

Functional consequences of plant-animal interactions along the mutualism-antagonism gradient

MARÍA C. RODRÍGUEZ-RODRÍGUEZ, PEDRO JORDANO, AND ALFREDO VALIDO¹

*Department of Integrative Ecology, Estación Biológica de Doñana (EBD-CSIC),
C/Américo Vespucio 26, Isla de la Cartuja, 41092, Sevilla, Spain*

Abstract. Plant-animal interactions are pivotal for ecosystem functioning, and usually form complex networks involving multiple species of mutualists as well as antagonists. The costs and benefits of these interactions show a strong context-dependency directly related to individual variation in partner identity and differential strength. Yet understanding the context-dependency and functional consequences of mutualistic and antagonistic interactions on individuals remains a lasting challenge. We use a network approach to characterize the individual, plant-based pollination interaction networks of the Canarian *Isoplexis canariensis* (Plantaginaceae) with a mixed assemblage of vertebrate mutualists (birds and lizards) and invertebrate antagonists (florivores, nectar larcenists, and predispersal seed predators). We identify and quantify interaction typologies based on the sign (mutualistic vs. antagonistic) and strength (weak vs. strong) of animal-mediated pollination and test the relationship with individual female reproductive success (FRS). In addition, we document pollinator movement patterns among individual plants to infer events of pollen transfer/receipt that define the plant mating networks and test the relationship with FRS. We identify six interaction typologies along a mutualism-antagonism gradient, with two typologies being over-represented involving both mutualists and antagonists and influencing FRS. Plants showing strong mutualistic interactions, but also (weak or strong) interactions with antagonists are relatively better connected in the mating network (i.e., with higher potential to transfer or receive pollen). Thus, mixed flower visitor assemblages with mutualists and antagonists give plants increased their importance in the mating networks, promote outcrossing and increasing both female and male fitness. Our approach helps characterize plant-animal interaction typologies, the context-specificity of diversified mutualisms, and a better forecasting of their functional consequences.

Key words: *antagonist; bird pollination; Canary Islands; female reproductive success; individual-based pollination networks; interaction strength; Isoplexis canariensis; mating network; mutualist.*

INTRODUCTION

Mutualistic plant-animal interactions are pivotal elements of the structure and dynamics of ecological communities (Bascompte and Jordano 2014, Kissling and Schleuning 2015). Unveiling the complexity of these interactions is a challenging task: each plant species frequently interacts with multiple mutualistic agents, and partner identities and their interaction strengths continually change over time and space (Thompson 2005). Recent research has examined not only the structural properties of these complex patterns of interaction, but also their ecological and evolutionary consequences for whole communities (Bascompte and Jordano 2014, and references therein). An outstanding issue is to understand how these multispecies networks, and their functional consequences, emerge from the structure of mutualistic interactions within populations and, in turn, from the heterogeneous distribution of interactions among individual plants and

animals (i.e., individual-based interaction networks; Dupont et al. 2011, Gómez et al. 2011, Dupont et al. 2014, Tur et al. 2014, Valverde et al. 2016). This variation and its functional consequences constitutes the raw material for coevolution (Thompson 2005).

Recent studies of pollination (Fortuna et al. 2008, Dupont et al. 2011, 2014, Gómez et al. 2011, Gómez and Perfectti 2012, Tur et al. 2014, Valverde et al. 2016), seed dispersal (Cantor et al. 2013) and ant-plant interactions (Dáttilo et al. 2014) have begun to unravel how biotic interactions are organized at the scale of individual partners. These studies largely examine a simplified interaction typology to include plants and their mutualistic partners. However, antagonistic partners can radically alter the outcomes of mutualistic interactions (Irwin and Brody 1998, Bronstein et al. 2003, Irwin 2003, McCall and Irwin 2006, Thompson and Fernandez 2006). Therefore, understanding the joint action of mutualists and antagonists at the plant individual level is crucial to clarify the costs and benefits of interactions in terms of female reproductive success (FRS hereafter).

Addressing the complexity in plant-animal interactions, and their consequences for individual plant fitness,

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¹Corresponding Author. E-mail: avalido@ebd.csic.es

can be achieved by the identification of interaction typologies describing different modes of interaction (Milo et al. 2002, Jordano 2010, Bascompte and Jordano 2014) (Fig. 1a). The study of recurring interaction typologies, called motifs, has been used to analyze a variety of complex webs of interaction (Milo et al. 2002). A gradient of interaction typologies can thus be defined, ranging from an extreme represented by individual plants with fully mutualistic interactions, to the other extreme with fully antagonistic interactions (Fig. 1b).

Our work represents a first attempt to empirically quantify the diversity of plant-animal interactions across individual plants, and their functional effects measured as reproductive outcomes. We hypothesize that such a quantitative typification of distinct interaction typologies based on the sign (mutualistic vs. antagonistic) and strength (weak vs. strong) of animal-plant relationships will have a functional correlate in terms of female reproductive success in plants. Besides, we expected that the increase of mutualistic interaction strength would enhance the contribution to overall pollen transfer within the mating network. To test these hypotheses, we use applications of complex network theory to the pollination of *Isoplexis canariensis* (L.) J. W. Loudon (Plantaginaceae) (1) to characterize individual-based interaction typologies emerging from the interactions of individual plants with mutualistic and antagonist agents, (2) to estimate the relationship between interaction typology and FRS, (3) to document pollinator movement patterns to infer the relative importance of each plant in the mating network, and (4) to describe the relationship between the relative position in the mating network with the interaction typology and FRS.

METHODS

Biological system

We focus on mutualistic and antagonistic agents interacting with the perennial shrub *Isoplexis canariensis*, a hermaphrodite and self-compatible ornithophilous species endemic to the Canary Islands (Valido et al. 2004). Opportunistic nectar-feeding passerine birds and lacertid lizards act as effective pollinators that increase FRS despite the potential for spontaneous autogamy (Rodríguez-Rodríguez and Valido 2008, Rodríguez-Rodríguez et al. 2013). However, the benefits provided by these vertebrate mutualists are counteracted by invertebrate antagonists (florivores, nectar larcenists and predispersal seed predators), which consume and damage reproductive structures (see Appendix S1: Table S1 for a species list).

Study site

The study area is located in Teno Alto (Teno Rural Park, NW Tenerife), at an elevation of 870 m a.s.l. The site is covered by “fayal-brezal” forest with *Erica arborea*

(Ericaceae), *Morella faya* (Aiton) Wilbur (Myricaceae) and *Ilex canariensis* Poiret (Aquifoliaceae) as dominant tree species. Populations of *I. canariensis* are generally found in highly aggregated patches on sun-exposed canopy gaps caused by falling trees, rock outcrops or abandoned agricultural lands. Within this forest we selected two representative, close patches as replicate plots with 67 (8.9×13.7 m) and 52 (17.5×19.70 m) adult plants each. We monitored tagged individuals during the flowering season (May–September 2008) until just prior to the dispersal of seeds (see Rodríguez-Rodríguez et al. 2015 for details).

