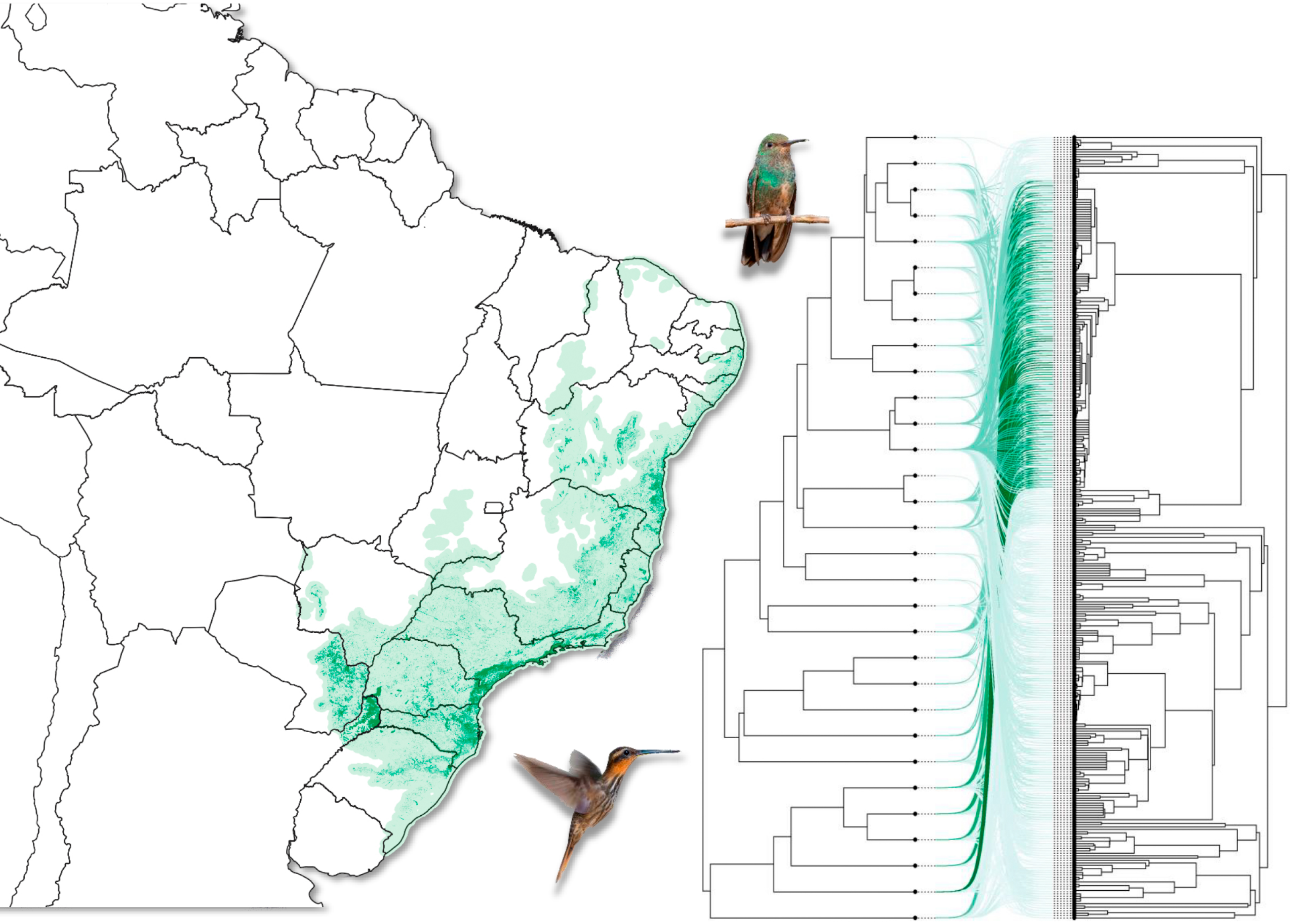
Joice Iamara-Nogueira

Organização das comunidades de flores e polinizadores vertebrados na Mata Atlântica brasileira

Organization of communities of plants and vertebrate pollinators in Brazilian Atlantic Rainforest



São Paulo

2020

Joice Iamara-Nogueira

Organização das comunidades de plantas e polinizadores vertebrados na Mata Atlântica brasileira

Organization of communities of plants and vertebrate pollinators in Brazilian Atlantic Rainforest

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Comissão Julgadora

Prof(a). Dr(a).

Prof(a). Dr(a).

Prof(a). Dr(a).

Orientadora

DEDICATÓRIA

Para minha mãe, Elenita e para meu pai, José

Por nunca duvidarem e sempre me apoiar

EPÍGRAFE

Mittler zwischen Hirn und Händen muss das Herz sein

O mediador entre o cérebro e as mãos deve ser o coração

Maria

(Thea von Harbou. **Metropolis**. São Paulo: Aleph, 2019)

AGRADECIMENTOS

Em 1927, Thea von Habou lançou o livro *Metropolis*, lançado em filme no mesmo ano por seu então marido Fritz Lang. O filme foi a produção cinematográfica europeia mais cara até então e é considerada um dos grandes expoentes do expressionismo alemão. No entanto, Fritz Lang não gostou de ter gravado o filme pois, em suas palavras, *"você não pode fazer um filme com consciência social no qual você diz que o mediador entre a mão e o cérebro é o coração. Digo, isso é um conto de fadas, sem dúvida. Mas eu estava muito interessado nas máquinas..."*. Lang pode estar certo sobre fazer filmes, mas sobre fazer essa tese, eu tenho que concordar com a Sra. Von Habou: a transformação das ideias e informações contidas no meu cérebro até este material feito pelas minhas mãos só foi possível por intermédio do coração. E por coração, eu me refiro às pessoas que por motivos diversos estiveram presente e colaboraram com a realização desta tese. Esta sessão é dedicada a elas.

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ÍNDICE

RESUMO

As interações entre espécies são extremamente importantes para a estrutura da comunidade porque elas influenciam o padrão de coexistência e a ocorrência de clados em determinadas áreas. Nos Neotrópicos, plantas e polinizadores vertebrados representam exemplos de história natural e interação biótica e são usados para interpretar resultados ecológicos e evolutivos complexos em florestas tropicais. O primeiro capítulo desta tese trata da organização e construção de um banco de dados para a interação entre flores e vertebrados polinizadores na Mata Atlântica da América do Sul. Apesar deste Bioma estar distribuído até a Argentina e Paraguai, não encontramos registros desta interação nestes paises. Verificamos também que há um forte viés nas amostragens, sendo que áreas de floresta localizadas no Rio de Janeiro e São Paulo contêm a maior parte dos registros. Observamos que, no geral, as características de flores – grande variação na tamanho da corola, baixa produção de néctar e baixo número de visitantes – e vertebrados – baixo número de plantas visitadas – favorecem a especialização neste sistema de polinização. Para beija-flores, as plantas visitadas por eremitas recebem visitas de menos espécies do que não-eremitas. As características de plantas e vertebrados envolvidos na interação não apresentaram influência de fatores ambientais, indicando que fatores bióticos pode ser mais importante para estruturar as comunidades. No segundo capítulo, baseado nas diferenças na distribuição das interações entre os eremitas e não eremitas nos questionamos se assimetrias nas interações entre as duas guildas poderiam ser percebidas na estrutura co-filogenética das comunidades. Esperávamos que a origem precoce dos eremitas e sua interação fiel a certos grupos de plantas pudessem gerar forças de interação mais forte do polinizador para a planta (assimetrias maiores), sendo sua marca histórica mais evidente que nas interações entre os não eremitas e suas flores. Nós amostramos as interações entre flores e beija-flores em uma metaweb composta por 327 espécies nativas de plantas, 31 espécies de beija-flores (26 não eremitas e cinco eremitas) e 1102 interações na Floresta Atlântica brasileira. A interação com sinal cofilogenético mais forte envolve as flores da família Bromeliaceae e os beija-flores eremitas, ao passo que para a interação entre não eremitas e flores, o sinal cofilogenético é praticamente ausente. Portanto, este estudo revela que os sinais cofilogenéticos nas redes de interação mesmo dentro do mesmo taxon pode ser distinto. Para beija-flores e flores residentes da Floresta Atlântica, os sinais de históricos de coevolução podem ser registrados somente para a interação entre eremitas. Para os não eremitas, não é possível registrar sinais históricos nas interações ecológicas contemporâneas.

Palavras-chave: Interações biológicas, mutualismo, cofilogenias, especialização, eremitas, não eremitas.

ABSTRACT

Interactions between species are extremely important for community structure because they influence the pattern of coexistence and the occurrence of clades in certain areas. In the Neotropics, plants and vertebrate pollinators represent examples of natural history and biotic interaction and are used to interpret complex ecological and evolutionary outcomes in tropical forests. The first chapter of this theses is the organization and construction of a database for interactions between flowers and pollinating vertebrates in the Atlantic Forest of South America. Although this Biome is distributed to Argentina and Paraguay, we did not find data of the interaction outside Brazil's boundaries. We also found that there is a strong bias in the sampling, with forest areas maturing in Rio de Janeiro and São Paulo determined most of the records. We observed that, in general, the characteristics of flowers – great variation in the size of the corolla, low production of nectar and low number of visitors – and vertebrates – low number of plants visited – favor the specialization in this pollination system. For hummingbirds, plants visited by hermits has fewer visitor species than plants visited by non-hermits. The characteristics of plants and vertebrates involved interaction has no influence of environmental factors, indicating that biological factors may be more important to structure as communities. In the second chapter, based on the differences in the distribution of interactions between hermits and non-hermits, we questioned whether asymmetries in the interactions between the two guilds are perceived in the co-phylogenetic structure of communities. We expected that the early origin of the hermits and their faithful interaction with certain groups of plants could generate frames of stronger interaction from the pollinator to the plant (larger asymmetries), their historical mark being more evident than in the interactions between non-hermits and their flowers. We sampled as interactions between flowers and hummingbirds on a metaweb composed of 327 native species of plants, 31 species of hummingbirds (26 non-hermits and five hermits) and 1102 interactions in the Brazilian Atlantic Forest. The interaction with a stronger co-phylogenetic signal involves flowers from the Bromeliaceae family and hermit hummingbirds, whereas for an interaction between non-hermits and flowers, the co-phylogenetic signal is practically absent. Therefore, this study reveals that cophylogenetic signals in the interaction networks even within the same taxon can be distinct. For hummingbirds and flowers resident in the Atlantic Forest, signs of historical coevolution can be recorded only for an interaction between hermits. For non-hermits, it is not possible to record historical signs in contemporary ecological interactions.

Keywords: Biological interactions, mutualism, cophylogenies, specialization, hermits, non-hermits.

INTRODUÇÃO GERAL

As diferenças na distribuição de espécies em diferentes partes do globo é um padrão que vem sendo investigado desde os primeiros naturalistas até os dias atuais (Hillebrand 2004, Pontarp et al. 2019). De acordo com o gradiente latitudinal de diversidade, há um amento no número de espécies em direção a regiões próximas aos trópicos (Hillebrand 2004). Diversas hipóteses relacionadas a limites ecológicos (como competição), taxas de diversificação, tempo de acumulação de espécies e clima foram levantadas para explicar tal padrão (Mannion et al. 2014, Pontarp et al. 2019, Rull 2020). Evidências empíricas apoiando estas hipóteses são difusas e não apresentam um consenso (Pontarp et al. 2019), fazendo com que este tema ainda seja recorrente.

O gradiente latitudinal de biodiversidade é particularmente proeminente na região Neotropical, exibindo grande diversidade tanto de plantas quanto de animais, como anfíbios, mamíferos, aves, borboletas e répteis (Rull 2020). Esta região também abriga seis dos maiores *hotspots* de biodiversidade do planeta, ou seja, regiões com excepcional taxas de diversidade e endemismo, principalmente de plantas e vertebrados e que tiveram grande perda do habitat original (Myers et al. 2000, Mittermeier et al. 2004). Nesta região, a Floresta Atlântica brasileira destaca-se por sua grande extensão geográfica e diversidade de ambientes, abrangendo várias faixas latitudinais (de 3°S a 30°S), longitudinais (de 35°W a 60°W), de elevação (do nível do mar até 2900 metros acima do nível do mar) e de climas (precipitação variando de 1000 a 4200 mm por ano)(Ribeiro et al. 2011). Além disso, a Floresta Atlântica possui uma grande variedade de fisionomias, incluindo florestas ombrófilas, florestas decíduas e semidecíduas, mangues, pântanos, restingas, campos de altitude e florestas subtropicais mistas (Florestas de Araucárias) (Peres et al. 2020).

A história evolutiva da Mata Atlântica é complexa e marcada por períodos de expansão e de contração (Ledru et al. 2005). Períodos de expansão permitiram a conexão com outros ambientes promovendo a troca de elementos da biota enquanto que os períodos de contração permitiram a ocorrência de especiação alopátrica (Ribeiro et al. 2011). Esta dinâmica evolutiva propiciou a formação de uma biota complexa com cinco centros de endemismo (Peres et al. 2020). No entanto, a partir do século XVI, o extenso crescimento da agricultura, a industrialização e o crescimento urbano promoveram a degradação da Floresta Atlântica brasileira, reduzindo sua extensão remanescente a cerca de 11.7% de sua área original (Ribeiro et al. 2009, 2011). A grande diversidade de elementos da flora e da fauna presentes na Floresta Atlântica associado à sua grande complexidade e desmatamento fazem com que esta região seja de grande interesse, não somente para fins de conservação, mas também para compreender quais fatores estão associados a distribuição e a abundância de espécies.

Dentre os diversos fatores levantados para explicar a estrutura de comunidades, interações mutualísticas podem desempenhar um papel importante neste processo (Sargent and Ackerly 2008). Fatores ambientais podem funcionar como filtros, permitindo apenas espécies com características ou fenótipos particulares de se estabelecerem em uma área, impedindo o estabelecimento ou persistência de todas as outras (Kraft et al. 2015). Assim, tais fatores determinam o padrão de coexistência de espécies pois influenciam a persistência de determinadas interações (Sargent and Ackerly 2008). Em comunidades tropicais, filtros ambientais parecem ser o processo dominante em áreas de altitude para a estrutura de comunidades de plantas polinizadas por beija-flores (Wolowski et al. 2017, Bergamo et al. 2020a). Além disso, a mudança na composição de grupos taxonômicos entre comunidades em diferentes altitudes em regiões Neotropicais é um fenômeno bem documentado na literatura (Buzato et al. 2000, Graham et al. 2009, Maglianesi et al. 2014).

Determinadas espécies de visitantes florais também podem atuar como filtros ambientais se a ausência de uma espécie de polinizador em um local prevenir o estabelecimento de uma espécie de planta (Sargent and Ackerly 2008). Em Gesneriaceae, a espécie *Sinningia allagophylla* possui três tipos florais com diferenças morfológicas (Nogueira 2013). Dentre eles, os indivíduos com flores pequenas e amarelas são restritos a porção sul da distribuição da espécie (Argentina, Uruguai e sul do Brasil, até o estado do Paraná), e essa restrição muito provavelmente é determinada pela distribuição geográfica de seu principal polinizador, a espécie de abelha *Centris tricolor* Friese 1899 (Zanella 2002, Nogueira 2013). Dessa forma, comunidades fortemente influenciadas por filtros ambientais – tanto fatores abióticos como a distribuição geográfica de polinizadores – tende a apresentar plantas com características florais similares (Sargent and Ackerly 2008).

A presença de determinadas espécies em uma área também pode influenciar o estabelecimento de outras através dos processos de facilitação e competição (Sargent and Ackerly 2008). A facilitação ocorre quando o estabelecimento de uma espécie de planta em uma área é influenciado positivamente pela presença de outras espécies que compartilham o mesmo visitante floral e que não depende diretamente de fatores abióticos (Sargent and Ackerly 2008). Este processo de atração conjunta depende da densidade de recursos florais é mais plausível de ocorrer quando a densidade de flores é baixa (Feinsinger 1987, Tur et al. 2016). Em uma comunidade depauperada na Floresta Atlântica, Bergamo e colaboradores (2020b) demonstraram que espécies com floração sincrônica e com fenótipo similar tiveram maior número de grão de pólen co-específico no estigma e maior número de grãos de pólen germinados quando comparados com o restante da comunidade. Tais resultados são indicativos de que mecanismos de facilitação organizam comunidades em determinados ambientes (Bergamo et al. 2020b). Assim como filtros ambientais, comunidades moldadas por facilitação também tendem a apresentar características florais semelhantes (Sargent and Ackerly 2008).

Em contrapartida, a competição é o processo pelo qual plantas experimentam redução no seu *fitness* devido ao compartilhamento de polinizadores (Sargent and Ackerly 2008). A redução no sucesso reprodutivo pode ocorrer pela preferência do polinizador ou pela transferência de pólen interespecífico (Waser 1983, Feinsinger and Tiebout 1991). Ao contrário dos processos anteriores, comunidades estruturadas por competição tendem a apresentar uma maior diversidade de características florais e, consequentemente, de síndromes de polinização (Sargent and Ackerly 2008). A maior variedade de tipos florais nas comunidades pode ser uma consequência de exclusão competitiva ou deslocamento de características promovido por seleção natural (Sargent and Ackerly 2008). Além disso, a seleção natural também deve favorecer a redução na sobreposição fenológica, fazendo com que espécies com baixa sincronia na fenologia tenham maior sucesso reprodutivo (Aizen and Rovere 2010). Dessa forma, a competição intraespecífica por recursos florais pode promover a partilha de recursos na comunidade e aumentar o grau de especialização dos polinizadores (Maglianesi et al. 2015).

Apesar da importância dos filtros ambientais, da facilitação e da competição, a história evolutiva das espécies não pode ser negligenciada na compreensão da estruturação das comunidades. O uso de filogenias em estudos de comunidade permite averiguar se espécies relacionadas possuem características similares e, assim, maior probabilidade de coexistirem (Webb et al. 2002). Se as características forem conservadas filogeneticamente e filtros ambientais e facilitação forem os fatores estruturando comunidades, tais comunidades serão compostas por espécies relacionadas evolutivamente (Sargent and Ackerly 2008, Wolowski et al. 2017). Porém se as características não forem conservadas, as comunidades serão compostas por espécies não relacionadas (Wolowski et al. 2017). Em contrapartida, se as características forem conservadas e a competição for o processo estruturando comunidades, é esperado que as comunidades sejam compostas por espécies não relacionadas (Sargent and Ackerly 2008, Wolowski et al. 2017).

Em interações entre plantas e visitantes florais, organismos relacionados normalmente compartilham características e tendem a interagir com espécies com fenótipos complementares – por exemplo, tamanhos de bicos e corolas similares (Rezende et al. 2007, Phillips et al. 2020). Esse agrupamento filogenético promove padrões de interações não aleatórios e aparecem como módulos em redes de interações (Olesen et al. 2007). A modularidade em redes ocorre quando um grupo de espécies interage mais fortemente do que outros grupos de espécies (Olesen et al. 2007). Tais interações podem ter sido resultado de processos coevolutivos, tanto par-a-par quanto difusos (Olesen et al. 2007, Aizen et al. 2016). A coevolução tem sido acessada pelo grau de congruência – sinal cofilogenético – entre árvores filogenéticas dos organismos: alta congruência indica que as interações são produtos que processos coevolutivos e a falta de congruência, por sua vez, indica aleatoriedade nas interações durante sua história evolutiva (Legendre et al. 2002).

Historicamente, a maioria dos estudos de cofilogenias são realizados com interações entre parasitas e hospedeiros (Demastes and Hafner 1993, Desdevises et al. 2002, Legendre et al. 2002) nos quais sinais de coevolução, ou seja, perfeita congruência, aparecem somente em grupos particulares nos quais as características biológicas dificultam ou impedem eventos de trocas de hospedeiros (Desdevises et al. 2002). Em interações difusas – como a que ocorre entre plantas e seus visitantes florais - há grande variedade de grupos taxonômicos envolvida e a perfeita congruência entre as árvores filogenéticas não pode ser esperada (Hutchinson et al. 2017). No entanto, em tais sistemas, mesmo um sinal cofilogenético fraco entre as espécies de plantas e seus visitantes fornecem evidências de que a tendências destas espécies interagirem provém de um processo de evolução conjunta (Hutchinson et al. 2017). Nestes casos, a estrutura filogenética das interações é predominantemente dada pela correspondência em grupos taxonômicos maiores (Famílias, Clados) do que espécies propriamente ditas (Aizen et al. 2016). Além disso, o sinal cofilogenético entre plantas e visitantes florais tende a ser maior em comunidades locais do que em comunidades criadas de forma aleatória (Hutchinson et al. 2017). Isso indica que a história evolutiva tem um papel importante na determinação das interações e, portanto, para a estrutura das comunidades (Hutchinson et al. 2017).

