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Research Article

Floral trait similarity at the community-level increases reproductive success suggesting facilitation through pollinator sharing

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The ability of plants to attract pollinators is context-dependent, influenced by floral traits, abundance, and resources from the plant community. Indirect interactions through shared pollinators, from competition to facilitation, may lead to varied reproductive outputs in plants, and the mechanisms behind these interactions remain to be fully elucidated in complex ecological communities. We aimed to disentangle the mechanisms by which the floral community may impact pollinator sharing and plant reproductive success in the highly biodiverse Campo Rupestre from Brazil. To do so, we investigated the relationships among species traits, ecological networks, pollen deposition and reproductive output (seed set) in variable community contexts, using a piecewise structural equation modeling (SEM) approach. Plant species with similar flowers in relation to its community showed higher seed set, indicating facilitation. In contrast, species with high flower abundance showed decreased visitation rates per flower and conspecific pollen deposition, suggesting intraspecific competition. Our study reveals that, while there is an interplay between facilitation and competition, the former had a stronger influence on the reproductive output of plants sharing pollinators in a highly diverse tropical community. These results show that traits and abundance mediate complex indirect interactions in plant–pollinator communities.

Keywords: flower diversity, network analysis, plant-pollinator community; plant reproduction, pollen deposition; seed set.

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Introduction

Most flowering plants require biotic pollination to ensure reproduction (Tong et al. 2023). In this context, pollinators constitute an important reproductive resource for plants, which are shared among individuals and species within communities (Pauw 2013). The indirect interactions through shared pollinators influence plant reproductive success, and vary from competition to facilitation (Sargent and Ackerly 2008). While competition for pollinators among plants in a community causes less attractive plants to receive reduced visitation and decrease their reproductive success (Ha et al. 2021, Johnson et al. 2022), facilitation has the opposite effect, as it increases overall attractiveness and reproductive success (Tur et al. 2016, Bergamo et al. 2024, De Amorim et al. 2025a). Understanding the mechanisms driving the relative importance of competition and facilitation in plant–pollinator communities is particularly important because this balance is a key driver of species coexistence and stability in plant communities (Pauw 2013, Benadi 2015, Guimarães et al. 2017, Duchenne et al. 2021).

Plants attract pollinators providing resources such as pollen and nectar, and advertise these resources via floral traits including color and shape (Dudash et al. 2011). Moreover, the abundance of flowers and individuals also influence pollinator attraction (Peuker et al. 2020). For instance, plant species with longer flowering periods and greater floral abundance tend to interact with more pollinators and experience higher reproductive success (Lázaro et al. 2020). However, the success in attracting pollinators is also context-dependent because floral traits, abundance, and the resources provided by the plant community also affect the plant's capacity to attract pollinators (Shibata and Kudo 2020, Sritongchuay et al. 2021). In situations of low abundance of pollinators and plants, facilitation might predominate leading to greater pollinator attraction and reproductive success for plant species with higher trait similarity and phenological overlap with plant communities (Bergamo et al. 2020, Lopes et al. 2022). On the other hand, competition may prevail when plants are abundant and pollinators become scarce (Rathcke 1983, Ye et al. 2023).

Quantifying the role that each plant species plays in the community according to their interaction with pollinators is a challenge, but this may be accessed by using species-level network metrics, such as specialization and partner diversity, which measure how plants distribute their interactions across multiple partners (Blüthgen et al. 2006, Dormann 2011). However, these metrics do not directly represent the influence that plants have on each other by sharing pollinators, i.e. indirect interactions. Therefore, metrics that are based on quantification of pollinator sharing may perform better to explain the influence that one plant species should have on or receives from others (Lázaro et al. 2020, Bergamo et al. 2022). By linking such metrics with estimates of plants reproductive success, we can assess how plants affect each other's fitness through pollinator sharing (Lázaro et al. 2020, Bergamo et al. 2022). For instance, target and acting degrees are network metrics based on the Müller's index, which quantify the potential indirect effects among plant species mediated by shared pollinators (Müller et al. 1999, Bergamo et al. 2022). A high acting degree indicates that a plant species has strong direct interactions with pollinators that also visit other plants, thereby indirectly influencing those co-flowering species. Conversely, a high target degree shows that a plant is indirectly influenced by other plants because its pollinators also strongly depend on them. Bergamo et al. (2021) highlighted that plant species with larger target degree, i.e. that are strongly affected by other plants because their pollinators mainly rely on other plant species, are expected to have greater fitness in facilitation scenarios but lower fitness in competition scenarios. While network metrics have been shown to greatly depend on species abundance and traits (Carvalheiro et al. 2014, Lázaro et al. 2020, Bergamo et al. 2021), disentangling their effects on plant reproductive success is still less explored.

An important functional consequence of indirect interactions among plant species in a community can be measured by heterospecific pollen deposition (Arceo-Gómez and Ashman 2014, Thomson et al. 2019). The flow of heterospecific pollen can go multiple ways or be almost unidirectional when a plant species sends more pollen than it receives (Fang and Huang 2013, Arceo-Gómez et al. 2020). In this context, deposition of heterospecific pollen mainly causes negative effects on plant reproduction (Ashman and Arceo-Gómez 2013). However, a few studies have shown indirect positive association between heterospecific pollen and seed set (Streher et al. 2020, Lopes et al. 2022). These positive effects can be related to generalized and closely related plant species showing higher tolerance to heterospecific pollen deposition (Streher et al. 2020). Teasing apart correlation from causation on the effects of heterospecific pollen deposition is also important (Ashman et al. 2020), since heterospecific pollen may suggest that the plant received a higher number of visits or a greater amount of conspecific pollen deposition concomitant with heterospecific pollen, which in turn increases seed set (Tur et al. 2016, Lopes et al. 2022). However, there are still few studies that link species traits, ecological networks and reproductive output at the community context, which is essential to understand how plant–pollinator interactions may be linked to ecosystem functioning.