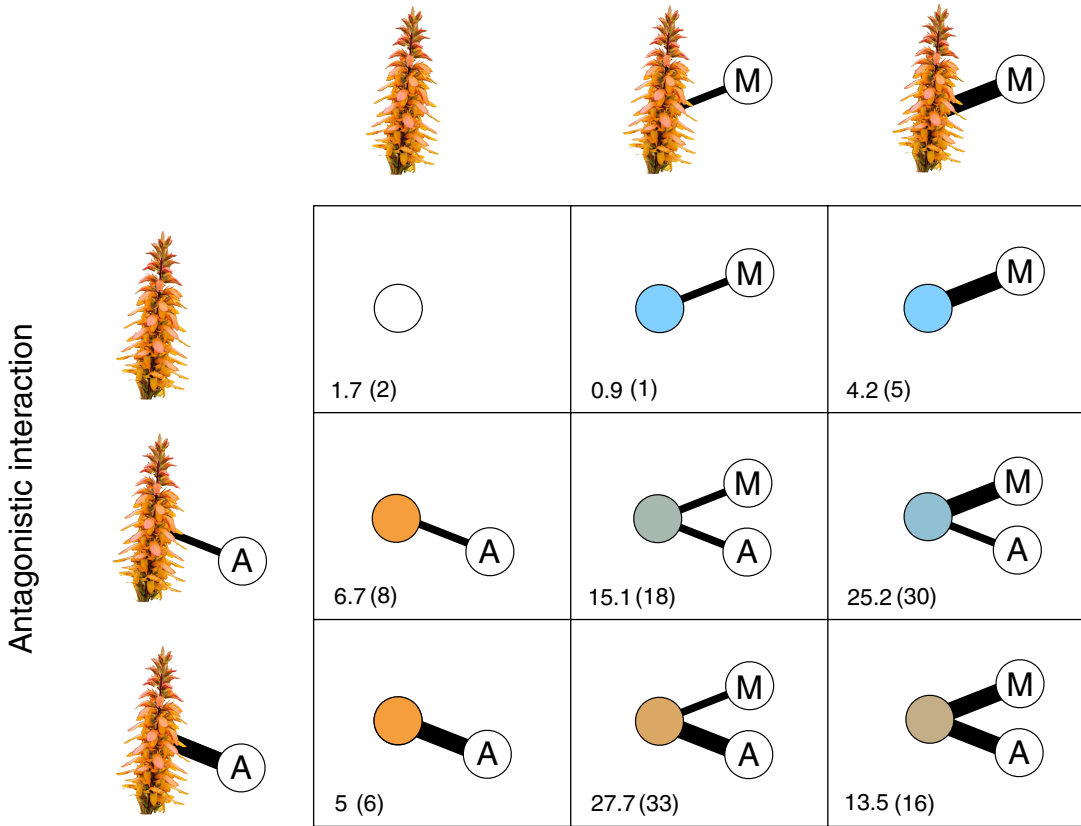
Plant-animal interaction typologies

We grouped animal assemblages into two functional categories: mutualists (M ; bird and lizard pollinators), and antagonists (A ; floral herbivores, nectar larcenists, and predispersal seed predators; Appendix S1: Table S1). For each individual plant, we defined the interaction strength as the frequency of interactions of specific animal groups with the plant, multiplied by the intensity of interaction. For mutualists, we estimated the interaction frequency as the proportion of censuses in which the plant-pollinator interaction was observed, and the intensity of interaction as the average proportion of flowers probed per plant visit. For antagonists, we estimated the frequency of interaction as the proportion of plant surveys in which we observed signs of damage, and the intensity of interaction as the average proportion of damaged reproductive units per plant survey. We defined the mutualistic interaction strength for the individual plant as the sum of the interactions with bird and lizard, and the antagonistic interaction strength as the sum of interactions with floral herbivores, nectar larcenists and predispersal seed predators. Both mutualistic and antagonistic interaction strengths were standardized (see Rodríguez-Rodríguez et al. 2015 and Appendix S2).

We used the interaction strengths to obtain a quantitative representation of interaction typologies based on an adjacency matrix among 119 plants (P) as rows, and two animal groups, mutualists (M) and antagonists (A) as columns. The matrix elements $a_{P,M}$ (individual plant—mutualists) or $a_{P,A}$ (individual plant—antagonists) were >0 if we detected any plant-animal interaction, and 0 otherwise. If the interaction occurred, we used the median values of the respective interaction strength as a cut-off to categorize into “weak” ($a_{P,M}$ or $a_{P,A} < \text{median}$) or “strong” ($a_{P,M}$ or $a_{P,A} \geq \text{median}$). We deconstructed the bipartite network into its constituent subgraphs to sort out the individual-based interaction patterns. These patterns were illustrated as undirected three-node subgraphs (triads), where each node represents an interacting partner (i.e., individual plant, mutualists, antagonists), and the links connecting nodes illustrate the interaction strengths between the plant and the respective animal group. We obtained 3×3 possible combinations of interaction with mutualists and/or antagonists resulting in

(a)

Mutualistic interaction



(b)

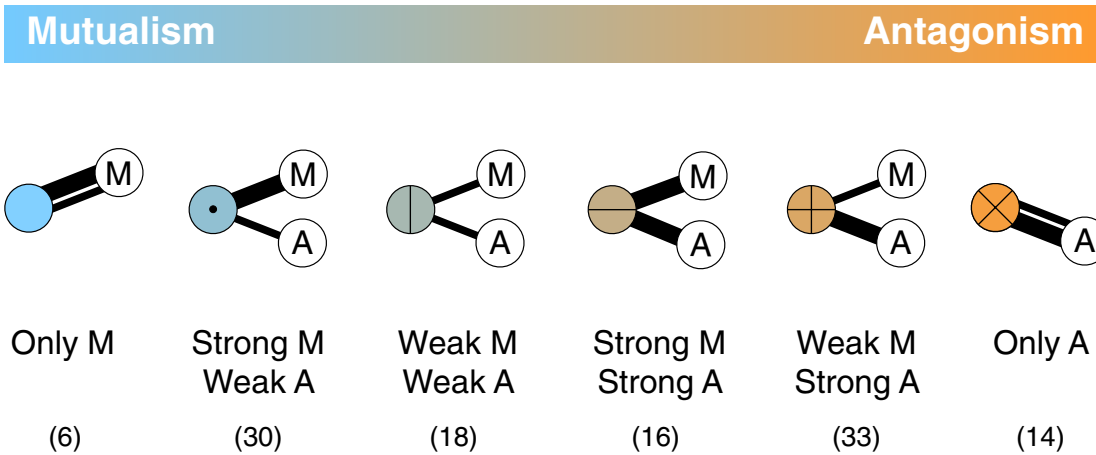


FIG. 1. Interaction modes between *Isoplexis canariensis* and mutualistic *M* and antagonistic *A* partners. Colors code groups of plants belonging to the same interaction typology (applicable to all figures). (a) The nine interaction triads based on the 3×3 possible combinations of mutualistic-antagonistic alternatives of interaction modes. Thick lines indicate strong interactions, while narrow lines depict weak interactions. Numbers in the lower-left corner of cells indicate the percentage (sample size in parentheses) of individual plants belonging to each triad (pooling all plants from the two studied patches). The two plants for which we did not record any interaction were later excluded (in white). (b) The six types of interaction typologies organized from the mutualistic to the antagonistic extremes. In the middle, those plants interacting with both animal groups (“diversified” interaction typologies) with all possible combinations of interaction strengths. Each interaction typology is accompanied by its respective label and observed frequency in parentheses (see Appendix S1: Table S1 for species assemblage including in the mutualist and antagonist groups).

nine types of triads (Fig. 1a). We recorded the number of plant occurrences in each typology to obtain the observed frequencies. Two plants with no interaction records were excluded from analyses (final $n = 117$).

Inferred plant contribution to the mating network

The relative contribution of individual plants to local pollen transfer was calculated in terms of their centrality within the mating network. The centrality of a node (plant) in the complex network of mating events is a measure of its relative importance within the graph (Freeman 1979), i.e., its potential role as a pollen source and/or pollen receiver. Plant centrality was estimated from unipartite weighted networks (one per patch) of individual plants connected by mating events. These mating events were inferred from the sequences of inter-plant movement by individual bird pollinators within the patch, recorded from direct field observations (Appendix S2). We assume these movements are surrogate indicators of actual events of pollen transfer, a safe assumption given the pollination effectiveness of flower visitation by the birds obtained from previous field experiments (Rodríguez-Rodríguez and Valido 2008, Rodríguez-Rodríguez et al. 2013). We focused on birds, instead of lizards, because they do the majority (>90%) of pollinator visits. Previous field experiments have also shown that visits by birds result in most cases in successful pollen deposition and removal; thus, visit and movement records of birds are a proxy to assess actual mating events.

The compiled information from all individual bird movements ($n = 172$ pooling from the two studied patches) was used to estimate link between nodes in the interaction network. Link width was proportional to the frequency of bird movements between each pair of plants, whether the plants acted as pollen donors or sinks (i.e., the bird moved from plant $A-B$ or vice versa). Although selfing events have relevant consequences for FRS (Rodríguez-Rodríguez and Valido 2008), here we focused only on among-plant interactions and, therefore, our networks showed no link connecting a plant to itself. Mating interactions were later represented as adjacency matrices with size $P \times P$, with the individual plants (P) from the same patch as rows (i) and columns (j). If the mating event occurred, a_{ij} values represented the number of events recorded between the specific pair of plants.

We characterized the role of each plant in the mating network by means of its centrality. Centrality indicates how well connected a given individual plant is (in terms of pollen transfer/receipt) to others into the patch as a function of the number of mating events they have shared. Specifically, we used the closeness metric C to estimate plant centrality by using `tnet` package in R (Opsahl 2015). This metric is positively related to the shortest number of direct and indirect interactions between one node and all other nodes in a network (shortest paths). C values specify which nodes can be reached fastest from any other node within the network

because it interacts with any node using no or few intermediaries (Freeman 1979). In our system where bird movements between plants determine path distance, the metric C would measure how well pollen originating from a plant reaches other plants via the shortest bird flights, or vice versa (i.e., how well pollen from conspecifics reaches the specific plant). We estimated weighted C measures to take into account both the number of intermediary nodes and the link weights, i.e., the number of mating events between any pair of plants (tuning parameter $\alpha = 0.5$) (Opsahl et al. 2010). Thus, links with larger weights were considered to have a much greater impact than links with smaller weights in the mating network. Finally, we normalized closeness measures dividing C by $N - 1$, where N is the number of plants in the corresponding patch, to have comparable values across patches.