Em regiões Neotropicais e, em especial na Floresta Atlântica, diversos trabalhos apontam para a importância das interações entre plantas e animais vertebrados nectarívoros para a organização de comunidades (Feinsinger 1976, Buzato et al. 2000, Fleming and Muchhala 2008, Bergamo et al. 2017, citando alguns). Os vertebrados que mais contribuem para a reprodução de plantas nos Neotrópicos são aves, em especial os pertencentes à família Trochilidae e morcegos nectarívoros da família Phyllostomidae (Fleming and Kress 2013). Com relação a morcegos e outros vertebrados, estudos voltados para a estrutura de comunidades são raros, sendo que a maioria é focada em grupos taxonômicos (Buzato and Franco 1992, Buzato et al. 1994, Marques et al. 2015). Para beija-flores, diversos processos foram apontados atuando na organização de redes de interação, como a competição (Wolowski et al. 2013, 2017), a facilitação (Wolowski et al. 2017, Bergamo et al. 2020b) e filtros ambientais (Araujo et al. 2018), geralmente associados a diferentes altitudes dentro do bioma (Wolowski et al. 2017). A história evolutiva das interações também influencia na estrutura das comunidades (Bergamo et al. 2017, 2017, mas veja Araujo et al. 2018)

Os fatores que determinam estrutura das comunidades visitadas por beija-flores são influenciados por diversos princípios, tais como a disponibilidade de néctar, o comportamento de forrageio dos beija-flores e a coevolução de características florais e dos animais (Feinsinger and Colwell 1978). A disponibilidade de néctar é correlacionada com a dispersão e com a morfologia das flores, que resulta em diferentes categorias relativas ao forrageio dos animais (Feinsinger and Colwell 1978). De acordo com Feinsinger e Colwell (1978), beija-flores que possuem comportamento trapilíneo, ou seja, que buscam alimento em rotas de captura pré-definidas, tendem a visitar flores dispersas e com corolas longas e especializadas, que fornecem grande quantidade de néctar. A maioria dos beija-flores eremitas tendem a apresentar este tipo de comportamento. Em contrapartida, beija-flores territorialistas, que exploram e defendem um território, tendem a visitar plantas aglomeradas que fornecem grandes ou moderadas quantidades de néctar. Os beija-flores podem ainda se comportar de forma generalista de acordo com a disponibilidade de recursos e a competição no ambiente. Beija-flores territorialistas e generalistas normalmente pertencem ao grupo dos não eremitas.

As diferenças no comportamento de forrageio dos beija-flores têm importantes consequências para a estrutura das comunidades. Beija-flores trapilíneos, por viajarem por grandes distâncias, transportam pólen geneticamente diversificado (Torres-Vanegas et al. 2019) contribuindo com o aumento da diversidade genética na comunidade. Além disso, beija-flores eremitas – que normalmente apresentam comportamento trapilíneo – são restritos a florestas de baixada enquanto que os não-eremitas são encontrados em uma grande variedade de elevações (Maglianesi et al. 2015). De fato, a dominância dos recursos em áreas de baixada por beija-flores eremitas (Sazima et al. 1995, Buzato et al. 2000) pode funcionar como um filtro biótico, favorecendo a presença de plantas que fornecem grandes quantidades de energia, resultando em comunidades com grandes semelhanças filogenéticas (Wolowski et al. 2017).

Na presente tese, nosso objetivo foi organizar informações e explorar a estrutura de comunidades entre flores e vertebrados nectarívoros na Floresta Atlântica, em especial beija-flores, levando em consideração a ecologia e a evolução das interações. O primeiro capítulo consiste na elaboração e organização de um banco de dados com toda a informação disponível sobre a interação para a Mata Atlântica brasileira. O objetivo deste primeiro capítulo é reforçar padrões que possam guiar futuros trabalhos voltados para a ecologia e evolução das interações e das suas comunidades na Floresta Atlântica. Além disso, apontamos tendências e lacunas no conhecimento acerca das interações. No segundo capítulo, nosso objetivo foi investigar a importância relativa de beija flores mais especializados – os eremitas que apresentam comportamento trapilíneos – e mais generalistas – os não eremitas, que são normalmente territorialistas – na estrutura da comunidade, considerando sua história evolutiva conjunta com as plantas que visitam e sua distribuição. Apesar de ser um sistema bem estudado na Floresta Atlântica, até o presente momento a importância do comportamento dos beija-flores e a história evolutiva conjunta dos mesmos não foi abordada. Para tanto, nós averiguamos a presença ou ausência de sinal cofilogenético nas respectivas redes de eremitas e não eremitas em comunidades em diferentes altitudes e latitudes. Com isso, nossas expectativas são encontrar maior sinal cofilogenético em redes de beija-flores eremitas do que na de não eremitas. Eremitas são considerados beija-flores especialistas, sendo provável que as interações tenham ocorrido por meio de evolução conjunta. Também esperamos encontrar maior sinal cofilogenético em menores latitudes e altitudes devido a distribuição de beija-flores eremitas ser concentrada nestas áreas (Stiles 1978; Feinsinger et al. 1979; Graham et al. 2009; Rodríguez-Flores et al. 2019).

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ATLANTIC FLOWER AND NECTAR-FEEDING VERTEBRATE INTERACTION: A DATASET FROM THE ATLANTIC FOREST OF SOUTH AMERICA

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INTRODUCTION

In the American tropics, wild plant species and their nectar-feeding vertebrates provide some of the most remarkable examples of natural history and biotic interactions (Sazima et al. 1995a, Agostini et al. 2006, Muchhala 2006, Temeles et al. 2009, Simon et al. 2011, Fleming and Kress 2013). The majority of nectar-feeding vertebrates are birds and mammals in the Trochilidae and Phyllostomidae families. Up to now, bird and bat floral visitors are present on ca. 12% and 6% of the flowering families, respectively (Fleming and Kress 2013), and they contribute to a very important ecosytem function by acting as pollinators. There are quite few records of other nectar-feeding vertebrates that can also act as pollinators (Buzato et al. 2012, Ratto et al. 2018). The proportion of vertebrate pollinated plant families varies between plant lineage with some lineages apparently more prone to display such interaction in some geographic areas (Buzato et al. 2000, Fleming and Kress 2013).

In spite of exhibiting relatively low taxonomic diversity (Fleming and Kress 2013), many studies of the relationship between flowers and nectar feeding vertebrates are used as a model to interpret complex ecological and evolutionary outcomes in tropical forests (Feinsinger et al. 1986, Tschapka 2004, Kay et al. 2005, Healy and Hurly 2013, Bergamo et al. 2017, 2020, Weinstein and Graham 2017). Such outcome are influecend by functional traits that affects the performance of individuals (McGill et al. 2006). Different functional traits are associated with different functional group of pollinators and defines the pollination niche of plants (Phillips et al. 2020). Some of the floral traits associated with pollination niche are: are corolla length and shape (resource accessibility), phenology and nectar production and concentration (resource availability), flower color and presence of fragance (attractiveness) (Muchhala 2006, Marten-Rodriguez et al. 2009, Lagomarsino et al. 2017, Bergamo et al. 2018).

Differences in morphology, physiology and behavior of vertebrates, even within sister clades, favor vertebrate potential to act as pollinators or larcenies (Feinsinger and Colwell 1978, Buzato et al. 2000, Boehm and Boehm 2018). When larceny occurs animal species obtain food rewards without transferring pollen on conspecific stigmas (Inouye 1980). Larceny can occurs in vertebrate-pollinated floras, apparently with few costs to the plant or changes on the mutualistic network properties (Maruyama et al. 2015a, Richman et al. 2018).

Inside the Neotropics, the Brazilian Atlantic Forest is considered one of the five hottest hotspots on earth, with a great number of endemic plants and vertebrates (Myers et al. 2000, Mittermeier et al. 2004). Nowadays, the Brazilian Atlantic Forest has only 11.4% to 16% of its original area (Ribeiro et al. 2009) due a long disturbance history since Brazil's colonization (Dean and Schwartz 1997, Joly et al. 2014). Fragmentation due habitat loss are considered the main cause of loss of global diversity (Foley et al. 2005, Butchart et al. 2010) and there have been declines in population trends in several groups of organisms (Butchart et al. 2010, Bogoni et al. 2018) with consequences to the plant-animal interaction and evolutionary trends of the biological systems (Galetti et al. 2013). In the past decades, bird and mammal pollinators have been moved to categories of higher extinction risk in IUCN Red List of Threatened Species (Regan et al. 2015). The loss of species in complex biological systems, such pollination networks, might trigger cascading effects of extinction and demographic impacts on multiple species thought direct and indirect effects (Säterberg et al. 2013, Pires et al. 2020).

In this study, we compile information about Brazilian Atlantic Rainforest flora in which interaction with nectar-feeding vertebrates contating plant reproductive structures are observed by focal and direct observation. There is a long research history on vertebrate pollination in this Bioma (Snow and Snow 1972, Snow and Teixeira 1982, Sazima et al. 1996, 1999, Machado et al. 1998, Buzato et al. 2000, Rocca and Sazima 2008, Vizentin-Bugoni et al. 2016). The dataset was assembled from 191 studies and 22 personal communications encompassing ca. 160 localities of Brazilian Atlantic Forest (Figure 1), representing 1920 unique interactions among 457 and 103 species of plants and nectar-feeding vertebrates, respectively. With this dataset, we intend to organize ecological information also useful for evolutionary studies, highlighting patterns towards flower and nectar-feeding vertebrate morphology, flower physiology and interaction features that can be observed from the collected data. This manuscript is part of the ATLANTIC SERIES datapapers which represents effort to organize information on the biodiversity of Atlantic Forest (e.g. ATLANTIC-FRUGIVORY - Bello et al. 2017, ATLANTIC-BATS - Muylaert et al. 2017 and ATLANTIC-BIRDS - Hasui et al. 2018).

METADATA

CLASS I. DATA SET DESCRIPTORS

A. Data set identity:

Title: ATLANTIC FLOWER AND NECTAR-FEEDING VERTEBRATE INTERACTION: A DATASET FROM THE ATLANTIC FOREST OF SOUTH AMERICA

B. Data set identification code:

Suggested Data Set Identity Codes:

ATLANTIC-nfvertebrateinteraction_plants.csv;
ATLANTIC- nfvertebrateinteraction _vert.csv;
ATLANTIC- nfvertebrateinteraction _int.csv;

ATLANTIC- nfvertebrateinteraction _refs.csv

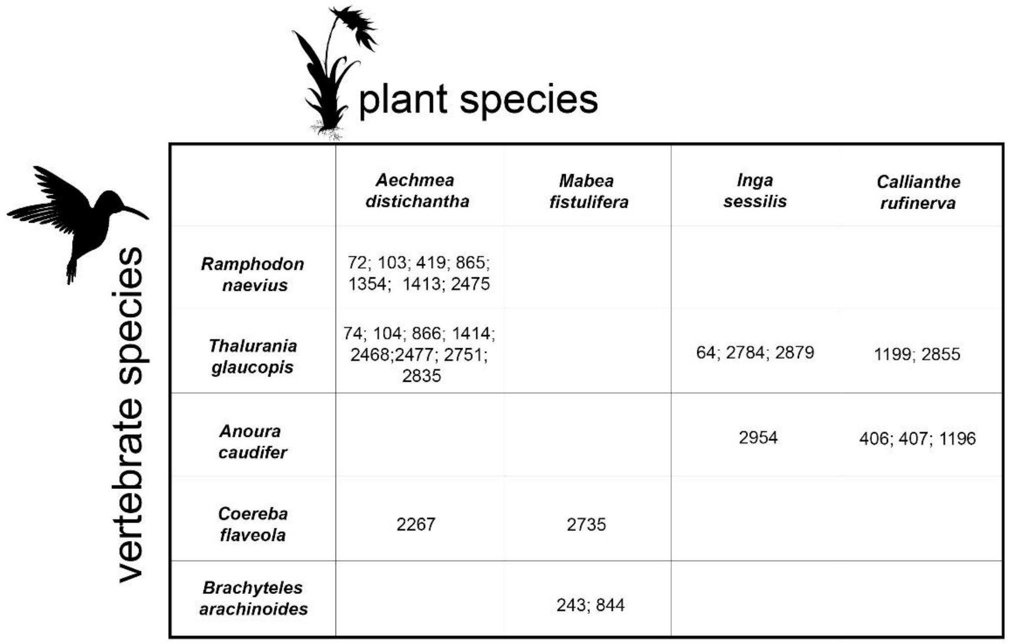
C. Data set description:

Originators: Joice Iamara-Nogueira; Nátalia Targhetta, Gina Chaves and Silvana Buzato Universidade de São Paulo (USP-SP), Instituto de Biociências, Rua do Matão, Travessa 14, 321, Butantã, São Paulo, SP, Brazil.

Abstract: Wild flowering plant species and their nectar-feeding vertebrates provide some of the most remarkable examples of natural history and biotic interactions in the Neotropics. In the Atlantic rainforests, a highly threatened Biome due to anthropogenic activities, several species of birds — specially hummingbirds, bats and other non-flying mammals as well as a few species of reptile are nectar feeders, acting also as pollinators, contributing to seed output of flowering plants. We present a dataset containing information on flowering plants visited by nectar-feeding vertebrates sampled in 160 localities in Atlantic Forest. This dataset provides information about 1920 unique interactions among 457 species of flowering plants and 103 species vertebrate pollinators. All plant-vertebrate interaction came from focal and direct observations of visits. No inferences of pollinators based on floral syndromes were included. We also provide information on the most common plant traits used to intrepreted association between flower and nectar-feeding vertebrates: corolla length, nectar production and concentration, flower color and shape, time of anthesis, presence or absence of odor and phenology. To the animals, IUCN classification, body mass, bill or rostrum size were also informed. Information on the frequency of visits and pollen deposition on the vertebrate's body were also informed if available on the original source. The highest number of unique interactions is registered for birds (1793) followed by bats (117). For plants, Bromeliaceae contains the highest number of unique interactions (614), followed by Fabaceae (248) and Gesneriaceae (106). It is evident the geographical bias of the studies throughout the southeast of Atlantic Forest and the highest efforts to flower-hummingbird interaction. However, there is a global tendency of higher interaction with birds rather other mammals species (Fleming and Kress 2013). In addition, the lack of similar protocols among studies to collect basic data makes some comparison and generalization difficult. This dataset represents a huge effort to organize and highlight the importance of vertebrate pollinators on this hotspot of biodiversity on the earth.

D. Key words: Atlantic Forest, Brazil, Floral traits, nectar-feeding vertebrates, Vertebrate pollinators

E. Description: The dataset is composed by four metadata that relates to each other as illustrated in the Figure 1. It comprises ca. 160 localities in Atlantic Forest Biome (Figure 2), following Biome limits defined by Ribeiro et al. (2009). The data set contains 1920 unique interactions among 457 identified plant species plus 21 unidentified plant species, and 103 identified vertebrate species plus 20 unidentified vertebrate species. There is a bias in the sampling effort related to the taxonomic groups and study localities. Studies involving only hummingbirds represent 57% of the dataset, while studies involving bats (alone or with another groups of vertebrates), which are also important floral visitors of the Atlantic Forest, represent only 25%. Most of these studies were carried out in southeast of Atlantic Forest (Figure 3).



	Aechmea distichantha	*Mabea fistulifera*	*Inga sessilis*	*Callianthe rufinerva*
Ramphodon naevius	72; 103; 419; 865; 1354; 1413; 2475			
Thalurania glaucopis	74; 104; 866; 1414; 2468;2477; 2751; 2835		64; 2784; 2879	1199; 2855
Anoura caudifer			2954	406; 407; 1196
Coereba flaveola	2267	2735		
Brachyteles arachinoides		243; 844		

Figure 1. User guide example to indicate the relationship among the four datasets in this datapaper: ATLANTIC-nfvertebrateinteraction_plants.csv, ATLANTIC-nfvertebrateinteraction _vert.csv, ATLANTIC- nfvertebrateinteraction _int.csv and ATLANTIC- nfvertebrateinteraction _refs.csv. **Vertebrate dataset** and **Plant dataset** contain taxonomic and traits related to nectar-

feeding vertebrate and plant species, respectively. **Interaction dataset** contain taxonomic identification of plant and floral visitors associated to the relative number of visits and original sources. Each interaction between a nectar-feeding vertebrate and plant has one or more indentifier *id_inter*, depending on how often the interaction was reported. The *id_inter* is also the same for **Reference dataset**. Some interactions do not occur and, in this case, no identifier has been assigned.

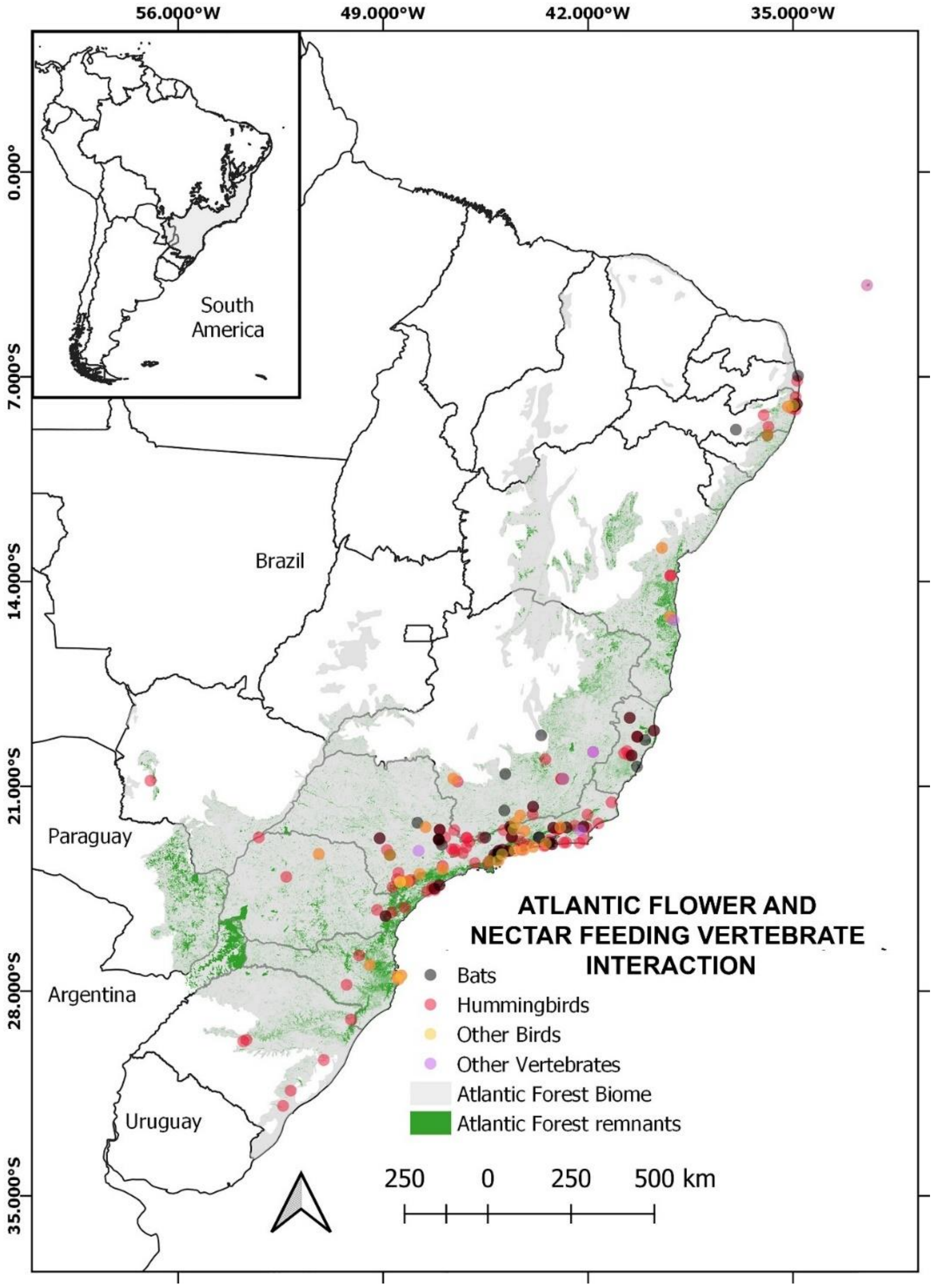


Figure 2. Distribution of the flower and nectar-feeding vertebrates interaction studies in the Atlantic Forest. The colors show the occurrence of the original Biome and the nowadays remnants areas of the Atlantic Forest. The dots show the locations of the original studies reporting flower and nectar-feeding interactions for each group. Light gray lines show the political division of Brazilian states.

