants and hummingbirds (Maruyama et al. 2014, Vizentin-Bugoni et al. 2014). We found that most abundant plant species in the communities, such as trees that flowers massively (e.g. *Erythrina speciosa*, *Spirotheca rivieri*) or species that exhibit year-round flowering (e.g. *Fuchsia regia*) had higher potential to affect other plants. The great number of flowers and extended flowering make these plants interact with many different hummingbird species in their communities (Canela 2006, Vizentin-Bugoni et al. 2014) and there seem to be a threshold on how abundant a plant species has to be to promote stronger effects. We did not found an effect for the differences in abundance between species pairs, showing that flower-abundant acting species can have a strong effect regardless the abundance of the receiving species. In fact only most abundant plant species exhibit disproportional higher effects.

Plant species with overlapped flowering phenology did not have a higher potential for indirect effects. Again, this was also unexpected based on the phenotypic matching patterns structuring plant-hummingbird networks (Maruyama et al. 2014, Vizentin-Bugoni et al. 2014). Instead, our results show that plants share hummingbird pollinators in a similar way independent of how its flowering overlaps. This may

indicate that indirect effects are distributed along the year and could vary its strength and direction depending on the different hummingbird-pollinated plant species in bloom. Accordingly, the phenological context was recently shown to influence plant-animal mutualisms as the variation observed between competition and facilitation among plants sharing bird seed-dispersers (Albrecht et al. 2015). Moreover, two hummingbird-pollinated plant species can indirect interact when its flowering overlap (via density-dependent mechanisms, e.g. Feisinger & Tiebout 1991) but also when there is sequential flowering (via pollinator support, e.g. Waser & Real 1979). Species with similar flower colour also did not share more hummingbird pollinators. Hummingbirds lack colour preferences, which has been shown in laboratory (Lunau et al. 2011) and in field experiments (Delph & Lively 1989) as well as under natural conditions (Bergamo et al. 2015). Our results suggest that petal colour is a less important cue for hummingbird foraging decisions at the community scale. Moreover, hummingbird-pollinated flower colours are more clustered than divergent in some communities, indicating that colour is more constrained by other factors such as habitat irradiance (Altshuler 2003), resource partition with bees (Rodríguez-Gironés & Santamaría 2004, Lunau et al. 2011, Bergamo et al. 2015) or higher attractiveness of the whole community (de Jager et al. 2011, Chapter 1). For instance, some hummingbird-pollinated plants also exhibit other attractive structures (e.g. floral bracts), but it remains to be tested how multicolored patterns could influence pollinator-sharing.

Most of the previous studies on pollinator sharing among plants focused on larger and less specialized insect-pollinated networks. Here we find that morphological barriers are more important in determining hummingbird sharing, while colour and resource production were more important for insect-pollinated species (Carvalheiro et al. 2014). Plant-hummingbird interactions are less constrained by the amount of signals

in a community or how nectar is produced at the individual plant level (Maruyama et al. 2014), since hummingbirds quickly associate colour with the amount of resources (Healy & Hurly 2001), and can forage for long distances (Sazima et al. 1995). Although we did not include nectar in our analyses, a next step would be to evaluate the influence of other nectar traits on pollinator sharing. We propose that rather than nectar production of an individual flower or of the total plant individual (Maruyama et al. 2014), the way that nectar is splitted among flowers would give a better relationship, since many hermit-pollinated flowers produce few flowers with large amounts of nectar, while territorial hummingbirds forage on plants that produce many flowers with variable nectar production (Buzato et al. 2000).

In sum, this study provides insights on how plants share its hummingbird pollinators and potentially affect each other indirectly. Species with similar nectar accessibility and with similar pollen placement are more likely to share hummingbird pollinators and engage in indirect interactions. Moreover, contrasting with what was reported for direct interaction with hummingbirds (Maglianesi et al. 2014, Maruyama et al. 2014, Vizentin-Bugoni et al. 2014), we showed that extremely abundant flowering plants can have higher impact on its co-flowering partners. Since many hummingbird-pollinated plant species are pollen limited (Wolowski et al. 2013), plant-plant interactions mediated by pollinators can have drastic consequences on fitness and impact plant populations (Sargent & Ackerly 2008). Finally, as many plant-hummingbird networks show similar structuring properties (Maglianesi et al. 2014, Maruyama et al. 2014, Vizentin-Bugoni et al. 2014), our findings should also extend to other plant-hummingbird networks throughout the Neotropics.