Female reproductive success

We estimated FRS of each individual plant as the product of two components: fruit set and viable seed set per fruit. Fruit set was estimated as the proportion of monitored floral pedicels that set fully developed fruits ($n = 8,452$ floral pedicels, range: 8–606 pedicels/plant). The viable seed set was estimated as the average proportion of viable seeds produced per fruit. We chose a random subset of fruits for each individual plant from similar basal positions in inflorescences to avoid bias caused by maternal effects ($n = 2,026$, range: 3–23 fruits/plant), and counted the number of viable and aborted seeds inside. Then, we calculated the proportion of seeds within the fruit (P_{vs}). Finally, we obtained viable seed set per fruit as the averaged P_{vs} calculated across all fruits analyzed for each plant (see Rodríguez-Rodríguez and Valido 2008, Rodríguez-Rodríguez et al. 2013, 2015 for details).

Data analysis

Identification of interaction typologies.—Based on the sign (mutualistic vs. antagonistic) and strength (weak vs. strong) of interactions (Fig. 1a) we tested whether typologies appeared more frequently than expected in a randomized network of the same size. Interaction typologies with observed frequencies above random expectation are known as motifs (Milo et al. 2002). To generate a random network, we resampled (9,999 times) the three alternatives of plant-animal interaction strengths (absent, weak, strong), keeping the probabilities of each of these alternatives found in the study population (0.10, 0.45, 0.45, respectively). Once the random network was built, we counted the number of each of the six predefined plant-animal interaction typologies (Fig. 1b) rendered by the iterated matrix following the procedure described in the *Plant-animal interaction typologies* section. We created six distributions of expected frequencies, which were later used to detect over-represented typologies (i.e., motifs) by one-tailed Z tests.

Reproductive consequences of interaction typologies.—The effect of the interaction typology on FRS was tested using generalized linear regression models (GLM; quasibinomial errors), with FRS as the response variable and plant-animal interaction typology as the explanatory variable. To control for potential external confounding factors, we also included a set of plant traits (Appendix S3), and patch identity as fixed effects. Prior to model fitting, plant traits were standardized and tested for multi-collinearity via Variance Inflation Factors (VIF < 2 for all predictor variables; HH package in R) (Heiberger 2013). The significance of regressors was tested by comparing the full model with models that excluded only the specific factor by means of likelihood ratio tests (Zuur et al. 2009). The relative weight of each regressor was assessed with the relaimpo package in R (Groemping 2006), which estimates relative importance of regressors by the R^2 contribution averaged over resampled orderings among regressors. Given that relaimpo only implements models with Gaussian errors, we also compared the standardized coefficients by expressing each as a percentage of the total sum of the absolute values of the estimates. This is an approximation to assess the relative importance of effects in GLM models with non-Gaussian errors. Finally, we tested for differences in FRS among interaction typologies by post-hoc pairwise comparisons. The comparisons were done with adjusted probability values by the single step method by using the R package multcomp (Hothorn et al. 2008).

Mating consequences of interaction typologies.—To establish the functional consequences of pollen transfer by birds' movements, we first explored the relationship between the closeness of each individual plant with their FRS. For this, we tested their relationships by GLM (quasibinomial errors). Again, we standardized plant traits and patch identity as fixed effects to control for potential confounding factors, and tested the significance of regressors by means of likelihood ratio tests. Secondly, we obtained the grand means of C and FRS per plant-animal interaction typology to explore graphically if interaction typologies with higher levels of mutualism were consistently associated with higher values of closeness and female reproductive outcome.

All analyses and graphical representations were generated with R software version 3.1.1 (R Development Core Team 2014).

RESULTS

Interaction typologies

We identified six interaction typologies of plant-animal interactions based on the interaction sign and strengths for mutualists (M) and antagonists (A) (Fig. 1b). The resulting triads simplified the complexity of interaction patterns found along the mutualism-antagonism gradient for the large number of individual plants studied.

One interaction typology, i.e., motif—plants that interacted weakly with mutualists but strongly with antagonists (“Weak M –Strong A ”)—was recorded significantly more frequently than expected by chance ($Z = 2.16$, $P = 0.02$, Fig. 2a). In addition, plants that interacted strongly with mutualists but weakly with antagonists (“Strong M –Weak A ”) were also marginally overrepresented ($Z = 1.46$, $P = 0.07$).

Reproductive consequences of interaction typologies

Female plant reproductive success was significantly associated with the interaction typology the plant belonged to (Table 1, Fig. 2b; see Appendix S4: Table S1A). This effect was significant even when statistically controlling for the rest of covariates, which did not have a significant effect on FRS ($P > 0.05$ in all cases; see Appendix S4: Table S1B).

We found a decreasing trend in female fitness from fully mutualistic to fully antagonistic interaction typologies (from left to right in Fig. 2b; see Appendix S4: Table S1A). Plants that interacted exclusively with mutualists (“Only M ”), or interacted with both animal groups but weakly with antagonists (“Strong M –Weak A ”, “Weak M –Weak A ”) had similarly high reproductive outcomes ($P > 0.05$ for all pairwise contrasts; grouped by letter a in Fig. 2b; see also Appendix S4: Table S1A). Conversely, those plants that interacted only with antagonists (“Only A ”), or interacted strongly with antagonists independent of their interaction strength with mutualists (“Strong M –Strong A ”, “Weak M –Strong A ”) showed similarly low reproductive success ($P > 0.05$ for all pairwise contrasts; grouped by letter c in Fig. 2b). The continuous variation in FRS shows that the combination of mutualistic and antagonistic interaction strengths is more accurate at predicting reproductive consequences when compared to simpler typologies. For example, mutualistic interactions explain just 23.14% of variation in FRS. By far, the largest relative effect on FRS is due to antagonist agents (68.85%) with floral herbivores contributing a 39.83% of the total (Appendix S5).

Thus, the quantitative typification of distinct interaction typologies based on the sign (mutualistic vs. antagonistic) and strength (weak vs. strong) of animal-plant relationships helps summarize the broad diversity of interaction “modes” occurring in nature, very often showing extreme complexity. In this way, the variation across interaction typologies (Fig. 2) adequately captured the continuous, quantitative effects of animal partners (Appendix S5). Overall, the analysis of FRS variation in relation to continuous values of interaction strengths with different groups of organisms supports the conclusions based on interaction typologies (see Results in Appendix S5).

Mating consequences of interaction typologies

The heterogeneous distribution of bird movements among plants within each patch resulted in contrasting

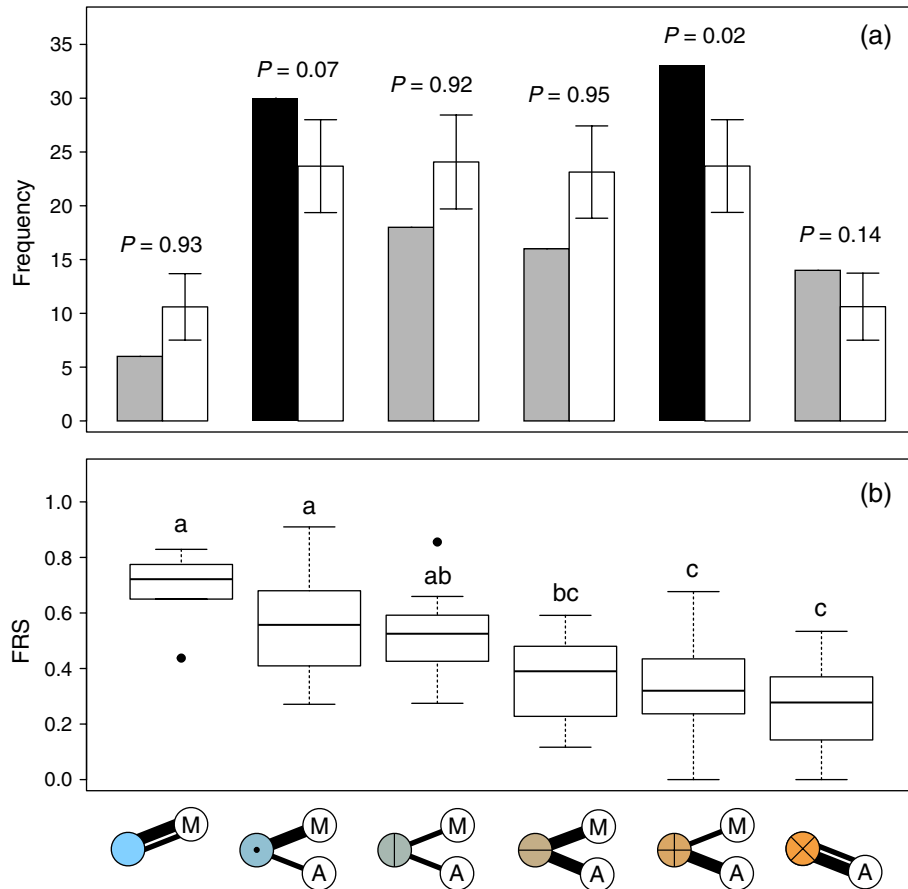


FIG. 2. Identification of plant-animal interaction typologies in the study system and their reproductive outcomes. (a) Observed (filled) and expected (unfilled) frequencies of the six interaction typologies. Mean \pm SD are represented for expected values. P values were obtained from upper-tailed Z tests ($\alpha = 0.05$). Black bars indicate identified interaction motifs (i.e., overrepresented). (b) Effect of the interaction typology on female reproductive success (FRS) analyzed by linear regression. FRS was defined as fruit set multiplied by viable seed set per fruit. Different letters indicate statistical differences in reproductive outcomes among interaction typologies ($P < 0.05$; see post-hoc multiple comparisons in Appendix S4).