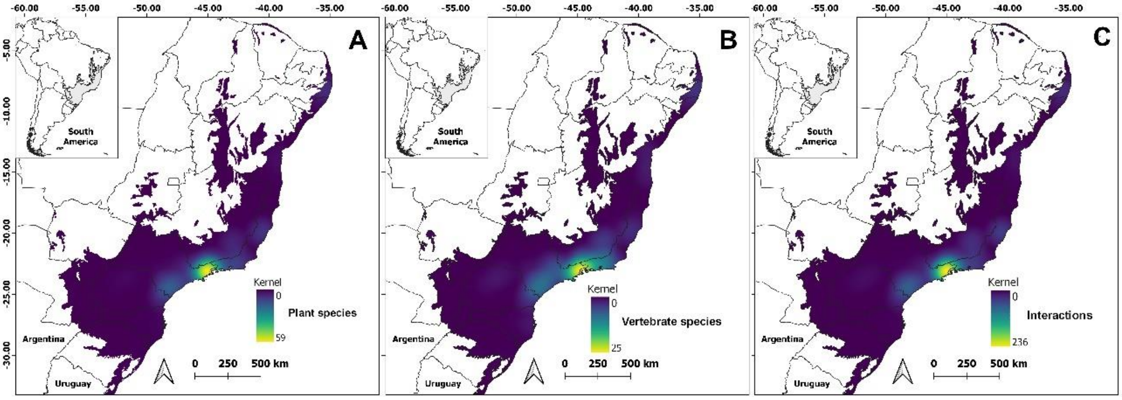


Figure 3. Kernel density of study sites in the flower and nectar-feeding vertebrate interaction dataset: plant species (A), nectar-feeding vertebrate species (B) and interaction (C). Kernel density map for 160 study sites, made with 10mm of radius. The color scale was made with five equal intervals, using 'viridis' color palette in QGIS.

Most plant species are epiphytes (ca. 35% of all species) and the minority are trees (4% of all species). This proportion are in accordance with nectar-feeding vertebrate visitor records, since epiphytes are visited largely by them in different habitats (Fleming and Muchhala 2008). Nonetheless, the low proportion of trees could represent a reflection of subsampling of nectar-feeding bats, since Glossophagine bats visit a great proportion of trees along with epiphytes (Fleming and Muchhala 2008). Despite of the intense search for data, we couldn't find any register of interaction by nectar-feeding vertebrates in the portion of Atlantic Forest outside Brazilian boundaries (Figures 2 and 3). We also include in the dataset 46 exotic species in areas of Atlantic Forest.

Plant species belong to 180 genera and 54 families. Bromeliaceae presents the highest number of interactions with 25 genera and 158 species, followed by Fabaceae with 18 genera and 33 species and Gesneriaceae with 6 genera and 33 species. Together, these three families have almost 50% of all the species used by nectar-feeding vertebrates (Figure 4, A-B). Vertebrate species belong to 70 genera and 20 families. Most vertebrates are birds (81 species), followed by bats (13 species), primates (6 species), opossum (2 species) and lizard (1 species). The most representative families are

Trochilidae with 24 genera and 41 species, Thraupidae with 12 genera and 19 species and Phyllostomidae with 10 genera and 13 species (Figure 5, A-B).

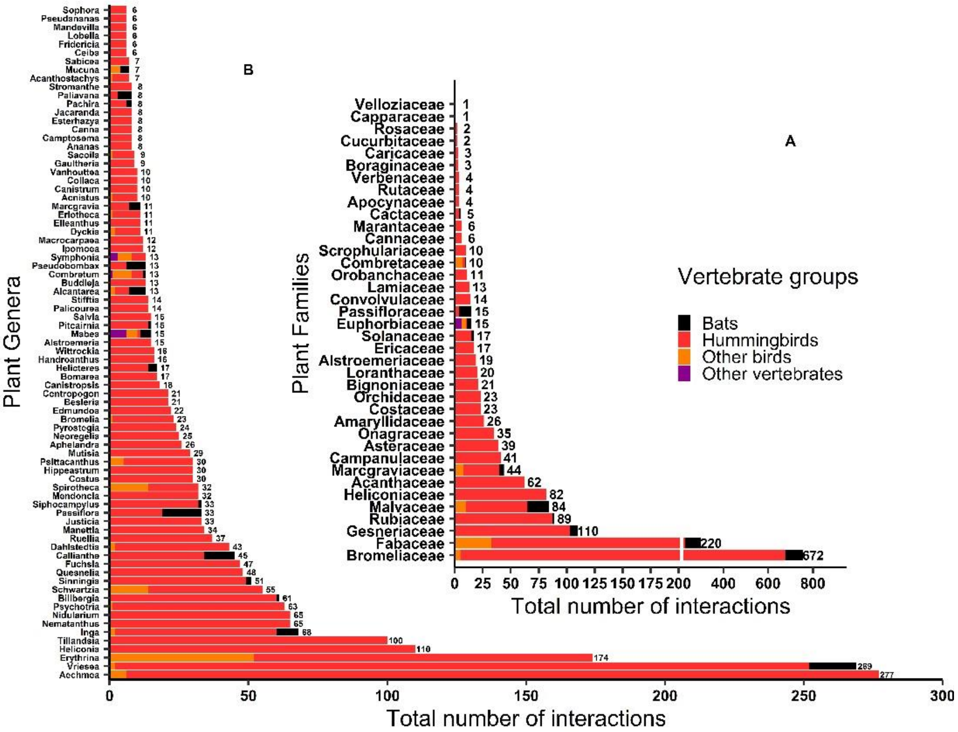


Figure 4. Distribution of the total number of interaction bewteen each nectar-feeding vertebrate group and fowering plant families (A) and genera (B) in the database Atlantic flower and nectar-feeding vertebrate interaction.

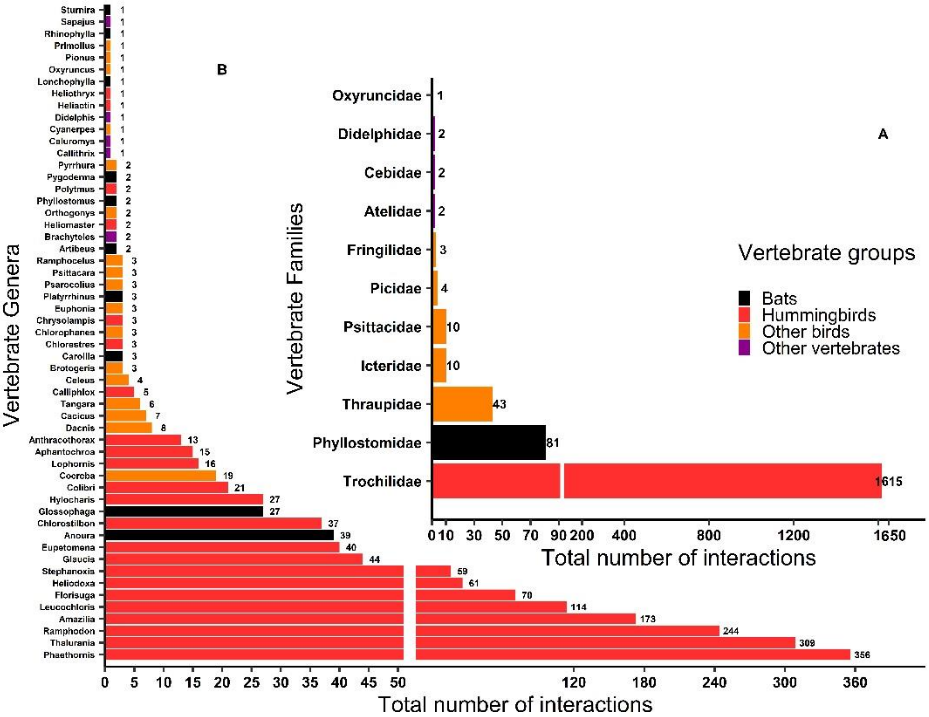


Figure 5. Distribution of the total number of interaction between each nectar-feeding vertebrate group on the families (A) and genera (B) of vertebrates database Atlantic flower and nectar-feeding vertebrate interaction.

Plants, bats, hummingbirds and other birds had high beta diversity (β_{SOR} = 0.94, 0.81, 0.82 and 0.91, respectively) and turnover (β_{SIM} = 0.82, 0.58, 0.63 and 0.75, respectively) while nestedness rates where low (β_{SNE} = 0.11, 0.23, 0.18 and 0.15, respectively). These values indicate that communities across latitudes are equally rich but different in species composition (Baselga and Orme 2012). Conservation status of plant species varies from least concern to critically endangered, considering the CNCFlora red list (Martinelli and Moraes 2013). Although most of plants are classified as least concern, only ca. 30% of plants in this database appear in the CNCFlora. Furthermore, key species from Bromeliaceae and Gesneriaceae family are in the most threatened conservation categories. For nectar-feeding vertebrates, a group with more information on the IUCN conservation list, ca. 14% of species are classified into most threatened groups. Of these, five are hummingbirds, five are other birds and five are primates.

Information on plant and animal traits relevant to the interaction such as flowering phenology or pollen placement on pollinator's body is not present for all species in the dataset (Table 1). For plants, the trait with more information is plant growth and with the least information is the species conservation status. For animals, few studies measured the features involved with nectar-feeding. Most of the information on the nectar-feeding vertebrate traits came from taxonomic research. We couldn't find any information about tongue size, an important characteristic related to nectar-feeding, and data available is derived from inference (Vizentin-Bugoni et al. 2016). Observation time of floral visitors on flowering plants was highly heterogenous from 48 minutes as the minimum time interval to 682 hours and 40 minutes as the maximum time interval. The frequency of visits was reported in only 61% of interactions (Table 1). It is also interesting to realize that most of the quantitative measure of plant features (corolla length and nectar volume and concentration) is related to bird visitors while qualitative description of flower features (anthesis time, color, shape and presence of fragence) are related to bat visitors.

Table 1. Summary of trait information presented in the flower and nectar-feeding vertebrate interaction dataset. For each trait we show the number of species presenting the information and the percentage of knowledge of each trait (n° of species with the information/total number of plants species in the dataset). The same metric was calculated to vertebrate species as well. Total number of plants are 457, total number of vertebrates are 103 and total number of interactions are 3120. For description of the traits, see the variable information section. *Data estimated from bill size.

	Traits	n° species	% knowledge
PLANT	Presence in the CNC Flora List	133	29.1
	Flowering start month	403	88.2
	Flowering period	405	88.6
	Plant growth	454	90.8
	Flower color	415	93.2
	Flower shape	426	93
	Presence or absence of odor	254	55.5
	Anthesis time	328	71.7
	Mean corolla length (mm)	338	73.9
	Standard deviation of corolla length (mm)	300	65.6
	Mean nectar production rate (µL/h)	259	56.7
	Standard deviation of nectar production rate (µL/h)	227	49.7
	Mean nectar concentration (%)	303	66.3
	Standard deviation of nectar concentration (%)	264	57.8
	Observation time	341	74.6
VERTEBRATE	Presence on IUCN list	95	92.2
	Mean body mass (g)	84	81.6
	Standard deviation of body mass (g)	30	29.1

	Mean bill or rostrum length (mm)	47	45.6
	Standard deviation of bill or rostrum length (mm)	30	29.1
	Mean tongue length (mm)*	9	8.7
INTERACTION	Body pollen deposition	1461	46.8
	Feeding behavior	2440	78.2
	Relative frequency of visits	1884	60.4

Most species of plants visited by vertebrate flowered during three to five months, representing an extended flowering pattern. In addition, most of flowering species provided small quantities of energy per flower (Figure 6 A-C). Considering both — flowering phenology duration and amounts of energy provided by nectar on flower, nectar-feeding vertebrates in the Atlantic Rainforest migth be able to recognize pattern on resource availabitily on these forests (extented flowering with small amount of nectar energy per flower). These traits promote trap-lining foraging behavior of most nectar-feeding vertebrates in this Biome, since territorial behavior occurs when resource availability makes up for the expense of defending the territory (Feinsinger 1976).

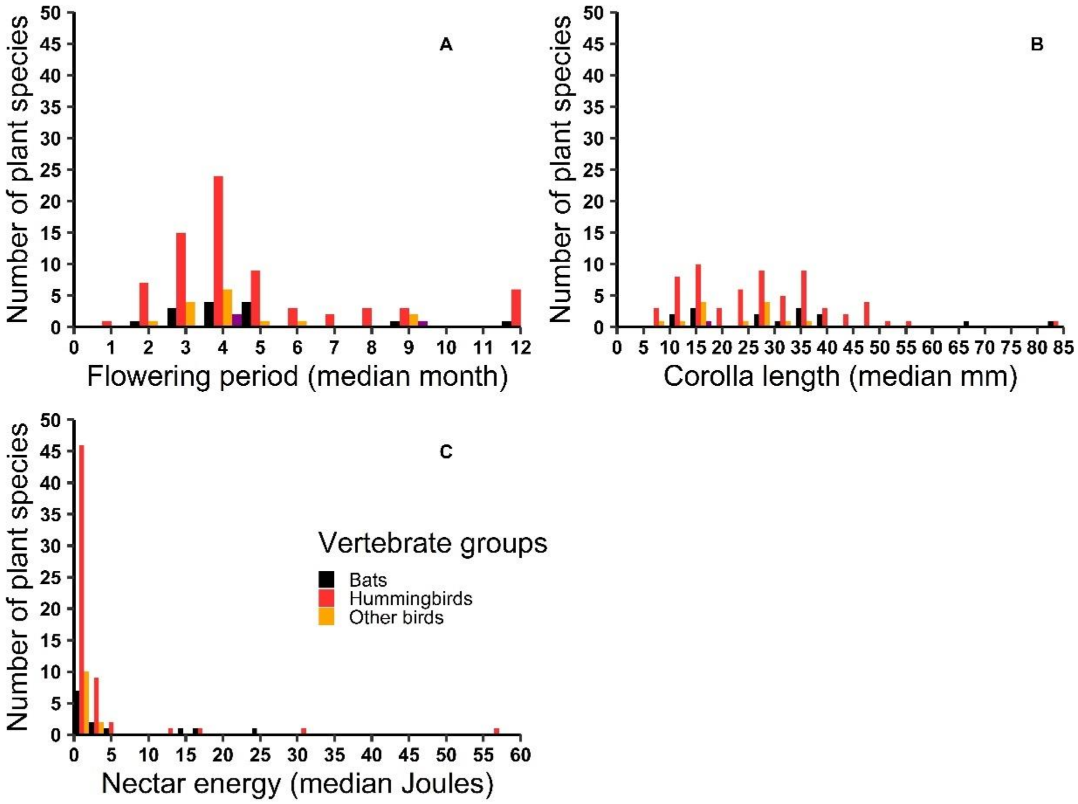


Figure 6. Frequency distributions of flowering period (A), corolla length (B) and nectar energy per flower (C) for plant species visited by each nectar-feeding vertebrate groups in the database Altantic flower and nectar-feeding vertebrate interactions.

Corolla length of flowers visited by nectar-feeding vertebrates are more heterogeneous for hummingbirds than for bats and other birds (Figure 6 B). This fact might be associated to the higher diversity of bill shapes of hummingbirds (Figure 7 A). With low frequencies of visits, small and medium bill size's hummingbirds share floral resources, visiting flowers with similar corolla lengths (Figure 7 B). The composition of nectar-feeding vertebrates and plant species related to the size and shape of flowers and bills might promote the resource sharing in some communities (Sazima et al. 1996, Bergamo et al. 2020). On the other hand, hummingbirds with large bill sizes and high frequency of visits have access to exclusive resources from flowers with larger corolla lengths (Figure 6B). In some communities, hummingbirds with larger bills might dominate the resource use for visiting a larger set of flowers (Sazima et al. 1995a, Buzato et al. 2000). No relationship was found between hummingbird body size and energy produced per flower (data not shown). Information about nectar production and concentration is collected in a myriad of unstandardized ways, making comparison difficult despite our best efforts to standardize data.

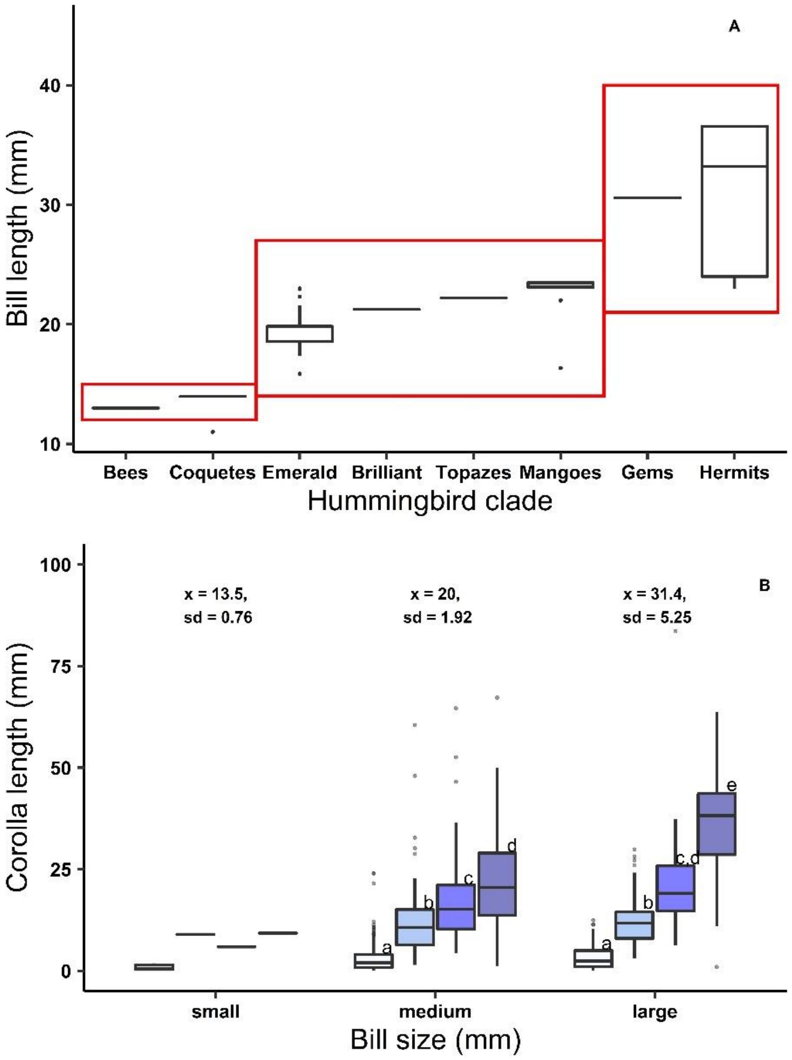


Figure 7. Classification of bill length following McGuire et. al. (2014) (A) and relation between corolla length and bill size (B) for plant species and hummingbirds in the database Atlantic flower and nectar-feeding vertebrate interaction.

The distribution of both the number of nectar-feeding vertebrate species per flowering plant (Figure 8) and the number of visited plant species per nectar-feeding vertebrate species (Figure 9) shows that specialization describes better the flower-vertebrate interaction than generalization. In special, for hummingbirds, the number of hermit species per plant species were lower than non hermit (Figure 8). So, generalization seems to be not the norm for plants visited by nectar-feeding vertebrates in the Atlantic Rainforests. As message, better understanding of the ecology and evolution of nectar-feeding vertebrates and flower interaction will require increased sampling of communities. There is so many places to be sampled throughout the Atlantic rainforest of South America. It is our challenge to safeguard this area. The distribution of the plant-pollinator interactions can help us to untangled many questions and could help us understand community properties such as resilience of these interactions necessary to support the anthropogenic perturbations.

