

Research

Trait patterns across space and time suggest an interplay of facilitation and competition acting on Neotropical hummingbird-pollinated plant communities

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Pollinators may influence plant community assembly through biotic filtering and/or plant–plant competition and facilitation. The relative importance of each process, however, vary according to the scale and how strongly plants share their pollinators, and possibly in relation to the pollinator groups considered. We here investigated the assembly of three Atlantic forest hummingbird-pollinated plant communities across space (among all species in the communities) and time, i.e. yearly flowering phenology (between pairs of co-flowering species), based on the pairwise distances of multiple floral traits (corolla length, anther and stigma height, colour and nectar). Because tropical hummingbird-pollinated plants are often subdivided in two pollination niches (hermits versus non-hermits), we also analyzed these groups separately. We found that trait structure across space was clustered for some floral traits, suggesting biotic filtering and facilitation. All floral traits had weak phylogenetic signal, indicating that closely related species were not more similar than distantly related species. Moreover, floral traits were randomly structured along the phenology when analyzing all plants together. On the other hand, we found similar corolla length but divergent anther height in co-flowering pairs within the same pollination niche. Thus, plants may benefit from flowering together and avoid competition through fine adjustments in reproductive traits. The results also suggest that clear signals of competition and facilitation among plants are only apparent when species strongly share their pollinators and depending on the traits that are considered. Our study illustrates a complex interplay of biotic filtering, facilitation and competition as processes structuring guilds of plants sharing the same functional group of pollinators.

Keywords: pollination ecology, functional structure, community assembly



Introduction

Multiple processes can simultaneously define species coexistence and community assembly, which may lead to contrasting functional trait patterns (Gerhold et al. 2015). Plant interactions with animals, such as pollination, have a major role in determining species composition in communities (Sargent and Ackerly 2008). Many plant species depend on pollinators for their reproduction (Ollerton et al. 2011), and can only persist in a community in the presence of such mutualists (Lundgren et al. 2016). In this scenario, only the plant species with reproductive traits fitting the local pollinator community will persist, implying that pollinators act as biotic filters (Shrestha et al. 2016). Plants also influence each other's fitness through pollinator sharing (Sargent et al. 2011), leading to the possibility of competitive exclusion, or stabilizing niche differences, structuring plant communities (HilleRisLambers et al. 2012, Nottebrock et al. 2016). In this context, plant species that share pollinators can benefit each other by flowering simultaneously via facilitative interactions, which increase overall visitation rates (Moeller 2004). One common expectation in this case is trait clustering in communities, a mechanism that enhances attractiveness of the whole community (Gumbert et al. 1999, de Jager et al. 2011, but see Ghazoul 2006). On the other hand, plants species with similar traits often suffer from inter-species pollinator visits, which may cause improper pollen transfer (Morales and Traveset 2008). In fact, plant communities may exhibit fine adjustments through interspecific differences in floral traits to avoid competition for pollinator attraction or heterospecific pollen deposition (Muchhala et al. 2014). Therefore, one can use the plant reproductive trait structure to understand the influence of plant–pollinator interactions on the assembly of plant communities.

The role of pollinators on the structuring of plant communities may become evident by considering distinct floral traits (Gegear and Lavery 2001). For instance, resource accessibility (corolla length) and availability (nectar sugar content) can influence the composition of pollinator assemblage associated to a flower and thus the degree of pollinator-sharing between plants and their potential indirect effects (Carvalho et al. 2014, Nottebrock et al. 2016, Bergamo et al. 2017). Meanwhile, floral signals and rewards influence pollinator attraction and foraging strategy among species. Thus, dissimilarity of floral signals may favor flower constancy, reducing competition (Chittka et al. 1997), while signaling similarity may lead to facilitation by enhancing pollinator attraction (Moeller 2004). Finally, anther and stigma height and position in the flower mediate pollen placement on pollinator's body and, consequently, the potential for heterospecific pollen transfer between plants (Morales and Traveset 2008, Stewart and Dudash 2017). Hence, using a multi-trait approach is required to assess the relative importance of distinct ecological processes on community assembly based on plant–pollinator interactions.

Tropical hummingbird-pollinated plants are considered a specialized system in the Neotropics (Stiles 1977, Feinsinger and Colwell 1978, Zanata et al. 2017). Further specialization into distinct pollination niches can be found within the hummingbird-pollinated plant communities, regulated by corolla–bill length matching and other morphological and behavioral traits (Murray et al. 1987, Maruyama et al. 2014, Maglianesi et al. 2015). Moreover, phylogeny-based analyses often show a low influence of evolutionary relatedness influencing plant–hummingbird interactions and, consequently the associated floral traits (Bergamo et al. 2017, Wolowski et al. 2017). Therefore, hummingbird-pollination could act as a filter on the community assembly, leading to communities composed by functionally similar plant species from distinct lineages (Wolowski et al. 2017). Thus, evaluating patterns on how multiple traits across communities are structured in the light of their phylogenetic structure may clarify the most likely process shaping the assembly of distinct communities.