topological positions of individual plants in the inferred mating network (Fig. 3). On average, plants occupied positions of moderate closeness ($C = 0.29 \pm 0.21$, range = 0–0.72, $n = 117$ plants). However, we found ample variation ranging from plants completely disconnected from the mating dynamics ($C = 0$, $n = 34$) to others with high integration ($C > 0.60$, range = 0.64–0.72, $n = 5$; Fig. 3).

Plant closeness had a significant effect on FRS: plants with higher C values had higher female fitness (Fig. 4; Appendix S6). The increase in plant closeness and associated reproductive benefits partially correlated with a transition from fully mutualistic to fully antagonistic interactions (Fig. 4). Hence, individual plants interacting exclusively with antagonists were totally decoupled from the mating network and showed the lowest reproductive outcomes (“Only A”, $C = 0$ for all plants, $n = 14$). However, increasing plant closeness and reproductive success were not associated with a decrease in antagonistic effects and a related increase in mutualistic interactions. This was contrary to our expectation of highest C

and FRS values in plants visited exclusively by mutualists. In contrast, the highest values of closeness were found in those plants that interacted with both functional groups: strongly with mutualists and weakly/strongly with antagonists (average $C = 0.43 \pm 0.15$, range = 0–0.72, $n = 46$). With intermediate values, we found plants that interacted exclusively with mutualists, or weakly with mutualists and weakly/strongly with antagonists (average $C = 0.24 \pm 0.19$, range = 0–0.59, $n = 57$; Fig. 4).

DISCUSSION

Studies addressing plant-animal mutualistic networks have provided novel insights on their functional consequences for natural communities (Bascompte and Jordano 2014). It has, however, been challenging to understand (1) how merging mutualistic and antagonistic interactions into a single network alters these consequences in terms of plant reproductive success (Fontaine et al. 2011), and (2) how these consequences are driven by the heterogeneous distribution of interactions at lower

TABLE 1. Summary of the generalized linear regression model showing the effects of plant-animal interaction typology, patch identity and standardized plant traits on female reproductive success (FRS)

Regression coefficients	Estimate \pm SE	<i>t</i> Value	<i>P</i> value
Intercept	0.282 \pm 0.404	0.70	0.48
Interaction typology “Only antagonists”	-1.749 \pm 0.374	-4.68	<0.001
Interaction typology “Weak M–Weak A”	-0.664 \pm 0.346	-1.92	0.05
Interaction typology “Strong M–Weak A”	-0.564 \pm 0.342	-1.65	0.10
Interaction typology “Weak M–Strong A”	-1.415 \pm 0.341	-4.15	<0.001
Interaction typology “Strong M–Strong A”	-1.202 \pm 0.363	-3.31	<0.001
Plant height	-0.074 \pm 0.069	-1.07	0.28
Nectar sugar reward	-0.022 \pm 0.068	-0.32	0.75
Flowering synchrony	-0.032 \pm 0.086	-0.37	0.71
Number of neighbours in $r = 2$ m	0.051 \pm 0.092	0.56	0.58
Distance to the nearest tree	-0.063 \pm 0.084	-0.75	0.45
Patch	0.307 \pm 0.186	1.65	0.10

Notes: FRS was estimated as the product of the proportion of fruits produced per plant and the averaged proportion of viable seeds per fruit (see *Methods: Female reproductive success*). Significance of regressors was tested by likelihood ratio tests (see also Appendix S4). Only interaction topology resulted in a significant effect (Deviance = 7.44, df = 5, $P < 0.001$).

organizational levels, i.e., among individuals within populations (Poiso et al. 2015). We address this challenge with new methods to characterize the intraspecific distribution of plant-animal interactions along the mutualistic-antagonistic gradient, and its functional correlates with plant reproductive success. Our study shows that even at small population scales, interacting animal assemblages vary considerably across individual plants, independently of spatial autocorrelation effects (Rodríguez-Rodríguez et al. 2015). However, this variation is not randomly distributed within the population, as illustrated by the presence of interaction motifs. Here, we find that the joint effects of mutualists and antagonists, depending on the relative interaction strengths, leave a signal in the relative contribution of plants as sources of viable propagules for the next generation. As expected, female reproductive success decreases from the fully mutualistic extreme to the fully antagonistic extreme of the interaction gradient. However, the existence of antagonistic damage, combined with strong mutualistic interactions, increases the participation of plants in the local dynamics of pollen transfer. Therefore, quantifying the strength of plant-animal interactions, rather than solely recording their presence or absence, improves our predictions of plant fitness and understanding of population dynamics.

Interaction typologies

Most plants involved in this study have in common that their animal assemblages include both mutualists and antagonists, but with variable interaction strengths. That is, if the strength of either type of interaction is strong, then the other type is weak. The two detected interaction motifs were “Weak M–Strong A” and “Strong M–Weak A”, significantly or marginally overrepresented, respectively (Fig. 2a). At this point, one might ask what drivers restrict individual plants from interacting with similar strengths

with both functional groups. In our system, we can reasonably explain this by considering the indirect effects of the interacting animal groups on each other. For example, it is known that pollinators are able to discriminate between damaged plants by antagonists (Irwin and Brody 1998, Krupnick et al. 1999, Carper et al. 2016). Alternatively, antagonists can also detect and reject plants depleted of floral resources by mutualists (Stout et al. 1998). The recognition of each other’s action results in a high frequency of plants that are greatly benefited from mutualists and poorly damaged by antagonists, and vice versa. In the case of *Isoplexis canariensis*, florivores seem to be the main drivers of the observed asymmetrical typologies because they interact with most plants in the population, and their action occurs even before the activity of pollinators. The early effect of florivores has great potential to influence the later movements of pollinators (i.e., the mating network), an explanation also supported by the negative spatial correlation between mutualistic and antagonistic interactions previously found in the two studied patches (Rodríguez-Rodríguez et al. 2015, see also Appendix S5).

Theoretical studies that have analyzed ecological networks with diversified interactions suggest that asymmetrical interactions may be prevalent in nature because of their associated benefits (Melián et al. 2009, Mougi and Kondoh 2012, 2014). First, the moderate mixture of mutualistic and antagonistic interactions gives greater stability and persistence to plant populations that scales up to maintain communities (Mougi and Kondoh 2012, 2014). Our divergent typologies assure the coexistence of mutualists and antagonists given that they appear in similar proportions (Fig. 2a). According to these theoretical approaches, stability drastically decreases when there is a skew towards either interaction type (Mougi and Kondoh 2012, 2014), a fact that may explain the relatively lower occurrence of plants that interact with a