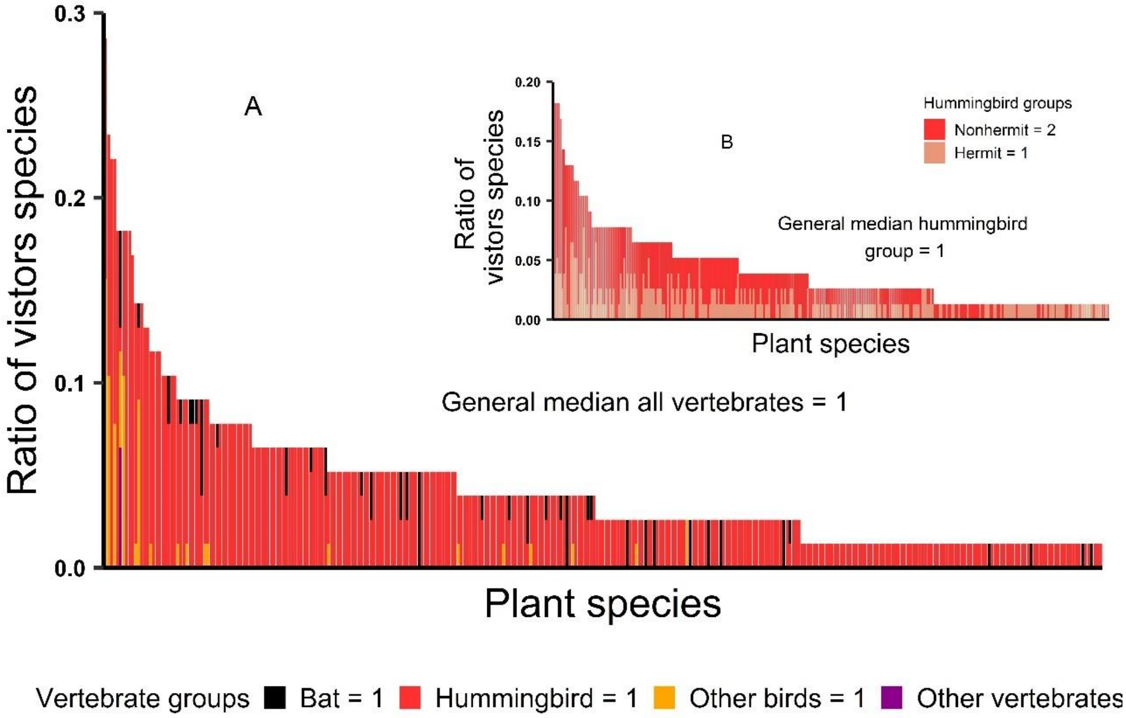


Figure 8. Distribution of the ratio of nectar-feeding vertebrate groups by flowering species (A) and the ratio of each hummingbird group by flowering species (B) in the database Atlantic flower and nectar-feeding vertebrate interaction.

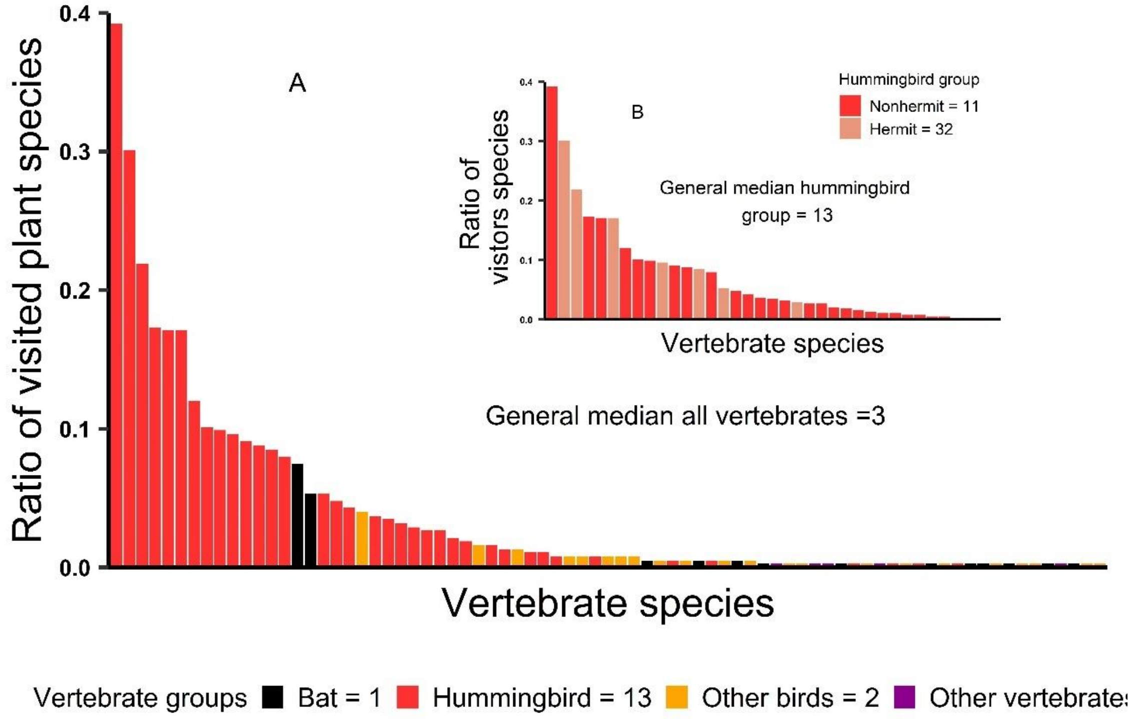


Figure 9. Distribution of the ratio of plant species visited by species of nectar-feeding vertebrates in each group (A) and the ratio of plant species visited by species in each hummingbird group (B) in the database Atlantic flower and nectar-feeding vertebrate interaction.

CLASS II. RESEARCH ORIGIN DESCRIPTORS

A. Overall project description:

Identity: Compilation of available data on nectar-feeding vertebrates in Atlantic Forest, including information about plants, vertebrates and their interaction.

Period of study: Dates of publication used as source range from 1949 to 2018.

Objectives: With this datapaper, we aimed to compiled and make available information about pairwise interaction of flowers and nectar-feeding vertebrates in the Atlantic Forest Biome, including traits of plants and animals that structure this interaction. We seek to highlight patterns about flower morphology and physiology, vertebrate morphology and interaction features observed through the compiled data that may guide further studies on the interaction between plants and vertebrates. W also point out gaps and bias in the knowledge on the distribution of the interaction and sampling efforts. We hope that this datapaper will be used as a baseline reference for future studies on the Atlantic Forest Biome related to the flower and nectar-feeding interaction.

Abstract: Same as above.

Sources of funding: See Acknowledgements

Site description: The Atlantic Forest is highly diverse with complex climate conditions, comprising tropical and subtropical vegetations, including a great variety of physiognomies, such as coastal evergreen ombrophilous forests, semi-deciduous and deciduous forests, mangroves, swamps, restingas, high-altitude grasslands and subtropical mixed forests (Morellato and Haddad 2000). It originally occupied an area of 150 million ha. (Ribeiro et al. 2009) ranging from 0° to 30°S, comprising a wide variety of climatic conditions (Ledru et al. 2005). The distribution of Altantic Forest is located mainly along the Brazilian coast and it shared limits with other biomes, such as Pampa (grassland open fields), Cerrado (Brazilian savanna) and Caatinga (Brazilian xeric vegetation) (Ribeiro et al. 2009). It supports 8% of the world's total species and is one of the areas with larger indexes of endemism (Morellato and Haddad 2000, Myers et al. 2000, Joly et al. 2014, Peres et al. 2020). As a result of its high complexity, the Biome presents high richness of plants (15519 species, Zappi et al. 2015), birds (891 species, Varzinczak et al. 2016) and bats (117 species, Lima 2014). During its history, the Atlantic Forest suffered several types of exploitation and unplanned occupation, leading to the fragmentation of the biome (Dean and Schwartz 1997, Morellato and Haddad 2000) and to a remaining area corresponding to only 11.4% to 16% of the original extension (Ribeiro et al. 2009). In this dataset we considered studies performed in areas of forests and associated vegetation like restingas and Araucaria Forest (Scarano 2002) and rock outcrops (Safford 1999a, 1999b, Scarano 2002, 2007).

Data compilation: We collected data through unpublished and published studies in articles, book chapters and dissertations and PhD thesis. We searched for information in the following sources: online databases (Web of Science, Scopus, Scielo, Research Gate, JStore, Google Scholar and Mendeley), digital library of state and federal universities and federal agency (CAPES), references cited in “gray” literature, references cited in other Atlantic papers (Muylaert et al. 2017, Hasui et al. 2018) and our own unpublished studies. We used the key words: “pollination + vertebrate”, “pollination + hummingbird”, “pollination + bat” and “pollination + hummingbird + bat”. We chose to use “pollination” because it is commonly associated with nectar feeding behavior. We controlled the search from 1980 to 2017 and, posteriorly, we expanded the start period to 1948, due a milestone in literature represented by Stephan Vogel’s work with bats and others that we found on the cross references. In addition, we invited several specialists to contribute with their own published and unpublished data. We validated all the information comparing data sent by the specialists with data in the database to check for inconsistencies and verify the reliability of the database.

Information on the interaction among nectar-feeding vertebrate and flowers were compiled from: (Ruschi 1949, Vogel 1968, 2015, Sazima 1976, Sazima and Sazima 1977, 1978, 1980, 1987, 1988, 1995, 1999, Assumpção 1981, Snow and Teixeira 1982, Machado 1983, Snow and Snow 1986, Rylands 1989, Silva 1991, 2008, Vieira et al. 1991, Buzato and Franco 1992, Ferrari and Strier 1992, Fischer et al. 1992, Franco and Buzato 1992, Piratelli 1992, 1993, Peracchi and Albuquerque 1993, Sazima et al. 1993, 1994a, 1994b, 1995a, 1995b, 1996, 1999, 2003, 2005, Araujo et al. 1994, 2004, Buzato et al. 1994, 2000, Fischer 1994, Martinelli 1994, Faria 1995, Passos and Sazima 1995, Pizo et al. 1995, Silva and Peracchi 1995, 1999, Araujo 1996, Pizo 1996, Vieira and Carvalho-Okano 1996, Dietz et al. 1997, Locatelli et al. 1997, Machado and Lopes 1998, 2000, Machado et al. 1998, Pereira 1998, San Martin-Gajardo and Freitas 1999, Almeida and Alves 2000, 2003, Alves et al. 2000, Neves 2000, Santos 2000, Singer and Sazima 2000, 2001, Braz et al. 2000, Vitali-Veiga and Machado 2000, Quirino and Machado 2001, Siqueira Filho and Machado 2001, Sluys et al. 2001, Wendt et al. 2001, 2002, 2008, Freitas and Sazima 2001, 2006, Varassin et al. 2001, Lopes 2002, 2007, Sigrist and Sazima 2002, Varassin 2002, Canela and Sazima 2003a, 2003b, 2005, Kaehler 2003, Siqueira-Filho 2003, Abreu and Vieira 2004, Almeida et al. 2004, Castro and Araujo 2004, San Martin-Gajardo 2004, Teixeira and Machado 2004, Mendonça and dos Anjos 2005, Sanmartin-Gajardo and Sazima 2005a, 2005b, Teixeira 2005, Kaehler et al. 2005, Correia et al. 2005, Agostini et al. 2006, Borges 2006, Canela 2006, Cruz et al. 2006, 2014, Freitas et al. 2006, Lenzi et al. 2006, Mendonça and Anjos 2006, Mendonça and Dos Anjos 2006, Rocca 2006, Rocca et al. 2006, Vosgueritchian and Buzato 2006, Costa 2006, Carvalho and Machado 2006, Fonseca 2007, 2012, Hmeljevski 2007, Leite and Machado 2007, Peterle et al. 2007, Piacentini and Varassin 2007, Vasconcellos and Freitas 2007, Lopes and Buzato 2007, Agostini 2008, Kriek 2008, Rocca and Sazima 2008, 2013, Rodrigues 2008, Costa and Morais 2008, Fonseca et al. 2008, 2015, 2016, Parrini and Raposo 2008, Aximoff and Freitas 2009, Borges et al. 2009, Koschnitzke et al. 2009, Paggi 2009, Rogalski et al. 2009, Braun 2010, Pelligrinotti et al. 2010, Piechowski et al. 2010, SanMartin-Gajardo and Vianna 2010, Scultori 2010, Silva et al. 2010, Avila and Freitas 2011, Kamke et al. 2011, Missagia and Verçoza 2011, Nunes 2011, Nunes-Freitas and Rocha 2011, Schmid et al. 2011b, 2011a, Scrok and Varassin 2011, Leone 2011, Meireles 2011, Bueno 2012, Gava 2012, Varassin and Sazima 2012, Verçosa et al. 2012, Amorim et al. 2013, Azevedo 2013, Benevides et al. 2013, Coelho 2013, Nolasco et al. 2013, Stein and Hensen 2013, Wolowski et al. 2013a, 2013b, 2016, Nogueira 2013, Hmeljevski et al. 2014, 2017, Malucelli 2014, Missagia 2014, Missagia et al. 2014, Silva and Piratelli 2014, Vizentin-Bugoni et al. 2014, 2016, Dias 2014, Souza et al. 2014, Cruz-Neto et al. 2015, El Ottra et al. 2015, 2016, Maruyama et al. 2015c, 2015b, Missagia and Alves 2015, 2016, 2017, 2018, Sato et al. 2015, Marques et al. 2015, Bergamo et al. 2016, Pansarin and de Pedro 2016, Capitani 2016, Bastos et al. 2017, Caballero-Villalobos et al. 2017, Pinto 2017, Malanotte 2018, Moreira 2018). We also compiled information from unpublished observations.

Research Methods: We included in the database all plant-oriented, animal-oriented and network studies reporting interaction between flowers and nectar-feeding vertebrates. We considered only information from directed observation of the interaction (animal visits to a flower). For each study, we extract geography coordination from the study itself when available or from the municipality or reserve where the study was performance using Google Earth. For plant features, we extract information about flowering phenology, growth form of species, flower colors and shape, presence of fragrance, anthesis time, mean corolla length and mean nectar rate production and concentration. For phenology, we used the first month in which the species was observed with flower and the number of month that the species remained with flowers; biannual species are signalized with an (*) on the data base. For nectar volume, information was collected in several different ways so, to standardize the data, we calculated the rate of nectar production per hour dividing the accumulated nectar volume by the period the flower remained bagged. When the study did not inform the period in which the flower remained bagged or didn't bagged flower before nectar removal, the dada was not included. For vertebrate features, we collected information on body weight and bill or rostrum length from the study itself or from taxonomic works. And finally, we compiled information from the interaction itself (time of observation, local of pollen deposition on animal's body, behavior of the animal at a flower – pollinator or larceny – and relative frequency of visits – number of flowers visited by total number of visits for each plant species in each community. Larceny was considered any behavior in which the animal visited the flower, consumed nectar or parts of the flower but did not touch the reproductive organs. The relative frequency of visits also includes invertebrates in the total number of visits in cases when the sum of frequencies in a given plant does not add up one. For all plants we checked the conservation status using CNC Flora classification (Flora do Brasil 2014) and for animals, we used IUCN classification (IUCN 2017). Plant habit was checked using Flora (Flora do Brasil 2014) and when more than one habit was assigning to a plant, we considered the one assumed in the original study or the first listed on Flora. When some of this information was missing, it was classified as NA.

Taxonomy and systematics: For plants, we used taxonomic information from Flora (Flora do Brasil 2014), The Plant List (The Plant List 2013), Kew Science (WCSP 2018), taxonomic books and from personal communication with specialists. For birds, we used the checklist of birds by the Brazilian Ornithological Records Committee (Piacentini et al. 2015); for bats we used the checklist of Brazilian bats (Nogueira et al. 2014); for mammals we used the Annotated checklist of Brazilian Mammals 2nd edition (Paglia et al. 2012) and for the reptile species we used (Rocha et al. 2009). We were able to verify and validated the taxonomy of all plant and animal species, except for *Conchocarpus rubrus* (A. St.-Hil.) Bruniera and Groppo (Rutaceae) present in one study. Another inconsistency is the presence of *Bromelia karatas* L. (Bromeliaceae) which, according to Flora do not occur in Brazil yet this species is present in three different works in the data base.

Statistical analysis: We performed descriptive statistical analysis for overview of the data. The biological diversity of plants and vertebrates was access dividing the data by 14 latitudinal ranges of 1° and excluding from analysis latitudes in which there was only one species of plants and/or vertebrates. Beta diversity (β_{SOR}), species turnover (β_{SIM}) and nestedness (β_{SNE}) among latitudes were computed with Sorensen index using the function *beta.multi* in betapart package (Baselga and Orme 2012) in R environment (R Core Team 2018).

The relation between corolla and bill length of hummingbirds and energy produced by the nectar/flower and body mass of hummingbirds was accessed by classifying bill lengths and body mass into three categories (small, medium and large) following clade classification in McGuire et al (2014). The relative frequency of visits was classified into four categories (0 to 0.25, 0.25 to 0.5, 0.5 to 0.75 and 0.75 to 1). Relative frequency of visits is the number of visits of nectar-feeding vertebrates in a flower by total of visits reported in each community and can vary from 0 to 1. The energy produced in the nectar was firstly calculated measuring the sugar production by the product of nectar volume (ml) and concentration (mg/ml). Since concentration of nectar is commonly measured in percentage, we transformed in mg/ml following Bolten et al. (1979). Lastly, we calculated the energy in Joules assuming that 1 mg of sugar correspond to 16.8 J (Dafni 1992). The comparison of corolla length and nectar energy per flower visited by hummungibds with different bill lenghts and body mas, respectively, was made using Kruskall-Wallis test followed by pairwise comparisons performed with Bonferroni adjustment (Zar 1998).

B. Data limitations and potential enhancements: We recognize that documenting the interaction between flowers and nectar-feeding vertebrates in a mega-diverse and forest Biome is a challenging task. This dataset is likely to contain only a subset of all interactions occurring in the Atlantic Forest because several sites is still to be sampled, therefore caution is needed when drawing conclusions.

The first limitation is the representativeness of the dataset. For plants, most of information comes from epiphytes, since Bromeliaceae is the plant family with the highest number of studies. In relation to nectar-feeding vertebrates, birds represent

84,64% of the interactions registered and, although bats are also important pollinators of Atlantic Forest (Fleming and Kress 2013), observations of the interaction involving nocturnal animals and flowers are particularly hard to perform. This data set is cleared biased towards the Trochilidae family. Although hummingbirds represent the main flower visitors in the tropics (Bawa 1990, Buzato et al. 2012, Fleming and Kress 2013), the number of studies involving only this family (122 in 195) is much higher than studies involving other groups. So, this database represents a subsample of possible interactions (Table 2).

Table 2. Representativeness of ATLANTIC flower and nectar-feeding vertebrate interaction to the species of nectar feeding vertebrates known to occur in the Atlantic Forest at all. Number of each class was obtained from literature:

Class	Family	N° of nectar-feeding species recorded in Atlantic forest	N° of nectar-feeding species in the dataset
BAT	Phyllostomidae	29	13
BIRDS	Cracidae	0	1
	Cuculidae	1	1
	Fringillidae	3	2
	Icteridae	3	4
	Oxyruncidae	1	1
	Picidae	1	1
	Pipridae	1	1
	Psittacidae	7	6
	Thraupidae	24	19
	Trochilidae	31	41
	Tyrannidae	31	1
	Vireonidae	13	1

Most studies containing information about flower traits (specially nectar volume) and interactions (specially time of observation and frequency of visits), but the information came as unstandardized way. Then, comparisons among species present in different studies must be made with caution.

Another important limitation of this dataset is the number of interactions listed by each group of nectar-feeding vertebrates. For birds, the dataset reports only 4.76% (1706) of all possible interactions based on 82 animals and 437 plants and for bats only 14.31% (93) of all possible interactions based on 13 animals and 50 plants. Studies of interaction between flowers and nectar-feeding vertebrate that involve the whole plant community may lead to a more comprehensive representation of the interaction network, especially in the subsampled areas of Atlantic Forest in the frontiers of Brazil, Argentina and Paraguay. It is also necessary more studies involving other groups of nectar-feeding vertebrates and birds besides Trochilidae, since they are poorly represented when compared to hummingbirds.

Future studies also should collect, when possible, all information about plants and vertebrates associated with the interaction and about the interaction itself, specially the relative frequency of visits, since this information is crucial to access the relative importance of nectar-feeding vertebrates to plant species. In addition, it would be interesting for specialist in the interaction between flowers and nectar-feeding vertebrates to standardize the data collection. Observation time should occur in similar range of time, since it corresponds to sample effort. Nectar concentration and, specially, volume, should be collected in bagged flowers in similar amounts of time.

CLASS III. DATA SET STATUS AND ACCESSIBILITY

A. Status

Latest update: Ago 2020

Latest archive date: Ago 2020

Metadata status: In review by coauthors

Data verification: Interaction information was compiled as published, except for taxonomic checking. Volume of nectar was presented as nectar production per hour.

Information on quantitative traits for each species of plants and animals is present as the average of the information presented on the studies they appear. Observation time is presented as the sum of the observation period performed in each study. Geographic coordinates in database consist in an approximation of reported decimal degrees (Datum WGS 84) converted with Google Earth. For records without this information, we used the geographic position of municipality or national park where the study took place.

B. Accessibility

Contact person(s): Joice Iamara-Nogueira (joice.iamara@gmail.com) or Silvana Buzato (sbuzato@usp.br).

Copyright restritions: No copyright or proprietary restrictions are associated with the use of this data set. Please cite this data paper when the data are used in publications or teaching events.

Costs: None.

CLASS IV. Data structural descriptors

A. Data set file

Identity: (1) ATLANTIC-nfvertebrateinteraction_plants.csv;
(2) ATLANTIC- nfvertebrateinteraction _vert.csv;
(3) ATLANTIC- nfvertebrateinteraction _int.csv;
(4) ATLANTIC- nfvertebrateinteraction _refs.csv

Size: (1) ATLANTIC- nfvertebrateinteraction _plants.csv, 118 KB;
(2) ATLANTIC- nfvertebrateinteraction _vert.csv, 17 KB;
(3) ATLANTIC- nfvertebrateinteraction _int.csv, 687 KB;
(4) ATLANTIC- nfvertebrateinteraction _refs.csv, 629 KB

Format and storage mode: data tables formatted as comma-separated values (*.csv).

