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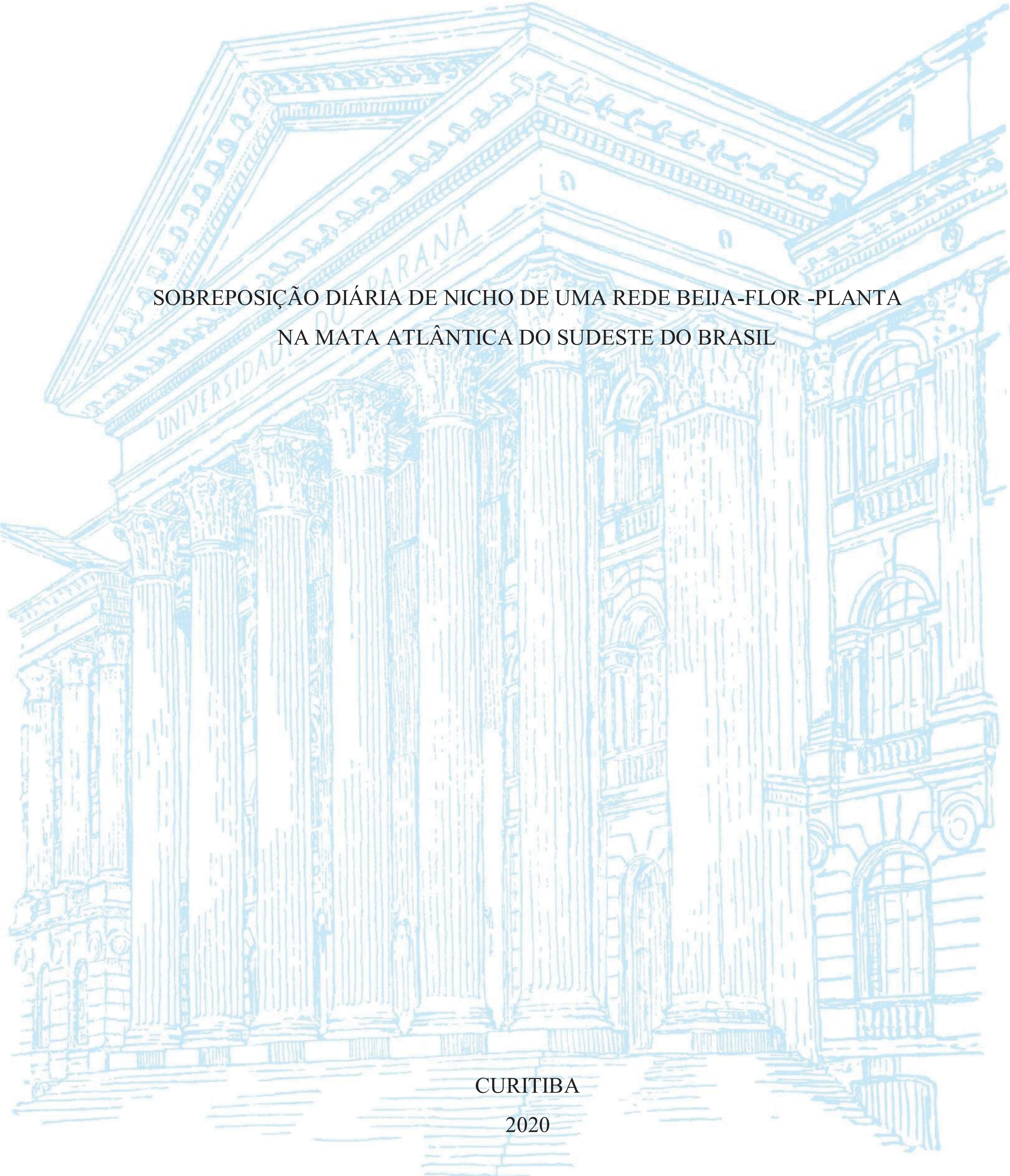

SOBREPOSIÇÃO DIÁRIA DE NICHO DE UMA REDE BEIJA-FLOR -PLANTA NA MATA ATLÂNTICA DO SUDESTE DO BRASIL

CURITIBA
2020

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SOBREPOSIÇÃO DIÁRIA DE NICHO DE UMA REDE BEIJA-FLOR -PLANTA NA MATA ATLÂNTICA DO SUDESTE DO BRASIL

Dissertação apresentada ao curso de Pós-Graduação em Ecologia e Conservação, Setor de Ciências Biológicas, Universidade Federal do Paraná, como requisito parcial à obtenção do título de Mestre em Ecologia e Conservação.

Orientadora: Profa. Dra. Isabela Galarda Varassin

Co-orientadora: Profa. Dra. Catherine Helen Graham

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TERMO DE APROVAÇÃO

Os membros da Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação em ECOLOGIA E CONSERVAÇÃO da Universidade Federal do Paraná foram convocados para realizar a arguição da Dissertação de Mestrado de **ANDREA VANESSA NIETO ORELLANA**, intitulada: **SOBREPOSIÇÃO DIÁRIA DE NICHO DE UMA REDE BEIJA-FLOR -PLANTA NA MATA ATLÂNTICA DO SUDESTE DO BRASIL**, sob orientação da Profa. Dra. ISABELA GALARDA VARASSIN, após terem inquirido a aluna e realizado a avaliação do trabalho, são de parecer pela sua APROVAÇÃO no rito de defesa.

A outorga do título de Mestre está sujeita à homologação pelo colegiado, ao atendimento de todas as indicações e correções solicitadas pela banca e ao pleno atendimento das demandas regimentais do Programa de Pós-Graduação.

Curitiba, 18 de Fevereiro de 2020.

ISABELA GALARDA VARASSIN
Presidente da Banca Examinadora

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JAMES J ROPER
Avaliador Interno

Dedico este trabalho àquele feixe de lua que nunca esquecerei, o meu pai.

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“Quieto
no en la rama
en el aire
no en el aire
en el instante
el colibrí”
(Octavio Díaz)

RESUMO

A partilha do nicho é um mecanismo que permite a coexistência de espécies, minimizando a competição. Este mecanismo tem sido amplamente estudado na escala trófica e espacial, enquanto que na escala temporal ao longo do dia tem permanecido pouco claro. Coletamos dados de beija-flores (horário da visita às flores) e plantas (produção de néctar e atributos morfológicos) da Mata Atlântica brasileira para explorar se eles segregam seus nichos em escala trófica (para beija-flores) e temporal diária (para beija-flores e plantas). Os beija-flores visitaram as mesmas espécies de plantas durante as mesmas horas do dia, indicando padrões de sobreposição e ausência de competição tanto na escala trófica quanto na escala diária. Por outro lado, a comunidade de plantas ofereceu néctar ao longo de todo o dia, não mostrando nenhum padrão de segregação da produção diária de néctar. A sobreposição de nicho na produção diária de néctar não diferiu entre espécies que co-floresceram ou compartilharam uma espécie de beija-flor. Também observamos que espécies de plantas com maior semelhança morfológica se sobrepuseram mais na produção diária de néctar. No geral, mostramos padrões de sobreposição no uso dos recursos tanto na escala trófica quanto na escala diária, indicando que a facilitação poderia estar estruturando a comunidade dos beija-flores. Para as plantas, a falta de segregação na produção de néctar e a elevada sobreposição dos beija-flores nas plantas, ao longo do dia, sugere que as plantas podem estar a facilitar-se mutuamente em vez de competirem pela polinização. Isso indica que interações indiretas, como a facilitação, podem estar estruturando a comunidade de beija-flor e plantas que eles visitaram na Mata Atlântica do sudeste do Brasil.