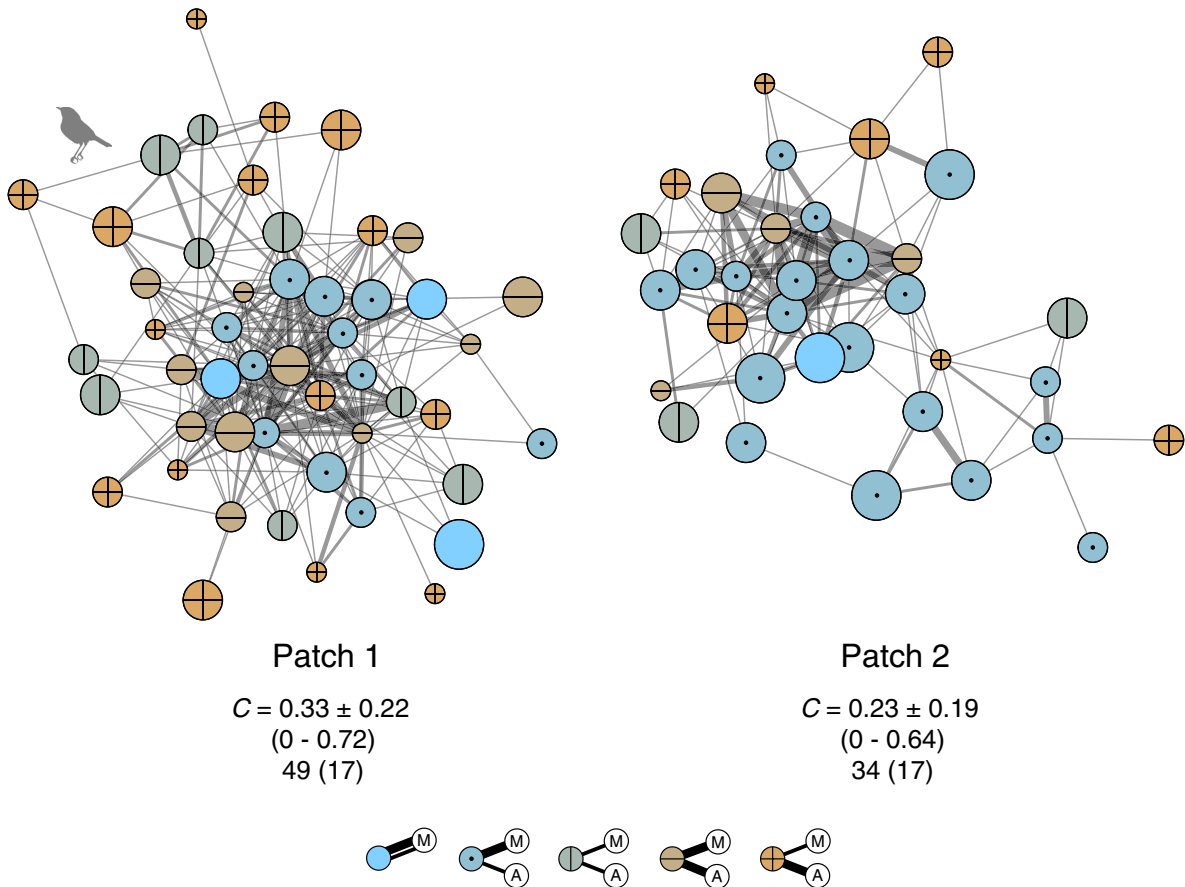


FIG. 3. Unipartite networks illustrating the inferred mating patterns (i.e., potential pollen transfer events) among individual plants originating from the $n = 172$ bird pollinator foraging movements. The links among nodes (plants) indicate the existence of at least one observed mating event between any pair of plants. Link width is proportional to the observed number of mating events at the patch scale. Node size refers to the female reproductive success (FRS) achieved by the plant, which was categorized into five levels for graphical representation: (1) $FRS = 0$, (2) $0 < FRS \leq 0.25$, (3) $0.25 < FRS \leq 0.50$, (4) $0.50 < FRS \leq 0.75$, (5) $0.75 < FRS \leq 1$. Network representation was generated with the Kamada-Kawai energy-minimization algorithm (Kamada and Kawai 1989). For each patch, we indicate mean \pm SD of closeness (range in parentheses), and below, the number of connected and disconnected plants (in parentheses).

single functional group (Fig. 2a). Second, the prevalence of asymmetrical interactions favors the maintenance of more complex biodiversity compared to populations with simpler typologies (Mougi and Kondoh 2012). Higher complexity increases the diversity of plant reproductive outcomes, which ultimately boosts variation fueling coevolutionary processes (Thompson 2005).

Reproductive consequences of interaction typologies

As expected, the predefined categories of distinct plant-animal interaction typologies along the mutualism-antagonism gradient correlated with individual plant female reproductive success. The fact that we consistently found a significant effect of interaction typology on FRS suggests that the combination of mutualistic and antagonistic interaction strengths within individual plants drives variation in FRS beyond the effects of plant traits and patch identity.

The continuous variation in FRS shows that the combination of mutualistic and antagonistic interaction strengths more accurately predicts reproductive consequences when compared to simpler typologies. Although the interannual consistency of this pattern needs to be evaluated, our results reveal that, even at the scale of small populations, the reproductive outcomes of plant-pollinator interactions are highly dynamic due to variation in antagonistic interactions (Irwin and Brody 1998, Krupnick et al. 1999, Herrera et al. 2002, Bronstein et al. 2003, Strauss and Irwin 2004, Thompson and Fernandez 2006).

Mating consequences of interaction typologies

Contrary to our expectations, plants with fully legitimate mutualistic interactions did not have the highest closeness values (did not contribute the most pollen transfer) despite having the highest female reproductive

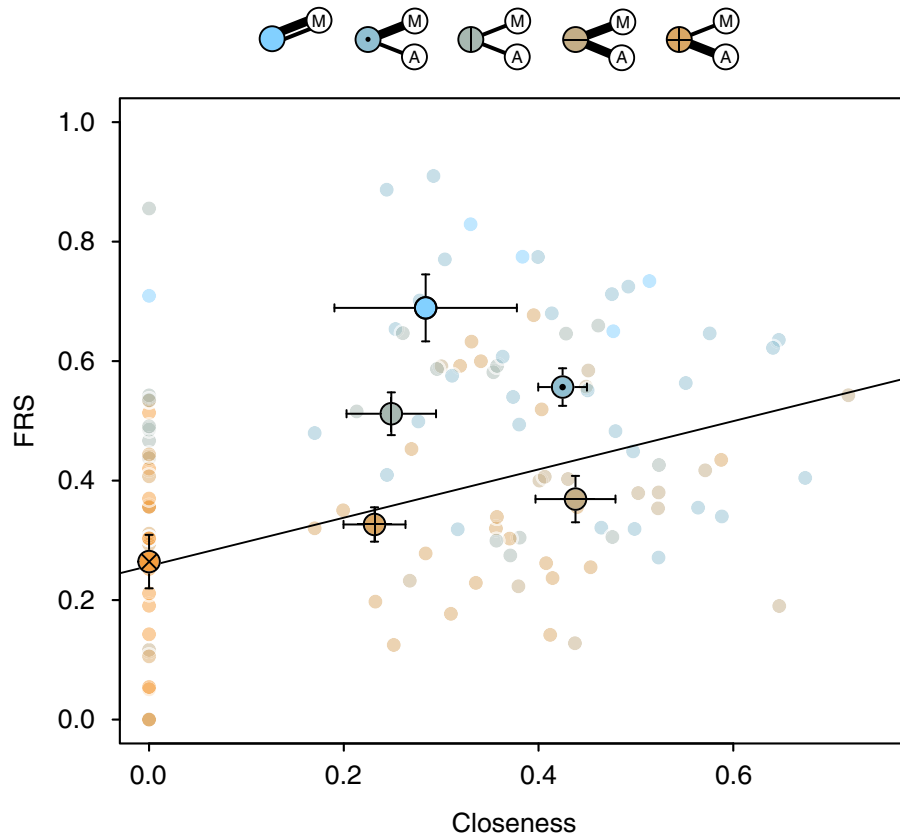


FIG. 4. Relationship between the centrality (closeness) of individual plants in the mating network and associated female reproductive success (FRS). Larger, plotted dots are group means \pm SE per plant-animal interaction typology. Smaller dots at the background represent values of individual plants (total $n = 117$). Model intercept and slope (β coefficient of closeness C) are given in Appendix S6. Averaged means \pm SD of closeness and fitness (C , FRS) per interaction typology: “Only M” ($C = 0.28 \pm 0.23$, FRS = 0.69 ± 0.14); “Strong M–Weak A”: ($C = 0.42 \pm 0.14$, FRS = 0.56 ± 0.17); “Weak M–Weak A”: ($C = 0.25 \pm 0.19$, FRS = 0.51 ± 0.15); “Strong M–Strong A”: ($C = 0.44 \pm 0.16$, FRS = 0.37 ± 0.16); “Weak M–Strong A”: ($C = 0.23 \pm 0.18$, FRS = 0.33 ± 0.17); and “Only A”: ($C = 0$, FRS = 0.26 ± 0.17).

success. In contrast, plants showing strong mutualistic interactions, but also (weak or strong) interactions with antagonists, occupied the most central positions in the mating network (i.e., higher closeness; Figs. 3 and 4). Thus, the presence of antagonistic interactions does not imply reproductive isolation within the mating network, but gives plants the potential to participate in the pollen flow and increase both female and male fitness. Our findings indicate that antagonistic interactions may indirectly promote outcrossing and increased pollen export/reception for individual plants.