Alphanumeric attributes: Mixed.

Data anomalies: If no information is available for any cell, this is indicated as 'NA'. In this data set there is NA values.

B. Variable information

B.1 Table 3. Plant information: Description of the fields related to plant features involved in the interaction

Variable	**Description**	**Level**	**Example**
id_plant	Identification of each plant species sampled. Each code is exclusive, so the same species sampled in the same locality by different studies will have different id.	1 to 514	1
order_ver	Verified order taxonomic classification.		Brassicales
family_ver	Verified family taxonomic classification.		Capparaceae
genera_ver	Verified genera taxonomic classification.		*Cynophalla*
species_ver	Verified specific epitope taxonomic classification.		*flexuosa*
author_ver	Species author after taxonomic verification.		(L.) J.Presl
tax_ver	Reference of taxonomic review.		REFLORA - Plantas do Brasil: Resgate Histórico e Herbário Virtual para o Conhecimento e Conservação da Flora Brasileira
nature_BR	Origen of the plant in relation to Brazil.	nat = native exo = exotic	nat
nature_AF	Origen of the plant in relation to Atlantic Forest.	nat = native intr = introduced	nat

Variable	**Description**	**Level**	**Example**
CNC_classification	Cnc Flora classification for threatened plants flowing Martinelli and Moraes 2013	cr = Critically endangered en = Endangered vu = Vulnerable nt = Near threatened lc = Least concern dd = Data deficient ne = Not evaluated	LC
floweringstart_month	First month of flowering.	1 to 12	1
floweringperiod_month	Number of months with flower.	1 to 12	3
plantgrowth	Form of plant growth.	bru = brush or shrub epi = epiphyte her = herbaceous lia = liana tre = tree trl = treelet	epi
flower_color_1	Principal color of petals.	blu = blue (green, etc) red = red (pink, orange, purple, etc) yel = yellow (cream, etc) whi = white	red

Variable	Description	Level	Example
flower_color_2	Secondary color of petals or bracts.	blu = blue (green, etc) red = red (pink, orange, purple, etc) yel = yellow (cream, etc) whi = white	yel
flower_shape	Shape of the corolla.	bel = bell dis = dish or capitula fla = flag gul = gullet hea = head or brush spu = spurred tub = tube	tub
odor	Presence of fragrance in the flower	abs = absence pre = presence	a
anthesis_time	Time of flower anthesis.	day = day (6h am to 6h pm) nig = night (6h pm to 6h am) bot = both (all day)	day
corolla_length_mm	Mean corolla length of flowers in millimeters.	1.24 to 144.15	25.55
corolla_length_mm_sd	Standard deviation of corolla length in millimeters.	0.05 to 25.6	3.23

Variable	**Description**	**Level**	**Example**
nectar_volume	Mean volume of nectar produced in microliters per hour. The rate of nectar production was estimated by the maximum volume measured in bagged flowers in pre-anthesis by the total of hours in which flowers kept bagged.	0 to 204.4	16.25
nectar_volume_uL_SD	Standard deviation of the nectar production rate in microliters per hour.	0 to 46.25	6.70
nectar_concentration_brix%	Mean nectar sugar concentration in brix (%).	6 to 60.6	29.35
nectar_concentration_brix%_SD	Standard deviation of nectar concentration in brix (%).	0 to 18.8	7.34
observation_time_hour	Time of observation of the interaction on plant species in hours.	0.8 to 682.72	40
n_input	Number of times in which the species was observed being visited by a vertebrate.	1 to 28	4

B.2 Table 4. Vertebrate information: Description of the fields related to nectar-feeding vertebrate features involved in the interaction

Variable	Description	Level	Example
id_vert	Identification of each vertebrate species sampled. Each code is exclusive, so the same species sampled in the same locality by different studies will have different id.	1 to 126	1
order_ver	Verified order taxonomic classification.		Passeriformes
family_ver	Verified family taxonomic classification after taxonomic verification.		Thraupidae
genera_ver	Verified genera taxonomic classification after taxonomic verification.		*Coereba*
species_ver	Verified specific epitope taxonomic classification after taxonomic verification.		*flaveola*
author_ver	Species author after taxonomic verification.		Linnaeus, 1758
ref_ver	Reference of taxonomic review.		Piacentin et al., 2015
IUCN_classification	IUCN classification for threatened plants following IUCN 2020	cr = Critically endangered en = Endangered vu = Vulnerable nt = Near threatened lc = Least concern ne = Not evaluated	LC

Variable	Description	Level	Example
body_weight_g	Mean body mass of the vertebrate in grams. When the species presents sexual dimorphism related to the body mass, the male mass was considered.	1.8 to 2000	10.5
body_weight_g_sd	Standard deviation of body mass of the vertebrates.	0.06 to 800	2.4
bill_rostrum_length_mm	Mean length, in millimeters, of the bill of birds or rostrum of mammals, specially nectarivores bats.	5 to 37.15	5
bill_rostrum_length_mm_sd	Standard deviation of length of the bill of birds or rostrum of mammals, specially nectarivores bats, in millimeters.	0.19 to 9.8	0.9
tongue_length_mm	Mean length, in millimeters, of the tong of birds and mammals, specially nectarivores bats.	9.6 to 27.2	9.6
n_input	Number of times in which the species was observed visiting a plant.	1 to 111	12

B.3 Table 5. Interaction information: Description of the fields related to the interaction between flower and nectar-feeding vertebrates in Atlantic Forest.

Variable	Description	Level	Example
id_inter	Identification of each interaction sampled. The codes are not exclusive, and the same code represents the same interaction but with	1 to 3120	1

Variable	Description	Level	Example
	different deposition of pollen in the animal's body.		
latitude	Latitude in decimal degrees (GCS – WGS84) from the locality where the interaction was observed.	-31.93 to -3.87	-24.38
longitude	Longitude in decimal degrees (GCS – WGS84) from the locality where the interaction was observed.	-56.95 to -32.47	-48.85
genera_plant	Genera taxonomic classification as it appears in published study.		Capparis
genera_plan_ver	Genera taxonomic classification after taxonomic verification.		*Cynophalla*
sp_plant	Specific epitope taxonomic classification as it appears in published study.		*flexuosa*
author_plant	Species author as it appears in published study.		(L.) L.

Variable	**Description**	**Level**	**Example**
sp_plant_ver	Specific epitope taxonomic classification after taxonomic verification.		*flexuosa*
author_plant_ver	Species author after taxonomic verification.		(L.) J.Presl
genera_floralvisitor	Genera taxonomic classification as it appears in published study.		*Coereba*
genera_floralvisitor_ver	Genera taxonomic classification after taxonomic verification.		*Coereba*
sp_floralvisitor	Specific epitope taxonomic classification as it appears in published study.		*flaveola*
author_floralvisitor	Species author as it appears in published study.		Linnaeus
sp_floralvisitor_ver	Specific epitope taxonomic classification after taxonomic verification.		*flaveola*
author_floralvisitor_ver	Species author after taxonomic verification.		Linnaeus, 1758
pollinator_group	Major type of vertebrate.	bat, bird, hummingbird, lizard, monkey, opossum	bird

Variable	Description	Level	Example
bodypollendeposition	Location of pollen deposition on pollinator's body.	bac = back bil= bill bel = belly che = chest chi = chin fro = front hea = head or crown lim = limb men = ment ros = rostrum tai = tail thr = troath win = wing	bil
behavior	Feeding behavior of nectar-feeding vertebrates once on flowers. Animals are considered legitimate pollinators when they touch the flower's reproductive structure with its body. Animals are considered larcenist when they visit flowers but don't touch the reproductive structures of the flowers. The behavior "larceny" may be robbers, thief, etc.	lar = laceny pol = legitimate pollinator	pol

Variable	Description	Level	Example
relativefrequency	Calculated as the number of visits in a species of plant by a species of nectar-feeding vertebrate by the total number of visits in this species of plant in each latitude and longitude (=community).	0 to 1	0.75

B.4 Table 6. References information: Description of the fields related to the references used in the dataset of plants and nectar-feeding vertebrates in Atlantic Forest.

Variable	Description	Level	Example
id_inter	Number of identifications of the interaction sampled and presented in Table 5.	1 to 3120	1
type	Type of bibliography	a = article b = book bc = book chapter t = thesis upd = unpublish data	a
Citation	Citation in Ecology style.		Abreu e Vieira 2004

Variable	Description	Level	Example
Reference	Reference in Ecology style.		Abreu, C.R.M. and Vieira, M.F. 2004. Os beija-flores e seus recursos florais em um fragmento florestal em Viçosa, sudeste brasileiro. Lundiana 5(2): 129-134.

CLASS V. SUPPLEMENTAL DESCRIPTORS

A. Data acquisition

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CAPÍTULO 2

EVOLUTIONARY INFERENCES ON THE COMMUNITY ORGANIZATION OF FLOWER-HUMMINGBIRD INTERACTIONS IN THE BRAZILIAN ATLANTIC RAINFOREST

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INTRODUCTION

Interactions between species is a key feature of communities structure because it can influence patterns of species coexistence (Sargent and Ackerly 2008; Louthan et al. 2015), and might contribute to the occurrence of clades in an area (Giannini et al. 2011). In addition, the degree of dependence between species also influence patterns of species coexistence and the structure of ecological networks (Thompson 2005; Olesen et al. 2007). In pollination systems, theory suggests that plants should specialize on the most effective or abundant pollinator because of the high pollinator contribution to the plant fitness (Stebbins 1970) or generalize when the availability of the most effective pollinator is unpredictable over time (Johnson and Steiner 2000). As a classical theme, specialization and generalization on plant-pollination has long been debated (Buzato et al. 1994; Waser et al. 1996; Johnson and Steiner 2000; Armbruster 2017). Some suggested that specialization is rare and generalization is the rule (Waser et al. 1996), while others pointed out that plants and pollinators occupy several places in a continuum from extreme specialization to extreme generalization (Johnson and Steiner 2000; Armbruster 2017). Specialization may also occur in a cryptic manner, in which floral visitors vary in their effectiveness as pollinators (Pellmyr and Thompson 1996). In fact, the degree of specialization vary widely in plant-pollination (Pauw 2019), probably due variation in morphological traits of interacting species and behavior (Ings et al. 2009; Armbruster 2017).

In bird pollination systems, the degree of dependence of interactors species is highly variable (Pauw 2019) but in plant-hummingbirds systems, the association might be more specialized (Feinsinger and Colwell 1978; Cotton 2008; Graham et al. 2009). Striking examples on such specialization are with plants from the genus *Heliconia* (Martén-Rodríguez et al. 2011; Temeles et al. 2013; Rodríguez-Flores et al. 2019) and *Nidularium* (Fonseca et al. 2016). The degree of specialization or generalization between hummingbirds and plants might be influenced by several non-mutually exclusive factors (Vizentin-Bugoni et al. 2014). The species trait hypothesis claims that morphology constrain the number, type and strength of interactions (Stiles and Stiles 1975; Maglianesi et al. 2014, 2015) and specialized morphologies enhance the quality of pollen receipt by plants (Betts et al. 2015). Furthermore, a lot of energy is required to hover, making hummingbird-plant associations a high energetic system (Feinsinger and Chaplin 1975; Suarez 1992). This may cause interference and exploitation competition among hummingbirds (Feinsinger et al. 1979). Taking together, differences in morphology and energetic requirements lead to differences in foraging behaviors (Feinsinger et al. 1979; Cotton 2008), generating two distinct ecological groups: hermits (former Phaethornithinae subfamily) and nonhermits (former Trochilinae subfamily). Hermits usually presents a more specialized morphology and trapiliner behavior, which allows them to visit multiple plants in a single bout while the aggressive behavior of territorial hummingibirds prevents visit from hermits in clumped plants (Torres-Vanegas et al. 2019). Associated with the episodic-like memory of hummingbirds and the fact that they are well oriented spatially (Jelbert et al. 2014; Pritchard et al. 2016), different foraging behaviors affects the patterns of gene flow in distinct fashion, with trapiliner, i.e. hermits hummingbirds having a higher impact on the genetic structure of communities (Torres-Vanegas et al. 2019).

Changes on the relative importance of hermits and nonhermits between communities might occur across spatial scales because of variation on local environmental conditions and differences in the metabolic rates between hermits and nonhermits associated with the wing disc loading (ratio of body mass and diameter of wing span) and costs of hovering (Feinsinger and Chaplin 1975; Feinsinger and Colwell 1978). In this context, environmental conditions act as a filter so that so that the distribution of hermits hummingbirds declines towards higher latitudes (Rodríguez-Flores et al. 2019) and elevations (Stiles 1978; Feinsinger et al. 1979; Graham et al. 2009). The absence of hermits hummingbirds in high elevations and latitudes might also acts as a habitat filter if it prevents the presence of certain plant species in the community (Sargent and Ackerly 2008; Louthan et al. 2015). Thus, communities of plant and hummingbirds should be more specialized in lower latitudes and elevations when compared to higher latitudes and elevations. Greater specialization is expected in tropics because its environmental conditions favors natural selection by biotic interactions, leading to a great variety of morphological adaptation (MacArthur 1969). Although this concept is prone to debate since empirical studies showed controversial results (Ollerton and Cranmer 2002; Dalsgaard et al. 2011; Morris et al. 2014), there is evidence for higher morphological matching and resource specialization in hummingbird and plants closer to the tropics (Sonne et al. 2020). As for elevation, montane communities tends to have less hummingbirds species than in lowland, leading to overlap in resource use (Sazima et al. 1996; Buzato et al. 2000; Maglianesi et al. 2015), non-conservatism of floral traits and even phylogenetic pattern (Wolowski et al. 2017). Both hummingbird species and individuals are more specialized in low and mid elevations than in high elevations (Maglianesi et al. 2015).

Hummingbird functional traits influencing the degree of specialization also determine the pollination niche of plants (Phillips et al. 2020). This concept is useful to understand the origins and the maintenance of species coexistence and distribution (Phillips et al. 2020). The pollination niche might been identify throughout modularity in interactions networks (Phillips et al. 2020). Modularity occurs when networks are organized in compartments of nodes that interacts more prominently with each other and they might be the result of a long term reciprocal selection and coevolution, leading to trait convergence between interacting species (Olesen et al. 2007). For many years, studies of interactions and coevolution have focused on pairwise interactions (Strauss and Irwin 2004) searching for congruency between phylogenies of parasites and their hosts (Demastes and Hafner 1993; Da Graça et al. 2018), based on Fahrenholz's Rule, in which coevolution can lead to similarity in phylogenies topologies, and host and parasite phylogeny would mirror each other (Brooks 1985). Although pairwise interactions are uncommon in plant-hummingbirds networks and they probably exerted selective pressure as a group (Janzen 1980; Cotton 2008), those networks have shown modularity in several instances (Maruyama et al. 2014; Zanata et al. 2017; Araujo et al. 2018; but see Rodríguez-Flores et al. 2019) indicating that interactions between extant plant and hummingbird species might have been a product of coupled evolution.

Despite the knowledge about the differences on the degree of specialization of different ecological groups of hummingbirds, little effort has been made to understand their relative role in the community structure (Maglianesi et al. 2014, 2015; Torres-Vanegas et al. 2019), especially when considering their evolutionary history with plants. Here we investigated the importance of each group of hummingbirds associated with their latitudinal and altitudinal distribution in shaping the community structure of the Brazilian Atlantic Rainforest using an evolutionary and ecological perspective. The geographical characteristics and the biological composition this biome make it an interesting spot to study community structure by tracking their coupled evolutionary history. Specifically, we intend to answer two questions: 1. How the cophylogenetic signal varies between communities pollinated mainly by hermits and nonhermits hummingbirds? We expect to find higher cophylogenetic signal between hermits hummingbirds and the plants they pollinate than nonhermits (Figure 1C) because the higher degree of specialization of hermits (Feinsinger and Colwell 1978; Cotton 2008) might be an indication of coupled evolution. 2. How the cophylogenetic signal in communities visited by these two groups of hummingbirds varies between latitudes and altitudes? We expect to find higher cophylogenetic signal in communities closed to the tropics and in lowlands because in those regions there is higher morphological matching and resource specialization (Sonne et al. 2020) and higher hummingbirds species, leading to partition of resources (Sazima et al. 1996; Buzato et al. 2000; Maglianesi et al. 2015). Futhermore, the distribution of the specialized hermits hummingbirds are centered in lowlands and lower latitudes (Stiles 1978; Feinsinger et al. 1979; Graham et al. 2009; Rodríguez-Flores et al. 2019).

MATERIALS AND METHODS

1. Study site

The Atlantic Rainforest originated, along with other Neotropical forest, 58-55 Ma. ago with higher expansion in early Eocene ca. 45 Ma, due warming and increasing moisture (Graham 2011). It originally occupied an area of 150 million ha. (Ribeiro et al. 2009) ranging from 0° to 30°S, comprising a wide variety of climatic conditions (Ledru et al. 2005). The historical formation of Atlantic Forest was influenced by global climatic changes during the Quaternary, when the dynamics of rainfall regime promoted consecutive expansion and retractions of the forest during the past 100.000 yr. (Ledru et al. 2005). Despite the hydrological and vegetational variability throughout the Quaternary, the diversity of species seems to have been intact in mountainous areas, which is considered interglacial microrefugia for the wildlife (Montade et al. 2014). The altitudinal range of Atlantic Forest vary from the sea level up to 2700 m above sea level (Joly et al. 2014).

In Brazilian Atlantic Rainforest, different patterns of precipitation define climatic boundaries between three areas with different phylogeographic patterns: the northern area (between 5°S and 15°S), with drier conditions and a moist cool semi-deciduous forest restricted to coastal zones, lowland galleries forest and mountaintops; a central area (between 15°S and 23°S) with rainy summers and dense evergreen forest and semi-deciduous forest in inland zones; and the southern area (between 23°S to 30°S), with permanent moisture or short winter dry season and prevalence of *Araucaria* forest mixed with evergreen forest (Ledru et al. 2016).

Nowadays, the remaining area of Brazilian Atlantic Rainforest correspond to only 11.4% to 16% of the original extension (Ribeiro et al. 2009), mainly due several types of unplanned human occupation (Joly et al. 2014). The Brazilian Biome have high endemism rates, for example of 30% in birds (Hasui et al. 2018), 73% in primates and 44% in plants (Mittermeier et al. 2004). Together, the intense fragmentation and the high endemism rates, places the Brazilian Atlantic Rainforest among the five hottest hotspot of biodiversity in the world (Mittermeier et al. 2004).

2. Study system

Hummingbirds splitted from swifts and treeswifts approximately 42 Ma. ago, in Eurasia and dispersed to South America about 22 Ma. (McGuire et al. 2014). In South America, the extant linages originated in Early Miocene from a common ancestor followed by a high rate of diversification, possible due the orogeny of the Andes and the diffuse coevolution with the plants they pollinate (McGuire et al. 2014). The Trochilidae family was classically divided into two subfamilies, Trochilinae and Phaethornithinae (McGuire et al. 2007), but recent studies have shown polyphyly in Trochilinae clade and a new classification of nine principal clades has been proposed (Bleiweiss 1991; McGuire et al. 2007, 2009, 2014). Overall, Emeralds, Mountain Gems and Bees have higher net diversification rates in contrast with Hermits and Topazes (McGuire et al. 2014).

Due the variable morphology and metabolic rates (Feinsinger and Chaplin 1975; Suarez 1992), despite the taxonomic and phylogenetic classification, hummingbirds are divided into two ecological groups with morphological, physiological and behavioral differences: the hermits, represent mainly by hummingbirds from Hermit clades (former Phaethornithinae subfamily) and the nonhermits, represented by all other hummingbirds. In general, the nonhermits are considered less specialized because they present a wide range of bills lengths and usually holds and defends territories (Feinsinger and Colwell 1978; Bleiweiss 1998b; Cotton 2008; Rodríguez-Flores et al. 2019). On the other hand, the hermits are considered more specialized because they have evolved adaptations in bill to correspond to flower morphology, ensuring access to almost exclusive resources in flower with long and/or curved corollas (Feinsinger et al. 1979; Rodríguez-Flores et al. 2019). These hummingbirds usually presents trapiliner behavior, feeding from scattered flowers (Snow and Snow 1972; Feinsinger and Colwell 1978; Cotton 2008). Nevertheless, all hummingbird species are prone to behave as a trapiliner and/or territorialist, depending on the community context (Feinsinger and Colwell 1978).