Acknowledgments

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Table 1.Model parameters for the potential indirect effects among hummingbird-pollinated plant species from the Atlantic forest. Fixed effects: phylogenetic (P); corolla length (CL); anther height (AH); colour (C) pairwise distance; phenological overlap (PO); acting plant species abundance (A); abundance difference between acting and target plant species (Ad). All models contain the random effects (acting plant species identity and community evaluated). For the best model, estimates of the factors are given in parenthesis. d.f. = degrees of freedom. Explained deviance = proportional difference between the deviance of the models and of a model including only the intercept and the random effects. ΔAIC = Akaike Information Criteria value after selection including models with all possible combinations among fixed effects.

Model	d.f.	Explained deviance	ΔAIC
P(-0.01)+CL(-0.03)+AH(-0.02)+A(0.01)	8	64.34%	0.0
P+CL+AH+A+Ad	9	64.44%	1.29
P+CL+AH+A+C	9	64.34%	1.90
P+CL+AH+A+PO	9	64.34%	1.98
Full	12	64.35%	6.93
Null	4	57.05%	174.14

Figure legend

Figure 1. Plants sharing hummingbird-pollinators at the Atlantic rainforest. A. *Aechmea disticantha* with short effective corolla length being pollinated by the short-billed hummingbird *Amazilia fimbriata*. B. *Centropogon cornutus* with long effective corolla length being pollinated by the long-billed hummingbird *Ramphodon naevius*. Photographs: I. Sazima and M. Sazima.

Figure 2.

Effect of each factor included in the best model on the influence of the acting plant on another species through shared hummingbird pollinators. Each dot represents the partial residuals (residuals after removing the variation explained by the other variables in the model) of the Müller's index of a plant species pair. The red line represents the regression line.

