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Pollinator-mediated facilitation is associated to floral abundance, trait similarity and enhanced community-level fitness

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Abstract

1. Pollinator-mediated processes (biotic filtering, facilitation or competition) are often inferred by patterns of plant reproductive trait diversity (clustering or evenness of reproductive traits within the community). However, one single pattern can be generated by distinct processes, making difficult to predict the main process of community assembly. Incorporating fitness estimates should improve the link between pattern and process.

2. We investigated patterns of flowering phenology and reproductive traits (floral color, floral size and anther height) along the season of a pollinator-depauperated and generalized community. We used data on fitness (pollen receipt and number of pollen tubes) to provide a functional link between trait patterns and assembly mechanisms. We also investigated if the degree of co-flowering depended on the floral abundance and pollination functional group (fly-, bee-, hummingbird-pollinated and generalist species) of the plant species.

3. High floral abundance in the flowering season was associated with low trait diversity in the community. Both features increased fitness at the community-level. This indicates that similar species are benefited at periods of high floral abundance, probably due to the joint attraction of generalist pollinators in this pollinator-depauperated community. In general, rare species flowered more synchronously with the community than abundant ones, although distinct patterns emerged depending on the floral trait and pollination functional group. Furthermore, species highly synchronous and possessing similar floral color in relation to the community had higher fitness indicating that facilitative mechanisms act favoring flowering synchrony and trait similarity.

Synthesis

Patterns of flowering synchrony and floral trait similarity indicate pollination facilitation in the studied community. Plants benefited from co-flowering with species

possessing similar floral color via shared pollinator attraction. Thus, we empirically demonstrated some of the predictions of community assembly theory.

Keywords: *campos de altitude*, community assembly rules, competition, highland grasslands, floral traits, pollination ecology, pollinator sharing, reproductive success

Introduction

Plant-animal interactions, such as pollination, may influence plant community assembly (Sargent & Ackerly, 2008). The evaluation of reproductive trait patterns has been used to infer which pollinator-mediated processes act on community assembly (Pellissier, Alvarez, & Guisan 2012; Eisen & Geber, 2018). For instance, high trait diversity and phylogenetic evenness are often associated to competition, indicating pressures that led to divergent uses of pollinators (Muchhala, Johnsen, & Smith 2014). On the other hand, low trait diversity and phylogenetic clustering may indicate biotic filtering, when the plants resemble each other due to ecological sorting and adaptation towards the dominant pollinator (Kemp, Bergh, Soares, & Ellis 2019) or facilitation, when phenotypically similar species benefit from sharing its pollination niche (de Jager, Dreyer, & Ellis 2011). To date, most studies reported static trait patterns including all co-occurring species. However, there is wide variation in flowering phenology within the community. Thus, how much species overlap its flowering and potentially compete or facilitate with each other through shared pollinators should vary within the community (Arceo-Gómez, Kaczorowski, & Ashman 2018). This is especially important in systems characterized by a long flowering season, on which the co-flowering community composition changes along time.

Incorporating the phenological dimension revealed important fine-scale processes structuring co-flowering communities. For instance, it has been shown that floral trait

composition in the community often changes over time (Filella et al., 2013), patterns of co-flowering are associated with floral trait similarity (Makino & Yokoyama, 2015; Bergamo, Wolowski, Maruyama, Vizentin-Bugoni, & Sazima 2018; Fantinato, Del Vecchio, Giovanetti, Acosta, & Buffa 2018) and floral traits mediate the temporal variation in pollination networks (Kantsa et al., 2018). Moreover, not only trait composition, but overall floral abundance also changes during the flowering season. Plants flowering in contrasting phenological environments (high vs. low overall floral abundance) deal with distinct contexts of pollinator-mediated interactions. High floral abundance may lead to strong competition for pollinators and, in this context, it is expected high trait diversity (implying divergent pollinator use), whereas high floral availability associated with low trait diversity (phenotypically similar co-flowering species) may lead to benefits of the joint attraction of pollinators (Moeller, 2004). Similarly, low floral abundance should foster competition and divergent pollinator use if the flower-pollinator ratio is high (Lázaro, Jakobsson, & Totland 2013), while if pollinators are scarce, facilitation is fostered due to benefits of joint attraction (Tur, Sáez, Traveset, & Aizen 2016). Nevertheless, other processes such as convergent evolution and biotic filtering would also generate low trait similarity (Briscoe Runquist, Grossenbacher, Porter, Kay, & Smith 2016). Therefore, studies should consider multiple processes generating the observed structure patterns.

Most studies inferring processes from floral trait patterns do not associate them with fitness estimates. This is problematic because floral trait diversity in the community was shown to influence the fitness of focal species (Albor, García-Franco, Parra-Tabla, Díaz-Castelazo, & Arceo-Gómez 2019). However, we lack fitness assessments at the community-level, which are necessary to link trait patterns to assembly processes. In this context, trait and phylogenetic diversity linked to competition or facilitation are predicted to enhance the overall fitness of the co-flowering community (“mean community fitness”, Wolowski,

Carvalho, & Freitas 2017). However, studies addressing how trait patterns determine overall fitness patterns have not been conducted within co-flowering communities.