The higher closeness values of plants with mixed mutualistic-antagonistic interactions may be due to individual plant characteristics, such as larger floral displays compared to other conspecifics ($P < 0.05$, Appendix S7; see also Gómez and Perfectti 2012, Dupont et al. 2014). These plant traits are especially attractive to both pollinators and antagonists causing conflicting reproductive pressures (Ågren et al. 2013). Here we propose an alternative, non-exclusive, hypothesis: the presence of antagonistic damage enhances plant centrality in the mating

network (Fig. 4). For example, the most central plants with diversified interactions incorporating antagonists (“Strong M–Weak A”, “Strong M–Strong A”) have higher levels of florivory and nectar larceny than less central plants with fully mutualistic interactions (“Only M”), which have no damage at all. Probably attracted by the large floral displays of these central plants, pollinators may detect partial floral damage during the visit, and/or reduced nectar rewards, and probe fewer flowers in less time compared to undamaged plants (Zimmerman and Cook 1985, Irwin and Brody 1998, Irwin 2003). These aspects may force pollinators to move more often among plants (Maloof and Inouye 2000).

Despite the higher closeness values of individual plants with diversified animal assemblages, their reproductive outcomes are lower compared to fully mutualistic typologies (Fig. 4). Female reproductive success is markedly reduced under strong antagonistic interactions, an obvious result if we consider that floral herbivores and seed predators consume pollen grains, ovules and seeds. The effect of antagonists can also reduce female fitness via

pollinators' behavioural changes since they are less frequently visited by pollinators, which probe a lower proportion of flowers and deposit less pollen (Thomson and Plowright 1980, Zimmerman and Cook 1985, Irwin and Brody 1998, Krupnick et al. 1999, Irwin 2003, McCall and Irwin 2006, Carper et al. 2016). However, centrality may enhance plant reproductive success in other aspects not evaluated in the present study. For example, the higher integration of plants in the mating network may lead to increased outcrossing. However, the relationship between floral damage and pollinator visitation is complex and unfortunately, we know relatively little about how antagonists may promote pollen and gene flow (Krupnick et al. 1999, McCall and Irwin 2006, Carper et al. 2016). Thus, future field experiments including paternal analysis of offspring to infer pollen dispersal patterns will shed light on the role of antagonists in pollination.

CONCLUSIONS

This paper aims to better characterize the complexity of plant-animal interactions occurring in natural populations and their functional consequences for plants (Gómez et al. 2011, Gómez and Perfectti 2012). We found extreme variation in interactions with six typologies identified but just 1–2 motifs, with strong effects on individual FRS. We demonstrate the expected decrease in FRS from mutualistic to antagonistic modes along with the unexpected finding that plants with damage are better connected in the mating network via increased pollen transfer/receipt. However, we realise that our results raise new questions that require further research. The question remains, how interaction typologies (and motifs) vary across space and time. The same species may interact in different ways when their local abundances vary, their trait distribution changes, or when the environment affects either of these factors (Siepielski and Benkman 2010, Ågren et al. 2013, Poisot et al. 2015). Secondly, even in the hypothetical situation that interaction typologies were consistent across plant species, whether they render similar reproductive outcomes for species with different breeding systems is unknown. For example, self-compatible plants can overcome strong antagonistic interactions more easily than self-incompatible plants, which might suffer a greater reduction in pollen transfer and seed production with greater damage. Third, further research in other pollination systems is needed to assess under which circumstances antagonistic damage may promote pollen and gene flow (i.e., outcrossing). Our study opens up a new approach to understanding how the building blocks of plant-animal interactions emerge within populations and, through their functional consequences, drive the dynamics of coevolution.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.1756/supinfo>

APPENDIX S1. Species assemblages in the mutualist and antagonist groups

The functional group of mutualists includes three animal guilds: bird and lizard legitimate pollinators, as well as facultative bird pollinators. Antagonists are represented by floral herbivores, nectar larcenists and predispersal seed predators (see Rodríguez et al. 2015 for details).

Table S1.

Functional group	Species	Family
Mutualists		
Legitimate bird pollinators	<i>Phylloscopus canariensis</i>	Phylloscopidae
	<i>Sylvia melanocephala</i>	Sylviidae
	<i>Sylvia atricapilla</i>	Sylviidae
	<i>Sylvia conspicillata</i>	Sylviidae
	<i>Fringilla coelebs</i>	Fringillidae
Facultative bird pollinators	<i>Cyanistes teneriffae</i>	Paridae
	<i>Serinus canaria</i>	Fringillidae
Legitimate lizard pollinators	<i>Gallotia galloti</i>	Lacertidae
Antagonists		
Floral herbivores	<i>Gymnoscelis rufifasciata</i>	Geometridae
	<i>Hypena obsitalis</i>	Noctuidae
	<i>Choristoneura simonyi</i>	Tortricidae
Nectar larcenists	<i>Plagiolepis barbara</i>	Formicidae
	<i>Camponotus hesperius</i>	Formicidae
	<i>Linepithema humile</i>	Formicidae
Predispersal seed predators	NA	cf. Kateritidae
	<i>Rattus rattus</i>	Muridae

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APPENDIX S2. Plant monitoring for mutualists and antagonists.

Within each studied plot, we target all the adult plants ($n= 119$) to obtain frequency and intensity of interaction by mutualists and antagonists. For this, we monitored individual plants every 3-4 days through the flowering period until no open flower remained within each plot (18 June to 15 August 2008) (see Rodríguez-Rodríguez et al. 2015 for details).

The frequency of interaction with mutualists was obtained from two alternative methods: focal and spot censuses. For focal censuses, each individual plant was watched from 9:00 to 21:00 h separately in 30-min periods (range: 25-271 periods/plant). For spot censuses, the observer stood in a corner of the patch at different times of the day and took a visual snapshot of all plant-pollinator interactions occurring within the patch at that moment (range: 25-186 snapshots/plant). With this information, we compiled the total number of focal and spot censuses done for each individual plant, and the frequency of interaction was calculated as the proportion of total censuses in which the pollinator guild visit the individual plant. Besides, we recorded the proportion of flowers probed by the individual pollinator per plant visit in relation to the total number of open flowers on the plant for calculate the intensity of interaction. Then, the interaction strength of each mutualist corresponds to the frequency of interaction multiplied by its intensity.

The frequency and intensity of interaction with antagonists was calculated in different ways depending on the antagonistic guild. For floral herbivores and nectar larcenists we recorded, in each individual plant survey, the number of flowers affected by floral herbivores and the number of inflorescences affected by nectar larcenists. We recorded the effect of nectar larceny at the inflorescence level instead of the floral level because ants, when present, often visit all flowers within the inflorescence. Floral

herbivory was visually identified by the existence of chewing damage on floral reproductive organs, silk/frass remains, corolla holes, and/or caterpillars inside the flower. Nectar larceny was identified by the presence of at least one ant feeding on nectar. The frequency of interaction was recorded for each individual plant as the proportion of surveys in which floral herbivory or nectar larceny were present. In the case of floral herbivores, we estimated the intensity of interaction as the average proportion of damaged flowers relative to the total number of open flowers, calculated across all plant surveys. In the case of nectar larcenists, we estimated the intensity of interaction to be the average proportion of inflorescences with presence of ants with respect to the total number of inflorescences, calculated across all plant surveys.

In the case of predispersal seed predators, we obtained infestation data from harvested fruits at the end of fieldwork. We chose a subset of 3-23 fruits/plant identified those that were infested. Fruit infestation was visually recognized by the presence of larvae (dead or alive), frass remains, partially consumed seeds, and/or holes in the capsule. Then, we estimated the proportion of viable seeds consumed by seed predators in respect of the initial number of viable seeds produced by the fruit. For this, we defined the proportion of viable seeds consumed by seed predators (P_{sc}) in the infested fruits as $P_{sc} = (S_i - S_r) / S_i$, where S_i is the initial number of viable seeds produced by the fruit, and S_r the number of remaining viable seeds after larvae predation. The estimation of P_{sc} was done in three steps. First, we separated the infested fruits in the focal plant (total $n = 185$ fruits from 71 plants) from the uninfested ones, and counted the number of remaining viable seeds within the infested fruits (S_r). Second, we estimated the initial number of viable seeds present in the fruit before predation (S_i) by linear regression. For this, we used data only from uninfested fruits produced by those plants that interacted with seed predators, instead of data from all studied plants. This

procedure avoided bias in the estimation of S_i caused by mother plant effects. Specifically, we fit a zero-inflated model with the number of viable seeds per uninfested fruit as response variable, and fruit width as explanatory variable (negative binomial family, log link function). After model fitting, we predicted S_i for the infested fruits substituting their respective values of fruit width into the regression equation. Third, we estimated P_{sc} using the above-mentioned formula after obtaining S_i and S_r values. Once the levels of infestation in the field were determined, we obtained “simulated surveys” by resampling the data associated with the collected fruits (infested and non-infested) from the same plant: presence/absence of fruit predation, accompanied by the respective proportion of viable seeds consumed. The resample was repeated as many times as the number of real periodical surveys done on the plant, and each simulated survey contained the same number of harvested fruits per plant. For each simulated survey, we calculated the proportion of infested fruits and the average proportion of seeds consumed per fruit. At the end, and calculated across all the surveys, we defined the frequency of interaction as the average proportion of infested fruits, and the intensity of interaction as the average proportion of viable seeds consumed per fruit (see Rodríguez-Rodríguez et al. 2015 for details).