The Brazilian Atlantic Rainforest has about 32 species of hummingbirds of which ten are endemic (Grantsau 1988; Hasui et al. 2018) and the floristic composition comprises several taxonomic groups, with some highly specialized in hummingbird pollination (e.g. Bromeliaeceae, Gesneriaceae and Heliconiaceae , Buzato et al. 2000, Iamara-Nogueira*,* Cap. 1). The principal clades of hummingbirds in Brazilian Atlantic Rainforest are Emerald with 44% of all species, Hermits with 25% and the remaining species are included in Mangoes, Coquetes, Bees, Brilliants, Mtn. Gems and Topazes (Iamara-Nogueira, Cap. 1).

3. Plant-hummingbird interaction data

The data on plant-hummingbird interaction was taken from the dataset from flower-vertebrate interaction of the Atlantic Rainforest (Iamara-Nogueira*,* Cap. 1). This dataset was built with data from 213 unpublished and published studies in articles, book chapters and dissertations and PhD thesis from 1977 to 2015. The database includes geographic information of directed observation of the interaction, e.g. focal observation of hummingbird species visiting flowering species. For the purpose of this study, we used information of presence or absence of the interaction.

4. Hermit and nonhermit pollination classification

To account the importance of each group of pollinator on the cophylogenetic signal between phylogenies, plants were divided into two categories: visited manly by nonhermits (when number of nonhermits hummingbirds visiting the plant species were > 66%) representing 31% of all interactions and visited manly by hermits (when number of hermits hummingbirds visiting the plants species were > 66%) representing 60% of all interactions. The remaining 9% plants were classified as mixed and left out of the analysis. In order to minimize the effect of higher number of nonhermits species, the number of hummingbird species of each group that visits a particular flower was divided by the total number of species in that group present in the database, that is, ten hermits and 30 nonhermits. This classification was also made considering the frequency of visits available in the datapaper, but comparison between the classification made with the number of species and the frequency of visits were not different ($t = 0.175$, $p = 0.861$). The number of species was used because there was more data available.

5. Latitudinal and altitudinal data

Considering the possibility of latitude and altitude promote changes in cophylogenetic signal between plant and hummingbird phylogenies, the latitudinal distribution of data was divided into eight ranges of 1° decimal and the altitudinal distribution in five ranges of 500 m, including only communities with more than 10 plant species and more than 5 hummingbird species (Figure 1A). The selected communities cover the latitudinal range of 8°S to 26°S and the altitudinal range from 0 to 2500 m above sea level. The data comprises the three areas of phylogeographic patterns defined by climatic conditions (Ledru et al. 2016) and almost the total range of elevation in Atlantic Forest (Joly et al. 2014). Beta diversity (β_{SOR}), species turnover (β_{SIM}) and nestedness (β_{SNE}) among sites across latitudes and altitudes were computed with Sorensen index using the function *beta.multi* in betapart package (Baselga and Orme 2012) in R environment (R Core Team 2018).

6. Plants and birds' phylogenetic trees

In order to access the importance of the history of interactions, it was used phylogenies of plants and hummingbirds. For plants, it was used an additive phylogenetic megatree with 356.305 species of seed plants, based on the Open Tree of Life project (Smith and Brown 2018). One caveat of this super-tree is the many polytomies due to absence of molecular data for several groups that were inserted based only on taxonomy, but previous work showed that the topology of trees does not interfere in the results of studies involving communities (Aizen et al. 2016; Li et al. 2019). Nevertheless, to account the possible effect of incomplete resolution on plant phylogeny on the results, we used the algorithm *PolytomyResolver* (Kuhn et al. 2011) that consist in a constant rate birth-death model that produces an input file to be applied on BEAST software (Suchard et al. 2018). This software randomly resolves the polytomies and adjusts branch lengths based on birth-death model. The BEAST software applies Markov Chain Monte Carlo (MCMC) that produces 10^4 alternative trees. To obtain the maximum clade fully resolved credibility tree we used BEAST output in TreeAnnotator with 25% of burning. The phylogenetic distance matrices of the original tree and the resolved credibility tree were compared using Mantel Correlation test. The correlation of its patristic distance with the fully resolved consensus tree were extremely high ($r = 0.99$, $p = 0$). For hummingbirds, it was used a fully resolved and well supported dated ultrametric tree based on 284 species of hummingbirds and six genes (four nuclear and two mitochondrial) in five loci (McGuire et al. 2014). After comparing and pruning matching species in the database and phylogenies, the three sets of data — the entire Brazilian Atlantic Forest as well this Biome subdivided by latitude and altitude — for this study contains 327 native plant species, 31 native hummingbird species (26 nonhermits and five hermits) and 1102 unique associations.

7. Relative importance of history and ecology to the organization of hermits and nonhermits-flower interactions

In order to verify the relative importance of history and ecology of interactions in the organization of plant and hummingbird interaction, the congruency between birds and plants phylogeny we accessed using Procrustes Approach to Cophylogenies (PACo) (Balbuena et al. 2013) and Random Tanglegram Partitions (Random TaPas) (Balbuena et al. 2020). PACo is a global-fit method that uses Procrustes technique to display datasets in their optimal superimposition (Balbuena et al. 2013). This method is used to quantify the degree of congruency between the topology of two given trees and to identify the associations with higher contribution to the cophylogenetic signal (Balbuena et al. 2013). The advantages of this method is that it allows non pairwise interactions, can handle large-scale cophylogenetic analysis and, since it used distance or dissimilarity matrices, does not require fully resolved phylogenies (Balbuena et al. 2013).

Despite these advantages, PACo analysis do not produces a clearly interpretable statistic regarding the strength of the signal (Balbuena et al. 2020), making comparisons complicated to make. Then, Random TaPas applies to a given global-fit method a series of random partial tanglegrams of fixed size based on number of unique interactions and returns the frequency of distribution of the statistic of the global-fit method in a small percentile where the highest cophylogenetic congruency is expected (Balbuena et al. 2020). The shape of this distribution can be expressed as a normalized Gini coefficient (G^*) that is expected to be inversely proportional to the cophylogenetic signal (Figure 1B): when each association between interactors contributes equally to the global-fit, the cophylogentic signal is at its maximum resulting in a $G^* = 0$ and when the associations contributes very unevenly to the congruency, the signal is very low and G^* would approach one (Balbuena et al. 2020). Normalized Gini values should be considered only when the PACo show significance. Since the plant phylogeny is an additive tree, the signal is considered strong when G* values is below the threshold of 0.72, moderate when it approaches the threshold and weak when it is above the threshold (see Balbuena et al. 2020 for details).

Another advantage of Random TaPas is that phylogenetic uncertainty can be incorporate in the analysis, which is an important step since phylogenies represent hypothesis of evolutionary history and may lead to wrong conclusions if not all clades are well supported. To this end, plants and hummingbirds well resolved probabilities trees were generated with the model *PolytomyResolver* (Kuhn et al. 2011)) applied in BEAST software (Suchard et al. 2018). From the generated trees, we draw 1.000 random plant trees and 1.000 random hummingbird trees and RandomTapas was applied for each pair of probability trees to obtain a range of residual distribution (i.e. G* values) (Balbuena et al. 2020). The observed G* values is then plotted against the range of simulated G* values to access the confidence of the results.

The application of RandomTaPas to our system and data is not without some caveats. (Balbuena et al. 2020). It is important to bear in mind that temporal congruence between the two phylogenies is relevant to get higher confidence in the strength of the signal and to infer the processes underling the phylogenetic congruency (Balbuena et al. 2020), so the results must be interpreted carefully. Another important observation is that, as we are working with a diffuse system of interaction between plants and hummingbirds, unique interactions are rare (Janzen 1980; Cotton 2008) and often it was not possible generate partial tanglegrams of fixed size with 10% of the number of total associations in each network, which is the recommended percentage of unique association in the tanglegram to estimate cophylogenetic signal (Balbuena et al. 2020). In this paper, the fixed size of tanglegrams to run Random Tapas were determined as the higher number of unique interactions to generate the higher number (up to 1000) of partial tanglegrams.

Despite these drawbacks, we are assuming that, due the diffuse nature of hummingbird pollination interactions, the analysis implanted here still sheds light on the shared evolutionary history of plants and hummingbirds (Hutchinson et al. 2017a). The analyzes were made for all hummingbirds and the plants they pollinated within the dataset from Atlantic Rainforest (MW) as well for each hummingbird groups, the hermits and their plants (HW) and nonhermits and their plants (NW). We applied the same analysis for the whole hummingbird web and hermtis and nonhermits web in each eight latitudinal and five altitudinal ranges. PACo analysis were performed with package paco (Hutchinson et al. 2017b) using patristic distances as input and Random TaPas was implemented using the script provided by the authors (Balbuena et al. 2020) using the function Gini_RSV of package GiniWegNeg (Raffineti and Aimar 2016) to calculate the normalized Gini Coefficient. All analyzes was performed in R environment (R Core Team 2018).

RESULTS

Interactions between hummingbirds and plants in the Brazilian Atlantic Rainforest (MW) showed an overall moderate cophylogenetic signal (Figure 2A). The cophylogenetic signal was present for both the interaction between hermits (HW) and the plants they pollinate and the interaction between nonhermits (NW) and their plants (Figure 2B, C) but it was stronger for hermits than nonhermits (Figure 2B, C). The number of plants visited by each group is given in Table 2. For hermits and their plants, the interactions contributing significantly to the signal were those related to the hummingbird *Ramphodon naevius* (Dumont, 1818) (Welch t-test: $t = 3.64$, $p = 0.00$, Figure 2). The Gini values obtained with hummingbirds and their plants and hermits and their plants were within the range of G*s obtained with 1000 pair of probability trees (Figure S1). There was no enough variation in simulated G* values to account for phylogenetic uncertainty in nonhermits web (Figure S1).

Across the latitudes, five out of eight communities presented cophylogenetic signal in the interaction between hummingbirds and plants. In general, the signal was weak, except for the lowest latitude where a moderate signal was present (Table 1, Figure 3A). The interaction between the hermit *Phaethornis ruber* (Linnaeus, 1758) and the non-hermit *Thalurania watertonii* (Bourcier, 1847) with Bromeliaceae species presented the smallest residuals at the lowest latitude (Table S1). Beta diversity and species turnover across latitudes were high for plants ($\beta_{SOR} = 0.88$, $\beta_{SIM} = 0.79$) and moderate for hummingbirds ($\beta_{SOR} = 0.67$, $\beta_{SIM} = 0.51$), while nestedness for plants (β_{SNE}

= 0.09) and hummingbirds (β_{SNE} = 0.16) were low, indicating that communities are equally rich but different in species composition. The number of plants visited by each group in each latitudinal range is given in Table 2. For the hermits hummingbirds and their plants, cophylogenetic signal was present in two communities – latitude -19 with a strong co-phylogenetic signal, and latitude -22 with a moderate co-phylogennetic signal (Table1, Figure 3A). In these communities, the smallest residuals were given by the interaction with plants of Bromeliaceae, Heliconiaceae and Costaceae families (Table S2, S3). For the nonhermit web, there were no evidences for phylogenetic congruency, except for a moderate signal in the community at latitude -22 (Table 1, Figure 3A). At this latitude, the small residuals were associated with a wide variety of interactions (Table S4). In general, the observed G* values of hummingbirds and plants, hermits and plants and nonhmerits and plants were within the range of G*s obtained with 1000 pair of probability trees, except for the hermits in some latitudes (Figure S2). In a few cases, the phylogenetic uncertainty could not be accessed (Figure S2).

Weak cophylogenetic signal for the plants and hummingbirds was found in lower elevations and there was a tendency to decrease the observed G* values with altitude (Table 1, Figure 3B). Only few species of hermits hummingbirds found in higher elevations, making it impossible to run the analysis. In lower elevations there was a weak signal only in the range 500 to 1000 m asl for both hermits and nonhmertis (Table 1, Figure 3B). Beta diversity across altitudes were high for plants (β_{SOR} = 0.84) and moderate for hummingbirds (β_{SOR} = 0.65) while and turnover for were high for plants (β_{SIM} = 0.67) and low for hummingbirds (β_{SIM} = 0.16). In contrast, nestedness were low for plants (β_{SNE} = 0.16) and relatively high for hummingbirds (β_{SNE} = 0.48), indicating that communities are different in plant and hummingbird species composition and lowland communities have higher number of hummingbird species than highland communities (Table 2). The number of plants visited by each group in each community is given in Table 2. Almost all observed G* values were within the range of G*s obtained with 1000 pair of probability trees, except for all hummingbirds and nonhermits hummingibirds in mid elevations (Figure S3). In elevations from 1500 m to 2000 m asl is was not possible to access the phylogenetic uncertainty (Figure S3).

DISCUSSION

The degree of dependence between plants and their pollinators has been shown to influence the community structure in different spatial scales (Maglianesi et al. 2014, 2015; Torres-Vanegas et al. 2019). Plant-hummingbirds networks are often modular (Maruyama et al. 2014; Zanata et al. 2017; Araujo et al. 2018), which indicates a high degree of specialization probably due long term reciprocal selection and coevolution (Olesen et al. 2007). Here, we explored the relative importance of two groups of hummingbirds with different degree of ecological specialization associated with their latitudinal and altitudinal distribution and their phylogenetic congruency to comprehend their influence in community structure of the Brazilian Atlantic Rainforest. Despite the strong congruence observed for the associations between hummingbirds and plants in Atlantic Rainforest, the cophylogenetic signal was different between hermits and nonhermits webs. Hermits hummingbirds are the main responsible for the congruence observed in the whole web and the higher cophylogenetic signal in this group was expected, since these birds shows a higher degree of ecological specialization (Feinsinger and Colwell 1978; Bleiweiss 1998b; Maglianesi et al. 2014, 2015). This result points out that coevolutionary process may be responsible for the organization of hermit's interactions with plant. Highlighted are the interactions between Bromeliaceae species and hermits, because they appeared as a consistent compartment strongly contributing to the cophylogenetic signal. This is an indication that hermit and Bromeliaceae species were probably under reciprocal selection and influence each other evolutionary history. (Olesen et al. 2007). In contrast, nonhermits webs didn't show cophylogenetic signal or modules. This result is also expected, since nonhermits are considered more generalists due its high variation on bill length, allowing visitation in flowers with wide range of morphologies (Feinsinger and Colwell 1978; Bleiweiss 1998; Cotton 2008; Rodríguez-Flores et al. 2019). This is an indication that past evolutionary history has little effect on the extant interactions and the organization of nonhermits webs is mainly made by current ecological factors.

The strong congruence between hermits hummingbirds and plants is reflected on their morphological affinity and higher pollination efficiency (Torres-Vanegas et al.

2019). According to previous studies (Buzato et al. 2000), these results indicate that hermits hummingbird are the main organizers of communities in Brazilian Atlantic Rainforest, especially for bromeliads. Bromeliaceae is a highly diverse family, found almost exclusively in Neotropics and are one of the most ecological diverse of flowering plants (Givnish et al. 2011). In the Brazilian Atlantic Forest, Bromeliaceae represents almost 40% of hummingbirds pollinated species (Iamara-Noguiera, Cap. 1) and are the main source of food for hummingbirds which are, in turn, their main pollinator (Buzato et al. 2000). A time-calibrated phylogeny for Bromeliaceae was provided by Givnish *et al* (2011) which, despite not containing all the species contemplated in this study, has three subfamilies well represented in our database (Tillandsioideae, Pitcairnioideae and Bromelioideae). The comparison of this bromeliad tree with the calibrated hummingbird phylogeny provided by McGuire *et al* (2014) can shed some light on the evolutionary history of these two groups. The extant subfamilies of Bromeliaceae probably began to diverge about 19 Ma (Givnish et al. 2011) coinciding with the diversification of extant hummingbird species 22 Ma ago (McGuire et al. 2014). Avian pollination arose 2-3 times in Bromeliaceae, once in core tillandsiods ca 15.2 Ma, once in ancestral tillandsioids 14.2 Ma and in the ancestor of Pticairnioideae-Puyoideae-Bromelioideae ca. 15.9-14.1 Ma (Givnish et al. 2014). All these events coincide in time with the origin of hermit's hummingbirds, ca. 15 Ma and also with the origin of the hermit hummingbird *R. naevius* (McGuire et al. 2014). However, despite the overlapping in time of divergence of some bromeliads and hummingbirds, ancestral state reconstruction of these two groups indicates that the place of origin is not always the same. This comparison reinforces our results about the importance of hummingbirds and plants interaction and, at the same time, calls attention to the joint evolution of these groups to be studied within the context of the Atlantic Forest. Among hummingbirds, the greater signal between Bromeliads and the hermit *Ramphodon naevius* also indicated a process of joint process of evolution, which leads to high specialized interaction. This hummingbird species is classified as a high reward trapliner and present aggressive behavior, dominating the resources at lowland communities (Sazima et al. 1995; Buzato et al. 2000). This species is found mainly in elevations below 500 m and in rare occasions they are found above this threshold, up to 900 m (Ridgely et al. 2016). The greatest contribution to the signal of this species of hummingbirds and bromeliads According to previous studies (Buzato et al. 2000), our results shows that the hummingbird *species R. naevius* have great importance on the organization of lowlands communities in Atlantic Forest.

Contrasting with the most-basal Hermits which are less diverse and restricted to lowlands and with the exception of Topazes, nonhermits hummingbirds are more diverse (McGuire et al. 2014). The greater diversification of this group is associated with the occupation of new areas and the specialization on different niches which allowed the coexistence of several species (McGuire et al. 2009). Indeed, Mangoes, Emeralds and Bess are over dispersed and are found in a great variety of habitats (Bleiweiss 1998a; Graham et al. 2009). Migratory habits of these hummingbirds guarantees a predisposition for long distance movements and toleration for a wide range of environmental conditions (Bleiweiss 1998a). Since hermits distribution are more restricted than nonhermits, the composition of hummingbirds species in different communities might promote chances in resource use and competition among species (Feinsinger 1976). The lack of congruency the we observed in most of the communities in this study might be an indicative that nonhermits hummingbirds are strongly influencing community structure depending not on historical process but rather on local ecological features. Since these birds do not show the same morphological match with flowers observed for hermits (Feinsinger and Colwell 1978; Bleiweiss 1998b; Cotton 2008; Rodríguez-Flores et al. 2019), the reciprocal selection might have been prevented from occurring (Thompson 2005). Besides hummingbird composition, the spatial distribution of plants (Morales and Vázquez 2008), morphological match (Feinsinger 1976; Vizentin-Bugoni et al. 2014) and phenological overlap (Vizentin-Bugoni et al. 2014) were identified as the main factors predicting interactions because the variation in these characteristics creates highly specialized interactions (Linhart 1973; Stiles and Stiles 1975; Maglianesi et al. 2014, 2015). In Brazilian Atlantic Rainforest, flowers might have clumped or dispersed distribution that are not species-specific and can vary across communities (Feinsinger and Colwell 1978; Buzato et al. 2000). Because beta diversity and turnover of species were high among communities, there should be a variation in floral and birds' morphologies and phenology and in the pattern of distribution of plants at different sites. Taking together, composition of hummingbirds at different sites, the availability of foraging behaviors in communities and the availability of resources

(Feinsinger 1976; Feinsinger and Colwell 1978; Buzato et al. 2000; Morales and Vázquez 2008), might allow or force nonhermits hummingbirds to assume more specialized foraging behaviors that shapes community structure (Torres-Vanegas et al. 2019). Therefore, the classification of hermits hummingbirds as specialists and nonhermits as generalists should be placed in a continuum (Buzato et al. 1994; Johnson and Steiner 2000) because it depends not only on morphology but also on ecological and historical context of communities. As an important example that rises from this study, the nonhermit *Thalurania watertonii* highly contributed with the cophylogenetic signal in the community at the lowest latitude, indicating that this species also had a coupled evolutionary history with Bromeliaceae. This species is endemic of Northeast of Brazilian Atlantic Rainforest (Las-Casas and Azevedo-Júnior 2009) and behaves both as territorialists and as trapilines (Siqueira Filho and Machado 2001).

Nonetheless, the results found for latitude and altitude should be interpreted carefully. Despite our study covered almost the entire latitudinal and altitudinal range of Brazilian Atlantic Rainforest and the differences in beta diversity are mainly due the turnover of species rather the loss of species across communities, our data is biased towards the coast of Southeast of Brazil and lowlands (Figure 1A, Table 2, Iamara-Nogueira, Cap. 1) and Bromeliaceae family (Iamara-Nogueira, Cap. 1). Therefore, it is important to note that the lack of cophylogenetic signal in some communities might be simply because not all possible interactions were observed. At the same time, the observed cophylogenetic signal for hermits' hummingbirds might been an artifact of the concentration of sampling in the main area of distribution of the hummingbird species *Ramphodon naevius*. In this sense, broader observations of interactions across Atlantic Forest and surveys on morphological, phenological and demographic data are essential to better understand how differences on the degree of specializations are related to the community structure. Furthermore, we used latitude and altitude as a proxy for environmental conditions that might be acting as a filter to pollinator range distribution and for the degree of specialization in communities. We treated latitude and elevation as independent factors, but it is very likely that the combination of these two variables generate very different climatic conditions from place to place, which can influence the degree of specialization at a finer scale. Therefore, the incorporation of environmental data known to influence species distribution might help understand how interactions shapes community structure.