Figure 1.
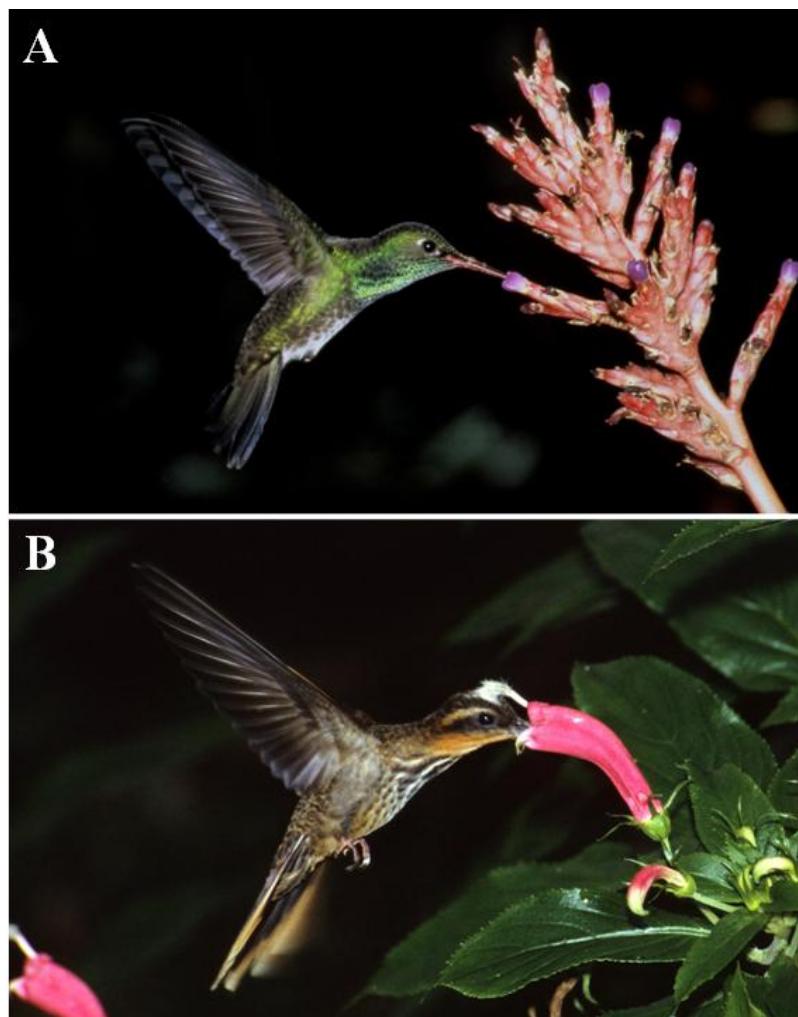
Figure 2.
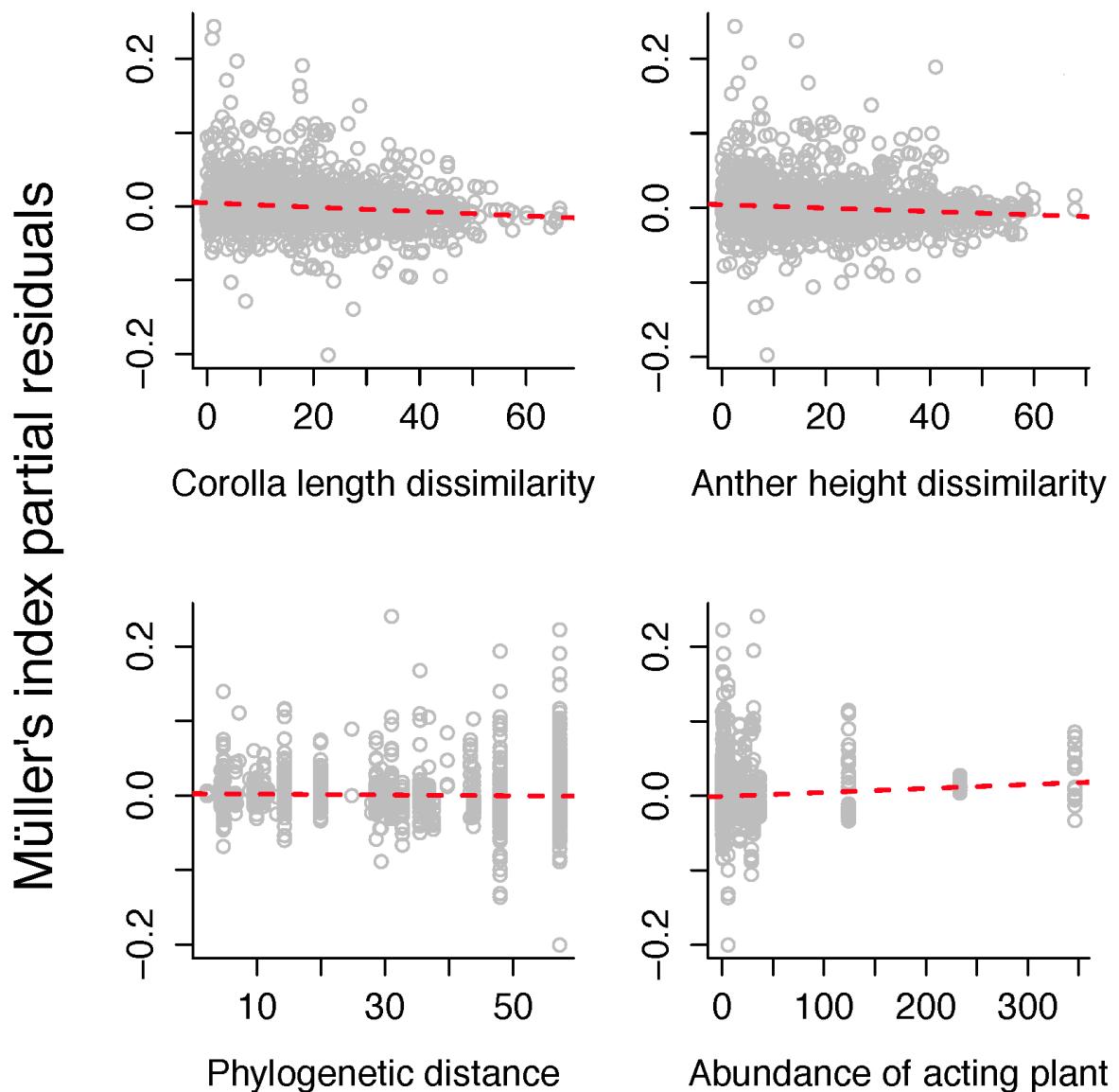
Supplementary material

Table S1. Species colour and morphological traits of hummingbird-pollinated plants of the Atlantic forest, Southestern Brazil. All data were collected in this study, except *Nematanthus fornix*, obtained from Canela 2006 (PhD Thesis). For colour, values indicate the number of samples. For the morphological traits, values on mean ± standard-deviation (number of samples).

