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Research article

Flowering synchrony modulates pollinator sharing and places plant individuals along a competition–facilitation continuum

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Indirect interactions among species within ecological communities govern ecological and evolutionary processes as much as, or even more, than direct effects. In insect-pollinated plant communities, indirect interactions between plants can be mediated by shared pollinators, and may influence plant fitness, population growth and community structure. As individuals are the entities actually interacting in nature, rather than species, downscaling a hierarchical level (i.e. from species to individuals) is essential to understand the underlying processes promoting these indirect interactions. We combined empirical data on plant–pollinator interactions collected in Mediterranean shrublands with a novel modelling framework to assess how the patterns of heterospecific and conspecific pollinator sharing between plant individuals are generated and their fitness implications. We found that the effects of flowering synchrony on pollinator sharing among conspecific and heterospecific plant individuals outperformed those of spatial distance. Our results revealed that plant individuals that shared more pollinators with conspecifics were also involved in a higher pollinator sharing with heterospecifics. For most plant species, the sharing of pollinator species between heterospecific plant individuals produced positive mean fitness outcomes, as long as plants did not share many pollinator interactions, which had negative effects on their fitness. At the level of plant individuals, we found that specific combinations of conspecific and heterospecific pollinator sharing lead to distinct reproductive outcomes that placed each individual along a competition–facilitation continuum. Interestingly, most plant species included a higher proportion of individuals likely experiencing competition compared to those potentially involved in facilitation processes. Our contribution provides novel insights into the factors responsible for local-scale indirect interactions within communities and their individual-level functional consequences. Such intricate patterns of indirect interactions have far-reaching implications, as the transitions of plant individuals along competitive or facilitative processes mediated by shared mutualists may contribute significantly to the functioning and coexistence of ecological communities.

Keywords: indirect effects, mutualism, phenology, plant fitness, pollination network, spatially-explicit network



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Introduction

Within mutualistic communities, most species interact directly with specific subsets of the available partners. For example, animal-pollinated plant species establish direct interactions with the animals that may act as pollinators. However, indirect interactions among species of the same trophic level also emerge as a consequence, playing a pivotal role, as they govern ecological and evolutionary processes as much as, or even more, than direct effects (Vandermeer et al. 1985, Strauss 1991, Benadi et al. 2013, Albrecht et al. 2015, Simmons et al. 2019). The sharing of pollinators between plants can lead to various indirect effects, which can be positive (i.e. facilitation), negative (i.e. competition), or neutral for one or both interacting plants (Sargent and Ackerly 2008, Braun and Lortie 2019). These indirect interactions mediated by shared pollinators have far-reaching effects, impacting population growth, coevolution of traits, and community structure (Hegland and Totland 2012, Guimarães et al. 2017, Losapio et al. 2019).

Despite the crucial role played by indirect interactions in ecological and evolutionary dynamics, our understanding of the mechanisms underlying their formation and maintenance in mutualistic networks is limited. So far, research has largely focused on determining these ecological processes behind entire species-level interaction network patterns (Carvalho et al. 2014) or evaluating conspecific and heterospecific effects of pollinator attraction on plant species' fitness (Hegland et al. 2009, Seifan et al. 2014, Lázaro et al. 2015). Yet, both approaches rely on pooling the interacting partners of all individuals at the species level. On the other hand, in recent years there have been efforts to study the indirect effects at the individual level in a single plant species (e.g. between plant individuals sharing pollinators, Gómez and Perfectti 2012, Arroyo-Correa et al. 2021), neglecting the potential for indirect effects between individuals from different species. Therefore, previous studies have left largely unexplored the factors responsible for local-scale individual patterns of indirect interactions at the community level as well as their functional outcomes for individuals.

Downscaling to the individual level is essential to understand the underlying processes promoting these indirect interactions between species, as individuals are the entities that are actually interacting in nature, rather than species (Guimarães 2020). Most animal-pollinated plant populations are composed of plant individuals that differ in the identity and abundance of pollinator species attracted (Soares et al. 2021, Arroyo-Correa et al. 2023). Indirect effects emerge as a consequence of sharing of pollinators, and may be driven by phenological overlap and spatial proximity (Rodríguez-Rodríguez et al. 2017, Arroyo-Correa et al. 2021). For example, plant individuals are expected to share more pollinators with plant individuals growing nearby and flowering at the same time compared to individuals farther away and/or with less phenological overlap. Hence, inter-individual differences in temporal and spatial aspects likely influence the probability

of plant individuals to share pollinators with both conspecifics and heterospecifics. However, there is limited information available on the relative importance of these spatial and temporal processes on the indirect effects mediated by pollinator sharing between plant individuals within communities.

The variation among plant individuals in pollinator sharing within and between species can be potentially translated into variation in plant reproductive success. First, pollinator sharing between conspecific plant individuals directly determines the potential effective pollen transfer events and therefore the production of seeds (Gómez and Perfectti 2012). Besides, this conspecific pollinator sharing may also affect plant individual's fitness via indirect effects, by increased attraction of pollinators that contribute to pollen flow among co-flowering individuals (i.e. facilitation) or reducing available pollinator resources due to intraspecific competition. Second, the sharing of pollinators between heterospecific plant individuals may have indirect negative effects on plant reproductive outcomes through competition for pollinator resources or heterospecific pollen competition on stigmas (Johnson et al. 2022). However, the fact that a plant individual shares pollinators with heterospecifics could also positively influence this plant individual's fitness indirectly by attracting pollinators that would otherwise not be present, counteracting their potential negative effects (Laverly 1992, Bergamo et al. 2020a, Hurtado et al. 2023). As a result, inter-individual differences in plant fitness may be generated by variation in how pollinators are shared with other co-flowering plant individuals, both within and between species in a community. Both facilitative and competitive effects, if any, would have measurable signals in fitness variation among individuals within populations in scenarios with some signs of pollen limitation and in absence of plant autogamy mechanisms. Because some plant individuals in the population may undergo competition while others may be involved in facilitative processes, it is likely that plant populations show inter-individual variation in the functional outcomes of these indirect interactions (Chamberlain et al. 2014). Therefore, plant individuals within populations may fall along a competition–facilitation continuum according to how they configure their indirect interactions in the community and what effects these interactions have on their fitness.

Patterns of inter-individual variation in resource use, such as pollinator use by plant individuals, can be visualized and analysed from an individual-based bipartite network perspective. For instance, in an individual-based plant–pollinator network, a set of nodes depicting plant individuals is connected to a set of nodes composed of the pollinator species visiting them (Gómez and Perfectti 2012, Arroyo-Correa et al. 2021). This individual-based bipartite network can be translated into a unipartite projection that represents patterns of pollinator sharing among pairs of plant individuals. Exponential random graph models (ERGMs) allow us to evaluate how the attributes of plant individuals (e.g. number of flowers produced, or spatial distance between them) shape pairwise interactions within the network depicting pollinator

sharing among these plant individuals. This is far from trivial, as this kind of modelling approach advances from descriptive metrics into a more cohesive predictive framework (Harris 2013). Besides, these models account for the fact that interaction establishment can be dependent on network topology (e.g. the observed density of interactions) together with node-specific ecological correlates, directly dealing with the nonindependence of the data. ERGMs have been previously used for mutualistic (Miguel et al. 2018, Arroyo-Correa et al. 2021), antagonistic (Isla et al. 2022) and animal social (Silk and Fisher 2017) networks.