Palavras-chave: beija-flor-planta, competição, partilha do nicho, polinização.

ABSTRACT

Niche partitioning is a mechanism that allows species to coexist by minimizing competition. This mechanism has been broadly studied at trophic and spatial scales while partitioning across a daily temporal scale has been less studied. We collected data of hummingbirds (visits to plants) and plants (nectar production and morphological traits) from the Brazilian Atlantic forest to explore niche segregation at trophic (for hummingbirds) and temporal daily (for hummingbirds and plants) scales. The hummingbirds visited the same plant species during the same hours throughout the day, indicating overlap patterns and lack of competition at both trophic and daily scales. On the other hand, the plant community offered nectar throughout the day, showing no pattern of segregation of daily nectar production. The niche overlap in daily nectar production did not differ between species that co-flowered or shared a hummingbird species. However, the plant species that shared hummingbirds showed the lowest niche overlap in daily nectar production. Also, we found that plant species with higher morphological similarity had higher overlap in daily nectar production. Overall, we show patterns of overlap in resource use both on the trophic scale and the daily scale, indicating that facilitation may be structuring the hummingbird community. For plants, the lack of segregation in nectar production and the high overlap of hummingbirds on plants throughout the day suggests that plants may be facilitating each other rather than competing for pollination. This indicates that indirect interactions, such as facilitation, may be structuring the hummingbird and plant community they visited in the southeastern Atlantic Forest.

Keywords: competition, hummingbird-plant, niche partitioning, pollination.

LIST OF FIGURES

LIST OF TABLES

INDEX

INTRODUCTION

Niche partitioning allows similar species to coexist through avoidance of competition (Schoener 1974, Chesson 2000, Levine and HilleRisLambers 2009). Within pollinator-plant networks, competition among pollinators may occur while foraging on limited floral resources. Therefore, species avoid direct confrontation through niche partitioning (Schoener 1974, Walter 1991) on diet, by selecting a subset of flowers (Maglianesi et al. 2015), or space, by foraging at inner or peripheral zones of a patch of flowers (Feinsinger 1976). On the other hand, plants blooming at the same time or sharing pollinators may avoid competing for pollination by asynchronous flowering (Oleques et al. 2017), by blooming in different seasons (Levin and Anderson 1970, Rathcke 1983), or by depositing pollen in specific body parts of their pollinators (Araújo 2010). Nevertheless, pollinators, as well as plants, may also avoid competition through finer temporal partitioning across the day. For instance, plants may release pollen, or nectar, at different hours (Armbruster and Herzig 1984, Stone et al. 1996) while pollinators may use different hours to visit the plants throughout the day (Lara et al. 2009, 2011). Niche partitioning has been well studied at spatial and seasonal scales, while finer temporal scales has been less considered within pollinator-plant systems. To understand temporal niche partitioning within pollinator-plant networks, we evaluated activity patterns of hummingbirds and plants to examine if they segregate their visits and nectar production, respectively, throughout the day to avoid competition and reduce niche overlap.

Generalized morphological traits allow pollinators to access any nectar reward and plants to be visited by any pollinator (Frame 2003, Ollerton et al. 2007), promoting niche overlap and leading to possible competition. As an alternative, both pollinator and plant species may partition their niche by segregating their activity patterns through a niche axis such as time (Kronfeld-Schor and Dayan 2003). For instance, pollinators sharing resources may synchronize their visits over the day to access pollen or nectar rewards. Some studies found niche segregation among hummingbird species throughout the day while foraging on limited floral resources (Cotton 2008, Lara et al. 2009, 2011). Plants, on the other hand, may differ in their flowering phenology by blooming at different seasons to avoid competition for pollinators (Levin and Anderson 1970, Feinsinger 1978, Aizen and Vázquez 2006). At finer temporal scales (i.e., throughout the day), plants sharing pollinators may time their pollen release (Armbruster and Herzig 1984, Stone et al. 1996) or nectar rewards at different hours throughout the day. Temporal segregation then could be a mechanism for plant species to avoid competition and reduce overlap (Kronfeld-Schor and Dayan 2003).

Competition among species may promote differential use of shared resources. Some hummingbird species have evolved morphological adaptations (e.g., curved and long bills) allowing them to forage optimally and avoid spending energy in seeking and handling other less profitable resources (Stiles 1978) . Such adaptations allow them to select a subset of resources as compared to species with generalist feeding morphologies (Futuyma and Moreno 1988, Forister et al. 2012). In mutualistic networks, pollinators tend to interact more often with those flowers that better fit their feeding morphologies (Thomson 2003, Stang et al. 2009, Vázquez et al. 2009). For instance, long-billed hummingbirds tend to visit flowers with long corollas even when flowers with shorter-corolla are readily available (Weinstein and Graham 2017). Furthermore, some studies have shown that morphology play an important role on predicting interactions frequencies and structuring the plant–hummingbird networks (Maruyama et al. 2014, Vizentin-Bugoni et al. 2014). From the plant perspective, floral morphology largely influences the visitation of pollinators and hence pollination efficiency. For instance, it can constrain access to nectar rewards (Castellanos et al. 2004, Muchhala 2007) to specific pollinators that will increase deposition of conspecific pollen, limiting the deposition of heterospecific pollen which may negatively impact seed production (Mitchell et al. 2009, Ashman and Arceo-Gómez 2013). By selecting a subset of pollinators, plant species may escape from the competition, reduce overlap and so promote coexistence.

Hummingbird-plant networks are well suited to explore temporal niche partitioning. In a highly diverse ecosystem such as the Atlantic Forest (Myers et al. 2000) many of the plant species pollinated by hummingbirds (e.g., Bromeliads – see Buzato et al. 2000) often bloom at the same time throughout the year over a brief period and have flowers that last only a single day (e.g., Martinelli 1995). Mutualistic hummingbird-plant networks might be a highly competitive environment where hummingbirds interact to feed on the same ephemeral floral resources (Feinsinger and Colwell 1978) over a short period. On the other hand, plant fitness relies on the deposition of conspecific pollen (Morales and Traveset 2008, Ashman and Arceo-Gómez 2013, Arceo-Gómez and Ashman 2016) delivered by floral visitors at a constrained schedule. Under this scenario, hummingbirds and plants might partition their niche by segregating their visits on flowers and pollen/nectar release at different hours throughout the day. Thus, the daily partitioning of foraging time by hummingbirds and nectar production by plants potentially promotes coexistence (Carothers and Jaksić 1984) and may reduce overlap among co-feeding and co-flowering species (Richards 2002).