The relationship between community patterns and plant reproductive success is particularly significant in habitats with high diversity, such as OCBIL (old, climatically buffered, infertile landscapes) ecosystems (Hopper 2009, Silveira et al. 2016). Species in these habitats have a long history of adapting to poor soils and limited climatic buffering in small areas (Hopper 2009, Hopper et al. 2021). Plants in OCBIL habitats often have restricted distributions and rely on long-distance pollinators, such as large bees and hummingbirds for gene flow between populations (Hopper et al. 2021, Monteiro et al. 2021). Brazil's Campo Rupestre is one of such OCBIL areas, characterized by high species endemism within a confined region (Monteiro et al. 2021). In Campo Rupestre, plant individuals may occur in variable

floral communities, from dense conspecific patches to highly diverse co-flowering patches (Loiola et al. 2023). Therefore, we aimed to understand the influence of the floral community on pollinator sharing and on the reproductive success of plants in this highly biodiverse tropical grassland ecosystem by characterizing the different process involved (Fig. 1): 1) the community context, which refers to floral trait similarity, floral abundance, and phenological overlap with the plant community; 2) the visitation rates by pollinators and the indirect effect between species quantified by target degree and acting degree; 3) heterospecific and conspecific pollen deposition; 4) the response variable representing plants' reproductive success: seed set. Facilitation and competition are expected to shape different relations between these different components (Fig. 1A versus 1B).

If facilitation will be a predominant process, we expected that species with greater functional similarity and phenological overlap would lead to higher values of both target and acting degree and visitation rate per flower, as higher floral similarity and phenological overlap would mean more shared pollinators (Bergamo et al. 2020, Lázaro et al. 2020). More abundant species are expected to receive more pollinators and, by sharing them with other plants, to show higher acting degree (Carvalheiro et al. 2014). Conversely, less abundant species are expected to have a higher target degree because they will share pollinators that interact frequently with other plants (Bergamo et al. 2021). Species with a higher target degree are expected to receive more heterospecific pollen deposition, but may also be more tolerant to its potential negative effects (Bergamo et al. 2021). In this context, flowering simultaneously with more abundant species could be advantageous for rarer plants, as they may benefit from receiving more visits, even though this incurs more heterospecific pollen. If facilitation is predominant, the impact of heterospecific pollen deposition is expected to be weak compared to the benefits of sharing pollinators, as sharing pollinators can increase both pollinator visitation frequency and the quality of conspecific pollen deposition (Streher et al. 2020, Lopes et al. 2022). Therefore, we anticipated a positive indirect relationship between heterospecific pollen and seed set. Heterospecific pollen affects seed set indirectly by being associated with greater conspecific pollen deposition and by influencing its quality, since it indicates that visitors also forage outside conspecific patches.

On the other hand, if competition predominates, higher plant functional similarity will lead to reduced visitation for each plant species (Albor et al. 2022). In this context, more abundant species are likely to 'hog' interactions, meaning they monopolize pollinators, thus increasing their visitation rate (Albor et al. 2019, Koptur and Barrios 2020), and acting degree (Bergamo et al. 2021), while less abundant species will mostly receive pollinators shared with other plants, increasing its target degree (Bergamo et al. 2021). Species with greater phenological overlap are likely to compete more with other species for pollinators, leading to a reduction in the visitation rate and an increase in their role in the network (target and acting degree). Species with a higher visitation rate and acting degree likely experience higher conspecific pollen deposition and less heterospecific pollen deposition, since they would receive most of the visits of their pollinators. Finally, we expect a direct negative effect of heterospecific pollen deposition on seed set due to the interference of heterospecific pollen on reproduction (Ashman and Arceo-Gómez 2013).

Material and methods

Area of study and sampling design

Fieldwork was carried out in an area of Campo Rupestre within the campus of Universidade Federal dos Vales do Jequitinhonha e Mucuri, Brazil (18°11′48″S, 43°34′08″W), which has 240 ha of area and is contiguous to the protected area of Biribiri State Park, with 16 998.66 ha. This region is situated at an altitude of 1300 m a.s.l. The climate is classified as a mesothermal, subtropical highland climate, characterized by humid temperate with dry and rainy seasons (Alvares et al. 2013). Campo Rupestre (mountainous rocky grasslands), a vegetation within the Cerrado, occupies less than 1% of the Brazilian territory but encompasses more than 10% of the country's plant diversity (Silveira et al. 2016). Field sampling was conducted during the rainy season between October 2022 and April 2023 (INMET 2020) as it is the period with the highest diversity of plant species in bloom (Monteiro et al. 2021, Luna et al. 2024).

To sample the community of diverse plant species and their interactions with pollinators, we delimited 32 plots for the study, aiming to select areas with the greatest environmental heterogeneity (e.g. sandy soil, higher rock density, greater vegetation cover), each one with an area of 2.5 m^2. In each plot, we identified plant individuals using numbered tags throughout the experiment. To identify plant species, we collected samples from outside the plots and cross-referenced them with the herbarium at the Universidade Federal dos Vales do Jequitinhonha e Mucuri and also consulted specialists when necessary. Examples of floral diversity are presented in Fig. 2. During the study period we conducted sequential steps involving 15 days of active work in the plots followed by a one-week break, totalling nine work periods interspersed with eight breaks. During the 15-days work periods, we collected data on the number of flowers per individual, conducted observation of floral visitors, collected stigmas to quantify pollen deposition, and marked flowers to estimate seed set at the end of the study across all 32 plots. During the breaks, we collected data on the flower traits of the plant species, but for this we used individuals from outside of the plots to avoid disturbing plant–pollinator interactions in the plots.

Floral resources and visitors

To estimate the flower abundance to each species we used the total number of flowers per species counted during the floral visitor observations. For species with inflorescences, such as Asteraceae, we counted these as attractive units instead of the number of florets (Bergamo et al. 2020). We measured morphological flower traits known to impact interaction with