The co-flowering patterns should also depend on the abundance and pollination system of each plant species. First, rare species are generally more subjected to competition for pollination (Ghazoul, 2005). In this context, rare species are expected to be less synchronous than abundant ones to reduce competition and ensure conspecific pollination (Gumbert, Kunze, & Chittka 1999). When facilitation is prevalent, synchrony would benefit rare species due to enhanced attraction of shared pollinators (Feldman, Morris, & Wilson 2004). Second, floral traits (e.g. floral color, size and anther height) that mediate competition and facilitation by pollinators differ among plants belonging to distinct pollinator systems (Carvalho et al., 2014, Bergamo et al., 2017). Therefore, the association between flowering synchrony and trait similarity should also differ among pollination functional groups within a community.

Two main mechanisms are discussed to structure co-flowering communities: flowering synchrony and trait similarity among species (Feinsinger, 1987). Reduced flowering synchrony is expected under competition, leading species with low synchrony with the community to present higher fitness (Waser, 1978; Aizen & Rovere, 2010), while aggregated flowering is favored under facilitation, with highly synchronous species presenting higher fitness due to benefits from joint attraction of pollinators (Moeller, 2004; Wolowski et al., 2017; Eisen & Geber, 2018). Trait similarity of each species within the community can also influence such outcomes on fitness (Sargent, Kembel, Emery, Forrestel, & Ackerly 2011). Therefore, low or high floral trait overlap of the plant species within the community is expected to be associated with competition or facilitation, respectively, both leading to higher fitness. However, it has rarely been tested the contribution of both

mechanisms structuring whole co-flowering communities (but see Wolowski et al., 2017 for a test with hummingbird-pollinated plants).

Here, we investigated flowering phenology and trait patterns in a plant community of a tropical highland grassland (Figure 1). Previous evidence showed that heterospecific floral density is positively related to visitation rates and pollination for several plant species in this community, indicating a prevalence of facilitation over competition (Bergamo, Streher, Traveset, Wolowski, & Sazima, 2019). This allowed us to test if facilitation is also predicted by reproductive trait similarity as proposed by the community assembly theory applied to plant-pollinator interactions (Sargent & Ackerly, 2008; Figure 1). Specifically, we explored if community-level trait similarity (low trait diversity) was associated with floral abundance (hypothesis 1). Then, we expected community-level fitness to increase with trait similarity (low trait diversity) and high floral abundance (hypothesis 2). We also investigated if flowering synchrony depended on the species abundance, trait similarity and pollination functional groups (hummingbird-, bee-, fly- or generalist-pollination, i.e., visited by three or more groups) (hypothesis 3). Finally, we tested if species with high flowering synchrony and trait similarity had higher fitness (hypothesis 4).

Material and Methods

Study system

The study was conducted in the Itatiaia National Park, southeastern Brazil, in a community consisting of highland grassland vegetation (~ 2300 m a.s.l., 22°21' S, 44°40' W). This vegetation is known as *campos de altitude*, which is characterized by extensive grasslands and small herbs growing in rocky outcrops and shallow soils at mountaintops surrounded by Atlantic Forest at lower altitude. There is a marked seasonality, with a warm and humid season in spring/summer and a cold and dry season in the winter. The mean

annual temperature is of 14.4 °C with minimum temperatures reaching -10 °C and mean annual precipitation of 2400 mm (Ribeiro, Medina, & Scarano, 2007). More than 150 plant species were previously registered in the study area (Ribeiro et al., 2007). Our study included flower counts for 76 plant species, with a detailed register of the flowering phenology and measurement of the floral traits for a subset of 63 species (Table S1).

Flowering phenology

Flowering phenology was registered on 17 monthly censuses (once per month, every four weeks) during two consecutive seasons (October/2016 to May/2017 season and September/2017 to May/2018 season). We did not sample in the peak of the dry season (June-August) because almost no plant species were flowering. Flower counts were conducted on 101 plots with 2 m² established on three transects. We established a minimum distance of 50 m between plots, totaling 0,34ha of area sampled. The number of flowers on each plant individual was counted monthly in all plots. For species with many flowers (e.g. the ones with large inflorescences), we estimated the number of flowers per inflorescence and extrapolated by counting the number inflorescences. For species with flowers arranged in capitula (e.g. Asteraceae) or other similar arrangements (e.g. Apiaceae), and therefore hard to individualize each flower, we used the number of inflorescences as a surrogate of abundance since each inflorescence functions as a pollination blossom (Bergamo et al., 2017). With the flower counts, we obtained a flowering phenology matrix with the number of flowers of each species on each month. Then, we calculated the overall floral abundance of the community and richness of species flowering per month. The floral abundance of each plant species was estimated as the sum number of flowers on each of the two seasons. We calculated flowering overlap among all pairwise species combinations (including only the 63 focal species) using the Czechanowski index (Feinsinger, Spears, & Poole 1981). This is an adequate index for

intensity of phenological measurements, since it is based on the overlap of the histograms representing the distribution of flowers along the months of two species.