Here, we collected data from the southeastern Atlantic Forest to evaluate temporal niche partitioning throughout the day within a hummingbird-plant system. We predicted that if competition is structuring hummingbird-plant interactions then 1) hummingbird species temporally and trophically partition resources, 2) plants temporally partition nectar production, 3) co-flowering plant species overlap less on nectar production than those that do not, 4) plant species sharing hummingbird species overlap less on nectar production than those that do not, and 5) less overlap in nectar production between plants with greater morphological similarity.

METHODS

We conducted this study within the Estação Biológica Santa Lúcia - EBSL (19°59′S, 140°32′W) southeastern Brazil. The annual temperature at the study site varies from 14.3° C to 26.2° C, with a mean of 19.9°C (Thomaz and Monteiro 1997). Average annual precipitation is around 1900 mm, with the highest rainfall in November and the lowest in June (Mendes and Padovan 2000). The area is mostly old-growth tropical rain forest (Atlantic Forest) (Mendes and Padovan 2000), and the understory tends to be dominated by bromeliads (Wendt and Coser 2010) as well as rocky outcrops (pers. obs.).

We observed birds and flowering plants along a 1.5 km by 10 m transect where we counted hummingbird-plant interactions, flowers abundance, nectar production and morphological floral traits of flowers visited by hummingbirds. We performed eight sample periods between November 2018 and July 2019.

To count hummingbird-plant interactions, we used time-lapse cameras (Plotwatcher Pro – 12 cameras). This method minimizes the time spent in the field for plant-hummingbird focal observations and increases data collection in time and space (Weinstein 2015, Weinstein and Graham 2017). We placed a single camera at a flower or group of flowers at 12 flowering plants (up to 2 m above the ground), on the transect for three days each. The cameras took an image every second from dawn to dusk (~12 hours), generating a total of 43,200 images per camera per day. We used a time interval of 20 seconds between visits to define independent visits. We tried to maximize the number of plant species at each sample period. Using Deep Meerkat software (Weinstein 2015), we found frames with motion, from which we took those with legitimate visits only (in which the birds inserted the bill into the corolla) and identified the bird species.

To estimate flower abundance along the transect, we counted all open flowers fitting the traditional ornithophilous syndrome (e.g., red to purple color, elongated corollas) (Fægri and van der Pijl 1972). Although flowers with bat or insect pollination syndromes are likely to be visited by hummingbirds (Dalsgaard et al. 2009), we did not count them because we recorded none interaction. When possible, we counted all open flowers on a plant; when we found a dense flowering plant, we counted flowers on five branches, calculated the average, and then multiplied that by the total number of branches, for the estimate of flower abundance of that plant.

To measure nectar production, we bagged floral buds from all plant species visited by hummingbirds. Once flowers opened, we collected nectar from 06:00 to 18:00 h every four hours. For each period, we extracted nectar from at least 10 new, freshly opened, flowers from different individuals of each plant species. By selecting new flowers, we avoided measuring nectar in previously damaged flowers (Kearns and Inouye 1993). We extracted nectar by using a microliter syringe (Hamilton syringe 50µl) or capillary tubes (20 and 60µl). This method allowed us to collect the entire reward offered by the flower. Total sugar content in nectar was measured, weight by weight (w/w), by using a handheld refractometer (range concentration 0 – 32% Brix degree) and corrected since brix degree values are temperature-dependent (Cruden et al. 1983). Flowers of three species (*Aechmea lamarchei, Billbergia amoena* and *Nidularium procerum*) were not abundant, so we repeated collecting nectar from those flowers. Nectar collected from new flowers provided a measure of accumulated nectar production, while repeated flowers provided an additional measure of dynamic nectar production (Gill 1988, Heil 2011). For those plant species with dynamic nectar, we modified some values before calculating sugar production (mg sugar) as follows: for extractions at 06:00, we used the original values for both volume and nectar concentration. For subsequent extractions that had zero volume, we used the volume and nectar concentration reported at the previous period, due to zero volume means no additional nectar production; thereby, we maintained the previous obtained values of nectar concentration. For flowers with volume different than zero, we added the volume obtained at the previous period, and we maintained the concentration value, because we expected little variation of nectar concentration within the same plant species (Varassin et al. 2001). For all plants, sugar production was calculated as the product of nectar volume (ml) by sugar concentration (mg/ml) following Kearns and Inouye (1993), although non-sugar constituents may also influence the refractive index (Inouye et al. 1980). .

To examine whether hummingbird activity follows nectar production throughout the day, we estimated sugar production hourly, from 06:00 to 18:00 h. Because sugar production has a lower bound of zero, we used a generalized linear model (GLM) with the Poisson distribution. A Poisson-GLM never predicts values below zero (Zuur et al. 2009). Since Poisson distribution works with integer values, we used sugar content expressed as µg (rounded to integers). For the model, we used a linear and a quadratic term to relate hours to sugar production for each plant species. We then used the fitted models to predict species-specific values of µg sugar at each hour (from 06:00 to 18:00 h). We estimated total resources availability of each plant species by multiplying sugar production (mg) by the number of flowers.

To measure floral morphological traits, we collected at least five flowers, each one from a different individual of each plant species visited by hummingbirds. For each flower, we took a scaled photograph to measure corolla length, an important trait that affects hummingbird-plant interactions (Temeles et al. 2009, Maglianesi et al. 2014). We defined corolla length as the distance from the base to the corolla opening. We used the ImageJ program (Schneider et al. 2012) to measure morphological traits. We collected one individual of each plant species as a voucher specimen, and these were deposited at the MBML herbarium – Instituto Nacional da Mata Atlântica. Plants were identified by comparison with plant vouchers by local specialists (see Acknowledgements).