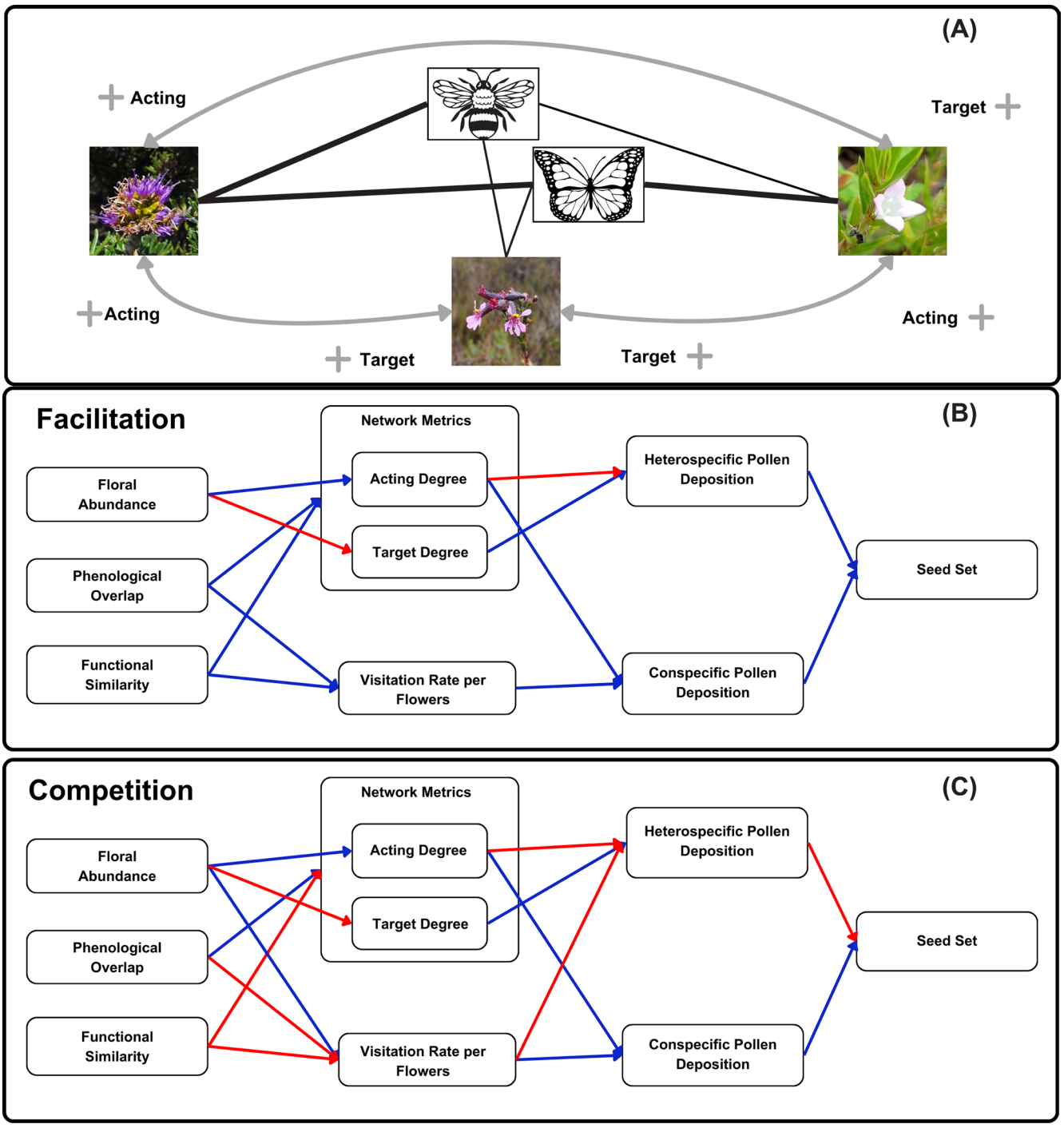

Figure 1. (A) Schematic representation of acting degree (+ Acting) and target degree (+ Target). Black lines and line thickness represent the frequency of interactions between plants and pollinators. Plant species with high acting degree (+ Acting) exhibit a higher frequency of interactions with a pollinator shared with other plant species, while plants with high target degree (+ Target) have a lower frequency of interactions with shared pollinators. (B and C) The analytical framework used in this study illustrates the division of variables into four parts and the flow of effects from left to right. The first part shows the community context (floral abundance, phenological overlap and functional similarity). The second part shows the acting and target degree and visitation rate that we used to understand the role of the plant species in the network. The third part displays conspecific pollen deposition and heterospecific pollen deposition, along with their effects on the fourth and final part, reproductive success (seed set). Blue and red arrows represent positive and negative relationships, respectively. (B) the scenarios in the facilitation context, (C) the scenarios in the competition context. The figure was created with Canva. Bee and butterfly illustrations were sourced from free elements provided by Pixabay and Graphixmania (via Canva).