By using pollinator visitation data recorded in plant individuals from multiple co-occurring species in Mediterranean shrublands, we aimed to investigate how indirect interactions are derived from the patterns of heterospecific and conspecific pollinator sharing between plant individuals and their fitness consequences. We first assessed the effects of the flowering synchrony and the spatial position of plant individuals on the sharing of pollinators with conspecific and heterospecific individuals. Second, we evaluated to what extent a

specific increase in the pollinator sharing of plant individuals with conspecifics changed the level of pollinator sharing among these plant individuals and heterospecifics. Third, we analysed the contribution of the conspecific and heterospecific components of pollinator sharing to plant individuals' fitness (i.e. total number of seeds produced). Overall, our modelling framework combining ERGMs and highly-resolved data (Fig. 1) enabled us to elucidate the local-scale mechanisms governing indirect interactions through shared pollinators, as well as their functional outcomes for the individuals involved in those interactions.

Material and methods

Study site and sampling

The study was performed in Doñana National Park (37°00'29.736"N, 06°30'24.919"W, 25 m a.s.l.), in the Atlantic coast of southwestern Spain (Supporting

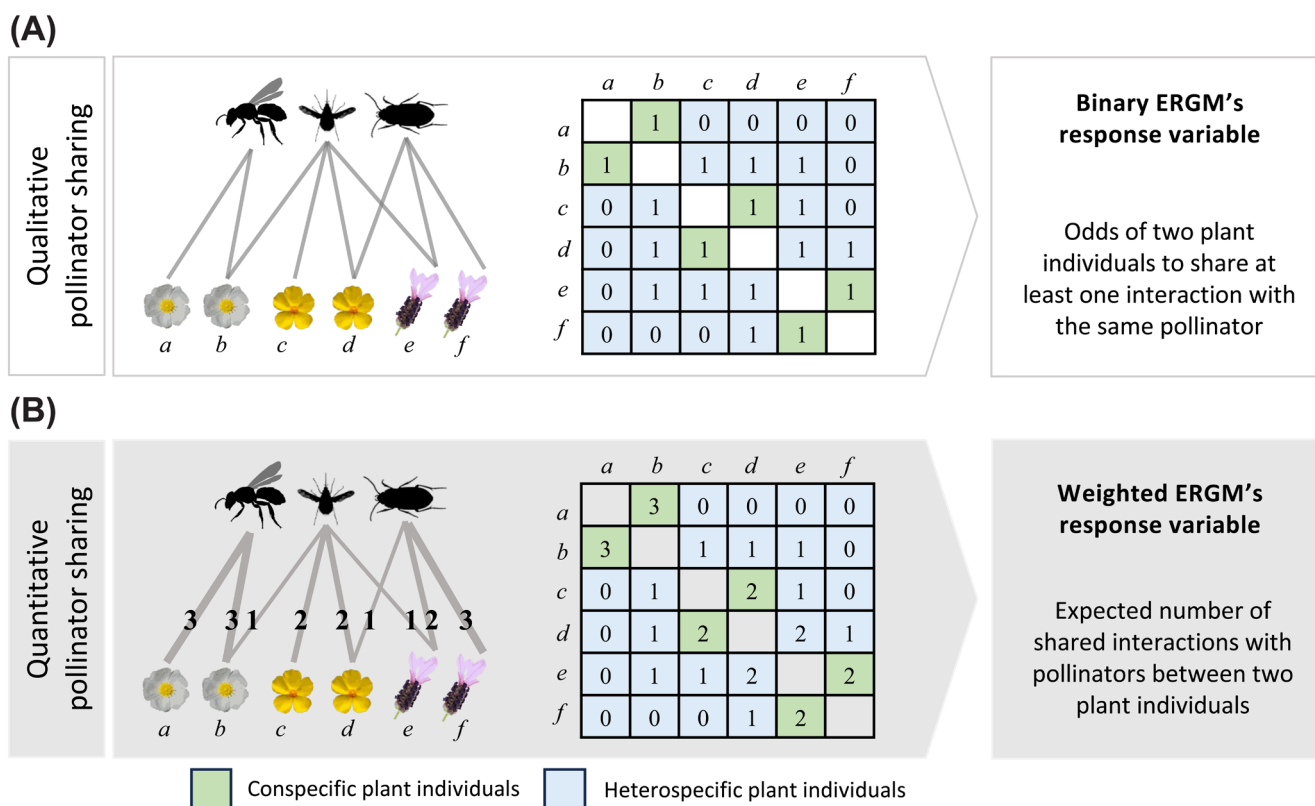


Figure 1. Conceptual illustration of the qualitative (A) and the quantitative (B) components of plant–plant pollinator sharing within conspecific and heterospecific contexts. Flower icons represent plant individuals (a–f). The qualitative pollinator sharing between plant individuals (A) is represented with a matrix in which elements depict the presence (1) or absence (0) of shared pollinators between any pair of plant individuals. In this qualitative matrix two plant individuals are linked (1) if they share at least one interaction with the same pollinator species. The quantitative pollinator sharing between plant individuals (B) is represented with a matrix in which elements contain the sum of the lesser values of the number of visits (bold numbers in network links) by each pollinator species shared between two plant individuals, so that sharing is driven by the lowest communality in interactions with pollinator species. Exponential random graph models (ERGMs) fitted with the qualitative pollinator sharing matrix (binary) model the odds of a given plant individual to share at least one pollinator with other plant individuals. Meanwhile, ERGMs fitted with the quantitative pollinator sharing matrix (weighted) model the expected number of shared interactions with pollinators of a given plant individual with all other plant individuals.

information). We selected six circular plots of 30-m radius that included 11 Mediterranean shrub species (Supporting information). These plant species are the only entomophilous shrub species growing in the area, and insect-mediated cross-pollination is essential to complete or improve seed production for all these plant species. We conducted surveys to record pollinator visits in the study plots during the peak flowering period only on sunny days (between early February and mid-July 2021). For each of the plant species, we selected individuals following a stratified random sampling (i.e. dividing each plot into four sections of the same size and selecting a similar number of plant individuals randomly within each section) to capture within-plot heterogeneity, totalling 700 individuals across plots (Supporting information). Within each plot, the spatial distance between plant individuals ranged between 0.24 ± 0.09 and 30.85 ± 2.44 m, averaged across plots [mean \pm SD]. We performed weekly surveys (19 weeks) on each flowering plant individual using video cameratogether with visual censuses along random transects (Supporting information). Pollinators were considered as all those insects touching flowers' reproductive structures, and were identified as pollinator morphospecies (hereafter 'species'), which were defined as groups of pollinator specimens with very similar or identical morphology (Arroyo-Correa et al. 2023, Supporting information). When a single pollinator visited several flowers of a plant individual, we counted each of those visits as a new visit. We excluded from analyses two plant species for which we did not gather sufficient visitation data due to the low abundance and the very early flowering period. We calculated the interaction sampling completeness for each plant individual as the proportion of the pollinator species recorded out of the total estimated using the Bootstrap asymptotic estimator (Smith and Van Belle 1984). For all plant species, the mean interaction sampling completeness of plant individuals was above 85% (Supporting information). Data obtained with video recordings were merged with those obtained with random transects by standardizing all interaction data as frequency of visits per minute to create an overall interaction dataset combining both methods (Supporting information). For each study plot we built a weighted bipartite network linking each plant individual from all plant species with the pollinator species visiting its flowers. We grouped pollinators at the species level assuming that pollinator individuals from the same species are likely to show more similar visitation patterns and fitness effects than pollinator individuals from different species (Gómez and Perfectti 2012). We used this proxy of pollinator sharing acknowledging the impossibility of tracking pollinator individuals at the scale of this study. This individual-based network was created by constructing an adjacency matrix A , where elements a_{ij} represent the frequency of interactions per unit time (min) between the pollinator species i and the plant individual j . With this network we characterized the pollinator resource usage patterns shown by plant individuals (Arroyo-Correa et al. 2023).