Statistical analysis

We evaluated niche overlap patterns of hummingbirds and plants at different scales. For hummingbirds, we examined niche overlap at trophic scale and throughout the day (hereafter, temporal scale), while for plants we only examined overlap on temporal scale. For the trophic scale, we followed the approach of Winemiller and Pianka (1990), while for the temporal scale, we followed Castro-Arellano et al. (2010). For the trophic scale, we built a hummingbird species (rows) by plant species (columns) matrix with each entry as the number of visits on each plant species. For the temporal scale, instead of using plant species as columns, we used hours (from 06:00to 18:00 h, every hour) with each entry as the number of hourly visits in the entire assemblage of plants. Both approaches calculate niche overlap between all possible pairwise combinations of hummingbird species in the assemblage based on the Pianka index (Pianka 1973). The index ranges from 0, for overlap (hummingbirds using different plants or hours), to 1 for complete overlap (hummingbirds using the same plants or hours). The observed niche overlap for the assemblage is then calculated as the mean of the overlap index derived from all possible pairwise combinations of hummingbird species. We calculated the probability of the observed niche overlap by comparing it with an appropriate null model. For the trophic level, our null distributions were created by using the ra3 algorithm (Albrecht and Gotelli 2001). We ran 10,000 iterations, in each iteration ra3 reshuffles the entries in each row of the matrix. Although the model allows utilization of any of the possible plants, it maintains the niche breadth of the observed hummingbird species (Albrecht and Gotelli 2001). Moreover, ra3 was devised for nominal unordered resources such as plants. For the temporal scale, our null distributions were created by using the ROSARIO algorithm (Castro-Arellano et al. 2010). We ran 10,000 iterations, in each iteration ROSARIO shifts the entire houly activity patterns of each species to estimate the assemblage niche overlap. We chose the ROSARIO algorithm because it considers time as a sequential, continuous and ordered resource. It also maintains temporal autocorrelation of temporal data by shifting only the distribution of activity patterns and not disrupting the shape of them, which biologically is more realistic (Castro-Arellano et al. 2010). For both trophic and temporal scales, the observed values lower than random values expressed segregated activity patterns (i.e., niche segregation), while observed values higher than random values expressed coincident activity patterns (i.e., niche overlap) (Castro-Arellano et al. 2010). We ran the simulations at trophic level by using the niche.overlap function of the EcoSimR package (Gotelli et al. 2015) for the R programming language (R Core Team 2018). While for the temporal scale, we used the Time Overlap software developed by Castro-Arellano et al. (2010) (http://hydrodictyon.eeb.uconn.edu/people/willig/Research/activity%20pattern.html).

From the plant perspective, we evaluated the temporal niche overlap, based on nectar production (mg sugar), both at the community and plant species pairwise levels. At the community level, we followed the same approach of Castro-Arellano et al. (2010) used for hummingbirds. We built a plant species (rows) by hours (columns – from 06:00 to 18:00 h, every hour) matrix (D) with each entry as the resource availability of each plant species at a given hour. From this matrix, we calculated the niche overlap of all possible pairwise combinations of plant species in the assemblage based on the Pianka index (Pianka 1973). The index ranges from 0, for overlap (plants producing nectar at different hours), to 1 for complete overlap (plants producing nectar at the same hours). The observed niche overlap for the assemblage is then calculated as the mean of the overlap from all possible pairwise combinations of plant species. We calculated the probability of the observed niche overlap as the proportion of times the observed value was included in 10,000 iterations of the ROSARIO algorithm (Castro-Arellano et al. 2010).

At the plant species level, to test if co-flowering plant species overlap less on temporal nectar production than those that do not, we used the matrix D to calculate the Pianka index for all possible pairwise combinations of plant species. Then, we pooled together all plant species pairs that co-flowered at least once as one group to compare it with those that did not co-flower as another group. We then compared the overlap in temporal nectar production, through Pianka index, between those groups by using a Wilcoxon rank test, calculated in R (R Core Team 2018).

To test if plants species pairs, sharing a hummingbird species, overlap less on temporal nectar production than those that do not, we used the matrix D to calculate the Pianka index for all possible pairwise combinations of plant species. Then, we pooled together all plant species pairs that shared at least one hummingbird species as one group to compare it with those that did not share any hummingbird species as another group. We then compared the overlap in temporal nectar production, through the Pianka index, between those groups using a Wilcoxon rank test.

To test whether species with flowers of similar corollas have less temporal overlap than expected, we correlated corolla length dissimilarity with temporal overlap in nectar production. We used overlap values obtained from matrix D and corolla dissimilarity was calculated as Euclidean distance in R (R Core Team 2018).

RESULTS

We collected data from 12 plant species visited by hummingbirds. For these, we recorded 488 legitimate interactions across four hummingbird species (Table 1) that included *Phaethronis eurynome*, *P. squalidus*, *Ramphodon naevius* and *Thalurania glaucopis*. Most of the plants visited by hummingbirds belonged to Bromeliaceae (88%) followed by Acanthaceae (12%). Most visits (56%) occurred between 06:00 – 10:00 h (Fig. 1A, B).

Across the study period, *Aechmea araneosa* produced the most flowers (n=103) in contrast to *Quesnelia quesneliana*, which produced the least (n=3). Nectar production ranged from 0.02 mg day^{-1} of sugar in *A. lamarchei* to 8.44 mg in *Vriesea ensiformis*. When we multiplied the sugar production by the abundance of flowers, *A. lamarchei* provided the least nectar (0.08 mg) and *A. araneosa* provided the most (426.4 mg) (Fig. 2). The corolla length ranged from 11.16 mm (SD = 0.13, n = 5) in *Tillandsia stricta* to 64.52 mm (SD = 0.31, n = 5) in *Vriesea simplex* (Table 2).

The overlap pattern of the hummingbird assemblage was similar at both trophic and temporal scales (Table 3). At the trophic scale (Fig. 3), the overlap was 0.50, and the daily scale was 0.83. In both cases, niche overlap was significantly greater than expected by chance (p= 0.99 for the trophic, and p = 0.99 for the temporal scale) (Table 3), indicating a lack of segregation. This suggests that hummingbirds not only visited the same plants but they also foraged on them at the same time throughout the day.

Flowers of most species had a peak of nectar production between 08:00 - 12:00 h (Fig. 2). Flowers of four species had a different pattern in nectar production; *Quesnelia strobilispica* decreased its production between 08:00 - 12:00 h; *Aphelanda margaritae*, *Vriesea ensiformis* and *Vriesea simplex* increased their production around 16:00 h (Fig. 2).

At the plant community level, temporal segregation based on nectar production did not differ from the expected under the null model. (p = 0.39, Table 3). All possible combinations between species resulted in 66 species-pair. At the species level, when we grouped the plants, they did not differ in their temporal overlap in nectar production when they co-flowered (one-tailed, W = 572, p = 0.36, Fig. 4A) or when they shared a hummingbird species (one-tailed, W = 319, p = 0.12, Fig. 4B). Contrary to our expectations, flowers with similar morphology had greater temporal overlap in nectar production (r = -0.36, df = 64, p = 0.002, Fig. 5).

DISCUSSION

We found that hummingbirds overlapped at both trophic and temporal scales, suggesting that resources were enough and therefore, competition might not be the main mechanism structuring the hummingbird-plant network. For plant species, the lack of temporal segregation in nectar production suggests a potential indirect effect, such as facilitation because even when plants co-flowered or shared a hummingbird species, they did not differ in their temporal overlap.

At the trophic scale, the hummingbird assemblage used similar resources. *P. eurynome* used most of the available resources resulting in overlap with morphologically similar species, especially *R. naevius*. The pattern of similar resource use between *P. eurynome* and *R. naevius* might be explained by their similar morphology (Zanata et al. 2019) and foraging behavior. Both hermit species are high-reward trap-liners (Stiles 1975, 1985, Feinsinger 1978, Stiles and Freeman 1993) that usually dominate the visits on hummingbird-pollinated flowers through floras of southeastern of the Atlantic Forest (Sazima et al. 1995, 1996, Buzato et al. 2000, Piacentini and Varassin 2007, Varassin and Sazima 2012). Also, they have been reported as common and resident hummingbirds of the EBSL (Ruschi and Simon 2012, Varassin and Sazima 2012), which could increase the likelihood of greater overlap on food resources among them and other hummingbird species, contributing to the overlap at the assemblage level.