The sequences of interplant movements by birds were obtained from direct observations during plant monitoring from 0900 to 2100, yielding a total of 257h over 34 days (18 June – 4 August 2008). We located at patch corners to minimize the impact on pollinator behaviour and waited until a bird arrived. Once the bird began to feed on nectar, we started to record the sequence of visited plants, including only those plants in which the bird probed at least one flower and contacted with floral reproductive organs (i.e. legitimate visits). The count of mating events was done in a ‘cumulative’ way. That is, we assumed that previously visited plants could act as pollen donors of subsequently

visited plants, despite not being directly connected by bird flights. For example, if an individual bird visited three plants in the following order: *A*, *B*, and *C*, we counted a total of three mating events instead of two. Thus, the first visited plant *A* acted as pollen donor for plants *B* and *C*; and the second visited plant *B* acted as donor for plant *C*.

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APPENDIX S3. Estimation of plant traits and their correlation with female reproductive success (FRS)

Methods

Estimation of plant traits

For each individual plant, we estimated five traits related with floral phenotype, local neighbourhood and microhabitat. To characterize floral phenotype, we measured plant height, nectar sugar reward produced in the flowers, and the level of flowering synchrony with conspecifics. Local neighbourhood was estimated by counting the number of *I. canariensis* plants in a radius of 2 m, and plant microhabitat by the distance to the nearest tree.

We chose these variables for the following reasons: (1) they influence interactions with animal mutualists and antagonists and subsequent plant reproduction in multiple systems (e.g. Heithaus *et al.* 1982; Hainsworth *et al.* 1984; Herrera 1993; Cariveau *et al.* 2004; Irwin *et al.* 2004; Elzinga *et al.* 2007), (2) they are spatially associated with female reproductive success (FRS) of *I. canariensis* (see the section *Spatial association between plant traits and plant reproductive success* below), and (3) these traits may have a direct effect on FRS, independently from their influence on mutualistic and antagonistic plant-animal interactions. In our study species, this influence could be important because *I. canariensis* is self-compatible and does not depend strictly on pollinators for seed production (Rodríguez-Rodríguez & Valido 2008).

Plant height (cm) was measured as the distance from plant base to the tip of the highest inflorescence. This biometric trait was used as a surrogate of floral display because it was positively correlated with the number of inflorescences (Spearman's rank

correlation, $r_s = 0.69$, $P < 0.001$) and total number of floral pedicels ($r_s = 0.61$, $P < 0.001$).

Nectar sugar reward was defined as the product of nectar volume and sugar concentration. For its estimation, we selected a subset of flowers located at basal positions in the inflorescences that we depleted and bagged during 24h ($n = 780$ flowers, range: 5-31 flowers/plant). In each flower, we used 50- μ L microcapillary tubes to probe the corolla base until no more nectar could be removed. Then, we measured with dial callipers the distance nectar had migrated up the tubes and converted it to volumes (μ L). To record sugar concentration (w/w% of sugar equivalents), we spotted the nectar within the tubes on a handheld refractometer (Bellingham & Stanley Ltd, Tunbridge Wells, Kent, UK). Calculated over all flowers analysed in the plant, we defined nectar volume as the average number of microliters produced per flower (μ L/flower), and nectar sugar concentration as the average percentage of sugar per flower (w/w% sugar/flower).

Flowering synchrony was estimated for any given plant in relation to coflowering conspecifics from the same patch. We used the Synchrony Index X_i (modified from Augspurger 1983), defined as follows:

$$X_i = (1/n-1) * (1/f_i) * \sum_{j=1}^n e_{j \neq i}$$

where n was the number of conspecific plants in the patch, f_i the number of plant surveys individual i was flowering, and e the number of plant surveys in which both individuals i and j were flowering synchronously $j \neq i$.

Local neighbourhood was defined as the number of conspecifics in a radius of 2 m (*spatstat* package in R, Baddeley & Turner 2005). We chose this distance because the majority of interplant movements made by passerine birds, the most frequent pollinators

of *I. canariensis*, were 100-200 cm long in the study area (median: 196 cm), which exceed the average distance to the nearest plant neighbour (70.3 ± 66.4 cm, further details in Rodríguez-Rodríguez *et al.* 2015).

Finally, we characterized plant microhabitat by measuring the Euclidean distance between the individual plant and its nearest tree (cm). We used this distance as a surrogate of the proximity to forest canopy, which determines a decreasing gradient of sunlight exposure and predation risk for interacting animals. For example, lower temperatures under forest canopy may determine reduced interaction frequencies between those plants close to the forest and ectothermic lizards (e.g. García *et al.* 2007).

Spatial association between plant traits and female reproductive success (FRS)

We tested if plant traits were spatially associated with FRS by spatial point pattern analysis with *Programita* software (Wiegand & Moloney 2004, 2014). To do this, we firstly mapped all the reproductive plants to the nearest centimetre by laying out two perpendicular measuring tapes to record the X- and Y-coordinates in each studied patch. Secondly, we created a data set per replicate patch, which included plants as a series of mapped point locations, and the estimated variables as quantitative marks assigned to each point: the five plant traits and FRS.

Conditionally on plant distribution, we then analysed the spatial association of the respective plant trait with FRS using bivariate mark correlation functions (Illian *et al.* 2008). We chose the Schlather's Index $I_{m_1m_2}(r)$ as the summary statistic for the correlations, which is a non-cumulative second-order statistics (Schlather *et al.* 2004; Wiegand & Moloney 2014). The rationale of this statistic is the following: all pairs of plants separated by distances within a specific interval ($r - dr/2$, $r + dr/2$) are determined, being dr the ring width. For each pair of plants, indexed by k , we have a

corresponding pair of marks (m_{k_i}, m_{k_j}) where m_{k_i} is the mark of the first plant i and m_{k_j} that of the second plant j . Schlather's I is then the Pearson correlation coefficient of the two variables m_{k_i} and m_{k_j} , taken over all k pairs at the distance r . The correlation coefficient is then estimated for different distances r to obtain the final functional summary statistics $I(r)$. In the bivariate analysis, the values of m_{k_i} and m_{k_j} values are taken from two different marks in two different plants (e.g. plant height of plant i and FRS of plant j). A value of $I_{m_1 m_2}(r) \sim 0$ would indicate there is absence of spatial autocorrelation among the marks m_1 and m_2 . In contrast, a value of $I_{m_1 m_2}(r) > 0$ would indicate mutual stimulation, and a value of $I_{m_1 m_2}(r) < 0$ would indicate mutual inhibition. In all spatial analyses, we normalized the mark correlation function with the mark variance to make it independent of the distribution and values of the marks (Wiegand & Moloney 2014). The normalization factor was represented by the covariance of the marks σ_{12} that belong to two different variables.

Independently of the plant trait analysed, we took into account that $r < 1/2$ length of the shortest side of the study patch (patch 1, max $r = 500$ cm), and estimated the summary statistics at distance bins of 10 cm and ring width of $dr = 110$ cm. The bin value indicates the interval of distances at which the summary is calculated from the focal point. We selected this value of ring width to assure a minimum of 30 plant pairs per distance class for each individual patch.