Pollinator-sharing networks

A total of 34 775 interactions between 583 plant individuals from nine species and 121 pollinator species were recorded in the study plots. To depict the patterns of shared pollinator species among plant individuals from different species, we generated two unipartite projections of matrix A that represent the pollinator sharing between any two plant individuals (Fig. 1). First, we created a qualitative unipartite projection of matrix A for the P plant individuals, in which elements represent the presence (1) or absence (0) of shared interactions with pollinators between two plant individuals. In this qualitative unipartite matrix two plant individuals are linked if they share at least one interaction with the same pollinator species (Fig. 1A). Second, we created a quantitative unipartite projection of matrix A for the P plant individuals, in which elements contain the sum of the lesser values of the number of visits by shared pollinator species between two plant individuals, so that pollinator sharing is driven by the lowest communality in interactions with pollinator species (Fig. 1B). Plant individuals that are strongly connected in these unipartite networks will be more likely to be involved in mating events (conspecific plants) and competition or facilitation processes promoted by conspecific or hetero-specific plant individuals (Gómez et al. 2011, Rodríguez-Rodríguez et al. 2017, Arroyo-Correa et al. 2021).

Flowering synchrony and spatial distance

To calculate the pairwise synchrony of plant individuals for each plot, we considered the presence or absence of flowers each week, defining flowering as a week when at least one flower was produced by a plant individual. We selected a qualitative version because plant individuals from different species have non-comparable patterns of quantitative flowering production. We quantified the pairwise flowering synchrony index for each pair of plant individuals by dividing the number of weeks that both individuals flowered by the total number of weeks that either of those individuals flowered (Ison et al. 2014), ranging from 0 (no overlap) to one (perfect overlap). For each plot we constructed a matrix for the P plant individuals where elements represent the flowering synchrony between each plant individual pair. This weighted adjacency matrix depicts therefore the temporal phenological overlap in bloom period between each plant individual pair. We also created a matrix of spatial distances among the P plant individuals on each plot, based on plant individuals' UTM coordinates using the 'sf' R package (Pebesma 2018). The elements of this spatial matrix depict the spatial distances (m) between each plant individual pair.

Plant fitness

For each plant individual, we calculated the fruit set as the proportion of flowers setting fruit. To do this, we randomly collected five inflorescences per plant and counted the total

number of flower buds produced initially and the number of fruits at the end of the season. All studied plant species produced flowers in inflorescences of different types, such as racemes (e.g. *Halimium calycinum*) or spikes (e.g. *Lavandula pedunculata*). To estimate seed production in each plant, we randomly sampled 10 fully developed fruits from different inflorescences and counted the number of seeds per fruit to obtain the average seed production per fruit. By randomly sampling inflorescences and flowers in each plant, we minimized the potential effects of phenological differences between inflorescences. Each week along the flowering season, we also counted the number of individual flowers in each plant individual and summed the weekly number of flowers as an estimate for the total number of flowers produced by a plant individual. An overall female reproductive success per plant (total number of seeds produced per plant, 'fitness' hereafter) was estimated as the product of the multiplication of the fruit set, the mean number of seeds produced per fruit, and the total number of flowers produced along the season.

Statistical analyses

Effects of flowering synchrony and spatial distance on pollinator sharing

To analyse the relative contribution of flowering synchrony and spatial distance on conspecific and heterospecific pollinator sharing, we used exponential random graph models (ERGMs, Lusher et al. 2013). The ERGM design is analogous to a classical generalized linear model (GLM) and implements a Markov chain Monte Carlo maximum likelihood parameter estimation. The use of these models for ecological networks allows us to test hypotheses about the underlying mechanisms shaping networks by modelling how link establishment (here pollinator sharing between plant individuals) is affected by specific predictor variables. These predictors can be structural, node-based or dyadic covariates. Structural covariates describe aspects of network topology that are expected to affect link formation. The most basic structural terms are the total number of unique links in binary ERGMs, referred to as 'edges' term, and the sum of link weights in weighted ERGMs, referred to as 'sum' term. The 'edges' term in binary ERGMs controls the proportion of possible links in the network that are actually observed (i.e. connectance) in log-odds. The 'sum' term in weighted ERGMs controls the general propensity (link weights) of nodes to be connected to other nodes (the logged, i.e. log-transformed, number of interactions established). The presence of these structural terms is equivalent to having an intercept within a GLM and is interpreted as the baseline odds of interaction establishment ('edges' term) and the baseline number of interactions established ('sum' term). Therefore, this framework allows us to account for the fact that link values can be dependent on any aspect of network topology, directly dealing with the nonindependence related to this (see the Supporting information for a more detailed interpretation of ERGM intercepts). Node-based

covariates model how node attributes (e.g. flower production) affect link establishment. Dyadic covariates explain differences in link establishment between nodes as outcomes of other kinds of relationships between them (i.e. link attributes, e.g. spatial distance or flowering synchrony).

We modelled the structure of the unipartite networks depicting the pollinator sharing between plant individuals. First, we modelled the binary unipartite network (i.e. binary ERGM, Fig. 1A) to assess the correlates of the odds that a given pair of plant individuals share at least one interaction with the same pollinator species. Second, we modelled the weighted unipartite network (i.e. weighted ERGM, Fig. 1B) to evaluate the correlates of the number of shared interactions with pollinators between any given pair of plant individuals. The 'edges' and the 'sum' terms were used as structural covariates in the binary and weighted ERGMs, respectively. For both types of models, we included the number of flowers as a node-based covariate to assess the main effect of this variable, accounting for the fact that plant individuals with more flowers were likely to attract more pollinators. We included the plant species identity (i.e. 'plant species' estimate) as a dyadic-based covariate to measure to what extent plant individuals tend to share pollinators with other plant individuals of the same species. This covariate allows us to evaluate how link establishment (i.e. pollinator sharing) changes within species (conspecific individuals) compared to between species (heterospecific individuals). We also included the matrices of flowering synchrony and spatial distance as dyadic covariates. Because we aimed to disentangle the effects of flowering synchrony and spatial distance on conspecific and heterospecific pollinator sharing separately, in each model we included two flowering synchrony matrices (one for conspecifics only and another one for heterospecifics only) and two spatial distance matrices (one for conspecifics only and another one for heterospecifics only). In the matrices of flowering synchrony and spatial distance only for conspecifics, the matrix elements between heterospecifics were set to 0, while in the matrix for heterospecifics the elements between conspecifics were set to 0. This approach allowed the model to simultaneously estimate the independent effects of these factors on pollinator sharing between conspecific and heterospecific individuals, as both the flowering synchrony and spatial distance matrices acting as predictor variables possessed identical dimensions to the corresponding unipartite network specified as response variable (Lusher et al. 2013).