Family *Species*	Colour	Corolla length (mm)	Anther height (mm)	Stigma height (mm)	Community
Acanthaceae					
Aphelandra colorata (Vell.) Wassh.	5	39.37 ± 0.95 (4)	52.99 ± 2.08 (4)	52.28 ± 1.17 (4)	SVG
A. longiflora (Lindl.) Profice	5	43.23 ± 2.58 (4)	40.23 ± 2.06 (4)	40.71 ± 2.11 (4)	SVG
Justicia carnea Lindl.	6	36.19 ± 0.75 (6)	59.50 ± 1.54 (6)	61.80 ± 1.79 (6)	FAR
J. sebastianopolitana Profice	5	29.49 ± 1.01 (4)	38.94 ± 0.34 (4)	39.49 ± 0.57 (4)	ITA
J. parabolica (Nees) Profice	9	31.53 ± 1.28 (7)	39.74 ± 2.48 (7)	41.19 ± 1.21 (7)	SVG
Justicia sp	7	15.92 ± 1.37 (7)	20.97 ± 0.75 (7)	21.84 ± 1.09 (7)	SVG

Mendoncia velloziana Mart.	1	29.81 ± 0.36 (2)	24.98 ± 3.13 (2)	28.15 ± 4.07 (2)	ITA, SVG
Odontonema barlerioides (Nees) Kuntze	7	44.72 ± 3.11 (7)	43.60 ± 3.29 (7)	43.06 ± 3.29 (7)	ITA
Staurogyne itatiaiae (Wawra) Leonard	8	17.12 ± 1.69 (6)	14.58 ± 1.14 (6)	15.79 ± 0.66 (6)	ITA
Alstroemeriaceae					
Alstroemeria inodora Herb.	5	25.69 ± 4.50 (8)	36.86 ± 6.52 (6)	41.2 ± 3.17 (5)	SVG
Bomarea edulis (Tussac) Herb.	6	22.79 ± 3.17 (6)	24.45 ± 2.29 (6)	22.13 ± 3.36 (6)	FAZ
Asteraceae					
Mutisia speciosa Aiton ex Hook.	4	23.81 ± 2.74 (6)	38.79 ± 4.69 (6)	38.79 ± 4.69 (6)	FAZ, SVG
Bignoniaceae					
Pyrostegia venusta (Kew Gawl.) Miers	4	34.52 ± 2.99 (4)	43.75 ± 5.07 (4)	46.14 ± 4.64 (4)	ITA, SVG
Bromeliaceae					
Aechmea coelestis (K.Koch) E.Morren	5	28.72 ± 1.88 (5)	26.60 ± 0.93 (5)	23.45 ± 0.51 (6)	FAZ