Community-level fitness

Fitness data were gathered from Bergamo et al. (2019). It was estimated as number of conspecific pollen grains in the stigma (hereafter, pollen receipt) and number of pollen tubes growing in the style (hereafter, pollen tubes). These two measurements are frequently used as quantitative and qualitative components, respectively, of the contribution of pollinators to the plant female fitness (Alonso, Herrera, & Ashman 2012; Tur et al., 2016). This was measured to a subset of 44 species in every monthly census (except October/2016 and September/2017 due to low floral availability). We selected species on which were possible to manipulate the flowers without moving pollen from the anthers to the stigmas (Table S1). The pistils of flowers at the end of the anthesis were collected and stored in 70% alcohol. Pollen grains and pollen tubes were counted in a fluorescence microscope. Since plant species vary in pollen receipt due to intrinsic differences in pollen production and pistil traits, we calculated z-scores (scaled to a mean of 0 and standard deviation of 1) within species for pollen receipt and pollen tubes. Then, mean community fitness was calculated as the mean pollen receipt and pollen tubes (after z-transformation) across all samples on each month (Table S2).

Pollination functional groups

We assigned each plant species in a pollination functional group using the plant-pollinator interaction data of Bergamo et al. (2019). For each month, a random subset of the plots with flowering individuals was observed and all visits to flowers registered.

Observation sessions lasted 1 h due to the low visitation rates in the area. Visitors were classified in major groups (bees, flies, wasps, beetles, ants and hummingbirds) and we accounted only visits with potential for pollination (i.e. when the visitor touched anthers and stigmas). Visits by *Apis mellifera* were not considered, since it is a supergeneralist invasive bee and would not indicate if that plant species evolved towards bee-pollination. Species visited in similar frequencies by two groups (e.g. ~50% bees and ~ 50% flies) were assigned to both pollination functional groups. Species visited by several groups (three or more) in similar frequencies were assigned to the “generalist” category. We included 15 species in the hummingbird-pollinated category, 22 species in the bee-pollinated category, 11 species in the fly-pollinated category and 21 species in the generalist category (Table S1).

Floral traits

We selected floral traits previously known to be relevant for plant-pollinator interactions, namely: floral reflectance (pollinator attraction), floral size (pollinator attraction and morphological fit between flower and pollinator), anther and stigma height (related to the site of pollen placement and pickup in the pollinator body). Since anther and stigma height were highly correlated, we removed the latter from subsequent analyses. Floral reflectance was measured as the petal spectral reflectance using a USB4000 spectrophotometer (OceanOptics, Inc., Dunedin, FL, USA) coupled with a deuterium-halogen light source (DH-2000; OceanOptics, Inc., Ostfildern, Germany), with a light emission range between 215 nm and 1700 nm. All reflectance measurements were taken at a 45° angle, using barium sulphate and a black chamber as white and black standards, respectively. Morphological features were measured directly in the field using a digital caliper. Floral size was measured as total petal length for tubular flowers and as maximum floral diameter for radial flowers. For species with capitula or similar arrangements, we measured the capitula/inflorescence diameter. We

measured anther height from the base of the flower to the top of the anther. We measured floral traits for all 63 focal species, with an average of 9.4 flowers per species and each sample from a distinct plant individual (Table S1).

We calculated the trait diversity in the community using the Rao's quadratic entropy index (Botta-Dukát, 2005), which is more related to trait convergence and divergence indexes commonly used to infer community assembly processes (Botta-Dukát & Czúcz, 2016). In this context, low trait diversity indicates trait clustering and high trait diversity indicates trait evenness. We calculated the same index weighted by each species abundance in the month (number of flowers in the month) and without abundance weighting (Table S2). Abundance-weighted indices give a better approximation of total appearance of the community and thus, how strong is trait convergence and divergence (Kantsa et al., 2018).

Floral reflectance and color

We first reduced the number of reflectance variables by applying a PCA in the 300-700nm range of the reflectance of all 63 species. Reflectances were standardized (by the maximum value per reflectance) prior to PCA procedures. We selected the first four PCA axes, which included 96.6% of the variation (see Appendix 1 for details) and used them with the floral size and anther height measurements to calculate the trait diversity per month (hypotheses 1 and 2).

For the analysis restricted to a single pollinator group (hypothesis 3), we used pollinator visual models to achieve meaningful color variables. We used the photoreceptor sensitivities of *Sephanoides sephaniodes* as hummingbird visual system (Herrera et al., 2008). For bees, we used sensitivities of the native stingless bee *Melipona quadrifasciata* (Menzel, Ventura, Werner, Joaquim, & Backhaus 1989) since Meliponini bees were the most common pollinators. For flies, we used sensitivities of the hoverfly *Eristalis tenax* (Lunau,

2014) since syrphids were the most common fly pollinators in the study system. Generalist species were mainly pollinated by hoverflies, muscoid flies, bees and wasps. For the generalist species, first we used fly vision models and then repeated the same analysis using bee vision models. We calculated the quantum catches (Q_i 's) for each plant species using its floral reflectance, corresponding photoreceptor sensitivities of its main pollinator group, a standard daylight function (D65) and a common green leaves reflectance function (AV400). To use them in color space models, we calculated relative quantum catches (q_i 's) with von Kries correction. We obtained perceptual distances as Euclidian distances in the tetrahedron model for hummingbirds (Vorobyev, Osorio, Bennett, Marshall, & Cuthill 1998), hexagon model for bees (Chittka, 1992) and categorical model for flies (Troje, 1993).