Binary ERGMs allow us to interpret the coefficients as the expected change (increase or decrease) in the log-odds that pollinator sharing exists between any plant individual pair as a function of a one-unit change in a specific predictor variable. Regarding weighted ERGMs, we used a Poisson structure of the interaction data, which effectively captured the underlying link distribution as the observed frequencies of pollinator sharing are based on visitation counts. To obtain integer counts we multiplied the number of visits per minute by a fixed number of minutes (1000 for all networks). The underlying Poisson distribution of the weighted ERGM allows the interpretation of the coefficients as the expected

change (increase or decrease) in the logged number of times that each plant individual pair shares an interaction with a pollinator as a function of a one-unit change in a specific predictor variable (results for specific interpretations of model coefficients). The fitting of ERGMs results in an expected interaction matrix generated based on the estimated parameters, incorporating the effects of predictors. In the case of binary ERGMs the matrix elements depict the pairwise odds of two plant individuals sharing at least one interaction with the same pollinator species. In the case of weighted ERGMs, these elements depict the expected number of interactions shared between two plant individuals. These models were fitted for each plot separately and were computed using 'sand', 'ergm' and 'ergm.count' R packages (Hunter et al. 2008, Kolaczuk and Csárdi 2014, Krivitsky et al. 2023).

Relationship between conspecific and heterospecific pollinator sharing

We evaluated to what extent pollinator sharing of plant individuals with conspecifics also involved pollinator sharing with heterospecifics. To do that, we used the expected interaction matrices mentioned above, which contained the odds of a given plant individual to share interactions with conspecifics and heterospecifics (binary ERGMs' output) and the expected number of shared interactions between a given plant individual and conspecifics and heterospecifics (weighted ERGMs' output, hereafter referred to as number of shared interactions). We assessed the relationship between conspecific and heterospecific pollinator sharing of plant individuals using linear mixed models. First, we used the log-transformed odds of heterospecific pollinator sharing as the response variable and the log-transformed odds of conspecific pollinator sharing as the predictor variable. Second, we set the log-transformed number of shared interactions with heterospecifics as the response variable and the log-transformed number of shared interactions with conspecifics as the predictor variable. The log-transformation in both axes allowed us to estimate the percentage of change in pollinator sharing with heterospecific plants for every 1% increase in pollinator sharing with conspecific plants (either odds of sharing interactions or number of interactions shared). We included plant species and study plot as random factors.

Consequences of conspecific and heterospecific pollinator sharing on plant fitness

We analysed the effects of conspecific and heterospecific pollinator sharing patterns on plant individuals' fitness by fitting a generalized linear models (GLMs) with an underlying Gamma error distribution with a log link. We fitted one model separately for each plant species. We set the total number of seeds produced by plant individuals as the response variable, and the odds of sharing interactions with conspecific plants, the odds of sharing interactions with heterospecific plants, the number of shared interactions with conspecific plants and the number of shared interactions

with heterospecific plants as predictor variables. All these measures of pollinator sharing derived from the ERGMs' expected matrices mentioned above. To account for the fact that the fitness of plant individuals can be affected by the number of pollinator visits that plant individuals receive, we also included the total number of visits as a predictor variable. All predictor variables were scaled to allow meaningful comparisons. We found that one specific predictor variable in the models for three plant species exhibited multicollinearity ($VIF > 10$, Supporting information). However, we included these predictors to not shift the model being tested across plant species and to accurately estimate the coefficients for those uncorrelated predictors by controlling for the effects of predictors that show signs of collinearity (O'Brien 2007). We removed *Helichrysum picardii* from these analyses, as the harsh environmental conditions in summer prevented this species from producing seeds. We fitted all models using the 'lme4' R package (Bates et al. 2015) and checked residuals with 'DHARMA' R package (Hartig 2022). The contribution of the conspecific and heterospecific components of pollinator sharing to plant fitness was assessed estimating their R^2 contribution using the 'relaimpo' R package (Grömping 2006).

Beyond evaluating the mean fitness effects for each plant species, we aimed to disentangle how pollinator sharing with conspecifics and heterospecifics can place plant individuals within populations into facilitative or competitive contexts. First, for both the odds of sharing interactions (i.e. binary ERGMs) and the number of interactions shared (i.e. weighted ERGMs), we categorized plant individuals into 'low' or 'high' conspecific pollinator sharing and 'low' or 'high' heterospecific pollinator sharing. Plant individuals exhibited either 'low' or 'high' pollinator sharing (conspecific or heterospecific, binary or weighted) when their levels of pollinator sharing fell within the lower or upper 50% range within their populations, respectively. Following this procedure, plant individuals were classified into four combinations depicting different conspecific and heterospecific pollinator sharing levels for both the binary and weighted versions. Second, we obtained the predicted fitness of plant individuals and estimated their z-scores based on the above generalized linear models. Plant individuals with positive z-scores have an increased fitness compared to the mean fitness in the population, and hence, they are more likely to have experienced a higher level of facilitation if they exhibit high pollinator sharing (with conspecifics and/or heterospecifics) compared to other plant individuals in their population. In contrast, plant individuals with negative z-scores have a decreased fitness compared to the mean fitness in the population, and hence, they are more likely to have experienced a higher level of competition if they exhibit high pollinator sharing (with conspecifics or heterospecifics) compared to other plant individuals in their population. This allows us to place individuals along a relative competition-facilitation axes. All analyses were performed using R software ver. 4.1.2 (www.r-project.org).