In this study we demonstrated that the relative importance of hermits and nonhermits for the structure of communities are related to different process. Hermits hummingbirds and their plants showed a high cophylogenetic signal, indicating that coupled evolutionary history is the main driver of these interactions. On the other hand, the lack of cophylogenetic signal for nonhermtis and their plants indicates that ecological process might be acting on these interactions. Moreover, the lack of cophylogenetic signal in communities in different latitudes and altitudes indicates that environmental and ecological particularities of each location might influence the feeding behavior of hummingbirds, changing the patterns of interactions and influencing the relative importance of each group of hummingbirds for the structure of communities. These results call attention to the classification of hermits and nonhermits as specialist or generalists because hummingbirds are able to behave in distinct manners depending on community's composition and visit flowers that otherwise would not be available. Furthermore, the survey of interactions spanning the whole Biome rather than local communities is essential to understand the dynamic of interactions and, to our knowledge, this is the first time that this large-scale research in Brazilian Atlantic Rainforest has been done.

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TABLES AND FIGURES

Table 1. Presence of cophylogenetic signal (PACo analysis, m^2_{xy} and p values) and its strength (RandomTAPAS analysis, G* values) for METAWEB (MW), hermits web (HW) and nonhermits web (NW) in each latitudinal and altitudinal range in Brazilian Atlantic Rainforest. Cophylogenetic signal is considered strong only when G* is higher than the 0.72 threshold. Only systems when the signal is present and strong are highlighted.

		MW			HW			NW		
		m^2_{xy}	**p**	**G***	**m^2_{xy}**	**P**	**G***	**m^2_{xy}**	**p**	**G***
Latitude	**-8**	**0.95**	**0.01**	**0.71**	0.98	0.67	0.66	0.54	0.19	0.57
	-13	0.93	0.32	0.67	**0.88**	**0.02**	**0.61**	---	---	---
	-19	0.97	0.01	0.81	0.97	0.31	0.66	0.45	0.84	---
	-20	0.96	0.37	0.72	---	---	---	0.77	0.32	0.65
	-22	0.97	0.00	0.73	**0.94**	**0.02**	**0.71**	**0.93**	**0.01**	**0.71**
	-23	0.98	0.00	0.73	0.98	0.22	0.82	0.94	0.50	0.73
	-24	0.97	0.00	0.72	---	---	---	0.94	0.77	0.64
	-25	0.95	0.10	0.72	---	---	---	0.87	1.00	---
Altitude	**0 – 500**	0.98	0.00	0.75	0.98	0.25	0.73	0.92	0.40	0.72
	500 – 1000	0.97	0.00	0.74	0.90	0.00	0.73	0.86	0.03	0.73
	1000 – 1500	0.97	0.00	0.72	---	---	---	0.92	0.84	0.62
	1500 – 2000	0.97	0.12	0.70	---	---	---	0.89	0.40	0.64
	2000 – 2500	0.95	0.09	0.68	---	---	---	0.94	0.15	0.67

Table 2. Characteristic of each community pollinated by hummingbirds in Brazilian Atlantic Rainforest, after consider the intersect with species present in plant and bird phylogeny. We present the number of hemits hummingbirds and the number of plants that they visit and the number of nonhermit hummingbirds with the number of plants that they visit.

	Community	Hermits	Hermit plants	Nonhermits	Nonhermit plants
	MW	5	180	21	84
Latitude	**-8**	3	27	4	5
	-13	3	9	--	--
	-19	4	38	3	3
	-20	2	18	10	7
	-22	5	53	14	44
	-23	5	69	15	30
	-24	2	31	11	10
	-25	2	16	5	4
Elevation	**0 – 500**	5	91	16	36
	500 – 1000	5	105	18	31
	1000 – 1500	1	42	9	11
	1500 – 2000	1	11	5	13
	2000 – 2500	--	--	5	13

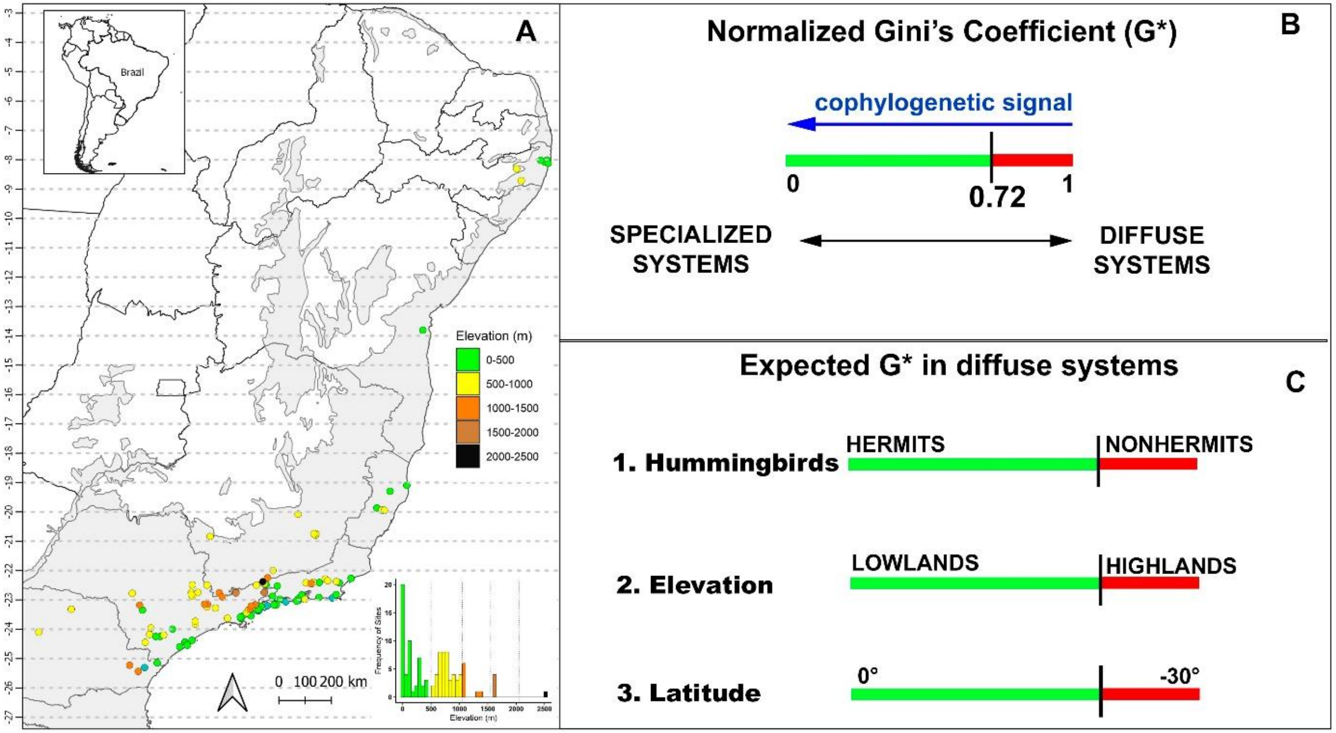

Figure 1. Latitudinal and altitudinal ranges of plant and hummingbirds' interactions used in this study to analyze the importance of altitude and elevation to cophylogenetic signal **(A)**, conceptual diagram about normalized Gini´s Coefficient on specialized and diffuse systems **(B)** and expectations on Gini's Coefficient regarding to group of hummingbirds, elevation and latitude **(C)**. See text for details.

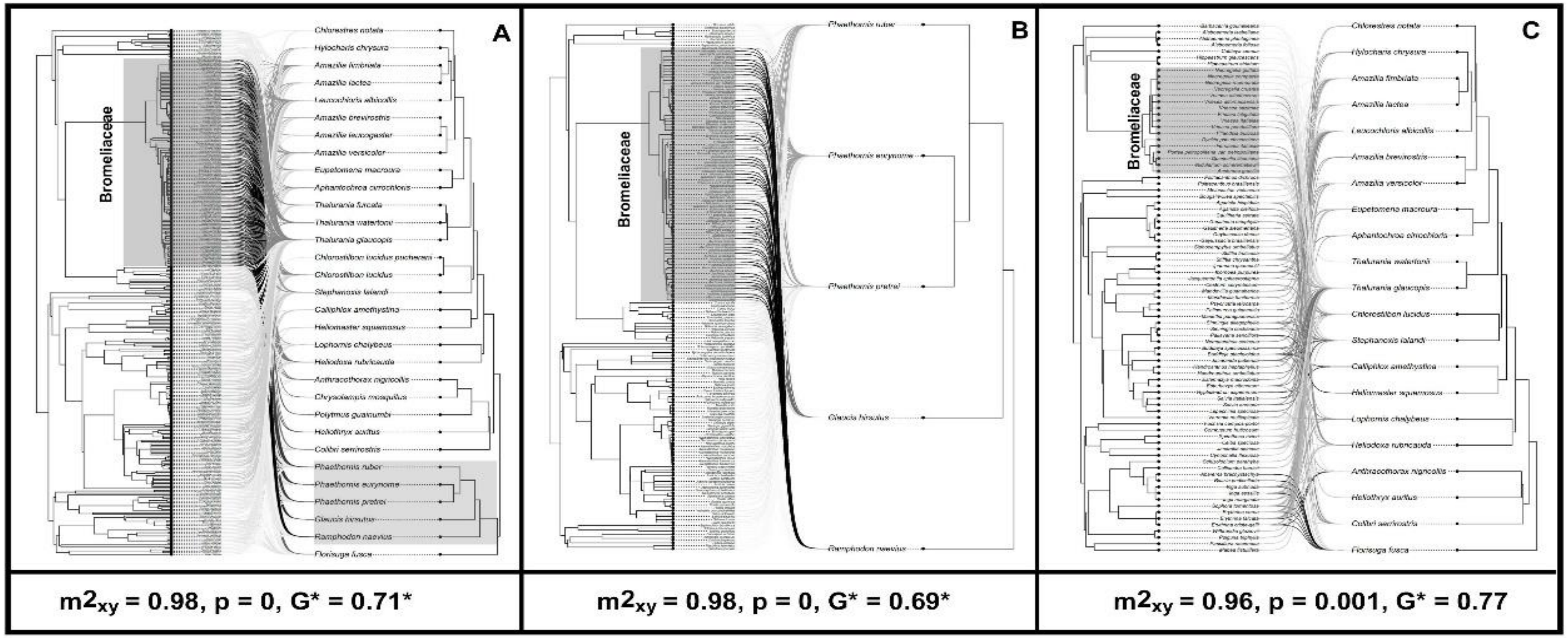

Figure 2. Tanglegram, PACo results and normalized Gini Coefficient (G*) of the associations between all hummingbirds and their plants (A - MW) and between hermits (B - HW) and nonhermits (C - NW) and their plants. The gray scale intensity of the links shows the contribution of each association to the congruency, varying from low contribution (light gray) and high contribution (black). Highlight sections shows clades with more specialized associations. The asterisk in G* values demonstrated values within the range of G*s obtained with 1000 pair of probability trees.

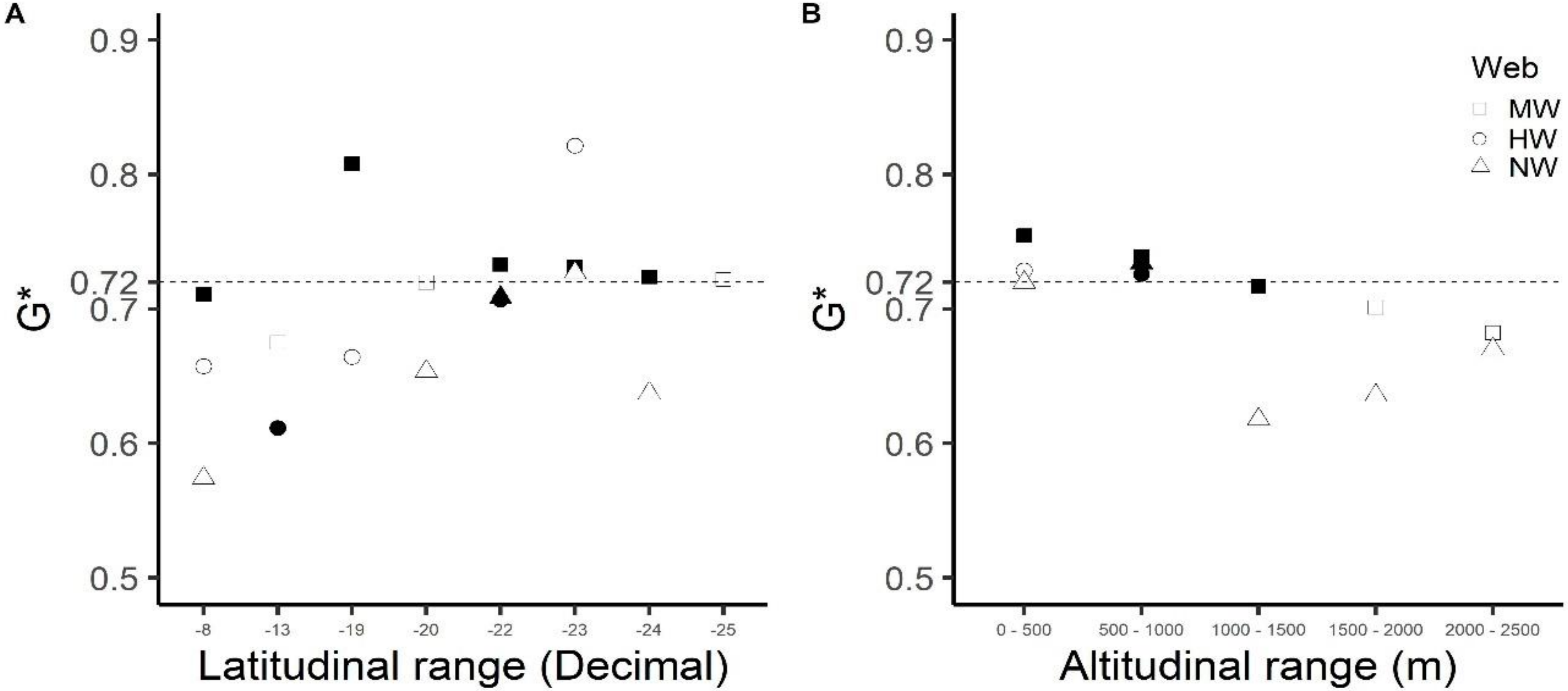

Figure 3. Normalized Gini Coefficient (G*) plotted against latitude (A) and altitude (B) for the three webs. Closed symbols indicate significant congruency between plants and hummingbirds' phylogenies (PACo $p < 0.05$) and values below the threshold of 0.72 represents a strong signal.

SUPPLEMENT MATERIALS

TABLE S1. The fifteen interactions with the smallest residuals for the MW in the communities at the latitudinal range -8.

Interaction	**procrustes residuals (10^2)**
Canistrum_aurantiacum-Phaethornis_ruber	6.64
Lymania_smithii-Phaethornis_ruber	6.64
Aechmea_muricata-Phaethornis_ruber	6.64
Billbergia_morelii-Phaethornis_ruber	6.64
Aechmea_tomentosa-Phaethornis_ruber	6.65
Aechmea_leptantha-Phaethornis_ruber	6.65
Aechmea_fulgens-Phaethornis_ruber	6.65
Bromelia_karatas-Phaethornis_ruber	6.68
Tillandsia_bulbosa-Thalurania_watertonii	6.68
Tillandsia_gardneri_var._gardneri-Thalurania_watertonii	6.69
Tillandsia_tenuifolia-Thalurania_watertonii	6.69
Guzmania_lingulata-Thalurania_watertonii	6.69
Vriesea_procera-Thalurania_watertonii	6.69
Vriesea_flammea-Thalurania_watertonii	6.69
Pseudananas_sagenarius-Phaethornis_ruber	6.70

TABLE S2. The fifteen interactions with the smallest residuals for the HW in the communities at the latitudinal range -19.

Interaction	**procrustes residuals (10^2)**
Aechmea_bromeliifolia-Glaucis_hirsutus	3.18
Aechmea_lamarchei-Glaucis_hirsutus	3.18
Nidularium_procerum-Glaucis_hirsutus	3.31
Billbergia_bradeana-Glaucis_hirsutus	3.34
Aechmea_saxicola-Glaucis_hirsutus	3.47
Aechmea_araneosa-Glaucis_hirsutus	3.48
Aechmea_perforata-Glaucis_hirsutus	3.52
Nidularium_espiritosantense-Ramphodon_naevius	5.29
Nidularium_cariacicaense-Ramphodon_naevius	5.29
Edmundoa_lindenii-Ramphodon_naevius	5.29
Nidularium_procerum-Ramphodon_naevius	5.29
Quesnelia_quesneliana-Ramphodon_naevius	5.29
Quesnelia_strobilispica-Ramphodon_naevius	5.29
Billbergia_euphemiae-Ramphodon_naevius	5.36
Billbergia_amoena-Ramphodon_naevius	5.36

TABLE S3. The fifteen interactions with the smallest residuals for the HW in the communities at the latitudinal range -22.

Interaction	**procrustes residuals (10^2)**
Billbergia_amoena-Phaethornis_pretrei	7.47
Billbergia_pyramidalis-Phaethornis_pretrei	7.47
Billbergia_horrida-Phaethornis_pretrei	7.47
Quesnelia_augusto-coburgii-Phaethornis_pretrei	7.48
Aechmea_fasciata-Phaethornis_pretrei	7.50
Canna_indica-Ramphodon_naevius	7.67
Heliconia_farinosa-Glaucis_hirsutus	7.75
Vriesea_psittacina_var._psittacina-Phaethornis_pretrei	7.76
Heliconia_spathocircinata-Glaucis_hirsutus	7.81
Heliconia_angusta-Glaucis_hirsutus	7.82
Costus_spiralis-Ramphodon_naevius	8.26
Costus_spiralis-Glaucis_hirsutus	8.36
Heliconia_spathocircinata-Ramphodon_naevius	8.38
Heliconia_farinosa-Ramphodon_naevius	8.38
Heliconia_angusta-Ramphodon_naevius	8.38

TABLE S4. The fifteen interactions with the smallest residuals for the NW in the communities at the latitudinal range -22.

Interaction	**procrustes residuals (10^2)**
Buddleja_stachyoides-Stephanoxis_lalandi	7.84
Buddleja_speciosissima-Stephanoxis_lalandi	7.85
Salvia_itatiaiensis-Stephanoxis_lalandi	7.97
Salvia_arenaria-Stephanoxis_lalandi	7.97
Gaultheria_sleumeriana-Chlorostilbon_lucidus	7.99
Gaultheria_eriophylla-Chlorostilbon_lucidus	7.99
Sinningia_cochlearis-Stephanoxis_lalandi	8.02
Sinningia_allagophylla-Stephanoxis_lalandi	8.02
Agarista_hispidula-Chlorostilbon_lucidus	8.05
Erythrina_falcata-Florisuga_fusca	8.20
Erythrina_verna-Florisuga_fusca	8.20
Erythrina_verna-Anthracothorax_nigricollis	8.23
Vriesea_penduliflora-Heliodoxa_rubricauda	8.38
Vriesea_itatiaiae-Heliodoxa_rubricauda	8.38
Vriesea_altomacaensis-Heliodoxa_rubricauda	8.38

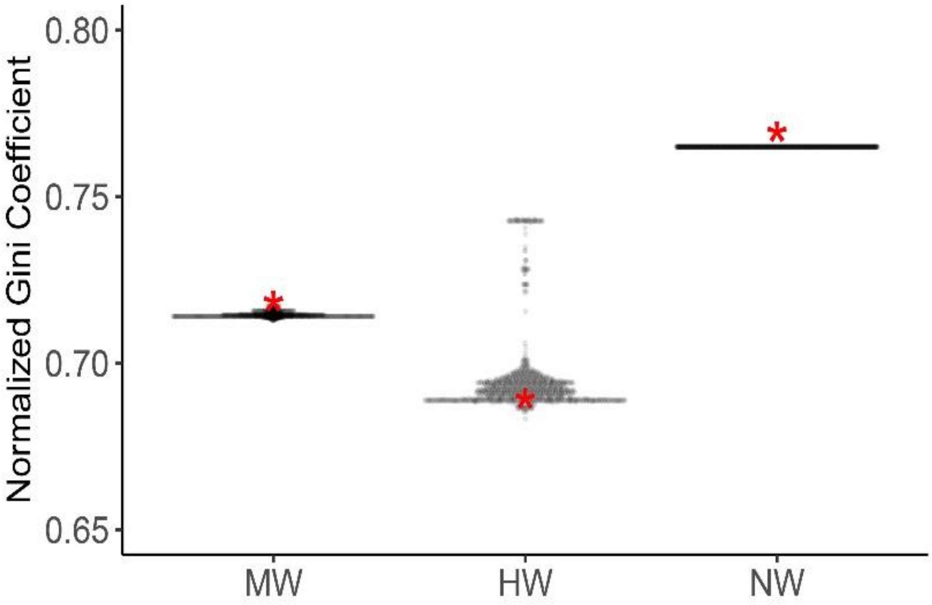

Figure S1. Observed normalized Gini coefficient (G*) of each web (asterisk) against the distribution of normalized G* for each 1000 pairs of posterior probability trees.