Besides the spatial variation among communities, the dynamics of plant–pollinator interactions changes within communities along the flowering phenology, meaning that community structure of plants interacting through shared pollinators will change depending on the phenological context being evaluated (Sargent et al. 2011). The temporal structure, defined here as the yearly flowering phenology of hummingbird-pollinated plant communities, is often referred to be staggered in the literature, and most interpretations point to the sequential flowering as a strategy to maintain hummingbirds in the community while avoiding competition for pollination (Stiles 1977, Aizen and Rovere 2010). At the same time, distinct flowering times of plants associated to long-lived pollinators may be associated to facilitation through joint maintenance of pollinators in an area (Waser and Real 1979, Moeller 2004). However, the presumed staggered flowering patterns are often not different from random expectations, and conversely, flowering overlap in an Atlantic forest hummingbird-pollinated plant community was associated to facilitation through joint attraction of pollinators (Wolowski et al. 2017). To disentangle the role of distinct processes, an important step is to incorporate trait patterns into the analyses of flowering overlap. In a scenario of similar pollinator use and facilitation through joint attraction, co-flowering species are expected to exhibit similar traits indicating benefits of enhancing overall attractiveness to the same shared pollinator species (Moeller 2004). On the other hand, co-flowering species with distinctive traits suggests a scenario to minimize competition for pollination. These patterns are not mutually exclusive, since species with similar corolla length and pollinators may minimize competition for pollination through fine adjustments in pollen placement (Rathcke 1983, Sargent and Ackerly 2008). Moreover, such fine adjustments are expected when plants strongly share their main pollinators, thus, belonging to the same “pollination niche” (Pauw 2013). Thus, incorporating the pollination

niche of the plants may reveal otherwise undetected trait patterns.

Here we assessed the patterns of trait structure for three hummingbird-pollinated plant communities in the Atlantic forest. For these communities, we have extensive knowledge on species composition, life history (i.e. flowering phenology, floral traits and pollen limitation), and pollination (Sazima et al. 1995, Buzato et al. 2000, Wolowski et al. 2013, Maruyama et al. 2015, Vizentin-Bugoni et al. 2016, Bergamo et al. 2017). We evaluated trait patterns among all plant species in the community and between co-flowering species pairs. For this, we used several floral traits important for the interaction with pollinators: corolla length (related to nectar accessibility), sugar content (resource availability), flower colour (attractiveness) and anther and stigma height (pollen placement and pick-up). We assessed 1) trait patterns across space (among communities); 2) trait patterns across the phylogeny; 3) trait patterns along time/phenology (between co-flowering species pairs). Moreover, we conducted separate analyses for each of the pollination niches that occur within these communities, to assess whether and how patterns change when the strength of pollinator sharing is considered.

Methods

Study system

We studied three hummingbird-pollinated plant communities from the Brazilian Atlantic forest, in southeast Brazil: Itatiaia – ITA (Wolowski et al. 2013), Santa Virginia

– SVG (Vizentin-Bugoni et al. 2016) and Picinguaba – PIC (Maruyama et al. 2015, specifically the ‘Praia da Fazenda’ area). These communities are characterized by two montane forests (ITA and SVG) and one lowland forest (PIC) (Supplementary material Appendix 1 Fig. A1). The species pool amounted to 103 plant species (32 occurring in ITA, 58 in SVG and 31 in PIC), belonging to several plant lineages, mostly represented by species of Bromeliaceae, Acanthaceae, Gesneriaceae, Malvaceae and Fabaceae (Supplementary material Appendix 1 Table A1, Fig. 1). All communities have hermit and non-hermit hummingbird species: five hummingbird species (two hermits) in ITA, nine species (one hermit) in SVG and 11 species (three hermits) in PIC (Supplementary material Appendix 1 Table A2). Visitation rates of the pollinators (i.e. number of visits/flower/time) were recorded by focal observation of each plant species (Wolowski et al. 2013, Maruyama et al. 2015, Vizentin-Bugoni et al. 2016). Each plant species was observed for at least 15 h and interactions were often recorded using video cameras, which allowed detailed examinations of the interactions. If a hummingbird made a legitimate visit (i.e. accessing the nectar through the corolla opening and touching the reproductive structures) it was considered a pollinator (Supplementary material Appendix 1 Table A3).