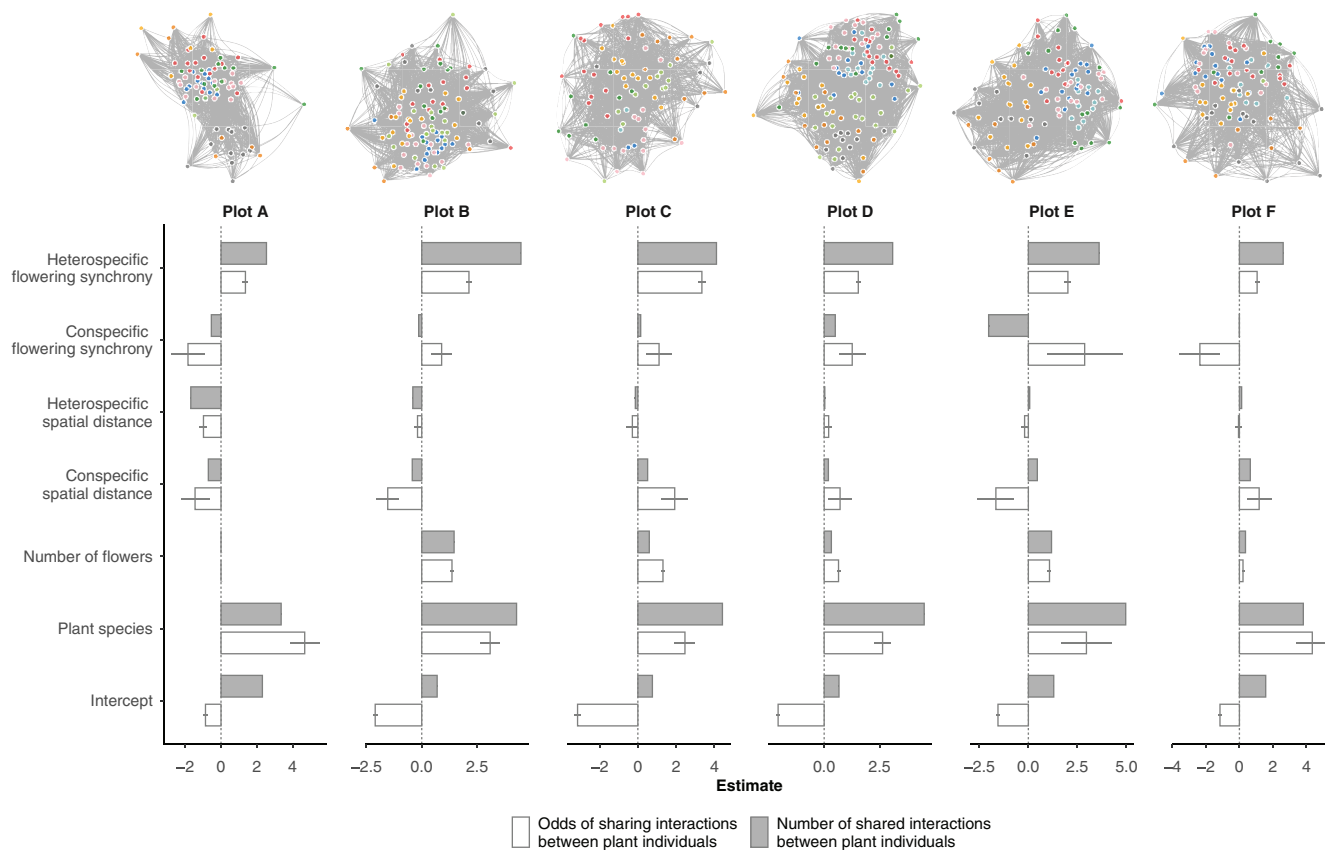


Figure 2. Ecological correlates of the odds of sharing interactions between plant individuals (binary ERGM, white) and of the expected number of shared interactions with pollinators between plant individuals (weighted ERGM, grey) within different plots (A–F). The intercept represents the log-odds that pollinator sharing exists between any plant individual pair (binary ERGM, white) and the logged expected number of shared interactions between any plant individual pair (weighted ERGM, grey). The plant species term indicates how these values change with plant individuals being conspecific compared to being heterospecific (i.e. homophily). Conspecific and heterospecific flowering synchrony and spatial distance refer to the effects of flowering synchrony and plant spacing on the pollinator sharing between plant individuals which are conspecific and heterospecific, respectively. The number of flowers represents the effect of plant individuals' flower production. A binary unipartite network illustrates the pattern of shared pollinator species among plant individuals from different species (colours) within each study plot. Two plant individuals are linked if they share at least one interaction with the same pollinator species.

Results

Effects of flowering synchrony and spatial distance on pollinator sharing

The baseline odds of a given plant individual to share at least one interaction with other plant individuals was 0.21 ± 0.14 (exponentially transformed intercept of the binary ERGMs, mean \pm SD across plots, Fig. 2, Supporting information). Meanwhile, the baseline expected number of interactions shared between a given plant individual and other plant individuals was 3.37 ± 1.53 (exponentially transformed intercept of the weighted ERGMs, mean \pm SD across plots, Fig. 2, Supporting information). We found that plant individuals' characteristics modulated these baseline levels of pollinator sharing (Fig. 2).

Conspecific plants had 34.14 ± 27.89 times more odds (averaged across plots) to share interactions than heterospecific plants. This is represented by the 'plant species' estimate

in binary ERGMs, which measures to what extent plant individuals tend to share interactions with other plant individuals of the same species compared to with plant individuals of different species (Supporting information). Conspecific plants shared 62.31 ± 52.99 more interactions than heterospecific plants (averaged across plots). This is represented by the 'plant species' estimate in weighted ERGMs, which measures to what extent plant individuals tend to share a higher number of interactions with other plant individuals of the same species compared to with plant individuals of different species (Supporting information).

Other model coefficients (Fig. 2, Supporting information) represent the effects of the number of flowers, distance to and flowering synchrony with other plants on the odds of sharing interactions between plant individuals (binary ERGMs) and the number of shared interactions between plant individuals (weighted ERGMs). For instance, the odds of a given plant individual to share interactions with other plants in plot B increased by a factor of 3.89 for every

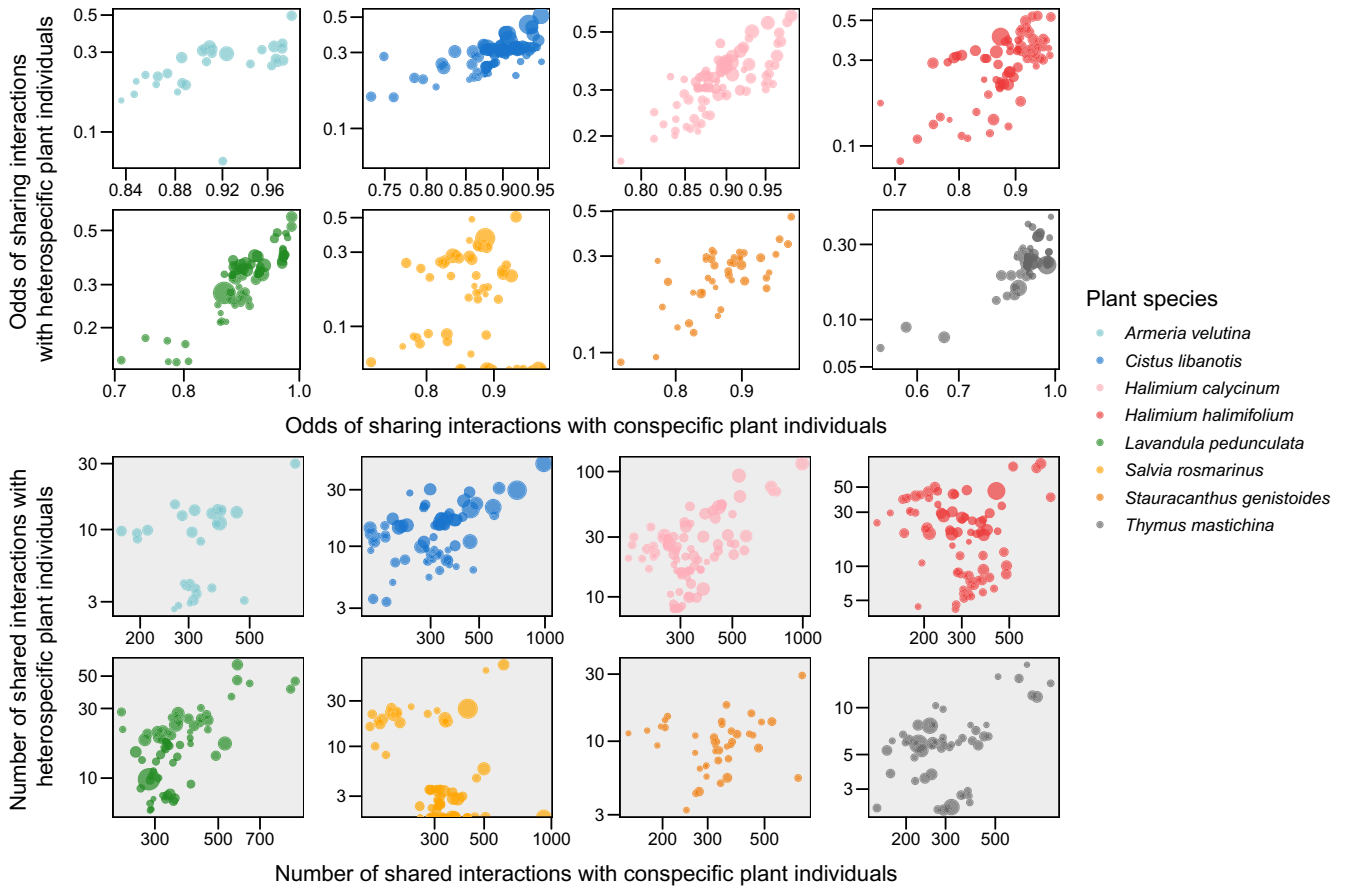


Figure 3. Changes in the odds of plant individuals to share interactions with heterospecifics as the odds of sharing interactions with conspecifics increase (white background), and in the number of shared interactions with heterospecifics as the number of shared interactions with conspecific increases (grey background) within different plant species (colours). Dot size is proportional to the number of pollinator visits of plant individuals. Note log scale in both axes.