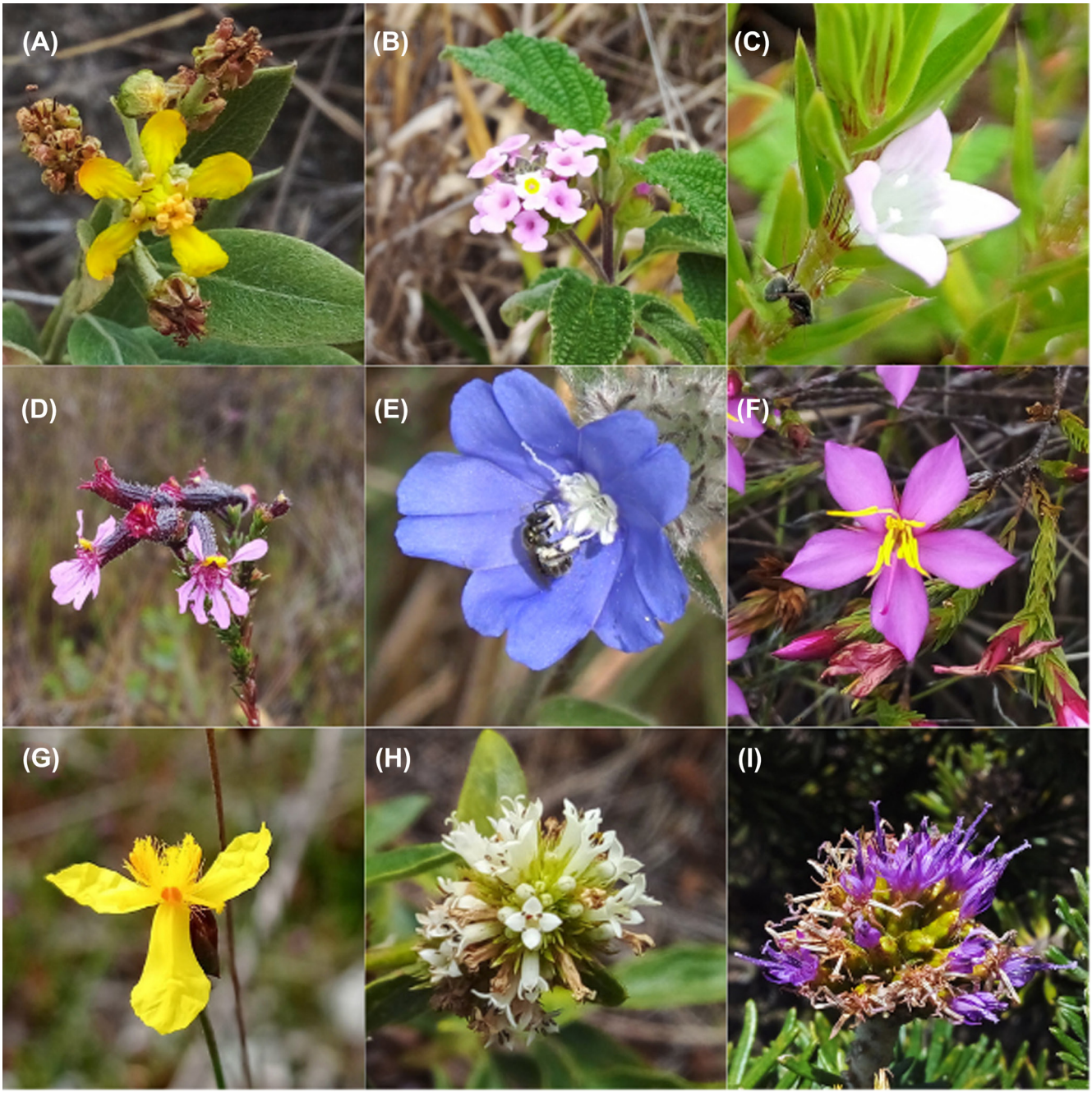

Figure 2. Examples of floral diversity found in the study. (A) *Tetrapterys microphylla* (Malpighiaceae), (B) *Lantana hypoleuca* (Verbenaceae), (C) *Richardia grandiflora* (Rubiaceae), (D) *Cuphea disperma* (Lythraceae), (E) *Evolvulus glomeratus* (Convolvulaceae), (F) *Microlicia* sp. (Melastomataceae), (G) *Xyris* sp. (Xyridaceae), (H) *Borreria verticillata* (Rubiaceae), (I) *Lychnophora pohlii* (Asteraceae). The figure was created with Canva.

pollinators, and thus pollinator sharing: corolla length, diameter of corolla opening, stigma and anther height for all species. Corolla length was considered as the distance from the base of the corolla up to the apex of the corolla. Additionally, each species was categorized according to the floral resource offered: nectar, pollen and/or oil (for Malpighiaceae; Supporting information). As the floral morphology of species may be related to their evolutionary history, we built a phylogenetic tree based on PhytoPhylo using the 'phytools' package (Revell 2024), and applied the *multiPhylosignal* function from the 'picante' package (Kembel et al. 2010) to test the phylogenetic signal (Blomberg's K) of species' morphology. The results indicate that only corolla length showed moderate phylogenetic signal (K = 0.60), while stigma height (K = 0.03), anther height (K = 0.04), and diameter of the corolla opening (K = 0.03) showed very weak phylogenetic

signal. Therefore, we did not include the phylogeny in the subsequent analysis.

For the observation of floral visitors, we arrived at the plots and recorded the number of blooming plants before starting. We then filmed each blooming plant individually within the plot for 30 minutes using video cameras. These observations were conducted between 7 a.m. and 3 p.m. throughout the study period, except on rainy days. By analyzing these recordings, we identified each visitor to the lowest taxonomic level possible, and counted the number of flowers visited. We determined whether the visitor made contact with the reproductive structures of the flowers, and when it did, we categorized these as potential pollinators. We recorded pollinators for 480 h (mean = 15 h and 30 min per species, according to flowering phenology; min = 30 min and max = 74 h). We used the number of observations divided by the time of observation and the number of flowers observed to calculate a visitation rate per flower.

Characterization of floral community

To characterize how similar each of the plants are in the community regarding functional floral traits, we calculated the functional distinctiveness for each species with interaction with pollinators using the *function distinctiveness* of the package 'funrar' (Grenié et al. 2017). Functional distinctiveness measures how different plant species are from each other. Thus, species with lower values of functional distinctiveness are more functionally similar to others in the community, whereas species with higher values are more functionally dissimilar. We constructed a matrix of species × mean floral traits and resources, including corolla length, corolla opening diameter, stigma and anther height, all of which were log transformed, and floral resource type as categorical variables, and another matrix with species abundances to weight their contribution to functional distinctiveness in the ordinal space.

To estimate the flowering overlap between plant species we calculated pairwise phenological overlap between species by adapting the index described by Freitas and Bolmgren (2008). This index incorporates the flowering time and flower abundance to measure the synchrony between pairs of species. The total phenological overlap with community for each plant species was estimated as the sum of the values obtained across all pairwise comparisons (Supporting information).

Pollen deposition and reproductive success

To quantify pollen deposition on flowers, we collected one stigma from each individual plant across all plots during the 15-day observation period. These stigmas were collected from flowers nearing senescence and transported to the laboratory. The stigmas were then placed on a microscope slide with glycerinated gelatin with fuchsin for pollen staining. In each stigma, we counted the number of conspecific and heterospecific pollen types.

To estimate heterospecific pollen deposition per species we used the following equation (McLernon et al. 1996):

Heterospecific pollen deposition $= £(x) / £(n)$, where:

x = heterospecific pollen deposited on stigmas to each plant species

n = number of stigmas collected to each plant species

To achieve more standardized conspecific pollen deposition measures, since pollen production varies between species, we used the 'min-max scaling' following equation:

Conspecific pollen deposition =sum(mean((x − min(x))/(max(x) − min(x))), where:

x = conspecific pollen deposited on stigmas to each plant species

min(x) = the minimum conspecific pollen found on the stigma to each plant species

max(x) = the maximum conspecific pollen found on the stigma to each plant species

For plant reproductive success, we marked open flowers in each individual plant across all plots during the 15-day observation period. These marked flowers were monitored until they developed into fruits. The fruits were then collected and placed in a fruit drying chamber. After drying, we counted the number of seeds per fruit. To compare seed production between species, we employed the same standardization used for conspecific pollen, considering the minimum and maximum seed production per species. Min-max standardization represents a relative reproductive success metric for the plants, useful in our case since we lack data on self-pollination or ovule number for the plant species. With this procedure, species with values closer to zero indicate that most individuals in that species had reproductive success closer to the individual with the fewest seeds, while higher values indicate that many individuals in that species had values closer to the maximum observed.