Phylogeny

Flowering phenology may be constrained by shared ancestry, leading to a phylogenetic signal in flowering overlap (i.e. closely related plants with similar flowering periods, Brito et al., 2017). Similarly, close related plants may share the same pollination niche, leading to phylogenetic signal in floral traits (Staggemeier, Diniz-Filho, & Morellato 2010). To account potential influences of evolutionary relatedness, we built a plant phylogenetic hypothesis for the 63 focal species based on the calibrated seed plant supertree of Zanne et al. (2014) (Figure S1). We used the updated version of this supertree implemented in the R-function S.Phylo.Maker (Qian & Jin, 2016). Flowering phenology, floral traits and floral abundance were all poorly correlated with phylogenetic relatedness in the studied community, therefore, we assumed that all models were robust to constraints of shared evolutionary history (Appendix S2).

Statistical analyses

Is trait similarity (low trait diversity) associated with floral abundance?

We used null models and linear models to investigate how floral abundance and trait diversity are associated. First, we calculated the trait diversity (abundance-weighted Rao's Q) per month. Then, the observed Rao's Q value of each month was compared with a null distribution generated by 10,000 random monthly communities created from the species pool (abundances across all months lumped together, Table S3). We used the independent-swap algorithm to create the null distribution (Gotelli 2000). To investigate if convergent evolution also contributed to the observed patterns, we used the same null model approach with the equivalent index for phylogenetic diversity, which is based on the phylogenetic distances between plant species (Table S4). Convergent evolution should lead high phylogenetic diversity to be associated with months of low trait diversity. Secondly, we fitted a model using monthly trait diversity (abundance-weighted) as the response variable and monthly floral abundance, phylogenetic diversity and season (2016/2017 or 2017/2018) as predictor variables. We repeated the same procedure with the Rao's Q index without abundance-weight to check if extremely abundant species were influencing the results. We also correlated floral abundance with richness of species flowering to check if floral abundant months were also richer, which may indicate that abundant species had not a strong influence in the results.

Does community-level fitness increase with floral abundance and trait similarity (low trait diversity)?

We fitted linear models to investigate the relationship between community structure and fitness. We used the mean pollen receipt and pollen tubes (mean community fitness, both z-transformed) per month as response variables. Since trait diversity and floral abundance

were associated (see Results), we fitted separate models: one with trait diversity and season and the other with floral abundance and season as predictors.

Does flowering synchrony depend on the species floral abundance, trait similarity and pollination functional group?

We tested if flowering synchrony was associated with floral abundance. Moreover, we also tested if such abundance relationships and traits associated with flowering synchrony differed among the pollination functional groups: hummingbirds ($n = 15$ plant species), bees ($n = 22$), flies ($n = 11$) and generalists ($n = 21$). For this, we fitted linear mixed models using the flowering synchrony of the 63 focal species as the response variable. We calculated the synchrony considering the flowering overlap within the species of each pollination functional group. Similarly, we used only the second season of flowering phenology to avoid overrepresentation of the pairwise flowering overlap. We also recalculated the floral reflectance, size and anther height similarity considering only the species within each pollination functional group. Then, floral abundance per species (total number of flowers counted per species, log transformed), all trait similarity variables and their interaction with pollination functional group (i.e. hummingbird-, bee-, fly- or generalist-pollination) were used as fixed predictors. Since some species were assigned to both bee- and fly-pollinated, we used plant species identity as random predictor. VIF values for all fixed terms were low (all < 3), indicating no collinearity (Zuur, Ieno, & Elphick 2010).

Does species fitness increase with flowering synchrony and trait similarity?

We fitted linear models to test how flowering synchrony and trait overlap per species influence fitness. Fitness was estimated as mean relative pollen receipt and relative pollen tubes per species, since relative measurements are necessary to achieve comparable fitness

values among species (Alonso et al., 2012). We relativized by dividing each sample with the maximum fitness value observed for each plant species. We did not use the z-scores since they were scaled to a mean of zero within species. This was restricted to a subset of 37 species that had more than eight sampled individuals for fitness data and all traits measured (Table S5). We fitted two linear models: one for pollen receipt and one for pollen tubes as response variables. As predictors, we used flowering synchrony and trait similarity of the species in relation to the community (Table S5). We had a single value per species and thus no random effects were needed. Flowering synchrony was calculated using the index proposed by Freitas and Bolmgren (2008), which also considers the flowering length of each species. We calculated the synchrony of the 37 species in relation to the flowering of all species (76) recorded in the study. To avoid inflating flowering synchrony, we used only the second season of flowering phenology. We took this decision based on the positive correlation of matrices of flowering overlap of both seasons (assessed by Mantel test), showing that interannual variation in flowering phenology was small ($r = 0.660$, $p = 0.001$). And because averaging across years would lead to overestimate flowering length of some species, also an important parameter of the synchrony index. We chose the second season because we sampled one month more (September) than in the first season. Trait similarity of the 37 species was calculated by generating trait distance matrices based on Euclidian distances of floral reflectance (PCA axes), size and anther height of the 63 species for which we had trait data. Then, trait similarity of each species in relation to its co-flowering community was calculated as abundance-weighted functional distinctiveness as proposed by Violle et al. (2017). High values of functional distinctiveness indicate less trait similarity of the species in relation to the co-flowering community.