While hummingbirds fed on the same plants, they also visited flowers during the same periods of the day between 06:00 - 11:00 h, the most active foraging period known for hummingbirds (Arizmendi and Ornelas 1990, Lange and Scott 1999, Lara et al. 2009). The lack of temporal segregation, as with trophic overlap, might be explained by resource availability. Theoretically, if shared resources are limited, then temporal partitioning is a mechanism for reducing resource competition (Schoener 1974), and therefore facilitating coexistence. Apparently, the resource availability in the study area, i.e. several flowering plant species and nectar rewards throughout the day, was enough for the hummingbird assemblage, probably resulting in no resource limitation, and thus limited competition or aggressive encounters among hummingbirds. However, because at the studied area, the patchy distribution of resources influenced the presence of pollinators (Varassin & Sazima 2012), there might occur segregation among hummingbirds, despite having available resources. Thus, the niche partitioning patterns could be influenced not only by the amount of resources but also by their spatial distribution.

Alternatively, closely related species are evolutionarily constrained to being active during the same time period limiting segregation at finer temporal scales (Daan 1981, Kronfeld-Schor et al. 2001a, b, c, Kronfeld-Schor and Dayan 2003). As a result of niche conservatism (Wiens and Graham 2005, Losos 2008), some species of hummingbirds could have similar time-use strategies resulting in overlap in their daily patterns instead of segregation. Also, environmental conditions may physiologically restrict hummingbirds to seek for food during the same hours of the day. After having no energy intake overnight, hummingbirds rely on immediate nectar rewards to fuel their energetic needs promoting them to use the same resources (Shankar et al. 2019). These ideas may explain our findings where all hummingbird were actively feeding through the first four hours in the morning. The high niche overlap among hummingbirds, at trophic and daily scales, suggests that resources were not limited among hummingbirds and that competition might not be the major mechanism structuring the hummingbird assemblage of the EBSL.

Daily segregation pattern of nectar production of the hummingbird-pollinated plant community did not differ from random expectations. Despite the random pattern, we found that nectar reward, mainly provided by bromeliads, was available for the hummingbirds throughout the day, reinforcing the idea that resources were not limited for hummingbirds. Plants with similar flower morphology showed greater temporal overlap in nectar production, and some species from the same genus had similar pattern of nectar production throughout the day. Plants with similar flower morphology may have converged on their floral traits (shape, color and nectar) and therefore some of them might be both related species and visited by similar pollinators (Brown e Brown 1979, Freeman et al 1984). As a result of evolutionary factors, some closely related plant species may have similar sugar concentration (Freeman et al 1984) and might be evolutionarily constrained to produce nectar during the same period throughout the day which may promote overlap patterns among plants. Nevertheless, plants can be highly plastic in their nectar production (Parachnowitsch et al. 2019) but environmental factors such as water availability, ambient humidity, temperature, soil factors and light may influence plants to produce nectar during coincident hours. This trait similarity may have important implications to coexistence, since that increasing similarity related to increased flowering synchrony have been reported as a mechanism to support facilitative interactions (Bergamo et al. 2020).

The similarity in temporal overlap in nectar production for plant species that co-flowered or shared a hummingbird suggest either the presence of other mechanisms increasing partitioning, such as partitioning of anthesis, or a benefit of co-flowering and sharing hummingbird pollinators. Some sympatric species flowering at the same time or sharing pollinators may reduce competition through partitioning of anthesis (time that flowers remain open) (Levin and Anderson 1970, Ollerton and Lack 1992) rather than segregation of nectar production. This strategy may allow plants to avoid heterospecific pollen transfer which may negatively impact seed production (Armbruster and Herzig 1984, Stone et al. 1996, Mitchell et al. 2009, Ashman and Arceo-Gómez 2013). Thus, instead of sugar segregation, the plant community visited by hummingbirds at EBSL might be timing their anthesis to avoid heterospecific pollen transfer and allowing coexistence among co-flowering sympatric species. The lack of segregation in nectar production among plant throughout the day and the high overlap among hummingbirds, suggest that there is a potential benefit of co-flowering and sharing hummingbird pollinators. Some studies (Callaway 1997, Bruno et al. 2003) propose that positive interactions, particularly indirect facilitation mediated by pollinators, can be a mechanism structuring pollinator-plant systems. The potential benefit of flowering at the same time is the joint attraction of pollinators resulting in increased fitness, especially for rare plants (Bergamo et al 2020). The negative side of joint attraction of pollinators, heterospecific pollen deposition, might be reduced through fine adjustments in floral morphological traits (e.g. differences in anther height) (Moeller 2004, Sargent and Ackerly 2008, Stewart and Dudash 2017), allowing them to place pollen on distinct body parts of the hummingbirds (e.g., neck, forehead, Araújo et al. 1994). For instance, recent findings in the Brazilian Atlantic Forest reported a positive relationship between fitness and flowering synchrony (Wolowski et al. 2017) and also, distinct anther heights and phylogenetic divergence of co-flowering species pairs (Bergamo et al. 2018) within hummingbird plant communities. Co-flowering patterns have been frequently observed for several bromeliads, the main plant family visited by hummingbirds in our study, that share same pollinators in the same study area (Martinelli 1995, Matallana et al. 2010, Wendt and Coser 2010), indicating that co-flowering is typical for a large part of the family. These patterns, along with our findings, suggest that facilitation (Bruno et al. 2003, Moeller 2004, Brooker et al. 2008) could be the mechanism structuring the hummingbird-pollinated plant community of the EBSL, as well as for the Atlantic Forest.

Our results serve to better understand the degree of niche partitioning within hummingbird-plant networks at a temporal scale that is rarely considered in pollination systems - a daily scale. Our results provide evidence of lack of niche segregation, but instead, clear overlap patterns at both trophic and daily scales among hummingbirds. Such findings indicate that competition for food was not intense for the hummingbird assemblage of the

EBSL. Nectar, offered mainly by Bromeliaceae, was available throughout the day, indicating that plants of this family are the most important nectar sources for hummingbirds. For plants, the segregation of nectar production was not different from random expectations at the community level, and no differences in temporal overlap of nectar production were detected for plant species that co-flowered or shared a hummingbird species. We thus suggest facilitation as a possible mechanism modulating the plant and hummingbird community in this area in the Atlantic Forest.

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FIGURE LEGENDS

Figure 1. Number of hummingbird visits throughout the day on a plant community recorded at EBSL, southeastern Brazil for A) the whole hummingbird assemblage and B) each hummingbird species.