Species	N	Col 1	Col 2	Col 3	Sites
A. disticantha Lem.	9	15.28 ± 1.66 (11)	13.41 ± 1.62 (11)	12.54 ± 2.04 (11)	FAZ, SVG
A. gamosepala Wittm.	1	19.97 (1)	18.62 (1)	18.10 (1)	SVG
A. nudicaulis (L.) Griseb.	5	13.56 ± 0.94 (6)	12.28 ± 0.70 (6)	10.26 ± 1.36 (6)	ITA, FAZ, SVG
A. vanhoutteana (Van Houtte) Mez	4	9.1 ± 1.02 (4)	19.6 ± 0.86 (4)	18.9 ± 1.42 (4)	ITA, SVG
Billbergia amoena (Lodd.) Lindl.	6	38,55 ± 2,08 (5)	49,31 ± 1,02 (5)	51,79 ± 0,44 (5)	SVG
B. distachia (Vell.) Mez	9	37.92 ± 3.41 (8)	50.41 ± 2.99 (8)	54.87 ± 3.48 (8)	ITA
B. vittata Brongn. ex Morel	1	26.97 (1)	43.42 (1)	46.77 (1)	ITA
Bromelia antiacantha Bertol.	2	18.61 ± 1.35 (2)	15.18 ± 1.12 (2)	12.17 ± 1.00 (2)	FAZ
Canistropsis seidelii (L.B.Sm. & Reitz) Leme	6	24.86 ± 1.87 (6)	21.20 ± 1.73 (6)	21.20 ± 1.73 (6)	FAR, FAZ
Canistrum perplexum L.B.Sm.	6	24.77 ± 2.13 (7)	23.03 ± 1.66 (7)	21.17 ± 1.49 (7)	SVG
Neoregelia johannis Carrière (L.B.Sm.)	5	33.60 ± 0.97 (5)	32.02 ± 2.08 (5)	30.89 ± 2.13 (5)	FAR, FAZ

Nidularium angustifolium Ule	5	38.59 ± 1.76 (5)	35.73 ± 1.76 (5)	34.07 ± 1.55 (5)	FAR, FAZ
N. innocentii Lem.	25	51.21 ± 6.05 (23)	47.25 ± 6.38 (23)	47.66 ± 5.95 (23)	FAR, FAZ, SVG
N. itatiaiae L.B.Sm.	2	45.42 ± 8.40 (2)	39.91 ± 7.03 (2)	39.37 ± 7.80 (2)	ITA
N. longiflorum Ule	8	63.36 ± 5.17 (6)	59.92 ± 5.27 (6)	62.23 ± 5.41 (6)	SVG
N. procerum Lindm.	11	41.73 ± 2.17 (7)	38.45 ± 1.16 (7)	37.43 ± 0.58 (7)	SVG
N. rutilans E.Morren	3	52.73 ± 2.43 (3)	47.94 ± 4.20 (3)	47.94 ± 4.20 (3)	SVG
Pitcairnia flammea Lindl.	9	36.56 ± 2.51 (9)	58.72 ± 2.38 (9)	63.47 ± 2.46 (9)	ITA
Quesnelia augusto-coburgii Wawra	5	48.70 ± 1.13 (5)	47.43 ± 1.06 (5)	47.43 ± 1.06 (5)	ITA
Tillandsia geminiflora Brongn.	9	17.61 ± 1.48 (9)	13.93 ± 2.29 (9)	14.70 ± 2.29 (9)	ITA, FAZ, SVG
T. stricta Sol.	5	17.60 ± 2.42 (5)	13.79 ± 2.49 (5)	14.26 ± 2.24 (5)	ITA, SVG
T. dura Baker	1	20.01 (1)	18.99 (1)	19.61 (1)	SVG

Vriesea carinata Wawra	12	42.26 ± 3.28 (7)	54.41 ± 5.23 (7)	57.64 ± 5.11 (7)	ITA, SVG
V. ensiformis (Vell.) Beer	3	50.39 ± 2.15 (2)	55.67 ± 1.15 (2)	60.84 ± 0.08 (2)	FAR, FAZ
V. erythrodactylon E.Morren ex Mex	3	41.17 ± 0.56 (3)	49.11 ± 2.28 (3)	51.73 ± 2.37 (3)	SVG
V. gradata (Baker) Mez	5	44.43 ± 3.23 (5)	56.28 ± 4.21 (5)	58.97± 3.57 (5)	ITA
V. incurvata Gaudich.	9	48.59 ± 3.84 (10)	56.96 ± 3.59 (10)	60.04 ± 4.61 (10)	SVG
V. inflata (Wawra) Wawra	4	47.01 ± 2.11 (6)	54.60 ± 3.77 (6)	57.37 ± 2.49 (6)	SVG
V. longicaulis (Baker) Mez	2	35.63 ± 1.30 (2)	40.39 ± 2.38 (2)	42.78 ± 1.90 (2)	ITA
V. procera (Mart. ex Schult. & Schult.f.) Wittm.	2	33.97 ± 0.93 (2)	31.67 ± 0.62 (2)	29.10 ± 1.00 (2)	FAZ
V. rodigasiana E.Morren	5	26.91 ± 1.37 (5)	32.79 ± 2.32 (5)	37.13 ± 2.47 (5)	FAR
V. simplex (Vell.)	6	51.56 ± 3.68 (5)	60.21 ± 5.90 (5)	62.45 ± 6.74 (5)	SVG
Vriesea sp	5	44.08 ±	49.91 ±	52.27 ±	SVG