All analyses were done in R environment (R Core Team, 2019) and specifically packages were used for each analyses: visual models were done in *pavo* package (Maia, Eliason, Bitton, Doucet, & Shawkey 2013), phylogenetic analyses were conducted in *phytools* package (Revell, 2012), and generalized linear models were fitted with *lme4* package (Bates, Maechler, Bolker, & Walker 2015).

Results

Trait similarity (low trait diversity) is associated with floral abundance

We found significant trait similarity (low trait diversity) in the months with high floral abundance (January/2017 to April/2017 and December/2017 to March/2018) and random trait structure in the other months (Figure 2A, Table S2-S3). Random phylogenetic structure predominated, except for November/2016 (evenness) and January/2018 (clustering, Figure 2B, Table S4). Accordingly, linear models showed that months with high floral abundance exhibited low trait diversity ($\beta = -0.014 \pm 0.001$, $R^2 = 0.44$, $F_{1,14} = 17.71$, $p = 0.001$, Figure 2C). Phylogenetic diversity ($\beta = 0.024 \pm 0.012$, $R^2 = 0.18$, $F_{1,14} = 4.27$, $p = 0.076$, Figure 2D) and season had no effect on trait diversity ($\beta = 0.594 \pm 0.324$, $R^2 = 0.03$, $F_{1,14} = 0.01$, $p = 0.964$). However, the removal of an outlier showed that phylogenetic diversity was positively related to trait diversity ($\beta = 0.042 \pm 0.091$, $R^2 = 0.49$, $F_{1,13} = 23.70$, $p < 0.001$). The relationship with floral abundance remained when using trait diversity without abundance-weight ($\beta = -0.013 \pm 0.001$, $R^2 = 0.28$, $F_{1,14} = 5.64$, $p = 0.034$). Similarly, phylogenetic diversity (without abundance-weight; $\beta = 0.003 \pm 0.022$, $R^2 = 0.08$, $F_{1,14} = 1.16$, $p = 0.301$) and season had no effect on trait diversity ($\beta = 0.212 \pm 0.550$, $R^2 = 0.04$, $F_{1,14} = 0.15$, $p = 0.705$). Phylogenetic diversity (without abundance-weight) had no effect on trait diversity after removal an outlier ($\beta = 0.005 \pm 0.022$, $R^2 = 0.06$, $F_{1,13} = 1.16$, $p = 0.809$). Floral abundance was positively correlated with richness of species flowering (Pearson' $r = 0.809$, t

= 5.33, $p < 0.001$). Therefore, we assumed that such relationship was not driven by few dominant species.

Community-level fitness increased with floral abundance and trait similarity

Months with high floral abundance ($\beta = 0.018 \pm 0.001$, $R^2 = 0.53$, $F_{1,12} = 13.65$, $p = 0.003$, Figure 3A) and with trait similarity ($\beta = -0.072 \pm 0.029$, low trait diversity, $R^2 = 0.36$, $F_{1,12} = 5.36$, $p = 0.039$, Figure 3B) had higher community-level pollen receipt. Months with high floral abundance also exhibited higher mean community-level pollen tubes ($\beta = 0.016 \pm 0.001$, $R^2 = 0.36$, $F_{1,12} = 6.39$, $p = 0.026$, Figure 3C) whereas trait diversity had no effect ($\beta = -0.049 \pm 0.035$, $R^2 = 0.14$, $F_{1,12} = 1.90$, $p = 0.194$, Figure 3D).

Flowering synchrony is dependent on floral abundance, trait similarity and pollination functional groups

Flowering synchrony depended on plant species abundance and pollination functional groups (Table 1, Figure 4). Rare species flowered more synchronically with the rest of the community than abundant ones ($\chi^2 = 5.98$, $p = 0.014$). The interaction between abundance and pollination functional group revealed that this relationship was mainly driven by bee- and fly-pollinated species ($\chi^2 = 7.57$, $p = 0.052$, Figure 4A). Species flowered synchronically if exhibiting similar floral color in relation to the community regardless of pollination functional group ($\chi^2 = 6.56$, $p < 0.001$, Figure 4B). Pollination functional group interacted with floral size similarity in determining flowering synchrony ($\chi^2 = 8.49$, $p = 0.039$, Figure 4C). In general, fly- and hummingbird-pollinated species flowered synchronously if exhibiting similar floral size in relation to the community. On the other hand, bee- and generalist-pollinated species flowered synchronously if exhibiting distinct floral size in relation to the community. Although we found an effect of anther height similarity alone (χ^2

= 4.17, $p = 0.041$), pollination functional group also interacted with this variable in determining flowering synchrony ($\chi^2 = 8.31$, $p = 0.040$, Figure 4D). Bee-pollinated species flowered synchronously if exhibiting similar anther height while fly- and generalist-pollinated species if exhibiting distinct anther height in relation to the community. Results were qualitatively similar when using bee-visual models for generalist species (Table S6).