Network metrics

We first constructed a plant–pollinator interaction matrix with plant species in the columns and pollinators in the rows, with cells indicating the number of flowers visited by each pollinator. The interaction matrix was built pooling the sampling across all plots. Because it was not always possible to identify pollinators at the species level through recordings, we categorized the pollinators into morphotypes in most cases (Supporting information). Since we were interested in pollinator sharing among plants more than in the importance of specific pollinator species, we assumed that our approach was able to represent the extent to which plants shared similar pollinators. We calculated target degree and acting degree for each plant species (Bergamo et al. 2022), as well as the closeness centrality that measures how one plant species is connected with others throughout pollinators. To calculate the values of target degree and acting degree we used the 'Müller's index' (Müller et al. 1999), that represent the indirect relation for ecological networks:

$$d_{ij} = \sum_{n} \left[\frac{\_ik}{£_l \_il} \frac{\_jk}{£_m \_mk} \right]$$

where,

d_{ij} = the effect of j plant species in the i plant species.
α_{ik} = the frequency of interactions between plant species i and pollinator k.
α_{jk} = the frequency of interactions between plant species j and pollinator k.
$\Sigma_i\alpha_{il}$ = the total of interactions of plant i.
$\Sigma_m\alpha_{mk}$ = the total of interactions of pollinator k.
n = number of samples

Using Müller's index, we obtained a plant–plant matrix, where rows represent the effect of other plants on the focal plant species and columns represent the effect a plant species had on all other plant species in the network. The target degree is calculated as the sum of the rows in the plant-plant matrix, excluding the focal species itself. It represents the effect of all other plant species on the focal plant species. The values range from 0 to 1, where 0 indicates no effect from the community, and 1 represents the maximum effect of the plant community on the focal plant species. The acting degree is calculated as the sum of the columns in the plant-plant matrix for each species, excluding itself. It represents the effect one plant species has on others. These values range from 0 (indicating no effect on other plants) to $n - 1$ (where n is the total number of plant species, minus the focal species itself), representing the maximum effect one plant species

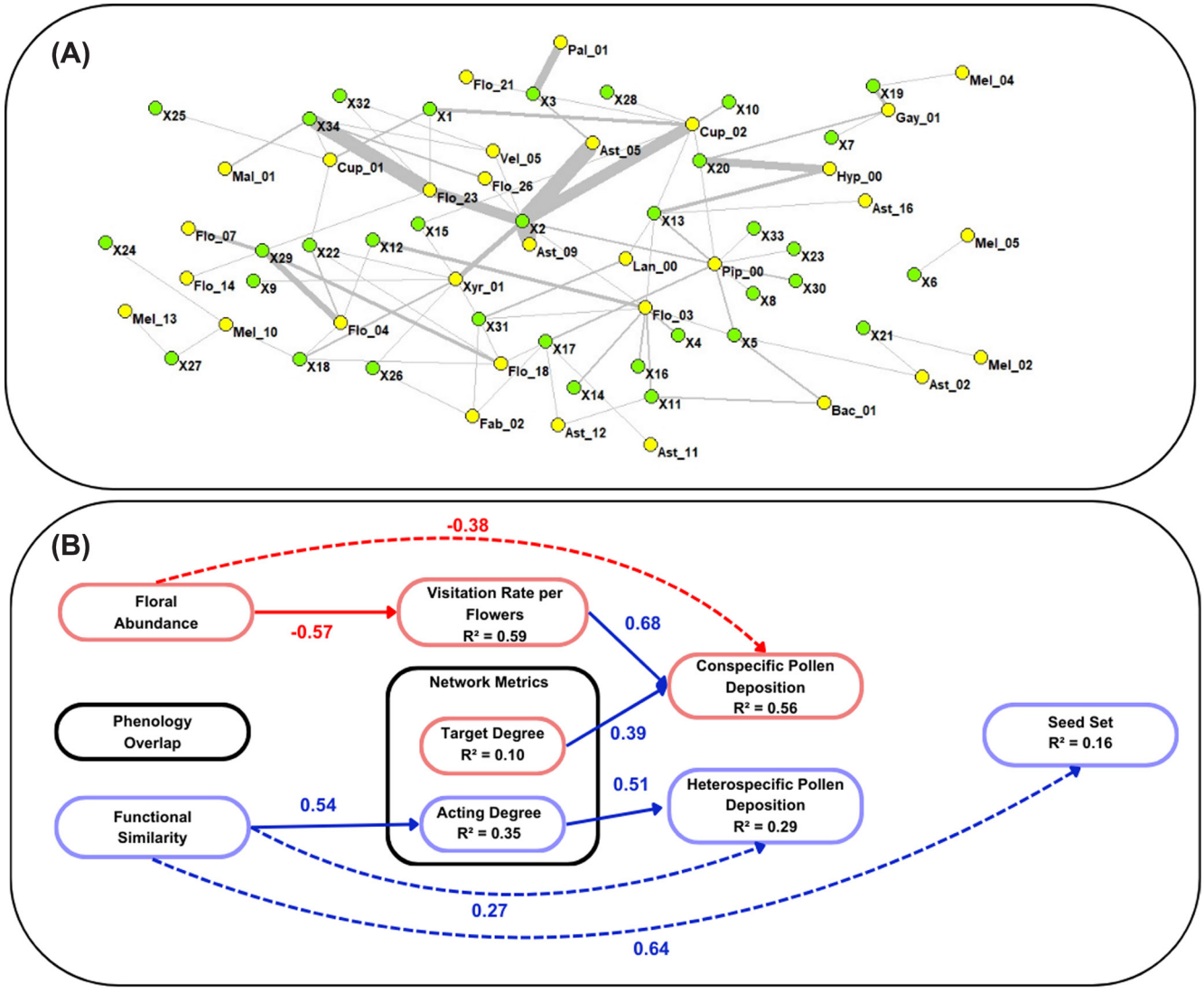

Figure 3. (A) Network of plant–pollinator interactions. Pollinators are depicted in green circles and plants in yellow circles. Line thickness represents the interaction frequency. Species codes refer to species names the Supporting information. (B) Results of the SEM analysis. Solid lines represent direct effects ($p < 0.05$). Dashed lines represent 'indirect' and 'TD' effects, which refer to results derived from recombination during the SEM analysis (Table 1). Dark blue arrows represent a positive relationship. Dark red arrow represents a negative relationship. Light blue squares represent the relationship of facilitation and light red squares represent the relationship of competition. The figure was created with Canva.

can have on others. However, the acting degree and closeness centrality were correlated ($R^2 = 0.35$, estimate = 56.24, $p < 0.01$), therefore we chose to focus on acting degree for the analyses. All network indices were calculated with the 'bipartite' R-package (www.r-project.org, Dormann et al. 2009).