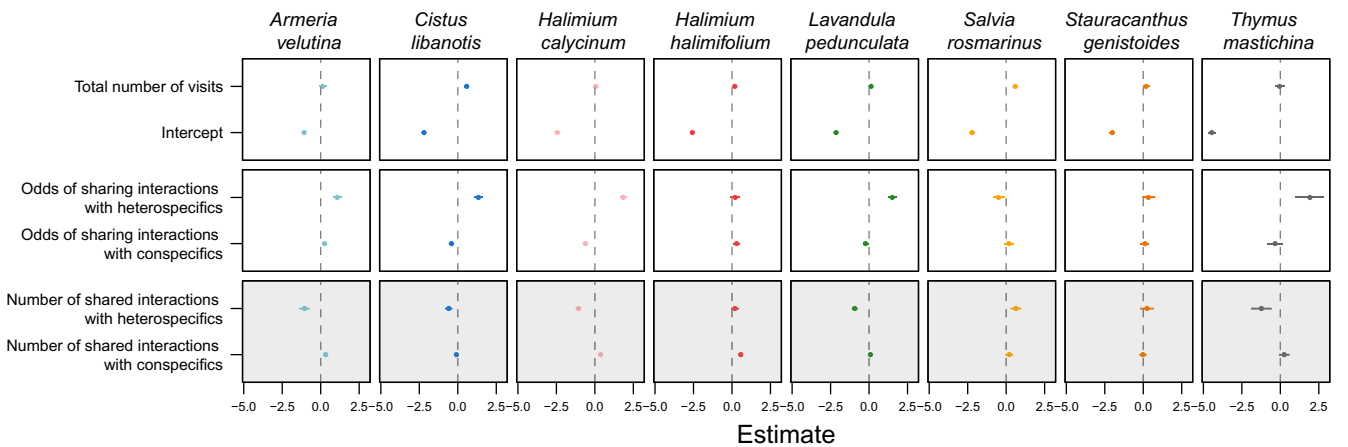


Figure 4. Effects of conspecific and heterospecific pollinator sharing on plant individual fitness (i.e. number of seeds produced) controlling for the total number of visits. The top panels include the intercepts (baseline number of seeds produced) and the effects of the number of visits. The middle panels represent the effects of the odds of sharing interactions with other plant individuals, separately for the conspecific and heterospecific counterparts. The bottom panels (grey background) include the effects of the number of shared interactions with other plant individuals, separately for the conspecific and heterospecific counterparts. Dots indicate the logged effect size of these predictor variables on the number of seeds (i.e. estimate), the range depicts the standard error of the effect, and colours represent different plant species.

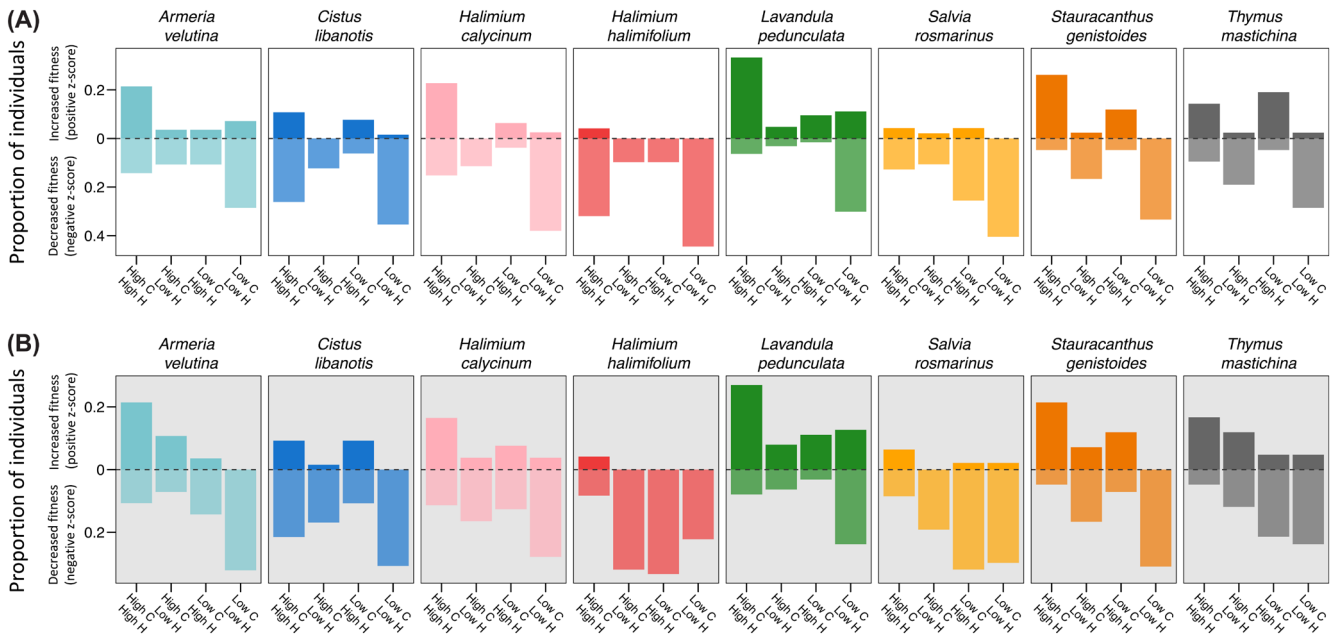


Figure 5. Relative fitness of plant individuals with different combinations of pollinator sharing with conspecific and heterospecific plant individuals. Plant individuals are classified into these combinations based on their odds of sharing interactions (A) and their number of interactions shared (B) with conspecifics ('Low' or 'High') and heterospecifics ('Low' or 'High'). The level of pollinator sharing with conspecifics (C) and heterospecifics (H), within each plant species, decreases from left (High C-High H) to right (Low C-Low H) along the abscissa. Fitness was predicted from the fitted models (GLMs) with the number of seeds as the response variable (methods) to control for the effects of the number of pollinator visits on seed production. Plant individuals' fitness is represented as the standard deviation from the mean number of seeds produced in the population (z-score). Individuals above the dashed line have positive fitness z-scores and are more likely to have experienced a higher level of facilitation if they exhibit high pollinator sharing. Individuals below the dashed line have negative fitness z-scores and are more likely to have experienced a higher level of competition if they exhibit high pollinator sharing.

unit increase in the number of flowers (i.e. 'number of flowers' estimate in binary ERGMs, Supporting information). Meanwhile, the number of shared interactions between a given plant individual and other plant individuals in plot B increased by a factor of 4.31, for every unit increase in the number of flowers (i.e. 'number of flowers' estimate in weighted ERGMs, Supporting information). The number of shared interactions between conspecifics decreased with flowering synchrony (in three out of six plots) and increased with spatial distance (in four out of six plots) (effect sizes in Fig. 2, Supporting information). As for the effects of flowering synchrony and spatial distance on the odds of sharing interactions, we did not find any clear patterns across study plots (Supporting information). Along all plots, the flowering synchrony increased both the odds of sharing interactions and the number of shared interactions between heterospecifics (Fig. 2, Supporting information).