		0.64 (2)	0.17 (2)	0.76 (2)	
Campanulaceae					
Centropogon cornutus (L.) Druce	7	46.63 ± 2.79 (7)	61.58 ± 4.00 (7)	65.52 ± 5.34 (7)	FAZ, SVG
Siphocampylus convolvulaceus (Cham.) G.Don	6	43.39 ± 2.64 (6)	52.81 ± 4.46 (6)	55.05 ± 5.03 (6)	SVG
S. longipedunculatus Pohl	7	42.01 ± 3.26 (10)	48.57 ± 3.67 (10)	50.18 ± 3.24 (10)	ITA, SVG
S. lauroanus Handro & M.Kuhlm.	6	42.03± 5.47 (6)	47.46 ± 3.80 (6)	49.72 ± 4.59 (6)	SVG
Cannaceae					
Canna paniculata Ruiz & Pav.	12	56.15 ± 8.73 (12)	69.59 ± 9.26 (12)	76.62 ± 10.14(12)	SVG
Fabaceae					
Dahlstedtia pinnata (Benth.) Malme	5	41.45 ± 1.53 (5)	37.48 ± 0.63 (5)	38.82 ± 1.49 (5)	FAR, FAZ
Erythrina speciosa Andrews	10	51.15 ± 3.67 (10)	44.04 ± 3.63 (10)	37.27 ± 4.29 (10)	FAZ, SVG
Inga subnuda Salzm. ex	2	12.92 ±	48.36 ±	44.17 ±	FAZ

Benth.		2.55 (2)	3.80 (2)	1.69 (2)	
Gentianaceae					
Macrocarpaea rubra Malme	5	28.50 ± 2.83 (5)	27.47 ± 3.57 (2)	23.43 ± 2.53 (5)	SVG
Gesneriaceae					
Besleria longimucronata Hoehne	12	23.57 ± 2.89 (11)	18.38 ± 2.41 (11)	16.79 ± 1.44 (11)	FAR, SVG
Nematanthus crassifolius (Schott) Wiehler	8	50.31 ± 4.87 (7)	48.84 ± 2.93 (4)	49.39 ± 2.77 (5)	ITA
N. fissus (Vell.) L.E.Skog	9	27.51 ± 3.35 (9)	22.19 ± 5.23 (5)	23.34 ± 3.84 (5)	FAR, FAZ
N. fluminensis (Vell.) Fritsch	13	53.30 ± 3.90 (14)	49.16 ± 5.02 (7)	51.62 ± 5.68 (11)	FAR, FAZ, SVG
N. fornix (Vell.) Chautems	5	26.50 ± 1.80 (35)	22.70 ± 0.20 (20)	22.90 ± 0.30 (16)	ITA
N. fritschii Hoehne	10	45.34 ± 4.34 (6)	42.82 ± 2.41 (4)	36.14 ± 0.30 (2)	SVG
N. gregarius D.L.Denham	5	24.85 ± 1.36 (5)	18.57 ± 3.48 (4)	19.78 ± 1.77 (4)	SVG
N. lanceolatus (Poir.)	4	26.10 ±	22.38 ±	23.63 (1)	ITA