Statistical analysis

To assess the effects of floral abundance, functional distinctiveness, phenological overlap, target and acting degrees, visitation rate, heterospecific and conspecific pollen deposition on reproductive success (seed set), we performed all analyses at the species level within the community. Specifically, we employed a piecewise structural equation model (SEM) with the function *psem* of 'piecewiseSEM' R package (Lefcheck 2016, following Lázaro et al. 2020). We used SEM because it allows the simultaneous evaluation of direct and indirect relationships among variables, enabling an integrated understanding of the system. This method combines predictors across different levels to evaluate their cumulative effects and test the global coherence of the hypothesized model. Additionally, SEM applies the concept of directed separation, which tests whether excluded paths (hypotheses) between variables remain significant, ensuring that the model structure captures essential relationships. The significance of predictor variables in SEM was assessed by examining the p-values of the models. For clarity, the SEM analysis was divided into four parts (Fig. 1). The first part of SEM included the effects of floral abundance, functional distinctiveness and phenological overlap on species level network metrics acting degree and target degree, as well as visitation rate per flower. For the second part, these variables were also included as predictors of heterospecific and conspecific pollen deposition. The third included all above mentioned variables plus heterospecific and conspecific pollen as predictors of reproductive success (seed set). We used the *simulateResiduals* function from the 'DHARMa' package (Hartig 2016) to stabilize the residuals' variance for better model fit. Log transformations were applied as part of model adjustment, not to achieve normality in the predictors. Therefore, we used log-transformed values for floral abundance and heterospecific pollen deposition. For this analysis, we removed 12 species without complete data (i.e. missing information on visitation rate, pollen deposition and/or seed set, sample size = 19; Supporting information). These checked models were included in the SEM. We also checked whether variables included as predictors were correlated, and proceeded with SEM after checking that they were not. For all models we used linear models with *lm* function and gaussian distribution.

All analyses were conducted using the R software (www.r-project.org) within the RStudio integrated development environment (www.posit.co). The data set used for the analyses is in the Supporting information.

Table 1. Results of the SEM. log(HPD) represents heterospecific pollen deposition log-transformed. Both R^2 and DF (degrees of freedom) represent parameters of the models. Bold and '*' mean significant values. Test: 'Direct' refers to results from the models in the SEM, while 'Indirect' and 'TD' refers to results derived from recombination during SEM analysis, not directly tested in the models. Indirect represents the subsequent relationship between variables, for example: visitation rates are affected by phenological overlap and, in turn, affect conspecific pollen deposition. TD refers to tests of directed separation.

Dependent	Independent	Test	R^2	DF	std estimate	Crit.value	p-value
Visitation rate			0.59	15			
	Functional distinctiveness	direct			−0.23	−1.33	0.20
	log(Floral abundance)	direct			−0.57	−3.20	**< 0.01***
	Phenological overlap	direct			−0.35	−1.87	0.08
Acting degree			0.35	15			
	Functional distinctiveness	direct			−0.54	−2.45	**0.02***
	log(Floral abundance)	direct			0.01	0.05	0.95
	Phenological overlap	direct			0.11	0.47	0.64
Target degree			0.10	15			
	Functional distinctiveness	direct			0.27	1.06	0.30
	log(Floral abundance)	direct			−0.12	−0.45	0.65
	Phenological overlap	direct			0.00	−0.01	0.98
log(HPD)			0.29	15			
	Visitation rate	direct			0.33	1.52	0.14
	Acting degree	direct			0.51	2.23	**0.04***
	Target degree	direct			0.17	0.78	0.44
	Functional distinctiveness	indirect			−0.27		
Conspecific pollen			0.56	15			
	Visitation rate	direct			0.68	3.87	**< 0.01***
	Acting degree	direct			0.11	0.62	0.54
	Target degree	direct			0.39	2.21	**0.04***
	log(Floral abundance)	indirect			−0.38		
Seed set			0.16	16			
	Conspecific pollen deposition	direct			−0.06	−0.29	0.77
	log(HPD)	direct			0.39	1.71	0.10
	Functional distinctiveness	TD		15	−0.64	−2.75	**0.01***

Results

We recorded 404 interactions between 31 plant species and 35 pollinator morphospecies, with less than one visit per hour on average. The most frequent visitor was the honeybee *Apis mellifera* with 143 interactions, followed by stingless bee *Trigona* sp. with 42 interactions (Fig. 3, Supporting information). During the study, species abundance ranged from 24 to over 700 flowers per species, flowering overlap from 0.75 to 8.09, and functional distinctiveness from 0.25 to 0.47 (Supporting information). Visitation rate ranged from 0.001 to 0.09, acting degree from 0.07 to 2.68, and target degree from 0.20 to 0.94 (Supporting information). All plant species received heterospecific pollen (0.3–45 grains per species) and conspecific pollen (6.08–146.58 grains). Reproductive success varied from 0.35 to 181.29 (Supporting information).

The SEM analysis showed good fit with the data (global goodness-of-fit: $C_{32} = 37.70$; $p = 0.22$; Fig. 3). Visitation rate per flower decreased with floral abundance (Table 1, Fig. 4A) and acting degree decreased with functional distinctiveness (Table 1, Fig. 4B). Target degree did not show relationship with any of the variables (Table 1). Heterospecific pollen increased with acting degree (Table 1, Fig. 5A) and had one indirect interaction: it decreased with functional distinctiveness (SE = −0.27; Table 1, Fig. 5B). Conspecific pollen deposition increased with visitation rate (Table 1, Fig. 5C) and with target degree (Table 1, Fig. 5D). Conspecific pollen deposition also had one indirect interaction: it decreased with floral abundance (SE = −0.38; Fig. 5E). Seed set did not show direct relation with conspecific and heterospecific pollen deposition (Table 1). However, seed set decreased with functional distinctiveness (estimate = −0.64; Table 1, Fig. 6).

Discussion

Here, we uncovered multiple direct and indirect relationships between species abundance, floral traits and phenology of the plant community, i.e. community context, on plant pollination and reproductive success. The positive effects of floral trait similarity on seed set support that pollination sharing has overall positive effects on plant reproductive success in the Campo Rupestre. This is because plant species exhibiting greater trait similarity tend to attract similar pollinators (Carvalheiro et al. 2014, Venjakob et al. 2016, Arroyo-Correa et al. 2024). Such positive impacts on seed set suggest facilitation as the main process driving pollination in the studied plant community (Ashman et al. 2020, Streher et al. 2020, Lopes et al. 2022, Arroyo-Correa et al. 2024).