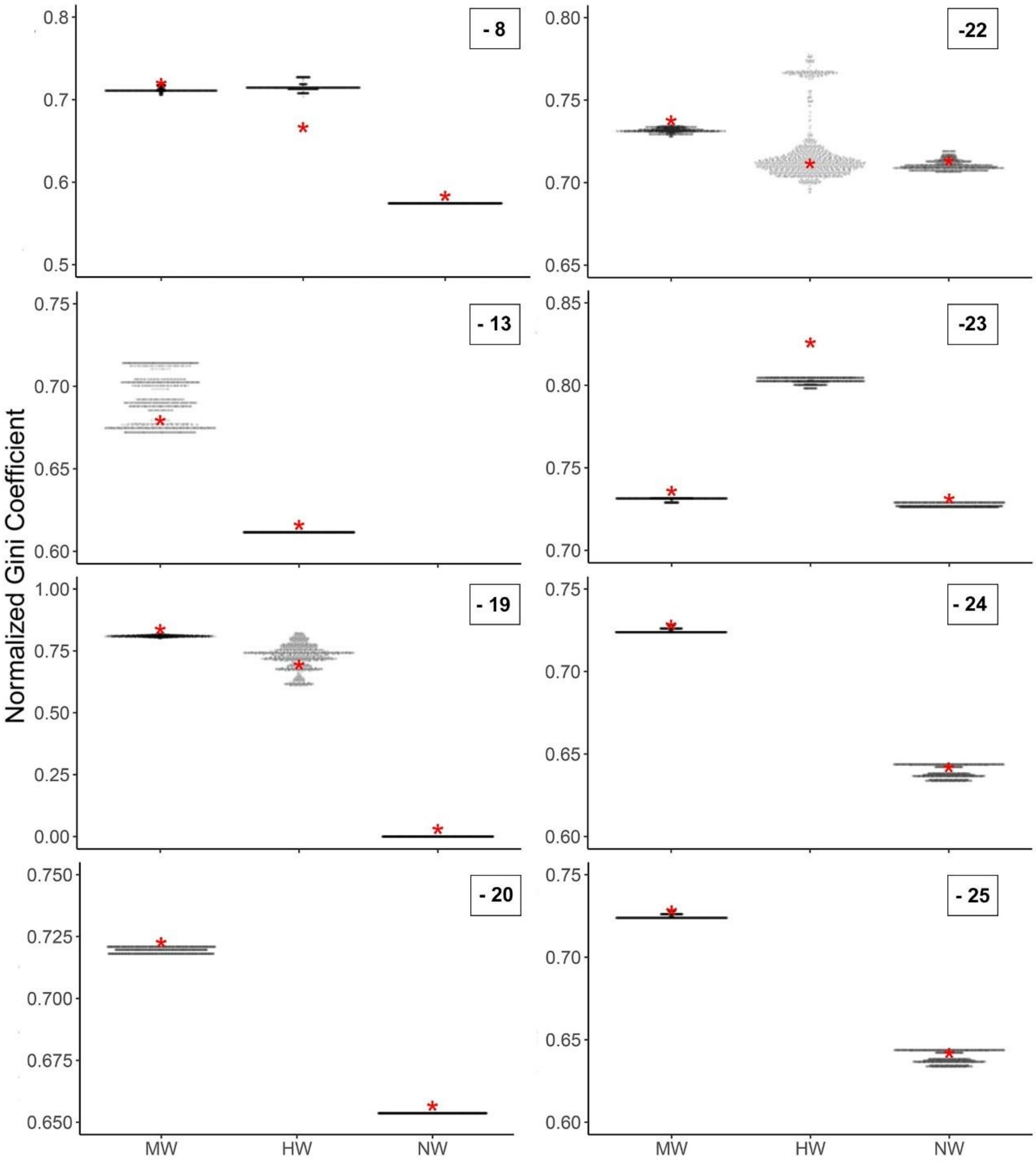

Figure S2. Observed normalized Gini coefficient (G*) of each web (asterisk) in each latitude against the distribution of normalized G* for each 1000 pairs of posterior probability trees.

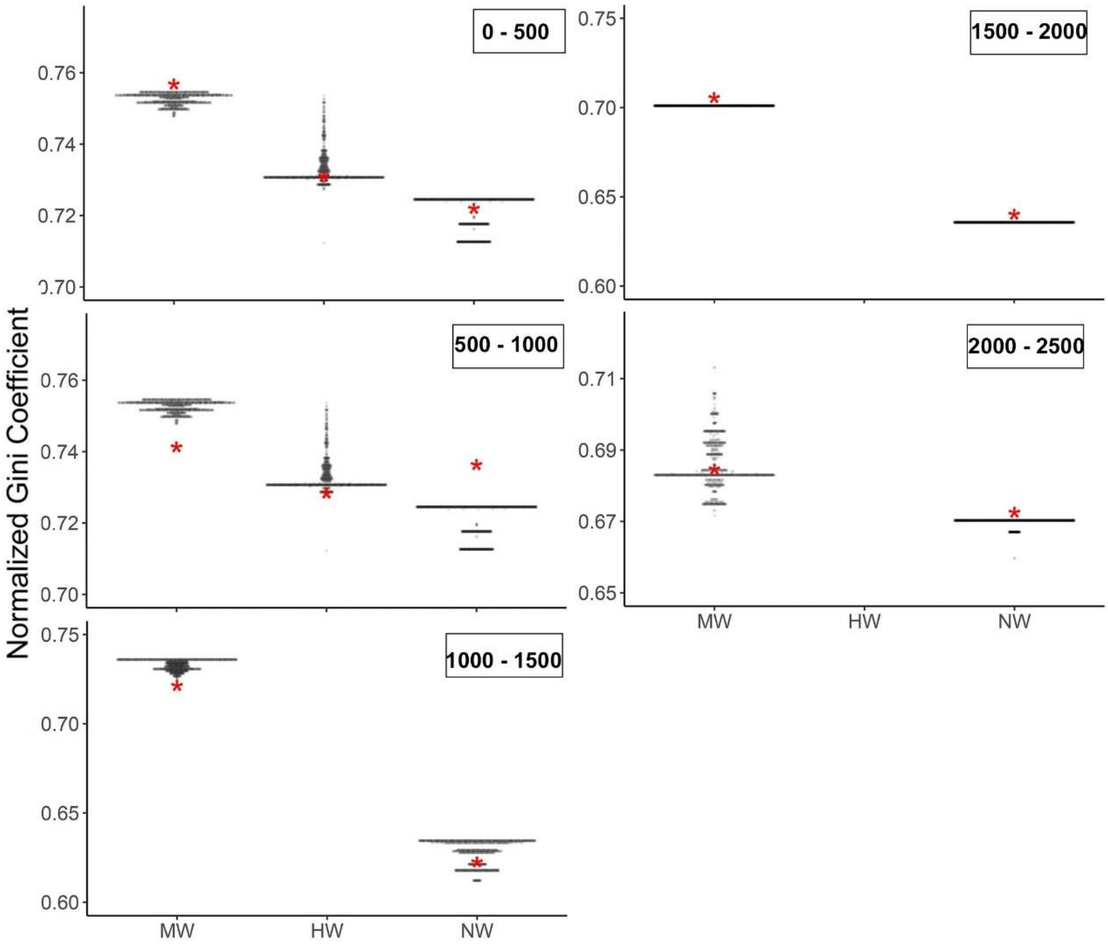

Figure S3. Observed normalized Gini coefficient (G*) of each web (asterisk) in each elevation against the distribution of normalized G* for each 1000 pairs of posterior probability trees.

DISCUSSÃO GERAL E CONCLUSÕES

O presente trabalho teve por objetivo geral organizar informações e explorar a estrutura de comunidades entre flores e vertebrados nectarívoros na Floresta Atlântica, em especial beija-flores, levando em consideração a ecologia e a evolução das interações.

No primeiro capítulo, nós elaboramos e organizamos toda a informação disponível até o presente momento sobre a interação para a Mata Atlântica brasileira na forma de um banco de dados. Este banco de dados foi composto de 213 trabalhos, incluindo dados não publicados e dados retirados da "literatura cinza" – dissertações e teses. Estes trabalhos abordaram um total de cerca de 160 comunidades na Floresta Atlântica brasileira, contendo 457 espécies de plantas (mais 21 não identificadas) e 103 espécies de vertebrados (mais 20 não identificadas). Cerca de 35% das plantas envolvidas nas interações presentes no banco de dados foram epífitas, principalmente as pertencentes à família Bromeliaceae enquanto que árvores representam somente 4% das interações. Com relação aos vertebrados nectarívoros, a maioria das interações registradas (57%) ocorreram com beija-flores, enquanto que para morcegos a porcentagem foi de apenas 25%. Além de beija-flores e morcegos, foram registradas em menores proporções outras aves, primatas, gambás e lagartos. Epífitas são importantes componentes da flora do Neotrópicos e são visitadas principalmente por beija-flores e morcegos (Fleming and Muchhala 2008). No entanto, morcegos também visitam flores de espécies arbóreas (Fleming and Muchhala 2008) e a baixa proporção destas no banco de dados indica viés de amostragem para este grupo de animais.

Com o Capítulo 1 também pretendíamos reforçar padrões relacionados às interações entre plantas e vertebrados na Floresta Atlântica. Nossos resultados demostraram grande diversidade beta e taxas de *turnover* para plantas, morcegos, beija-flores e outras aves em diferentes comunidades ao longo de 14 faixas latitudinais de 1°. Ao mesmo tempo, as taxas de aninhamento foram baixas. Isto indica que a Floresta Atlântica é um ambiente bastante diverso e rico ao longo de sua extensão geográfica, resultado este que já tem sido demonstrado em diversos trabalhos (veja Peres et al. 2020 para uma revisão). A maioria das espécies de plantas florescem ao longo de três a cinco meses, caracterizando um padrão estendido de floração. Este padrão de floração associado à grande diversidade florística na Floresta Atlântica representa previsibilidade na oferta de recursos. No entanto, a produção de energia foi baixa na grande maioria das flores. O padrão fenológico e a quantidade de recursos nas comunidades podem influenciar os vertebrados nectaríovos a adotarem comportamentos de forrageio em rotas de captura – trapilíneo – uma vez que a baixa quantidade de energia oferecida pelas plantas pode não compensar a defesa de território (Feinsinger 1976).

Verificamos uma grande variação no com o comprimento da corola e, uma vez que os traços florais são correlacionados (Armbruster et al. 1999), estes resultados reforçam a grande diversidade de espécies de plantas na Floresta Atlântica. Flores polinizadas por beija-flores apresentaram maior variação floral, o que pode estar relacionado a grande diversidade de formatos e tamanhos de bicos deste grupo de vertebrados nectarívoros (Maglianesi et al. 2014). O comprimento da corola e dos bicos destes animais influenciam a forma com a qual o recurso é compartilhado nas comunidades (Sazima et al. 1996). Beija-flores com bicos longos têm acesso a recursos exclusivo a algumas espécies de plantas, as quais eles visitam com grande frequência. No entanto, beija-flores com bicos longos e médios podem ainda compartilhar recursos florais, diminuindo a frequência relativa de visitas de cada um destes grupos. Com isso, beija-flores de bicos longos – que comumente também forrageiam em rotas de captura – podem dominar o uso do recurso e a organização de algumas comunidades (Buzato et al. 2000, Wolowski et al. 2017).

O padrão fenológico e a baixa disponibilidade de recursos podem estar influenciando a forma com a qual as visitas estão organizadas na comunidade. De forma geral, as interações na Floresta Atlântica tendem a ser especializadas. Isso ocorre porque a distribuição do número de espécie de vertebrados por espécie de plantas e o número de espécie de planta visitada por espécie de vertebrado é baixo para todos os grupos de vertebrados. Além disso, plantas tendem a ser visitas por menos de espécies de beija-flores de bicos longos (eremitas) do que de bicos curtos (não eremitas), reforçando que os primeiros são mais especialistas no uso do recurso.

Por fim, no primeiro capítulo da tese, nós pretendíamos apontar tendências e lacunas na informação acerca da interação entre vertebrados e flores na Floresta

Atlântica. Observamos que há um viés de amostragem com relação a localização dos estudos e a grupos taxonômicos. A maioria das observações foram realizadas na região Sudeste do bioma. Os motivos para essas lacunas muito provavelmente estão relacionados a razões históricas e políticas, tais como pouco financiamento para pesquisa em algumas regiões, pouca tradição no estudo da polinização ou problemas logísticos de amostragem em áreas remotas (Vizentin-Bugoni et al. 2018). Além disso, como apontado anteriormente, a maior parte dos estudos foram realizados com beija-flores. Apesar destes animais serem os principais vertebrados nectarívoros dos Neotrópicos, morcegos nectarívoros são importantes elementos para a reprodução de plantas nestes ambientes (Fleming and Kress 2013). Não há uma padronização na coleta de dados relacionados a polinização, principalmente produção de néctar e tempo de observação, fazendo com que comparações sejam difíceis de serem realizadas. Neste banco de dados, nós padronizados essas informações, porém é importante que especialistas entrem em consenso para futuros trabalhos. Por fim, a maioria dos trabalhos são voltados para a ecologia de plantas e dados morfológicos dos vertebrados nectarívoros são raramente coletados.

No Capítulo 2 da tese, nosso objetivo foi investigar a importância relativa de diferentes grupos de beija-flores na estrutura da comunidade, considerando sua história evolutiva conjunta com as plantas que visitam e sua distribuição. Beija flores podem ser divididos em dois grupos: os eremitas – mais especializados, de bico longo e que apresentam comportamento trapilíneos – e os não eremitas – mais generalistas, com grande variedade no comprimento dos bicos que são normalmente territorialistas. Para tanto, nós averiguamos a presença ou ausência de sinal cofilogenético nas respectivas redes de eremitas e não eremitas em comunidades em diferentes altitudes e latitudes. Nós esperamos encontrar maior sinal cofilogenético em redes de beija-flores eremitas do que na de não eremitas, devido ao fato de que os primeiros são mais especializados, sendo provável que as interações tenham ocorrido por meio de evolução conjunta. Também esperávamos encontrar maior sinal cofilogenético em menores latitudes e altitudes, relacionados com a distribuição de beija-flores eremitas.

De forma geral, encontramos sinal cofilogenético entre as redes de beija-flores e das plantas que eles polinizam. No entanto, esse sinal é dado principalmente pelas interações com e eremitas, uma vez que as filogenias deste grupo de beija-flores e plantas apresentaram maior congruência. Eremitas são beija-flores mais especializados (Feinsinger and Colwell 1978, Maglianesi et al. 2014, 2015) e possivelmente as interações com este grupo de beija-flores tenham sido resultado de evolução conjunta. Além disso, beija-flores eremitas e plantas da família Bromeliaceae aparecem como um compartimento que contribuem de forma significativa para o sinal encontrado, indicando que estes dois grupos taxonômicos tiveram pressões seletivas similares e influenciaram na evolução de forma recíproca (Olesen et al. 2007). Além de bromélias e beija-flores terem uma ligação ecológica importante, a diversificação destas plantas parece coincidir no tempo com a diversificação de beija-flores eremitas, ambos se originando por volta de 20 milhões de anos atrás (McGuire et al. 2014, Givnish et al. 2014).

Dentre os eremitas, destaca-se a espécie de beija-flor *Ramphodon naevius* (Dumont, 1818), cuja contribuição pra o sinal cofilogenético na rede de eremitas foi significantemente maior do que das outras espécies. Essa espécie apresenta comportamento trapilíneo e é extremamente agressiva, dominando os recursos em comunidades de baixada (Sazima et al. 1996, Buzato et al. 2000), áreas nas quais esta espécie é restrita (Ridgely et al. 2016). A origem deste beija-flor data de 15 Ma. (McGuire et al. 2014) e coincide com a origem da polinização por aves em alguns clados de bromélias que ocorrem na Floresta Atlântica, como as Tillandsioides e no ancestral Pticairnioideae-Puyoideae-Bromelioideae (Givnish et al. 2014).

Em contrapartida, a filogenia de beija-flores não eremitas e as plantas que eles polinizam apresentou sinal cofilogenético fraco, sem interações contribuindo de forma significante. Este grupo de beija-flores é mais diversificado (McGuire et al. 2014) e mais generalista na ocupação de diferentes áreas e na utilização do recurso (McGuire et al. 2009). Além disso, a maioria das comunidades localizadas em diferentes altitudes e altitudes não apresentou sinal cofilogenético forte, tanto para redes de eremitas quanto para de não eremitas. No entanto, a maioria das comunidades com sinal cofilogenético forte estava situada em áreas de baixas elevações (até 1000 m) e em regiões tropicais (até 23°S). Essa falta de congruência é um indicativo de que a história evolutiva tem menos importância do que fatores ecológicos locais na organização das comunidades polinizadas por este grupo de beija-flores. De fato, este grupo apresenta menor acoplamento morfológico com as plantas quando comparado com os eremitas (Feinsinger and Colwell 1978; Bleiweiss 1998b; Cotton 2008; Rodríguez-Flores et al. 2019), indicando que seleção recíproca pode não ter ocorrido (Thompson 2005).

A distribuição restrita de beija-flores eremitas pode ser um fator importante para a organização de comunidade de não eremitas, pois a composição das espécies em diferentes comunidades pode promover mudanças no uso do recurso (Feinsinger 1976). Beija-flores eremitas podem ser considerados como um filtro biótico para a existência de outras espécies (Wolowski et al. 2017) e sua ausência pode permitir a dominância de beija-flores não eremitas. Além disso, a variação na distribuição espacial das plantas (Morales and Vázquez 2008), no acoplamento fenotípico (Feinsinger 1976, Vizentin-Bugoni et al. 2014) e na sobreposição fenológica (Vizentin-Bugoni et al. 2014) pode promover interações especializadas, sendo fatores importantes para estruturação das interações (Linhart 1973; Stiles and Stiles 1975; Maglianesi et al. 2014, 2015). Na Floresta Atlântica brasileira, a dispersão das espécies pode variar entre comunidades (Feinsinger and Colwell 1978; Buzato et al. 2000) e, levando em consideração as altas taxas de diversidade beta e *turnover* encontrados, deve haver também grande variação na morfologia de plantas e beija-flores e na fenologia das plantas. Tais fatores podem promover comportamento especializados em não eremitas, moldando diferentes estruturas em diferentes comunidades. Assim, a classificação de diferentes clados e espécies de beija-flores deve ser considerado dentro de uma escala contínua ao invés de seus extremos Buzato et al. 1994; Johnson and Steiner 2000), pois ela depende não somente da morfologia e da história evolutiva, mas também do contexto ecológico.

Apesar da grande diversidade beta e taxas de *turnover*, os resultados que encontramos neste segundo capítulo podem ser influenciados pelo viés de amostragem para a região Sudeste da Floresta Atlântica. Assim, a falta de sinal em algumas comunidades pode ser devido a falta de observação de interações. Da mesma forma, o forte sinal cofilogenético encontrado para os eremitas pode ser devido a uma concentração das observações nas áreas onde este grupo está mais presente. Assim, um aumento na área de observação, bem como a coleta de dados demográficos, fenológicos e morfológicos são essenciais para compreender como as diferenças entre a especialização de beija-flores e sua história evolutiva influenciam na estrutura das comunidades. Além disso, a incorporação de dados ambientais que limitam a distribuição de plantas e beija-flores pode ajudar a compreender como essas interações estruturam comunidades.

Apesar dessas tendências e lacunas de amostragem, nossos dados apontam que a história evolutiva foi um fator importante para a estrutura de comunidades de eremitas e suas plantas, enquanto que processos ecológicos estão atuando nas interações de não eremitas e suas plantas. Diferenças na ecologia local de cada comunidade pode promover mudanças na competição pelo recurso e influenciar no comportamento de forrageio dos beija-flores, mudando os padrões de interação e influenciando na importância relativa de cada grupo.

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