Species-level fitness increased with flowering synchrony and trait similarity

Species highly synchronous with the community had higher pollen receipt ($\beta = 0.612 \pm 0.232$, $R^2 = 0.21$, $F_{1,33} = 10.70$, $p = 0.003$, Figure 5A) and pollen tubes ($\beta = 0.527 \pm 0.226$, $R^2 = 0.19$, $F_{1,33} = 9.44$, $p = 0.004$, Figure 5C). Species with similar floral reflectance in relation to the community had higher pollen receipt ($\beta = -1.315 \pm 0.519$, $R^2 = 0.24$, $F_{1,33} = 4.33$, $p = 0.045$, Figure 5B) and pollen tubes ($\beta = -1.301 \pm 0.510$, $R^2 = 0.24$, $F_{1,33} = 4.74$, $p = 0.037$, Figure 5D). Relative fitness was not explained by floral size (pollen receipt: $\beta = 0.001 \pm 0.008$, $R^2 = 0.08$, $F_{1,33} = 1.49$, $p = 0.231$; pollen tubes: $\beta = -0.002 \pm 0.007$, $R^2 = 0.09$, $F_{1,33} = 1.82$, $p = 0.187$) nor anther size similarity (pollen receipt: $\beta = -0.053 \pm 0.090$, $R^2 = 0.08$, $F_{1,33} = 0.34$, $p = 0.561$; pollen tubes: $\beta = -0.016 \pm 0.089$, $R^2 = 0.08$, $F_{1,33} = 0.03$, $p = 0.861$).

Discussion

Trait similarity (low trait diversity) is associated with floral abundance

We found significant low trait diversity (trait clustering) in floral abundant months. Moreover, floral trait diversity linearly decreased with floral abundance in the community, which indicates an overall pattern of increasing floral similarity between co-flowering species. These patterns are consistent with facilitation. The linear models also revealed high trait diversity in months of low floral abundance. However, we found no significant trait structure in months of low floral abundance, indicating a minor role of competition in the

community assembly. Phylogenetic diversity was predominantly random and the removal of an outlier showed a positive relationship with trait diversity, making convergent evolution unlikely. The relationship between phylogenetic and trait diversity vanished when using phylogenetic diversity without abundance-weight, indicating that some abundant plant lineages generated this association. Overdominance of few plant species leading to functionally homogenous communities was also unlikely since the relationship remained when using functional diversity indexes with no abundance weight and plant species richness increased with floral abundance. Finally, we argue that such trait clustering was not generated due to a dominant pollinator group selecting or sorting similar plant species (biotic filtering), since this community is marked by high levels of generalization, from the perspective of both plants and pollinators (Freitas & Sazima, 2006; Danieli-Silva et al., 2012). Therefore, we suggest pollinator facilitation as the major process driving the co-flowering of similar species assuming that increased trait similarity leads to high pollinator sharing (Junker, Blüthgen, & Keller 2015).

Community-level fitness increased with floral abundance and trait similarity

Community-level fitness was higher in floral abundant periods with functional similarity, as predicted when pollination facilitation is the major process (Wolowski et al., 2017). The studied community is a grassland surrounded by tropical forests and periods of high floral abundance probably attracted more pollinators from adjacent areas and maintained them in the area. Such increase on fitness was widespread in the community probably due to the benefits of sharing generalist pollinators. Pollination networks of other generalized tropical communities showed less interaction partitioning (and thus, high pollinator sharing) when floral abundance is high (Souza et al., 2018). Our results also suggest a similar mechanism in the studied community. Furthermore, it was shown that high floral trait

diversity in the community decreases pollinator visitation frequency to focal plant species (Fornoff et al., 2017; Albor et al., 2019), probably due to stronger searching costs for generalist pollinators in a functionally diverse array (Cakmak et al., 2009). Facilitation between similar flowers in the studied community may operate similarly, with effects also on pollen receipt.

The effect of trait similarity disappeared when evaluating pollen tubes at the community-level. Accordingly, the prevalence of facilitation in the community diminished when evaluating pollen tubes (Bergamo et al., 2019). Benefits of pollinator sharing may be offset by costs due to heterospecific pollen transfer (Thomson, Fung, & Ogilvie 2019). This may also indicate a “diffuse facilitation” scenario (*sensu* Feldman et al., 2004), on which some species strongly benefit from shared attraction while others have weak benefits or remain neutral. Other possibility is that that density-dependent processes are more important than trait-mediated ones in the studied community. In fact, intraspecific negative density-dependence in pollination coupled with low occurrence of density-dependent interspecific competition was shown to stabilize plant coexistence in the studied community (Bergamo et al., 2019). Instead of the community-level patterns used here, trait-mediated processes may be observed only between plant species pairs (Lanuza, Bartomeus, & Godoy 2018). Future studies that assess pairwise fitness differences would be important to determine the relative importance of density-dependence vs. trait-mediated processes mediating plant coexistence.