Figure 2. Sugar production (mg) throughout the day of the hummingbird-visited plants recorded at EBSL, southeastern Brazil.

Figure 3. Pianka overlap index (0.50) of the hummingbird assemblage at trophic scale at the EBSL, southeastern Brazil. The observed overlap is represented by the red line. Solid and dashed black lines indicate the 90th and 95th quantile of the random distribution (blue bars). The observed overlap is higher than random distribution (blue bars) indicating lack of segregation ($p=0.98$).

Figure 4. Overlap in daily nectar production (mg) of plant species pairwise that A) co-flower (YES) and do not co-flower (NO), and B) that share (YES) and do not share (NO) a hummingbird species at EBSL, southeastern Brazil. Box-plots show the median values (tick lines), the interquartile (the box) and the confidence intervals (whiskers).

Figure 5. Correlation between overlap in daily nectar production (mg) and corolla dissimilarity of plants species. Each dot represents a pair of plant species belonging to the plant community visited by the hummingbirds. We recorded a total of 66 pairs of plant species.

TABLES

Table 1. Interactions (x) between hummingbird (columns) and plant (rows) species recorded at EBSL, southeastern Brazil

	Phaethornis eurynome	*Phaethornis squalidus*	*Ramphodon naevius*	*Thalurania glaucopis*
Aechmea araneosa	x	x	x	x
Aechmea lamarchei	x		x	x
Aechmea mutica	x		x	
Aphelandra margaritae	x			
Billbergia amoena			x	
Nidularium cariacicaense	x		x	
Nidularium procerum	x		x	
Quesnelia quesneliana			x	
Quesnelia strobilispica			x	x
Tillandsia stricta	x			
Vriesea ensiformis	x			
Vriesea simplex	x		x	

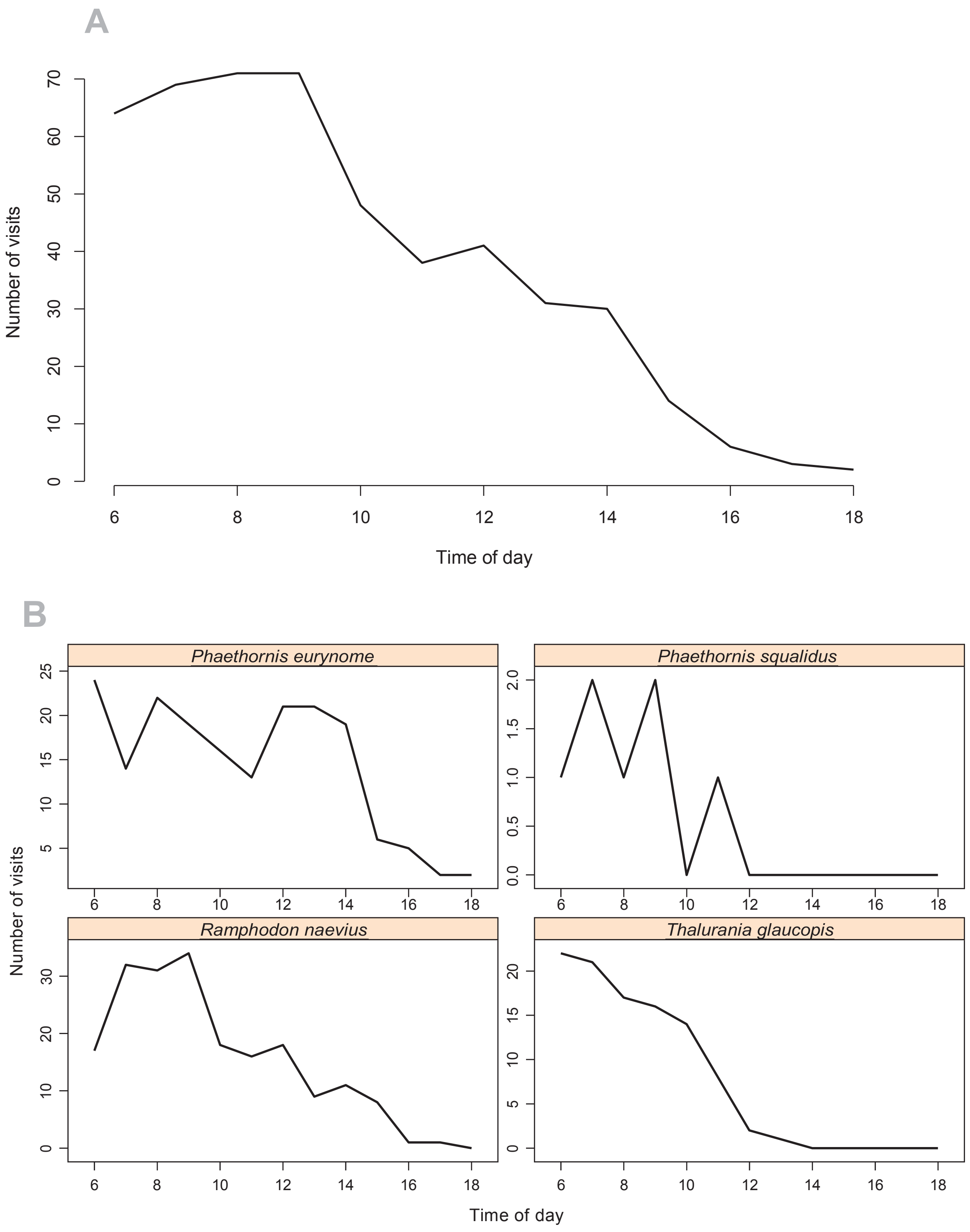
Table 2. Corolla length and nectar production equation of the hummingbird-visited plant species recorded at EBSL, southeastern Brazil. On the equation the x= time and, y = nectar production (mg sugar).