Relationship between conspecific and heterospecific pollinator sharing

The odds of conspecific individuals to share interactions ranged between 0.70 ± 0.10 and 0.97 ± 0.02 [mean \pm SD across species] while the odds for heterospecific individuals to share interactions ranged between 0.06 ± 0.05 and 0.49 ± 0.08 . The number of shared interactions between conspecifics ranged between 157.00 ± 36.20 and 837.00 ± 139.00 while

the number of shared interactions between heterospecifics ranged between 3.25 ± 2.59 and 52.30 ± 33.40 (based on a 1000 min basis). We found that plant individuals that shared more pollinators with conspecific plants also shared more pollinators with heterospecific plants (Fig. 3). Specifically, for every 1% increase in the odds of interaction sharing with conspecific plants, the odds of sharing with heterospecific plants increased by about 2.50% (estimate = 2.47 ± 0.16 , $t = 15.04$, $p < 0.001$). Meanwhile, for every 1% increase in the number of shared interactions with conspecific plants, the number of shared interactions with heterospecific plants only increased by 0.65% (estimate = 0.65 ± 0.06 , $t = 11.36$, $p < 0.001$). These relationships between the conspecific and heterospecific components of pollinator sharing were mediated by the total number of flowers and visits of plant individuals (Supporting information), as more generalized plant individuals (producing more flowers and receiving more visits) were more likely to share pollinators with conspecifics but also with heterospecifics.

Consequences of conspecific and heterospecific pollinator sharing on plant fitness

After accounting for the effects of the number of visits received, the effects of the odds of sharing interactions with conspecific plant individuals on individual seed production varied from negative, no effect and positive across plant

species (Fig. 4, see the Supporting information for effect sizes). In three out of eight plant species, plant individuals' seed production increased with the number of shared interactions with conspecific plant individuals. Meanwhile, two out of eight plant species showed a decrease in seed production with the odds of conspecific pollinator sharing. For five out of eight plant species, seed production increased with the odds of sharing interactions with heterospecific plant individuals and decreased with the number of shared interactions with these heterospecifics. This result means that for a given plant individual, sharing a few pollinators with plant individuals of other species may be beneficial as long as it does not share large quantities. The conspecific component of pollinator sharing explained the $13.12 \pm 10.93\%$ [mean \pm SD across species] of the variance in individual seed production across plant species, while the heterospecific counterpart on average accounted for the $24.50 \pm 11.38\%$ of the variance (Supporting information).

We found that different combinations of pollinator sharing with conspecifics and heterospecifics left different imprints on the fitness of plant individuals across different species (Fig. 5, Supporting information). Plant species were composed of a mixture of plant individuals experiencing either higher (i.e. more facilitation) or lower (i.e. more competition) fitness relative to the mean as a result of pollinator sharing with conspecifics and heterospecifics. The proportion of individuals with an increased fitness (i.e. positive z-scores) compared to its population exceeded the proportion of individuals with a decreased fitness (i.e. negative z-scores) only in *L. pedunculata*. All the remaining plant species comprised a higher proportion of individuals experiencing a decreased fitness ($0.74 \pm 0.14\%$ across plant species) compared to those exhibiting an increased fitness. Hence, in those plant species, most individuals were likely involved in more competitive or less facilitative processes, and only few individuals experienced high levels of facilitation in response to high pollinator sharing either with conspecifics or heterospecifics. In five out of eight plant species, more than 50% of the plant individuals with high levels of conspecific pollinator sharing had an increased fitness, which may be associated both with higher chances of being involved in mating events and experiencing conspecific facilitation. Meanwhile, in five out of eight species, more than 50% of the plant individuals with high odds of heterospecific pollinator and low odds of conspecific pollinator sharing had increased fitness and therefore, they were likely to have experienced heterospecific facilitation (Fig. 5).

Discussion

Indirect interactions among plants mediated by pollinator sharing may have important implications for the structure and functioning of mutualistic communities (Mitchell et al. 2009). Over the past years, there has been substantial progress in understanding the processes that drive indirect plant–plant interactions mediated by pollinator sharing (Moeller 2004,

Sargent and Ackerly 2008, Carvalheiro et al. 2014), as well as for other mutualists (e.g. seed dispersers, Carlo 2005 and antagonists, Rathcke 1983). Yet, we still fail to understand how these interactions vary in space and time and how it translates into functional outcomes. Our analytical approach allows us to disentangle the spatial and temporal drivers of pollinator sharing patterns by downscaling to the plant individual level and incorporating the community context. The effects of flowering synchrony on the sharing of pollinators between conspecific and heterospecific plant individuals outperformed those of spatial distance. We also found that plant individuals that shared more pollinators with conspecifics were also involved in a higher pollinator sharing with heterospecifics. The fitness of plant individuals was more influenced by heterospecific pollinator sharing compared to conspecific pollinator sharing. Increasing the odds of plant individuals to share pollinators with heterospecifics produced positive fitness outcomes, as long as these plant individuals did not share many interactions, which had negative effects on their fitness. At the level of plant individuals, specific combinations of conspecific and heterospecific pollinator sharing lead to distinct positive or negative outcomes that placed those individuals along a competition–facilitation continuum.

The synchrony between co-occurring plant individuals in their flowering periods represents one of the main mechanisms which may allow them to share pollinators, giving room to potential facilitative or competitive effects (Moeller 2004, Lázaro and Santamaría 2016). Both conspecific and heterospecific plant individuals generally increased the odds of sharing pollinators and the number of pollinators shared when increasing their flowering synchrony. Besides, in most cases these positive effects were higher for heterospecific plant individuals than for conspecific ones, which is in line with previous findings on heterospecific facilitation for pollinators (Rathcke 1983, Ghazoul 2006, Bergamo et al. 2018). The smaller effects of flowering synchrony on conspecific pollinator sharing may be partially a consequence of pollinators' learning abilities. This learning leads pollinators to visit similar flowers throughout their lives, so that conspecific plants that share pollinators do not necessarily overlap in flowering (Waser 1986). Certain study plots exhibited a decrease either in the odds of sharing pollinators or in the number of shared pollinators between conspecific plant individuals when their flowering periods overlapped. In a scenario of a peak conspecific flowering, there could be a 'dilution effect' (i.e. the pollinator community distributes its visits over a larger number of conspecific plants), which would decrease pollinator sharing between conspecific plant individuals. These findings might also suggest a pattern of individual specialization among plant individuals within the same species, in which they partition available pollinator resources in a scenario where intraspecific competition for pollinators is likely to arise within the same time frame (Cope et al. 2022). In most study plots, spatial distance decreased the odds of sharing pollinators and the number of pollinators shared for both conspecific and heterospecific plant individuals. This result aligns with the observation that pollinators tend to move at

short distances as a consequence of optimal foraging strategies (Pasquaretta et al. 2017). Interestingly, the temporal scale, specifically the flowering synchrony of plant individuals, had a greater impact on pollinator sharing than the spatial scale. This result may be related to the fact that the maximum distance between plant individuals in our study plots (30.85 ± 2.44 m) was unlikely to pose strong spatial constraints for the movement of most pollinator species. In any case, it is clear that temporal limitations throughout the 19 weeks of the flowering season played a crucial role on pollinator species' activity, and hence on interaction patterns (Olesen et al. 2008, CaraDonna and Waser 2020).