Flowering synchrony is dependent on floral abundance, trait similarity and pollination functional groups

We found that bee- and fly-pollinated rare species flowered more synchronically with the community than abundant ones. Rare species are often in disadvantage due to pollinator-mediated Allee effects (Evans, Cavers, Ennos, Vanbergen, & Heard 2017). Our abundance

measurements may also reflect species-level differences on floral display, with the rare species also bearing few flowers per plant. Species with small displays also suffer disadvantages due to pollinator-mediated Allee effects (Ghazoul, 2005). In high-altitude grasslands, Allee effects were shown to be weak (Bergamo et al., 2019) and our findings indicate that these rare and/or small display plants may not experience such effects due to the benefits of co-flowering. However, the effect of abundance was weak for hummingbird- and generalist-species. This may be related to hummingbird preferences for patches possessing a high number of flowers (Justino, Maruyama, & Oliveira 2012), and thus, rare and small display species would benefit less from co-flowering. On the other hand, generalist species shares a distinct fraction of their pollinators making benefits of co-flowering largely diffuse and not dependent on species abundance. Overall, we showed that relationships between co-flowering and species floral abundance differ for each pollination functional group within the community.

Species with similar floral color were the most synchronous with the community regardless of their pollination functional group. This general effect of color similarity agrees with the community-level patterns of trait similarity and fitness. As expected, the relation between co-flowering and the other floral traits differed among pollination functional groups. Floral color similarity had a clear relationship with synchrony for fly-pollinated species. This concurs with other fly-pollinated communities also marked by high color similarity (Bergamo, Telles, Arnold, & Brito 2018; Ishii, Kubota, Tsujimoto, & Kudo 2019). Moreover, the most synchronous fly-pollinated species had distinct anther height, which may reduce reproductive interference when sharing pollinators (Stewart & Dudash, 2017; Bergamo et al., 2018a, Fantinato et al., 2018). For hummingbird-pollinated plants, the most synchronous species had similar floral color and size. These patterns indicate facilitative interactions mediated by trait similarity, in contrast with the weak relationship with abundance for this

pollination functional group. These mixed patterns suggest a balance between competition and facilitation, which concur with other assembly studies on hummingbird-pollinated plants from the Atlantic forest (Wolowski et al., 2017; Bergamo et al., 2018a).

The importance of high color similarity for bee-pollinated species found here was also reported as a mechanism of facilitation in other bee-pollinated plant communities (de Jager et al., 2011). Moreover, we found the counter-intuitive pattern of synchrony associated with anther height similarity for this pollination functional group. This could reflect the restricted safe sites to deposit pollen on the bee's body without the risk of grooming (Koch, Lunau, & Wester 2017). Interestingly, bee-pollinated species flowered more synchronically when distinct in floral size. This could be associated to divergent use of pollinators (and thus, competition). However, the prevalence of facilitation among bee-pollinated species (Bergamo et al., 2019) suggests that such pattern may be driven by the frequently unnoticed mechanism of facilitation through floral diversity (Ghazoul, 2006). In this context, plant species with distinct traits attract and maintain a diverse pollinator community (in this case, a diverse bee community), which ultimately leads to benefits through pollinator sharing (Ghazoul, 2006). Such a scenario is even more likely between generalist species, on which flowering synchrony was associated with distinct floral size and anther height. For generalist species, the benefits of attracting a diverse pollinator community is more likely since all of them could share most pollinators.

Species-level fitness increased with flowering synchrony and trait similarity

Synchronous species and with similar colors in relation to the community were the most fit, consistent with facilitation (Wolowski et al., 2017). This suggests that joint attraction may favor high flowering synchrony and color similarity (Geber & Moeller, 2006; Eisen & Geber, 2018), leading to the observed high floral abundance coupled with low trait

diversity at the community-level. In this community, flowers are exposed to a bright environment since it is an open habitat and vegetation is composed mainly by shrubs and herbs. It is known that bright habitats enhance color conspicuousness (Endler, 1993), which may increase the importance of floral color as a reliable signal for pollinators in this community. Interestingly, floral color similarity explained relative fitness per species for both pollen receipt and pollen tubes, although trait diversity was not related to the latter at the community-level. This discordance indicates that even if several species benefit by being similar, these trait-mediated relationships should be context-dependent with some neutral and competitive outcomes also operating at the community-level (Tur et al., 2016). Floral size did not have an effect, which may indicate that this trait is more related to specific pollinator groups, as found for some pollination functional groups in the flowering synchrony analysis. Nevertheless, our findings support a structuring role of pollinator-mediated interactions via both flowering phenology and floral traits.

Conclusion

We found flowering and floral trait patterns consistent with pollination facilitation. Since previous assessments in the studied community showed that facilitation prevailed over competition for pollination, we could empirically demonstrate some of the community assembly theoretical predictions. Moreover, the link between patterns and process is likely due to reproductive advantages of species highly synchronous and similar in floral color in relation to the community, especially for rare plant species. Nevertheless, distinct patterns emerged depending on the floral trait and pollination functional group being analyzed. Although most plant species benefited from facilitation, some presented functional patterns consistent with competition. Therefore, distinct pollinator-mediated processes may act on the same community. We stimulate measurements of fitness at the community-level to help

disentangling by which mechanisms pollinator-mediated assemblage processes generated the observed flowering and trait patterns.