The strong positive influence of visitation rate on conspecific pollen deposition was expected but, contrary to our hypotheses, abundant plants were associated with decreasing conspecific pollen and visitation rate per flower (Fig. 1). These negative relationships could be related with intraspecific competition (Wei et al. 2021, Ye et al. 2023), where plant species with high numbers of flowers experience less visits per flower and less conspecific pollen as plant individuals compete for pollinator attraction (Pauw 2013, Monasterolo et al. 2022). However, the less abundant species, which received more conspecific pollen, did not produce more seeds (Fig. 1). The lack of effect of conspecific pollen could be related to geitonogamy, where species that attract floral visitors end up depositing their own pollen or that of close relatives (Mitchell et al. 2004, Karron et al. 2009). A negative relationship between seed production and geitonogamy makes sense, as Campo Rupestre plants generally are self-incompatible but have low dispersal ability, leading to isolated populations that are genetically similar to each other (Silveira et al. 2016, Monteiro et al. 2021). On the other hand, many plants we found during this study have few ovules, such as Asteraceae plants, *Lantana* and *Palicourea*. Therefore, they would require only a few pollen grains to produce seeds, meaning there would not be a direct correlation between conspecific pollen deposition and seed production.

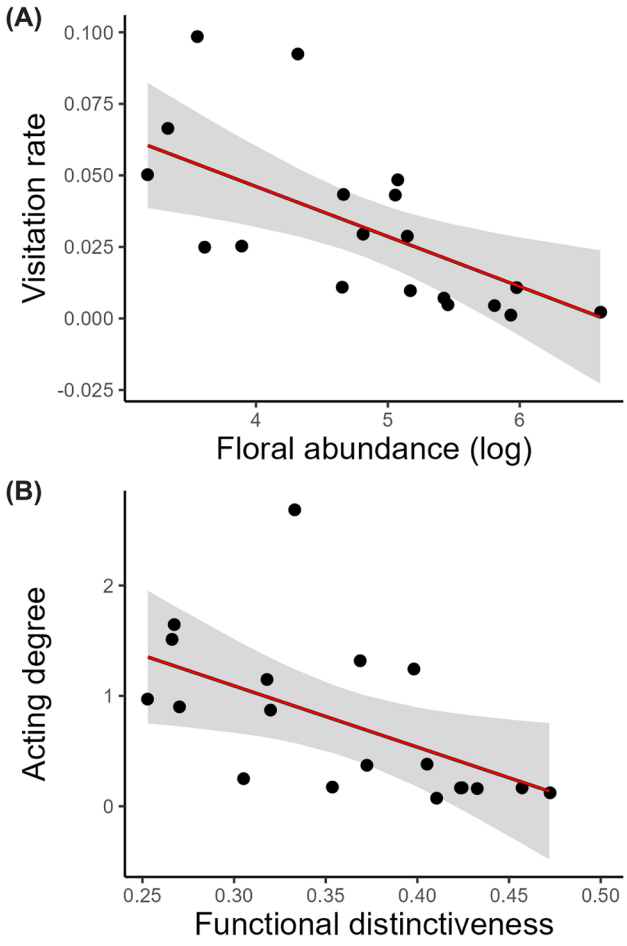

Figure 4. (A) Negative relationships between visitation rate and floral abundance and (B) negative relationships between acting degree and functional distinctiveness. Thus, plants with greater functional similarity (i.e. lower distinctiveness values) shared more pollinators. Plants with a higher acting degree are those that receive more frequent visits from shared pollinators.