Beyond disentangling the drivers of indirect plant–plant interactions mediated by pollinator sharing, by using exponential random graph models, we were also able to link these patterns with their consequences for plant fitness, which may influence plant establishment and community structure (Benadi et al. 2013, Kraft and Ackerly 2014). Hence, this approach enabled us to bridge the gap between structure and function when it came to assessing the functional outcomes of indirect interactions. By incorporating the community context, we improved our ability to predict the consequences of the heterospecific pollinator sharing relative to its conspecific counterpart, as most plant species overlap in space and time with other plant species. In generalized communities, plant individuals receiving many pollinator visits are expected to have more chances of sharing pollinators both with conspecifics and heterospecifics. The odds of plant individuals to share interactions with heterospecifics increased faster than the odds to share interactions with conspecifics (Fig. 3). This outcome might stem from the fact that there are more heterospecific plant individuals present in the community compared to conspecifics, leading to an increased likelihood of engaging in interactions with heterospecifics. Meanwhile, the number of shared interactions between plant individuals and heterospecifics increased slower compared to the increase in the number of shared interactions with conspecifics (Fig. 3). This trend could be attributed to the greater number of pollinator species shared by conspecific plant individuals, as opposed to heterospecifics, such that conspecifics are more likely to accumulate shared interactions at a faster rate. These findings highlight the importance of considering the broader plant community context when estimating the effects of pollinator sharing on individual plant fitness, as the increased odds of sharing or number of interactions shared with heterospecifics may modulate the potential positive or negative outcomes of increased conspecific pollinator sharing (Arceo-Gómez and Ashman 2011, Phillips et al. 2020). In fact, our results revealed a twofold increase in the impact of heterospecific pollinator sharing on plant fitness compared to the effects of conspecific pollinator sharing, which was mainly driven by the flowering synchrony between plant individuals.

After accounting for the effects of the number of visits, we found that pollinator sharing modulated plant individual fitness in all plant species. Therefore, the fitness outcomes of both less visited individuals and highly visited individuals were

affected by the levels of pollinator sharing (Fig. 4). Besides, in response to different levels of conspecific and heterospecific pollinator sharing, plant individuals with less visits had similar effects on fitness compared to plant individuals with more visits (dots of different sizes in the Supporting information). At the level of mean plant species' responses, increasing the odds of sharing pollinator species with heterospecific plants produced positive fitness outcomes, as long as plants did not share many pollinator interactions, which promoted negative fitness effects. This result suggests a facilitation effect of increasing the odds of heterospecific pollinator sharing (Braun and Lortie 2019, Bergamo et al. 2020a, b), as a given plant individual might be more likely to be visited by pollinator species attracted by heterospecific plant individuals, compared to a scenario without heterospecific neighbors. This increased likelihood of a given plant individual to receive any pollinator visit would in turn enhance its fitness (Lopes et al. 2022). This is consistent with evidence from other mutualisms, where heterospecific indirect interactions facilitate positive outcomes (Carlo 2005, Ghazoul 2006). Even though the odds of sharing pollinators with heterospecifics could promote plant fitness via facilitation, the positive heterospecific effect could not compensate for the negative effects of sharing a high number of pollinators with those heterospecific plant individuals. These negative effects could be a sign of heterospecific pollen competition on stigmas, which may be enhanced when increasing the events of visitation by pollinators that also visit other plant species (Ashman et al. 2020). However, when pollinators visit plant individuals from different species, their distinct flower structures may lead the pollinators to deposit pollen on different body parts, diminishing the potential transfer of heterospecific pollen and subsequent pollen competition (Waser 1978). Therefore, while we observed that plant individual fitness generally decreased with an increasing number of pollinators shared with heterospecific plant individuals, the potential limitations imposed by flower morphology differences may have reduced this negative impact of heterospecific indirect interactions (Muchhala and Thomson 2012, Huang et al. 2015). Our findings underscored the relevance of heterospecific interactions for plant fitness. In contrast to generalized systems such as ours, plant individuals' fitness in communities composed of plant species more specialized in pollinator use is expected to be less governed by these heterospecific indirect interactions, as plant individuals would share a higher proportion of pollinators with conspecifics than with heterospecifics.

Two plant species belonging to the Cistaceae family exhibited a reduction of individual fitness with increasing odds of conspecific pollinator sharing. Since these odds can be associated also to a higher number of flowers being visited within a given plant individual in a single foraging bout of a pollinator, they may increase geitonogamous pollination of that plant individual, which will import self-pollen that might be incompatible (Wilcock and Neiland 2002, Rodger and Ellis 2016). Besides, increased odds of sharing pollinators could also increase the chance of interacting with competitors, promoting intraspecific competition. However, other plant

species increased the mean fitness when increasing the number of interactions shared with conspecifics. For a given plant individual, a higher number of visits by pollinators which also visit conspecific plants can increase the amounts of conspecific pollen grains received, reducing pollen limitation, promoting realized mating events and increasing plant fitness (Aizen and Harder 2007, Lázaro et al. 2015).

When downscaling to individual-level responses, our findings suggest that the unique context of plant individuals and how they shared mutualists with both conspecifics and heterospecifics caused those individuals to fall along a continuum spanning from more competitive to more facilitative processes. The prevalence of these indirect interactions varied across different plant species, indicating that the balance between facilitation and competition, either conspecific or heterospecific, is intricately linked to the specific characteristics of each plant species and its interactions with both conspecifics and heterospecifics. These findings challenge the notion of universal facilitation or competition dynamics at the species level in plant communities, perhaps underappreciated in previous studies. Our results also revealed that plant individuals with few interactions (Supporting information, e.g. small plants with lower flower production, spatially peripheral in communities with clearly defined habitat boundaries, or phenological outliers) experienced improved fitness when they displayed any signs of pollinator sharing. These facilitation processes observed in individuals with few interactions align with earlier research emphasizing the importance of facilitation for rare species (Bergamo et al. 2020a, b, Wei et al. 2021). Our findings highlight that the effects of indirect interactions in mutualistic systems are not dichotomous but rather exist on a competition–facilitation spectrum (Fig. 5). These results are in line with previous findings that underscored the context-dependent nature of the outcomes of direct interactions (Bertness and Callaway 1994, Chamberlain et al. 2014, Fichtner et al. 2017), and also of indirect interactions within antagonistic systems (Veblen 2008) and food webs (Paine 1980). Our study builds upon this knowledge by quantifying the role of indirect interactions in natural mutualistic communities on the short-term balance between facilitation and competition at the individual level. This insight could only be gained by examining responses at the individual level, rather than analysing responses across entire species within communities, which might obscure the processes underlying community assembly.

By leveraging the ERGM framework, we were able to link the patterns of phenological and spatial overlap between conspecific and heterospecific plant individuals with variation in fitness outcomes via indirect interactions. This type of subtle balance between the consequences of sharing ecological partners at the intra and interspecific levels might be extended to other types of ecological interactions where partner sharing has been repeatedly documented (Atsatt and O'Dowd 1976, Carlo 2005, Zhang et al. 2021). We found

that the flowering synchrony of plant individuals defined how they shared pollinators with heterospecifics and conspecifics, which in turn modulated the position of those plant individuals along the competition–facilitation continuum. Such intricate patterns of indirect interactions have far-reaching implications, as the transitions of plant individuals along competitive or facilitative processes mediated by shared mutualists contribute significantly to the overall coexistence of ecological communities. Such comprehensive understanding is instrumental in formulating effective conservation strategies that can safeguard the functioning of plant–pollinator communities.

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Author contributions

Blanca Arroyo-Correa: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Software (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

Ignasi Bartomeus: Conceptualization, Funding acquisition (equal); Investigation, Methodology, Project administration, Supervision, Validation, Writing – review and editing.

Pedro Jordano: Conceptualization, Funding acquisition (equal); Investigation, Methodology, Project administration, Supervision, Validation, Writing – review and editing.

Data availability statement

Data and R code are available from the Zenodo Digital Repository: <https://doi.org/10.5281/zenodo.8337910> (Arroyo-Correa et al. 2024) and the GitHub repository (<https://github.com/BlancaAC>).

Supporting information

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

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