Functional traits

Data on floral traits were collected in all communities for most species and completed with information from the literature. We measured directly in the field all morphological features using a digital caliper: corolla length, i.e. the measure from the base of the nectary to the flower tube opening

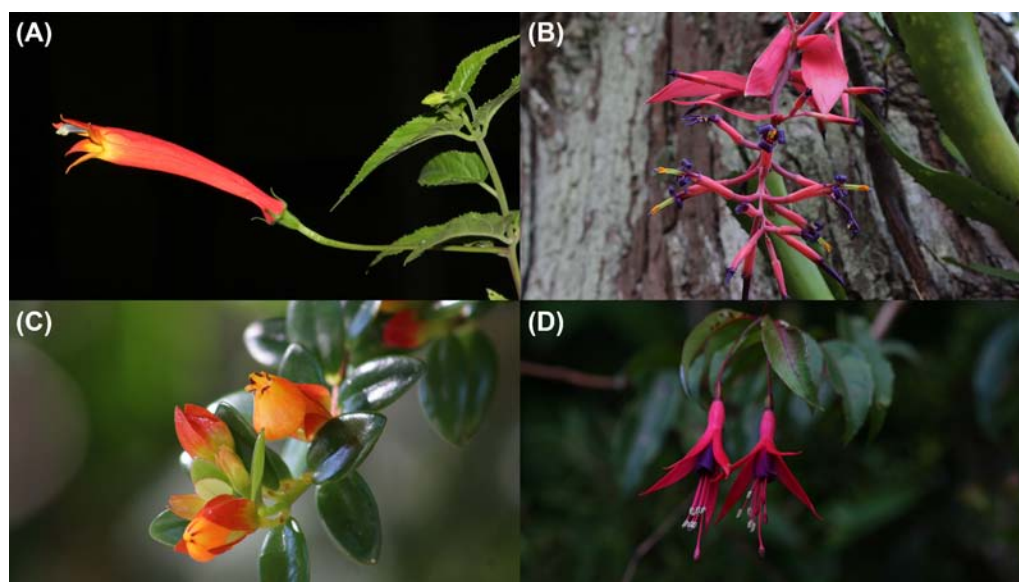


Figure 1. Hummingbird-pollinated plants of the Atlantic forest, southeastern Brazil. (A) *Siphocampylus longipedunculatus* (Campanulaceae); (B) *Billbergia vittata* (Bromeliaceae); (C) *Nematanthus gregarius* (Gesneriaceae) and (D) *Fuchsia regia* (Onagraceae). (A) and (B) have long corollas pollinated by hermit hummingbirds, while (C) and (D) have short corollas pollinated by both hermit and non-hermit hummingbirds. In relation to the corolla tube there is also difference on anther and stigma position: inside (A, C) and outside (B, D). Photo credits: Jeferson Vizentin-Bugoni (A, C) and Marina Wolowski (B, D).

(effective corolla length sensu Wolf et al. 1976) as a proxy of resource accessibility; and stigma and anther height, from the base of the nectary to the top of each structure as the estimate of the position of placement and transfer of pollen on the hummingbird body. We measured the spectral reflectance of the petals using a spectrophotometer coupled with a deuterium-halogen light source, with a light emission range between 215 nm and 1700 nm. We took all reflectance measurements at a 45° angle, using barium sulphate and a black chamber as white and black standards, respectively. To analyse the colour in the hummingbird subjective view, we modelled hummingbird vision following procedures in Bergamo et al. (2017; also see Supplementary material Appendix 1 for details). Nectar volume was collected with a micro-syringe and nectar concentration measured with a pocket refractometer in flowers bagged before the anthesis and kept isolated from visitors for at least 12 h. We only complemented nectar data from the literature when measures of nectar production were collected in flowers also isolated from visitors for at least 12 h. As the functional trait for nectar, we considered the nectar sugar content, calculated following Galetto and Bernardello (2005). From the 103 species included in this study, the final dataset included corolla length for 102 species (99.03%), anther and stigma height for 94 (91.26%), colour for 92 (89.32%) and nectar for 90 (87.34%). Species' floral traits and source of the data are available in the Supplementary material Appendix 1 (Table A4–A5). Each sample was measured from a distinct plant individual.

Trait structure among communities

We calculated abundance-weighted mean pairwise distance (MPD) between all species for each floral trait (i.e. corolla length, anther and stigma height, colour and nectar sugar content) for each community as the measure of trait structure. The abundance of each species was calculated as the relative number of flowers produced by a plant species recorded during one year of flowering phenology census. To avoid differences caused by species richness and/or sampling design, we calculated the relative number of flowers produced per species per community along 12 months as a proxy of flower abundance. For this, we divided the total number of flowers of a given species in a community by the total number of flowers across all species in that community. Then, the observed MPD value of each community was compared with a null distribution generated by 10 000 random communities created from the species pool. To create the random communities, we used the independent-swap algorithm in which the original species richness is preserved and the probability of a species to be included in a community is weighted by its frequency (Gotelli 2000). The analysis for each floral trait was done using the subset of species for which we had information (Supplementary material Appendix 1 Table A4–A5). A significant MPD value higher than expected by chance indicates trait evenness, while a significant lower MPD value indicates trait clustering. These analyses were performed using the

package *picante* in R (Kembel et al. 2010). We calculated the trait distances between species as the Euclidian distance for each floral trait. For flower colour, we calculated perceptual distances using the logarithm version of the receptor noise-limited model (Vorobyev et al. 2001, Supplementary material Appendix 1). We chose the logarithm version because it better represents the photoreceptor responses to the amount of light captured by the eye system (Vorobyev et al. 2001). Results were qualitatively similar when using the tetrahedron colour space model (Vorobyev et al. 1998) instead of the receptor noise-limited model (Supplementary material Appendix 1 Table A6), and we present only the receptor noise-limited results in the main text. However, it should be noted that these models do not consider potential colour variability within target and receiver species.