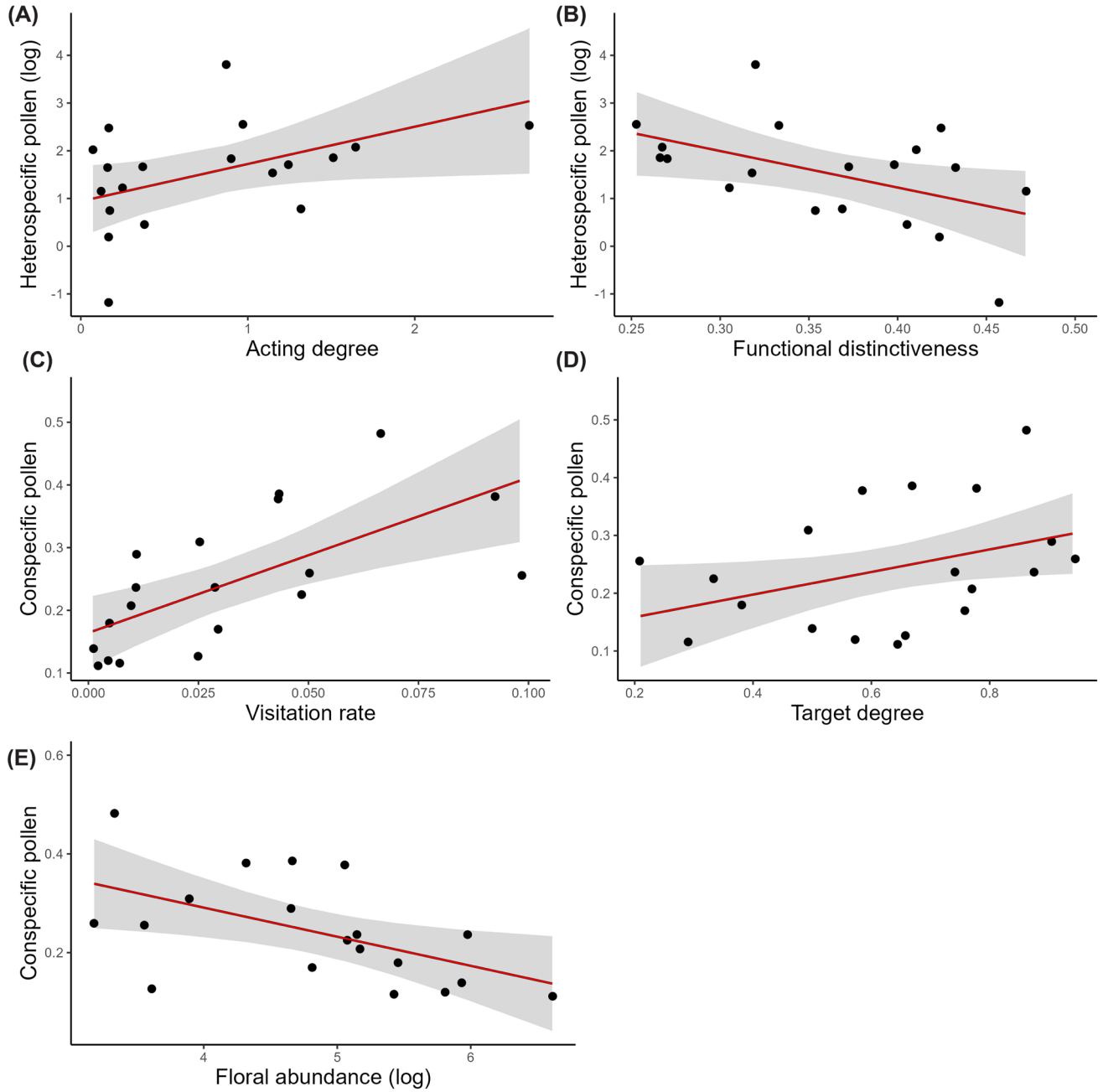

Figure 5. Relationship between heterospecific and conspecific pollen deposition and their predictors. (A) Positive relationship between heterospecific pollen deposition and acting degree (B) and indirect relationship between heterospecific pollen deposition and functional distinctiveness (SE −0.27), indicating that more functionally similar plants (i.e. lower distinctiveness) receive more heterospecific pollen. Relationship between conspecific pollen deposition and (C) visitation rate and (D) target degree. (E) indirect relationship of conspecific pollen and floral abundance (SE −0.38).

This possibility is further supported by the fact that plants in the Campo Rupestre experience low pollen limitation levels (Lopes et al. 2023), reinforcing that a lack of pollen would not be the factor severely affecting their reproductive success.

We found that species with similar floral traits tended to share more pollinators with other plant species, occupying a more central role in the network and increasing heterospecific pollen deposition. This result supports our initial hypothesis based on the facilitation ecological process, which predicted that trait similarity would promote greater pollinator sharing among species, ultimately enhancing the transfer of heterospecific pollen (Fig. 1; Arceo-Gómez et al. 2020, Bergamo et al. 2020, Lázaro et al. 2020). However, we found an opposite pattern than expected, as we hypothesized that

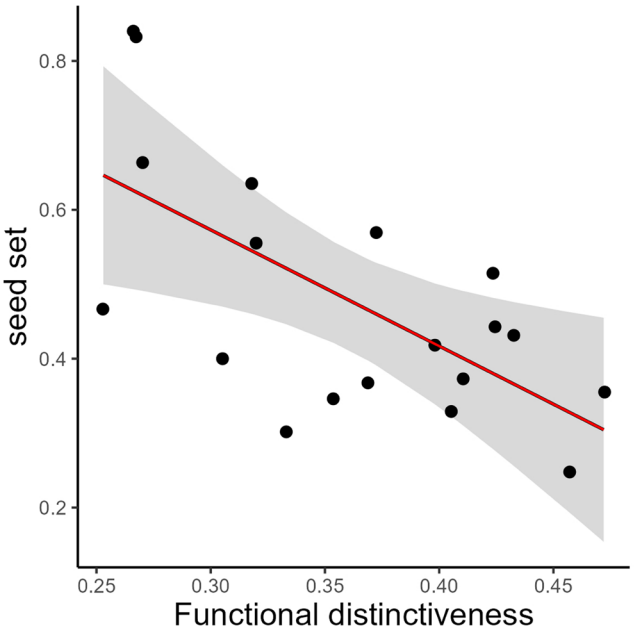

Figure 6. Indirect relationship between the seed set and functional distinctiveness (SE: −0.64) from tests of directed separation of SEM analysis, indicating that more functionally similar plants (i.e. lower distinctiveness) indirectly achieve higher seed set.

species with a higher acting degree would receive less heterospecific pollen and more conspecific pollen while species with a higher target degree (relying on pollinators that also visit many plants) would receive more of both heterospecific and conspecific pollen (Bergamo et al. 2022). This surprising result could be related to the correlation between acting degree and closeness centrality (Supporting information), as central species in the network, sharing more pollinators with all plant species, are expected to receive more heterospecific pollen. In addition, our results show that acting and target degree metrics reveal directional pollen flow patterns, helping to uncover how species interact through pollinator sharing, even when the effects diverge from initial expectations.

Facilitation is an important strategy for plant survival in environments with low pollination, due to the low abundance of either pollinators or plant species (Ghazoul 2006, Tur et al. 2016, Bergamo et al. 2020, Hederström et al. 2024, Arroyo-Correa et al. 2024). The Campo Rupestre are one of these habitats; besides the high plant endemism, the heterogeneity of soil features restricts the species to small, non connected areas (Silveira et al. 2016). Additionally, generalization in pollination systems is common in Campo Rupestr*e*, where interactions between plant and pollinators appear to be characterized by some opportunism (co-occurrence and co-flowering) and floral abundance than to strict morphological specialization (Carstensen et al. 2014, Lopes et al. 2022, Monteiro et al. 2021, Amorim et al. 2022, De Castro et al. 2025). Therefore, generalized plant species are expected to strongly share pollinators in this ecosystem. In this context, facilitation through trait similarity may be an important mechanism ensuring reproductive success of co-flowering plant species. On the other hand, both intraspecific competition and tolerance to heterospecific pollen may weaken interspecific competition. High floral abundance appears to reduce flower visitation and conspecific pollen deposition, indicating a cost to producing many flowers simultaneously. Meanwhile, tolerance to heterospecific pollen may benefit species that flower simultaneously with others, as it allows them to share pollinators without suffering strong fitness costs from heterospecific pollen transfer. This tolerance may reduce the selective pressure for temporal or morphological segregation and instead promote co-flowering and trait similarity, ultimately favoring facilitation over competition in this system.

In summary, our study revealed that plant species with high abundance had lower per flower visitation rates, which was associated with reduced conspecific pollen deposition, suggesting intraspecific competition. At the same time, plant species with higher floral morphology similarity in relation to the community produced more seeds, indicating that facilitation predominated over competition at the seed set stage. Specifically under low pollination probability scenarios, these positive interactions between plant species show the potential to increase plant coexistence in the habitat. Therefore, plant diversity in the community and indirect interactions between plant species positively affected the reproduction of plants. To conclude, floral similarity and floral abundance shape the positive and negative indirect effects between plants in the whole pollination process in this highly diverse ecosystem.

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Data availability statement

Data available on Figshare: https://doi.org/10.6084/m9.figshare.29264300 (De Amorim et al. 2025b).

Supporting information

The Supporting information associated with this article is available with the online version.

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