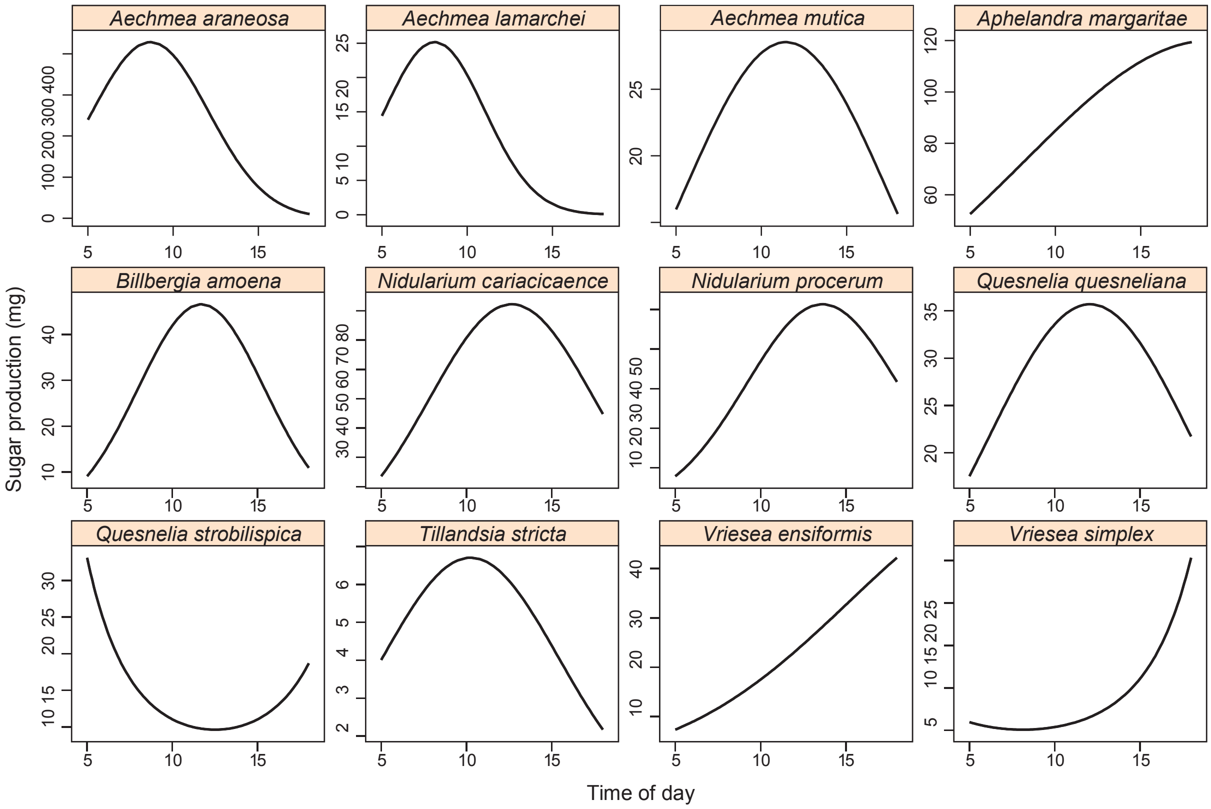
Plant species	**Corolla length (mm)**	**Nectar production equation x = time, y = nectar production (NP, mg sugar)**
Aechmea araneosa	15.96	NP = exp (5.086 + 0.749time – 0.043 x^2)
Aechmea lamarchei	27.7	NP = exp (4.927 + 0.943time – 0.058 x^2)
Aechmea mutica	23.85	NP = exp (6.227 + 0.320time – 0.014 x^2)
Aphelandra margaritae	39.7	NP = exp (5.906 + 0.157time – 0.004 x^2)
Billbergia amoena	49.85	NP = exp (3.684 + 0.852time – 0.036 x^2)
Nidularium cariacicaense	52.04	NP = exp (4.409 + 0.539time – 0.021 x^2)
Nidularium procerum	50.98	NP = exp (3.343 + 0.685time – 0.025 x^2)
Quesnelia quesneliana	36.9	NP = exp (6.466 + 0.342time – 0.014 x^2)
Quesnelia strobilispica	50.66	NP = exp (10.66 – 0.549time + 0.021 x^2)
Tillandsia stricta	11.16	NP = exp (4.362 + 0.383time – 0.018 x^2)
Vriesea ensiformis	50.2	NP= exp (6.183 + 0.246time – 0.004 x^2)
Vriesea simplex	64.52	NP = exp (8.235 – 0.267time + 0.016 x^2)

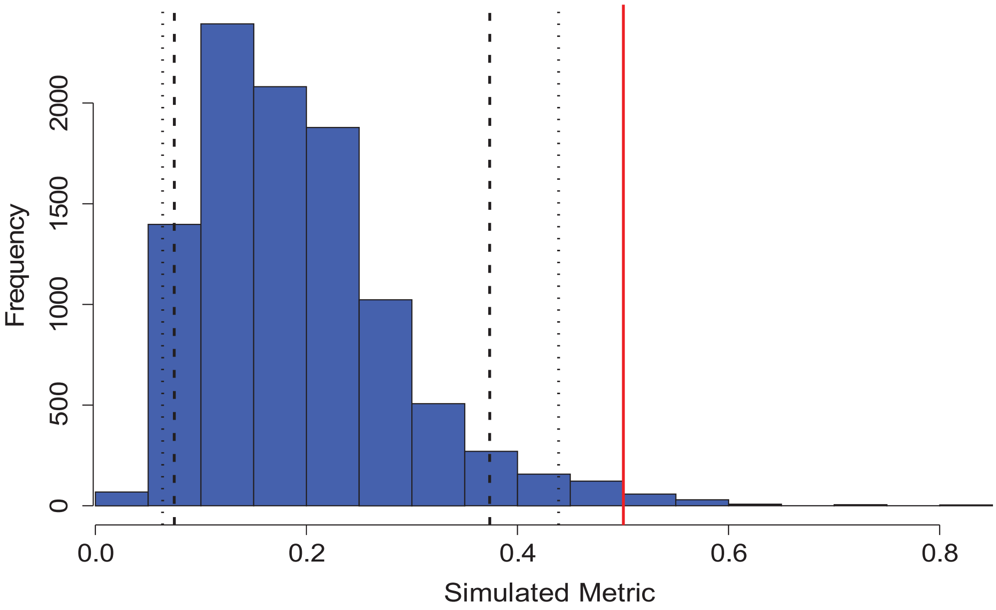
Table 3. Patterns of overlap in resource use for hummingbirds at trophic and daily scale and nectar production for the plant community on a daily scale. Observed values are the observed overlap for the hummingbird assemblage and the plant community visited by hummingbirds at EBSL, southeastern Brazil. P-values are one-tailed probabilities of finding segregated patterns. P-value was calculated as the proportion of randomizations that resulted in an overlap that is equal to or less than the observed overlap. Non-significant values indicate coincident patterns of niche overlap.