Phylogenetic signal of floral traits

To assess the phylogenetic signal of each floral trait, we built a plant phylogenetic hypothesis for the species pool based on the consensus supertree of the APG III (Tree R20120829) in Phylomatic (Webb and Donoghue 2005). For Bromeliaceae, we assumed monophyly for subfamilies and polytomies for genera following the relationships reported in Givnish et al. (2011). Then, we calibrated branch lengths with the BLADJ function in Phylocom (Webb et al. 2008), using the Angiosperms major lineages divergence times proposed by Bell et al. (2010). Supplementary material Appendix 1 Fig. A2 illustrates the evolutionary relationships among all species.

For the quantitative traits (morphological features and nectar sugar content), the phylogenetic signal was measured by the *K* statistic (Blomberg et al. 2003), using the *phytools* package in R (Revell 2012). The *K* statistic assesses the amount of variation among species traits that is correlated with its phylogenetic relationships. Values of *K* > 1 means that closely related species are more similar than expected by the Brownian motion model of evolution while a *K* < 1 indicates that closely related species are less similar than expected (Blomberg et al. 2003). To assess significance, we compared the observed *K* for each trait with a null distribution generated by 10 000 random trees assembled by reshuffling species into the null phylogenies. If the observed *K* significantly differs from 1, the trait under question departs from the expected evolution under Brownian motion. We also assessed if the observed *K* was significantly different from 0, which would indicate that some degree of phylogenetic signal exists. For floral colour, for which we had only a perceptual distance matrix, we calculated the phylogenetic signal as the correlation between colour and phylogenetic distances matrices using a Mantel test.

Determinants of pairwise flowering overlap

Phenological data was collected monthly in each community (Wolowski et al. 2013, Maruyama et al. 2015,

Vizentin-Bugoni et al. 2016). The number of flowers per species was recorded each month along pre-existing trails. In Itatiaia, the phenology census was conducted by counting the number of flowers for plant individuals occurring in permanent plots. In Santa Virginia and Picinguaba, the phenology census was made by counting flowers of every plant individual along trails. Therefore, we had a matrix for each community with the number of flowers produced by a given species at each month (for 12 months). Then, we quantified flowering overlap among all pairwise species combinations for each community using the Czechanowski index, based on the overlap of the histograms representing two temporal distributions (Feinsinger et al. 1981). This is a more adequate index for quantitative phenological data since it accounts for the flowering intensity at each temporal unit evaluated (i.e. the number of flowers at each month). For communities with more than one-year survey (ITA and SVG), we selected the year with the higher number of flowering species recorded as interannual variation in flowering of a given species in the same community was revealed to be small by Mantel tests in Bergamo et al. (2017).

We assessed whether pairwise temporal overlap among species of each community was explained by the evolutionary relatedness or trait similarity by fitting the pairwise temporal overlap with the phylogenetic and trait distances as fixed variables in mixed-models. For this, we used the package *lme4* (Bates et al. 2015) in R. We included in these analyses 84 species (81.55% of the total of species) for which we had information for all floral traits. However, anther height and stigma height were highly correlated, as indicated by the variance inflation factor (anther height: 14.54; stigma height: 13.86). We removed stigma height because this trait is more variable among flowers within species than anther height (Bergamo et al. 2017). Nectar was not included as we only had this data for 68.93% of the 84 species mentioned above. We used the species pair nested within community as random effects to account for the dependency related to species identities and local species composition. Since many species pairs had no flowering overlap, we performed two sets of models to deal with zero-inflation (Carvalho et al. 2014). First, we converted the response variable into a binomial variable to investigate which factors influence the probability of flowering overlap ('Probability models'). For these models, we assigned 0 when there was no temporal overlap and 1 to all positive values, assuming a binomial-distribution error structure. Second, the variability in the phenological overlap was tested using the subset of positive values and assuming Gaussian-distribution error structure ('Variability models'). For the variability models, we applied a logit transformation on the response variable to meet model assumptions. We run both sets of mixed models with combinations between all fixed effects and a null model with only the response variable and the random effects. The best models were selected based on its ΔAIC values, assuming models with $\Delta AIC < 2.0$ as equivalents.