Chautems		1.58 (2)	1.75 (2)	
Nematanthus sp	10	50.52 ± 1.77 (6)	47.04 ± 4.14 (5)	49.65 ± 3.21 (6)	SVG
N. sericeus (Hanst.) Chautems	5	36.45 ± 2.18 (5)	30.66 ± 1.84 (5)	31.73 ± 5.45 (3)	SVG
Sinningia cooperi (Paxton) Wiehler	6	38.92 ± 1.78 (9)	59.68 ± 2.77 (5)	65.94 ± 2.45 (4)	ITA, SVG
S. gigantifolia Chautems	1	37.76 (1)	32.22 (1)	37.60 (1)	ITA
S. glazioviana (Fritsch) Chautems	10	42.50 ± 1.64 (7)	47.75 ± 3.32 (7)	51.80 ± 1.99 (7)	SVG
Heliconiaceae					
Heliconia angusta Vell.	7	30.97 ± 1.02 (3)	53.36 ± 1.71 (3)	46.90 ± 0.81 (3)	FAR, FAZ
H. farinosa Raddi	6	36.74 ± 5.84 (6)	49.85 ± 3.24 (6)	46.12 ± 1.58 (6)	FAR
Lamiaceae					
Salvia sellowiana Benth.	9	40.86 ± 9.29 (9)	50.11 ± 5.80 (9)	55.05 ± 5.13 (9)	ITA, SVG
Loranthaceae					
Psittacanthus dichroos	5	28.69 ±	44.47 ±	47.88 ±	FAR, SVG

(Mart.) Mart.		1.24 (5)	1.17 (5)	0.76 (5)	
Malvaceae					
Callianthe bedfordiana (Hook.) Donnel	7	27.03 ± 4.16 (5)	24.82 ± 1.35 (5)	25.96 ± 2.88 (5)	ITA
C. rufinerva (A. St.Hil.) Donnel	9	16.74 ± 3.70 (6)	13.72 ± 4.08 (6)	13.85 ± 5.11 (6)	SVG
Eriotheca gracilipes (K.Schum.) A.Robyns	2	0 (1)	15.76 (1)	15.76 (1)	FAZ
Spirotheca rivieri (Decne.) Ulbr.	1	5.91 (1)	28.12 (1)	32.32 (1)	SVG
Marantaceae					
Stromanthe thalia (Vell.) J.M.A.Braga	4	7.42 ± 0.74 (3)	6.41 ± 0.66 (3)	6.73 ± 0.96 (3)	ITA
Marcgraviaceae					
Schwartzia brasiliensis (Choisy) Bedell ex Gir.-Cañas	5	7.28 ± 1.08 (5)	7.28 ± 1.08 (5)	7.28 ± 1.08 (5)	FAZ
Onagraceae					
Fuchsia regia (Vell.) Munz	5	25.24 ±	52.77 ±	51.42 ±	ITA, SVG

		3.08 (10)	4.74 (4)	5.88 (6)	
Orchidaceae					
Elleanthus brasiliensis (Lindl.) Rchb.f.	3	8.12 ± 0.78 (3)	6.45 ± 0.97 (3)	5.41 ± 0.87 (3)	ITA
Orobanchaceae					
Velloziella dracocephaloides (Vell.) Baill.	5	73.72 ± 2.64 (5)	52.11 ± 1.45 (5)	63.64 ± 1.65 (5)	ITA
Rubiaceae					
Manettia cordifolia Mart.	5	49.17 ± 3.67 (5)	48.10 ± 3.89 (5)	45.50 ± 1.65 (5)	SVG
M. mitis (Vell.) K.Schum.	5	25.41 ± 0.73 (5)	31.29 ± 1.98 (5)	34.34 ± 2.33 (5)	ITA
Psychotria nuda (Cham. & Schltdl.) Wawra (brev/long)	8	19.88 ± 1.75 (10)	18.34 ± 0.43 (5) / 16.29 ± 1.71 (5)	12.42 ± 2.30 (5) / 19.53 ± 1.91 (5)	FAR, FAZ
Sabicea grisea Cham. & Schltdl.	2	15.7 ± 0.61 (2)	12.64 ± 0.13 (2)	14.38 ± 0.49 (2)	FAZ

CONSIDERAÇÕES FINAIS

A abordagem funcional e filogenética tem sido utilizada para responder diversas questões em ecologia: de organização de comunidades a funções ecossistêmicas (Gerhold et al. 2015). É crescente o uso desta abordagem para entender como os polinizadores podem estruturar as comunidades de plantas (Sargent & Ackerly 2008). No primeiro capítulo, verificamos estrutura filogenética aleatória e predomínio de estrutura funcional e temporal agregadas para comunidades de plantas polinizadas por beija-flores. Ao avaliar uma escala espacial maior, um estudo prévio em comunidades de plantas polinizadas por beija-flores encontrou estrutura filogenética dispersa e agregada e estrutura funcional aleatória (Wolowski et al. *em revisão*). Desta maneira, nossos resultados demonstram que processos relacionados a história evolutiva destas plantas deixam de atuar na escala avaliada, ao passo que processos relacionados ao nicho das espécies aumentam em importância. Este estudo ilustra como abordagens englobando diferentes escalas e atributos relevantes na interação planta-polinizador, associados a conhecimentos de história natural da interação planta-polinizador, são necessários para um entendimento mais completo da influência da polinização na estruturação das comunidades de plantas.