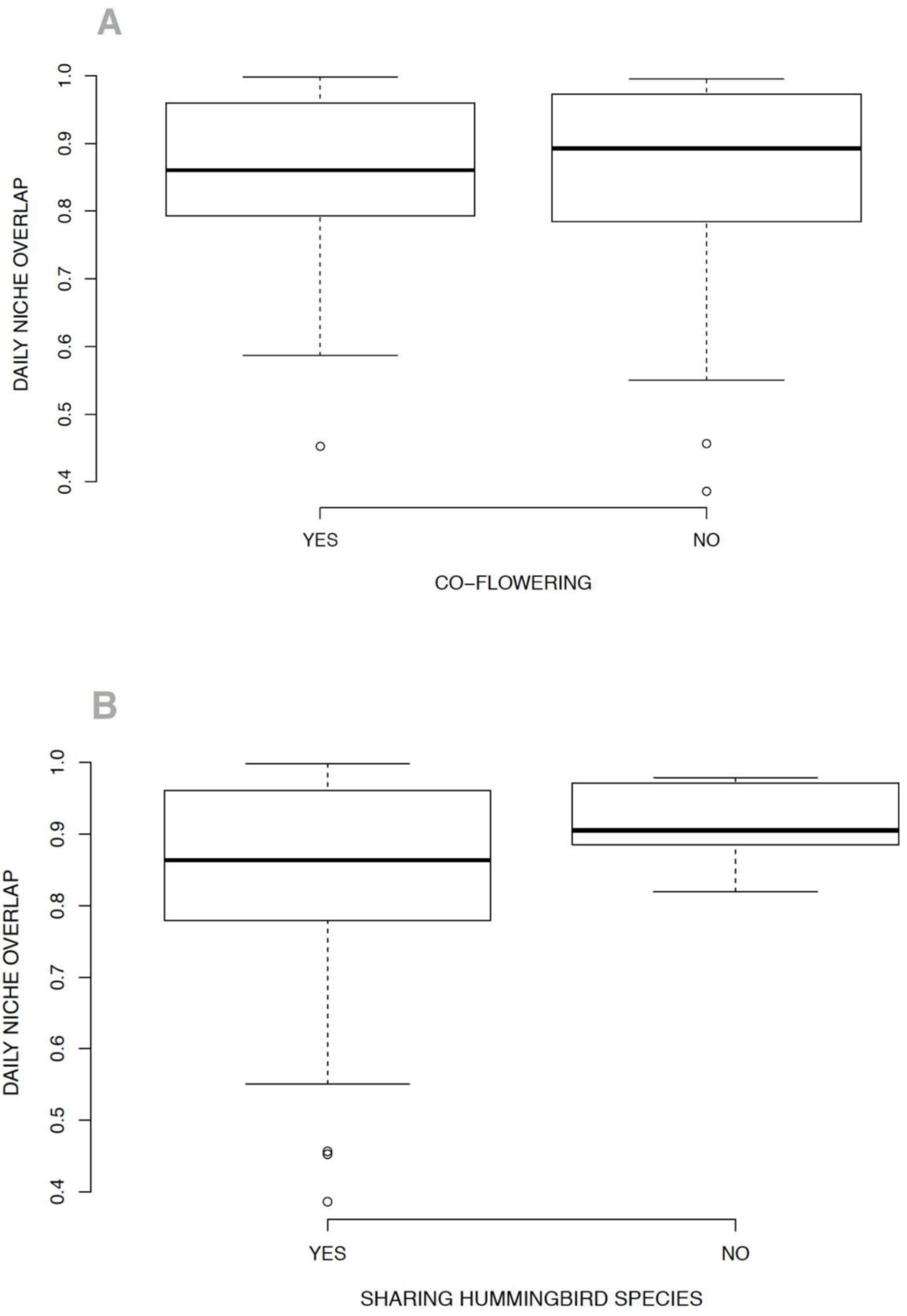
	Model	**Observed**	**P-values**
Hummingbird assemblage (trophic scale)	ra3	0.50	0.98
Hummingbird assemblage (daily scale)	ROSARIO	0.83	0.99
Plant community (daily scale)	ROSARIO	0.85	0.39

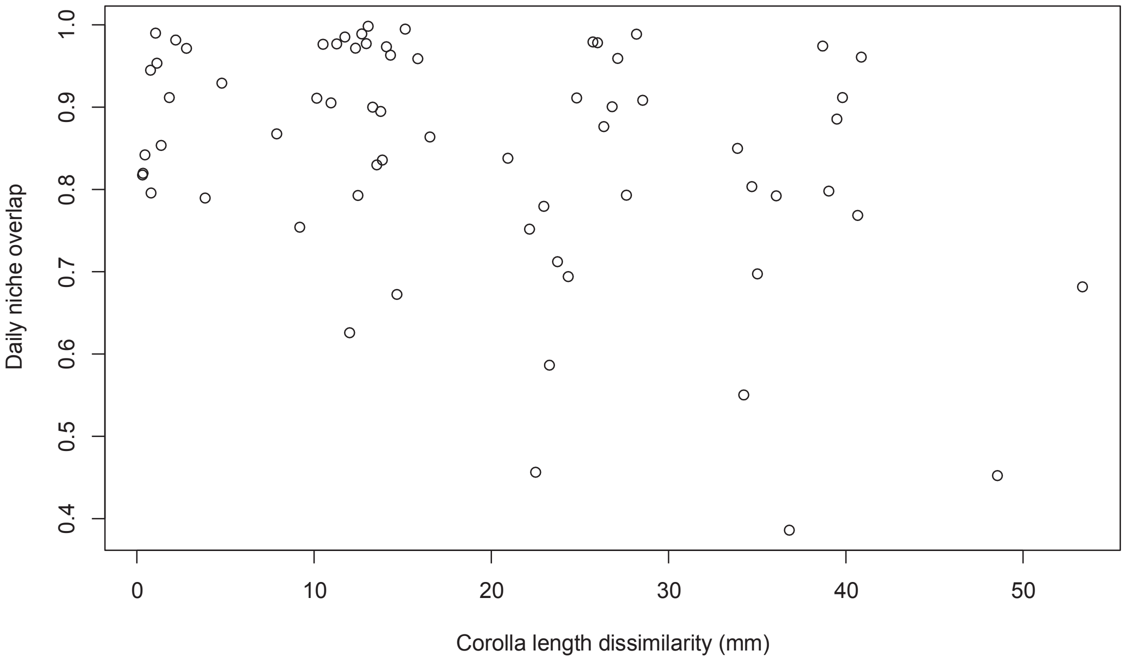
FIGURES


A
Number of visits
0
10
20
30
40
50
60
70
6
8
10
12
14
16
18
Time of day
B
Phaethornis eurynome
Phaethornis squalidus
Ramphodon naevius
Thalurania glaucopis
Number of visits
5
10
15
20
25
0.0
0.5
1.0
1.5
2.0
0
10
20
30
0
5
10
15
20
6
8
10
12
14
16
18
Time of day


Aechmea araneosa
0
100 200 300 400
5 10 15
Aechmea lamarchei
0
5 10
15 20
25
Aechmea mutica
20
25
Aphelandra margaritae
60
80
100
120
Billbergia amoena
10
20
30
40
Nidularium cariacicaence
30 40 50 60 70 80
Nidularium procerum
10 20 30 40 50
Quesnelia quesneliana
20
25
30
35
Quesnelia strobilispica
10 15
20
25
30
Tillandsia stricta
2
3
4
5
6
Vriesea ensiformis
10
20
30
40
Vriesea simplex
5
10 15 20 25
Sugar production (mg)
Time of day


Frequency
0
500
1000
1500
2000
0.0
0.2
0.4
0.6
0.8
Simulated Metric


A
DAILY NICHE OVERLAP
1.0
0.9
0.8
0.7
0.6
0.5
0.4
YES
NO
CO–FLOWERING
B
DAILY NICHE OVERLAP
1.0
0.9
0.8
0.7
0.6
0.5
0.4
YES
NO
SHARING HUMMINGBIRD SPECIES


Daily niche overlap
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0
10
20
30
40
50
Corolla length dissimilarity (mm)