We also performed these set of model analyses for each pollination niche: the subsets of hermit-pollinated and

mixed-pollinated plant species in each community ('hermit assemblage' and 'mixed assemblage', respectively). We classified the pollination niche based on the visitation frequency data of hermits and non-hermits of each plant species in each community. The hermit pollination niche was composed by plant species for which at least 80% of the visits were performed by hermit hummingbirds. We chose this threshold based on our own data, as few plant species have hermits performing 60–79% or below of the visits, supporting such separation (Supplementary material Appendix 1 Fig. A3). Moreover, this visitation threshold included ca 53% of the species of each community, which is consistent with the number of interaction partners of hermits in most Atlantic forest communities (Buzato et al. 2000, Wolowski et al. 2013, Maruyama et al. 2015, Vizentin-Bugoni et al. 2016). Using the same criteria for the non-hermits, we would include only 26.3% of the species in the exclusively non-hermit category. Instead, we classified all other plant species as mixed-pollinated, which also included the species visited by both hermits and non-hermits at similar frequencies. The hermit category included all *Phaethornithinae* species, except *Phaethornis ruber*, since this hummingbird usually has opportunistic foraging strategy, often acting in the community as a non-hermit (Maruyama et al. 2015).

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.qt7nr84>> (Bergamo et al. 2018).

Results

Trait structure among communities

Overall, floral trait structure within communities did not differ from the random expectation (Fig. 2, 3, Supplementary material Appendix 1 Table A6). However, the montane communities showed trait clustering for some floral traits: anther height, stigma height and flower colour in SVG and nectar sugar content in ITA (Fig. 2, 3, Supplementary material Appendix 1 Table A6).

Phylogenetic signal of floral traits

All traits departed from the expected pattern of evolution under Brownian motion and had phylogenetic signal with $K < 1$ (corolla length: 0.13, anther height: 0.12, stigma height: 0.12, nectar sugar content: 0.13, all $p = 0.001$). This suggests that closely related species were less similar than expected. All K -values did not differ from zero (corolla length: $p = 0.47$, anther height: $p = 0.89$, stigma height: $p = 0.91$, nectar sugar content: $p = 0.51$). These two analyses suggest a weak phylogenetic signal, i.e. only 12–13% of the trait variance was explained by phylogenetic relatedness (sensu Blomberg et al. 2003). In addition, flower colour also lacked phylogenetic signal (Mantel test, $r = -0.035$, $p = 0.94$).

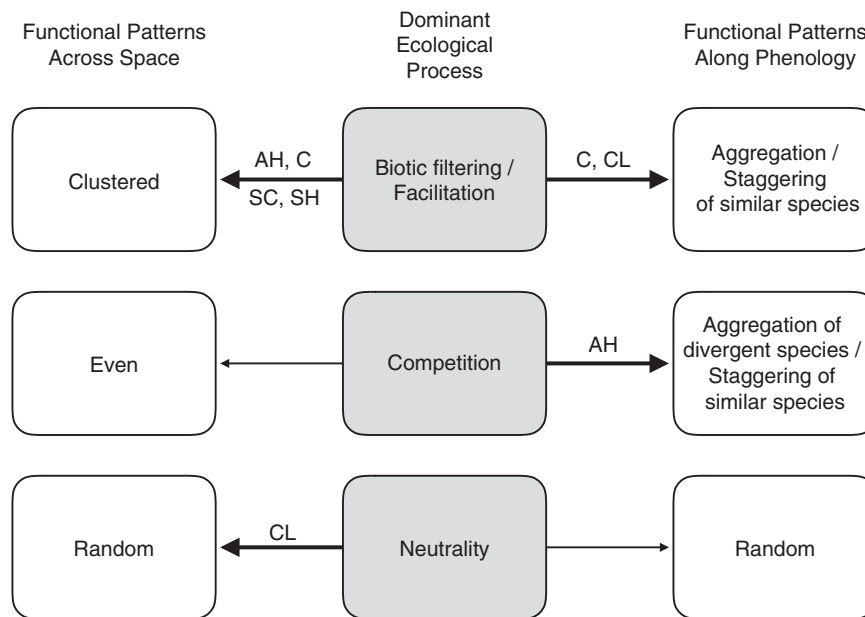


Figure 2. Framework illustrating the expected functional patterns across space (among communities) and along time (yearly phenology within communities), related to the structuring processes of plant–pollinator interactions (combining the frameworks of Moeller 2004 and Sargent and Ackerly 2008). The first and third columns indicate the expected pattern under the dominant ecological process of the second column. Note that biotic filtering and facilitation may lead to phenological aggregation of similar species (‘facilitation through joint attraction’) or staggering of similar species in the case of long-lived pollinators (‘facilitation through joint maintenance’) (sensu Moeller 2004). Thicker arrows indicate the functional patterns found in at least one of the hummingbird-pollinated plant communities of this study in the Atlantic forest, southeastern Brazil. AH – anther height, C – flower colour, CL – corolla length, SH – stigma height and SC – nectar sugar content.