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Table 1. Parameters of the models explaining flowering synchrony of the plant species of highland grasslands in Itatiaia National Park, Brazil. Floral abundance, floral trait similarity and pollination functional group, i.e. bee-, fly-, hummingbird- and generalist-pollination, were used as predictors. Generalist pollination represent species pollinated by three or more pollinator groups. Floral color distances were calculated with fly-vision models for the generalist species. Flowering synchrony index followed Freitas and Bolmgren, (2008) and trait similarity calculated as proposed by Violle et al. (2017). β = estimate of the effect, χ^2 = linear mixed effect value. Bold values indicate significant effects at $p < 0.05$.

Predictor variables	β	χ^2	p
Pollination functional group	-	22.80	< 0.001
Floral abundance	-0.04 ± 0.01	5.98	0.014
Floral color similarity	-0.26 ± 0.10	6.56	0.010
Floral size similarity	0.04 ± 0.08	0.05	0.826
Anther height similarity	-0.07 ± 0.07	4.17	0.041
Pollination functional group * Abundance	-0.35 ± 0.04	7.57	0.052
Pollination functional group * Color	-	5.60	0.133
Pollination functional group * Size	-	8.49	0.039
Pollination functional group * Anther height	-	8.31	0.040

Figure legends

Figure 1. Framework of the expected functional patterns (based on plant reproductive traits) and responses on fitness related to the structuring processes of plant-pollinator interactions on plant community assembly. Plant species can be sorted from the community pool into each co-flowering community under two scenarios: competition for pollination or facilitation for pollination as the main structuring process. **Competition scenario:** at the community-level, it is expected high trait diversity and functional evenness, indicating divergent pollinator use. Therefore, high trait diversity would enhance community-level fitness. At the species-level, it is expected plant species to flower asynchronously or to possess distinct reproductive traits when flowering synchronously with the community. These plant species would benefit due to divergent pollinator use and diminished competition. **Facilitation scenario:** at the community-level, it is expected low trait diversity and functional clustering, indicating similar pollinator use. Thus, low trait diversity would enhance community-level fitness. At the species-level, it is expected plant species to flower synchronously and to show similar reproductive traits with the community. These plant species would benefit due to pollinator sharing and facilitation.

Figure 2. Assembly patterns of the co-flowering community in highland grasslands in Itatiaia National Park, Brazil. Trait and phylogenetic diversity were calculated as the Rao's Q index (Botta-Dukát, 2005) and floral abundance as the sum of flowers counted. A) Floral trait diversity per month. B) Phylogenetic diversity per month. Grey triangles represent the observed diversity value per month while white circles represent average diversity values across a null distribution (Gotelli, 2000). "C" letter indicates significant clustering and "E" letter significant evenness structure. C. Relationship of trait diversity and abundance. D.

Relationship of trait diversity and phylogenetic diversity. Each black dot represents a monthly census. The red line represents the regression coefficient.

Figure 3. Relationships between mean community fitness with floral abundance and floral trait diversity of the co-flowering community in highland grasslands in Itatiaia National Park, Brazil. Community fitness was estimated as mean pollen receipt (after z-transformation), or as mean pollen tubes (after z-transformation). Floral abundance was estimated as total number of flowers counted in the monthly census and floral trait diversity was calculated as the Rao's Q index (Botta-Dukát, 2005). Black dots represent each monthly census. The red line represents the regression coefficient of the model including the predictor variable + season of census. A) Effect of flower abundance and B) Effect of floral trait diversity on mean community-level pollen receipt. C) Effect of flower abundance and D) Effect of floral trait diversity on mean community-level pollen tubes.

Figure 4. Relationships between flowering synchrony with species abundance, floral trait similarity and pollination functional group in highland grasslands in Itatiaia National Park, Brazil. Flowering synchrony was estimated as proposed by Freitas & Bolmgren, (2008) and trait similarity followed Violle et al., (2017). A) Effect of floral abundance (log transformed). B) Effect of floral color similarity. C) Effect of floral size similarity. D) Effect of Anther height similarity. Grey dots represent the partial residuals (after eliminating the contribution of the other predictor variables) and the colored lines are the regression coefficients. Each color represents a pollination functional group: bee-, fly-, hummingbird- and generalist-pollination. Generalist pollination represents species pollinated by three or more pollinator groups.

797 Figure 5. Relationships between species fitness with flowering synchrony and floral trait
798 similarity in highland grasslands in Itatiaia National Park, Brazil. To achieve comparable
799 values among species, fitness measurements were relativized by dividing the corresponding
800 fitness value with the maximum observed within each species. Flowering synchrony index
801 followed Freitas and Bolmgren, (2008) and trait similarity calculated as proposed Violle et
802 al., (2017). Black dots represent each plant species and the red line is the regression
803 coefficient. A) Effect of flowering synchrony and B) Effect of floral reflectance similarity on
804 pollen receipt. C) Effect of flowering synchrony and D) Effect of floral reflectance similarity
805 on pollen tubes.