Plantas que compartilham beija-flores como polinizadores podem interagir indiretamente entre si, da competição à facilitação (Rathcke 1983). Porém, estudos que investigaram que mecanismos levam plantas a compartilhar polinizadores foram restritos a espécies polinizadas por insetos (Carvalheiro et al. 2014). Além disso, plantas formam redes de interações mais especializadas com beija-flores que com outros grupos de polinizadores em comunidades (Danieli-Silva et al. 2012). Desta maneira, também era esperado que processos relacionados aos atributos das espécies de plantas fossem importantes para determinar o potencial para efeitos indiretos. No segundo capítulo

verificamos que, de acordo com as restrições fenotípicas que estruturam as interações entre plantas e beija-flores, plantas com atributos florais semelhantes possuem maior potencial para efeitos indiretos (Maglianesi et al. 2014, Maruyama et al. 2014, Vizentin-Bugoni et al. 2014). Contudo, mesmo que abundância não estruture as interações diretas entre plantas e beija-flores, verificamos que espécies de plantas mais abundantes têm maior potencial para efeitos indiretos nas comunidades. Desta maneira, este estudo demonstra que mesmo propriedades estruturadoras não tão importantes para a interação entre plantas e beija-flores podem ser relevantes quando se analisa os efeitos indiretos entre plantas em comunidades.

Padrões em comunidades são contingentes a história evolutiva e atributos das espécies (Vellend 2010). Além disso, os processos que geram estes padrões atuam em diferentes escalas temporais e espaciais (Chave 2013). Portanto, um dos atuais desafios em ecologia é entender como e em quais escalas a história evolutiva e atributos das espécies moldam as comunidades observadas atualmente. Em conjunto, os resultados deste estudo apontam que interações indiretas entre plantas polinizadas por beija-flores são influenciadas por suas histórias evolutivas e atributos, e de forma semelhante, estes processos podem passar para o nível da comunidade e influenciar sua estruturação. A convergência evolutiva e a similaridade entre os atributos reprodutivos das espécies polinizadas por beija-flores levam a um balanço entre facilitação e competição. Este balanço, por sua vez, produz diferentes padrões estruturais nas comunidades dependendo da escala de observação. Dessa forma, associar conhecimento de história natural, evolução e atributos das espécies se mostra como uma abordagem promissora para compreender os mecanismos de coexistência das espécies nas comunidades.

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APÊNDICES

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Declaração

As cópias de artigos de minha autoria ou de minha co-autoria, já publicados ou submetidos para publicação em revistas científicas ou anais de congressos sujeitos a arbitragem, que constam da minha Dissertação/Tese de Mestrado/Doutorado, intitulada **Estruturação de comunidades e potencial para efeitos indiretos de plantas polinizadas por beija-flores na Floresta Atlântica**, não infringem os dispositivos da Lei n.° 9.610/98, nem o direito autoral de qualquer editora.

Campinas, 12 de janeiro de 2016

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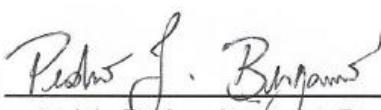
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Em observância ao **§5º do Artigo 1º da Informação CCPG-UNICAMP/001/15**, referente a Bioética e Biossegurança, declaro que o conteúdo de minha Dissertação de Mestrado, intitulada "*Estruturação de comunidades e potencial para efeitos indiretos de plantas polinizadas por beija-flores na Floresta Atlântica*", desenvolvida no Programa de Pós-Graduação em Ecologia do Instituto de Biologia da Unicamp, não versa sobre pesquisa envolvendo seres humanos, animais ou temas afetos a Biossegurança.

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