Determinants of pairwise flowering overlap

We found evidence for phylogenetic and trait determinants in the pairwise flowering overlap only when evaluating pollination niche assemblages (Fig. 2). Trait similarity and evolutionary relatedness did not explain the probability, nor the variability, in pairwise flowering overlap among all hummingbird-pollinated plants (Table 1). However, pairs with similar corolla length had higher probability of flowering together within hermit-pollinated plant species (Table 1). Additionally, a positive effect of phylogenetic distance was included in the second best model, indicating that more distantly related hermit-pollinated plant species pairs had higher chance of flowering together (Table 1). Thus, there is weak phylogenetic signal for co-flowering hermit-pollinated plant species. A third best model included only a negative effect of anther height, indicating that hermit-pollinated plant species pairs with distinct anther height had more chance of flowering together (Table 1). For mixed-pollinated plant species, corolla length, anther height, colour and phylogenetic distance were included in the best models explaining the probability of flowering overlap (Table 1). Overall, mixed-pollinated plant species pairs with similar corolla length and floral colour, but with distinct anther height had more chance of flowering together (Table 1). Also, there was a weak positive effect of phylogenetic distance, indicating that distantly related species flowered together. When considering the variability in pairwise

flowering overlap, however, trait similarity and evolutionary relatedness had no influence within each pollination niche assemblage (Table 1).

Discussion

Here we show that hummingbird-pollinated plant communities present trait patterns suggesting influence of plant–pollinator interactions across space and time. Specifically, we found random and clustered structure of floral traits across space, coupled with convergent trait evolution. Along the temporal dimension, co-flowering plant species within the same pollination niche exhibited a combination of some similar and other divergent floral traits. These results evidence the interplay of biotic filtering, facilitative and competitive interactions operating at different scales and influencing the structure of guilds within communities.

Trait patterns across space

The use of multiple floral traits revealed specific trait patterns among these communities. Although most floral traits within communities were random samples from a larger species pool, four traits were clustered in two montane communities (anther height, stigma height and flower colour in SVG and nectar sugar content in ITA). In these communities, there is a higher proportion of hermit-specialized plant species than in

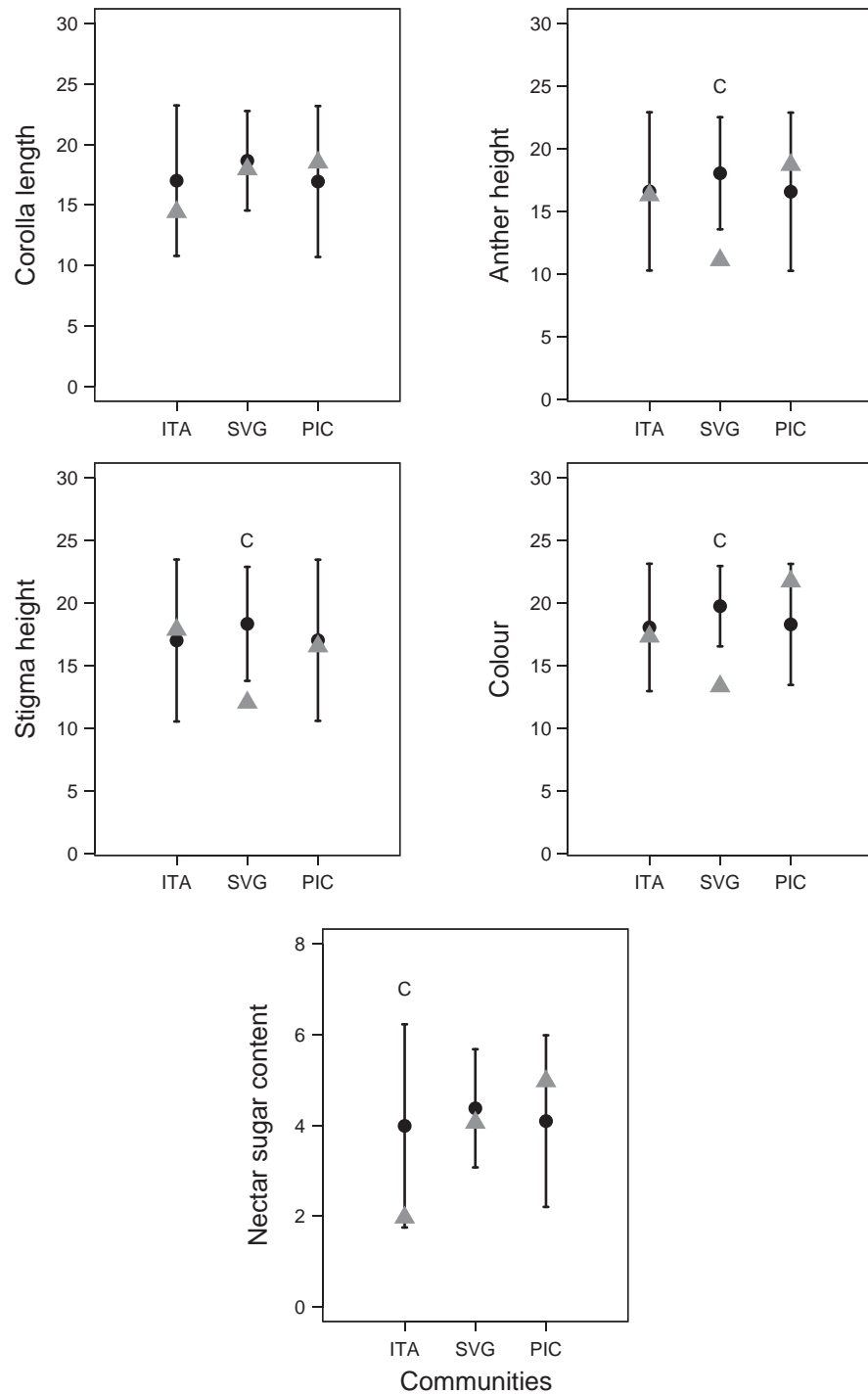


Figure 3. Functional structure of hummingbird-pollinated communities in the Atlantic forest, southeastern Brazil. Functional structure was evaluated with the species pool comprising all communities (ITA=Itatiaia; SVG=Santa Virginia; PIC=Picinguaba). Grey triangle = mean pairwise distance (MPD) observed for each community. Black circle = mean MPD of 10 000 null assembled communities with independent swap algorithm (Gotelli 2000), with bars representing 95% confidence interval. Letter 'C' indicates a clustered structure at $p < 0.05$ level.

coastal lowland communities (57% in ITA and 55% in SVG versus 29% in PIC, Wolowski et al. 2013, Maruyama et al. 2015, Vizentin-Bugoni et al. 2016). Thus, the trait signature on these communities may reflect the role of biological

filter played by hermit hummingbirds, favoring plants with some specific floral traits (Shrestha et al. 2016). For instance, anther and stigma height were higher on average for montane than lowland communities (in mm; ITA: 36.19 and 37.89,

Table 1. Model parameters for the determinants of pairwise co-flowering of hummingbird-pollinated plant communities ('Whole community') and the hermit and mixed plant assemblages. The probability (Binomial model) and variability of phenological overlap (Gaussian model) were evaluated with mixed models. Fixed effects: anther height (AH); colour (C); corolla length (CL) and phylogenetic distance (P). All models included species pair identity nested within community as random effects. Estimates of the factors in the best models (in italics) are given in parenthesis. Explained deviance = difference between the deviance of the models and of a model including only the intercept. ΔAIC = the difference in Akaike information criteria between the best selected model and the model under consideration, after selection including models with all possible combinations among fixed effects. Significance is assessed by comparison of AIC values. The models with lowest AIC values, generally < 2.0 , are considered significant (in bold).

	Explained deviance	ΔAIC	weight
Whole community (Binomial)			
Random effects only	38.28%	0.00	0.22
AH+C+CL+P	38.35%	6.23	0.01
Whole community (Gaussian)			
Random effects only	42.98%	0.04	0.17
AH+C+CL+P	43.02%	5.07	0.01
Hermit assemblage (Binomial)			
<i>CL(-0.04)</i>	53.33%	0.0	0.19
<i>CL(-0.04) + P(0.008)</i>	53.62%	0.63	0.11
<i>AH(-0.02)</i>	53.13%	1.29	0.10
Random effects only	44.83%	2.27	0.06
AH+C+CL+P	53.93%	4.42	0.02
Hermit assemblage (Gaussian)			
Random effects only	43.04%	0.0	0.18
AH+C+CL+P	43.18%	4.61	0.02
Mixed assemblage (Binomial)			
<i>AH(0.03) + CL(-0.05) + P(0.002)</i>	57.31%	0.0	0.31
<i>AH(0.03) + C(-0.006) + CL(-0.05) + P(0.002)</i>	57.35%	0.87	0.20
<i>CL(-0.05) + P(0.002)</i>	57.24%	0.96	0.19
Random effects only	49.73%	7.17	0.01
Mixed assemblage (Gaussian)			
Random effects only	40.67%	1.19	0.13
AH+C+CL+P	41.02%	5.58	0.01

SVG: 39.02 and 40.33, PIC: 30.38 and 30.15, respectively). Since hermits have longer bills than non-hermits, plants with longer reproductive structures are able to export more pollen in suitable parts of the hermit body (e.g. forehead or throat, Rocca and Sazima 2013). The colour similarity may promote faster pollinator learning of floral resources and lead to higher visitation rates (Gumbert et al. 1999), a mechanism not yet explored for hummingbird pollination studies. Additionally, facilitative interactions were suggested based on the association between flowering synchrony and lower pollen limitation in a hummingbird-pollinated montane plant community (Wolowski et al. 2017). Similar floral resource availability also reinforces the role of facilitative interactions, since it is less likely that pollinators will exhibit resource-based preferences among different plant species if these are equally profitable (Ghazoul 2006). Thus, trait patterns that were different from random expectations suggest that biotic filtering and facilitation play a structuring role in these guilds across space.

The patterns observed for traits, in combination to even or random phylogenetic structure found in these communities (Wolowski et al. 2017), offer deeper insights on the assembly process of studied communities. Since one montane community (SVG) had a predominance of clustered trait patterns, and we found weak phylogenetic signal for all floral traits, we

propose that biotic filtering may lead to the co-occurrence of similar species regardless of its evolutionary relatedness, generating random phylogenetic patterns. Conversely, the lowland community (PIC) exhibited only random trait patterns. For this community, our results do not support the role as biotic filter of the large hermit *Ramphodon naevius*, a mechanism proposed to explain clustered phylogenetic patterns for other two lowland communities (Wolowski et al. 2017). The fact that the PIC community exhibits both more hermit and non-hermit hummingbirds, with *R. naevius* pollinating only 46% of the plants in contrast to other lowland communities where this proportion is 60–82% (Wolowski et al. 2017), may decrease the dominance of this large hermit and its possible sole effect as a biotic filter. Overall, the low phylogenetic signal of floral traits, coupled with biotic filtering when there is a dominant pollinator, generate clustered trait structure associated to distinct phylogenetic structures across space.

Trait patterns along the phenology

Trait similarity and phylogenetic relatedness did not influence the probability or variability in flowering overlap when considering all hummingbird-pollinated plant species of a given community. A possible explanation is that tropical plant–hummingbird networks are trait-structured according

to two distinct hummingbird groups, with long- and short-corolla flowers being visited preferentially by long- (hermits) and short-billed (non-hermits) hummingbirds, respectively (Stiles 1977, Feinsinger and Colwell 1978, Maruyama et al. 2014, Maglianesi et al. 2015). Furthermore, this is expected to produce stronger pollinator sharing among plants with similar floral traits (Bergamo et al. 2017). Following these interaction patterns, evolutionary and trait-based processes mediated by the pollinators would operate more strongly only among subgroups of plants. Therefore, we only found trait and evolutionary relatedness determining patterns of flowering overlap when separating these communities based on their pollination niches.

In both hermit- and mixed-pollinated plants, species with similar corolla length had higher probability of co-flowering. Moreover, mixed-pollinated co-flowering plant species pairs also had similar floral colour, which can enhance overall attractiveness of the flower assemblage (Moeller 2004). These results give support to the “joint attraction of pollinators” mechanism of facilitation (*sensu* Moeller 2004). Given that corolla length determines the hummingbird pollinators associated to plants in the Atlantic forest (Vizentin-Bugoni et al. 2016, Bergamo et al. 2017), species with similar corolla length flowering together may enhance attraction of shared pollinator species. Such joint attraction should then translate in higher fitness, which was shown for synchronous hummingbird-pollinated species in ITA (Wolowski et al. 2017). Although co-flowering pairs showed similar corolla length, they also showed distinct anther height and phylogenetic divergence (for both hermit and mixed assemblages). These results suggest that plant species can benefit from the facilitation of flowering together while avoiding heterospecific pollen deposition through fine adjustments on pollen placement (Moeller 2004, Sargent and Ackerly 2008, Stewart and Dudash 2017). Moreover, heterospecific pollen deposition has stronger negative effects between closely related species (Arceo-Gómez and Ashman 2016), including hummingbird-pollinated plant species (Fonseca et al. 2016). Thus, if only distantly related species are flowering together, there is a reduced chance of negative effects due to hummingbirds sharing. These results illustrate a complex combination of plant–plant facilitative and competitive indirect interactions structuring the flowering phenology of plants sharing the same functional group of pollinators.

Conclusions

Our results support the role of plant–pollinator interactions on the structure of plant communities, adding up to the growing evidence of plant communities being organized based on floral traits. Importantly, we show that trait patterns are stronger when evaluating specific pairwise combination of plants and pollination niches along time. This indicates that trait-based processes are more likely to operate and be detected at smaller scales of evaluation, which is

in accordance with predictions based on scale (Chase and Myers 2011). We also demonstrated a complex combination of trait similarity and divergence through fine adjustments in floral traits, which points out to the importance of both facilitative and competitive interactions, despite the common claim that competition is the sole major biotic process driving species organization within communities (Rathcke 1988, HilleRisLambers et al. 2012). Instead, we propose a complex interplay of biotic filtering, facilitative and competitive interactions shaping the organization of plant–pollinator systems.

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Supplementary material (available online as Appendix oik-05571 at <www.oikosjournal.org/appendix/oik-05571>).
Appendix 1.