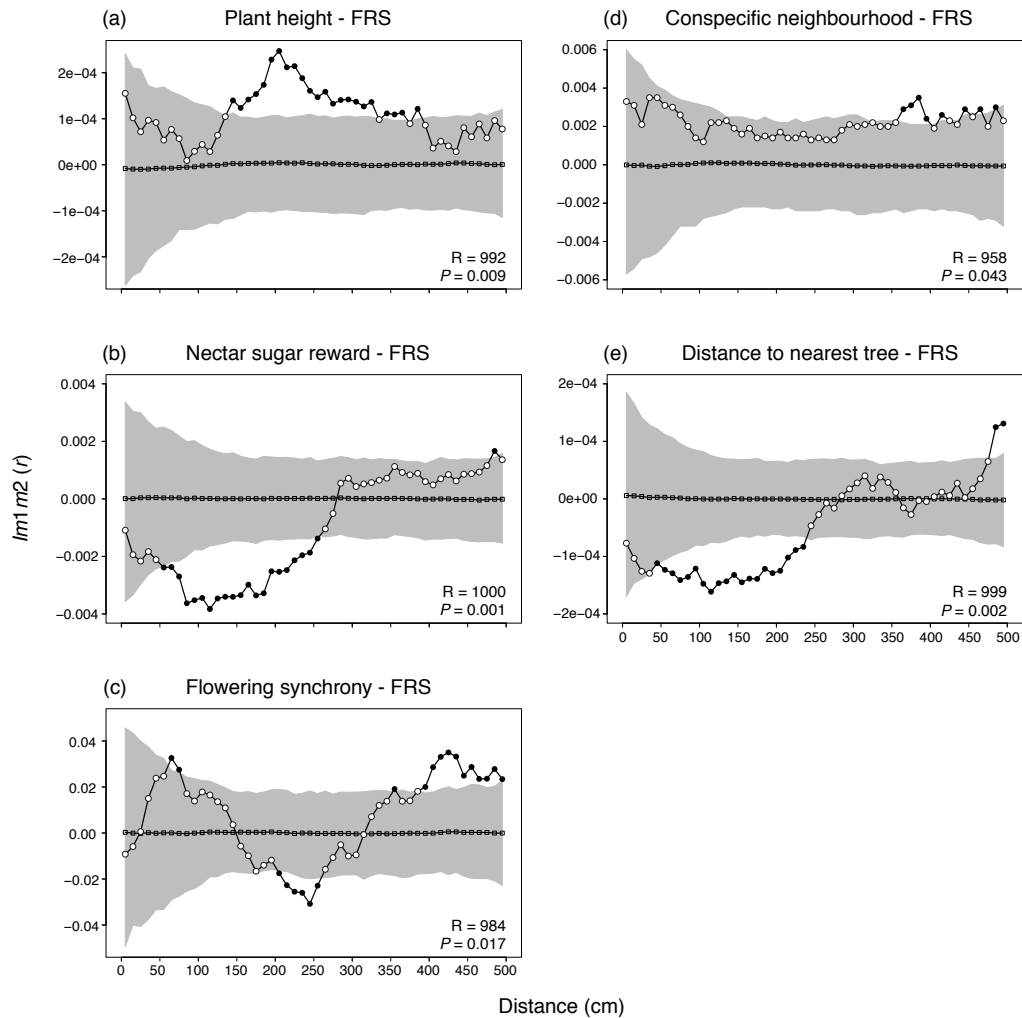
We calculated the summary statistic per patch and combined the results from the two patches into a mean, weighted value (see formula for combination in Wiegand & Moloney 2014). The empirical values for each statistic were compared with theoretical values from the chosen null expectation following Monte Carlo simulation. We chose the null model of *independent marking*, which shuffles the marks independently and randomly among all plant locations (Wiegand & Moloney 2014). Significance was

assessed by comparing the observed data with simulation envelopes from 999 simulated patterns of the null model ($P = 0.05$). Since we simultaneously tested the null hypothesis at several scales of distance r , we used a Goodness-of-Fit (GoF) test that collapses the scale-dependent information contained in the test statistics into a single index u_i to avoid Type I error inflation (Loosmore & Ford 2006). There is a significant departure from the null model when the rank of the index of the observed pattern u_0 is > 950 with $\alpha = 0.05$ among all u_i .

Results

Bivariate mark correlation analysis with Schlather's Index $I_{m1m2}(r)$ between female reproductive success (FRS) and the estimated plant traits: (a) plant height, (b) nectar sugar reward, (c) flowering synchrony, (d) conspecific neighbourhood, and (e) plant microhabitat (see figure below). Dots, mean-weighted summary statistic of the data; black squares, expectation under the null model; and grey shading, simulation envelopes marking the 25th lowest and highest values taken from 999 simulations of the null model. Black dots indicate statistical difference from the null model ($P < 0.05$), and R and P values indicate, respectively, the rank of the index of the observed pattern and the statistical significance of the Goodness-of-Fit (GoF) test.

Fig. S1



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APPENDIX S4. Relationship between plant-animal interaction typology and female reproductive success (FRS).

Table S1A. Post-hoc pairwise comparisons of regression coefficients among interaction typologies from the full model. s.e. Standard error. Code for statistical significance: * P , <0.05; ** P , <0.01; *** P , <0.001.

	Estimate ± s.e.	t value	P value	
‘Only A’ – ‘Only M’	-0.407 ± 0.081	-5.011	< 0.001	***
‘Weak M - Weak A’ – ‘Only M’	-0.157 ± 0.077	-2.031	0.321	
‘Strong M – Weak A’ – ‘Only M’	-0.131 ± 0.076	-1.727	0.506	
‘Weak M – Strong A’ – ‘Only M’	-0.337 ± 0.075	-4.489	< 0.001	***
‘Strong M – Strong A’ – ‘Only M’	-0.289 ± 0.081	-3.566	0.007	**
‘Weak M - Weak A’ – ‘Only A’	0.249 ± 0.060	4.165	< 0.001	***
‘Strong M – Weak A’ – ‘Only A’	0.275 ± 0.060	4.627	< 0.001	***
‘Weak M – Strong A’ – ‘Only A’	0.069 ± 0.052	1.323	0.763	
‘Strong M – Strong A’ – ‘Only A’	0.118 ± 0.065	1.819	0.447	
‘Strong M – Weak A’ – ‘Weak M - Weak A’	0.026 ± 0.051	0.507	0.996	
‘Weak M – Strong A’ – ‘Weak M - Weak A’	-0.180 ± 0.049	-3.668	0.005	**
‘Strong M – Strong A’ – ‘Weak M - Weak A’	-0.131 ± 0.058	-2.279	0.203	
‘Weak M – Strong A’ – ‘Strong M – Weak A’	-0.206 ± 0.046	-4.439	< 0.001	***
‘Strong M – Strong A’ – ‘Strong M – Weak A’	-0.157 ± 0.052	-3.042	0.032	*
‘Strong M – Strong A’ – ‘Weak M – Strong A’	0.049 ± 0.054	0.911	0.940	

Table S1B. Summary of the generalized linear regression model showing the effects of different interaction typologies (mutualists, antagonists; Fig. 1b) and plant traits on female reproductive success (FRS). FRS was estimated as the product of the proportion of fruits produced per plant and the averaged proportion of viable seeds per fruit (see *Methods: Female reproductive success*). Significance of regressors was tested by likelihood ratio tests. Significance: ***, $P < 0.001$.

	d.f.	Deviance	<i>P</i> value
Full model	116	21.624	-
Model without interaction typology	8	-5.300	< 0.001***
Model without plant height	12	-0.134	0.28
Model without nectar sugar reward	12	-0.015	0.75
Model without flowering synchrony	12	-0.016	0.71
Model without conspecific neighbourhood	12	-0.036	0.58
Model without distance to nearest tree	12	-0.065	0.456
Model without patch	12	-0.316	0.097

APPENDIX S5.- Relationship between interaction strengths (both mutualistic and antagonistic) and FRS with respect to interaction typologies.

Interaction typologies are a categorical summary of the quantitative, continuous, outcomes of diversified interactions with antagonistic and mutualistic taxa. Such a quantitative typification of distinct interaction typologies based on the sign (mutualistic vs. antagonistic) and strength (weak vs. strong) of animal-plant relationships helps summarize the broad diversity of interaction “modes” occurring in nature, very often showing extreme complexity. Here we report the analyses of covariation between FRS and interaction strengths of the two groups: mutualists, antagonists (Table S1), and summarize the mean strength value associated for each taxon to each type of interaction categorized by the typologies (Table S2). Interaction typologies effectively capture the quantitative variation of interaction strengths, illustrate the ample diversity of interaction modes, and provide a link with the mating network patterns we examine (Figs. 3 and 4). In this way, the variation across interaction typologies (Fig. 2) can be compared with the continuous, quantitative effects of animal partners.

Table S1. Summary of the generalized linear regression model showing the effects of different functional groups (mutualists, antagonists; S1A) and different species and taxa (S1B) on female reproductive success (FRS). FRS was estimated as the product of the proportion of fruits produced per plant and the averaged proportion of viable seeds per fruit (see *Methods: Female reproductive success*). Significance of regressors was tested by likelihood ratio tests (see Appendix S4: Table S1B). The relative importance of effects for different taxa was estimated with the *relaimpo* package in R (see *Methods* for

details). Significance: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. See Appendix S1 for details of species assemblages and Fig. 1 for sample sizes for each interaction typology.

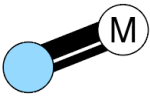
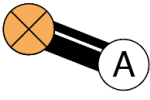
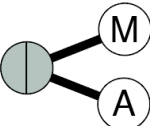
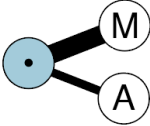
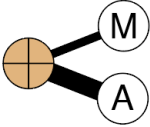
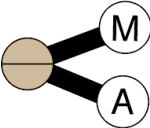
Table S1A. Functional groups.

Regression coefficients	Estimate \pm s.e.	t value	P value	% Effect
Intercept	-0.359 \pm 0.074	-4.85	< 0.001***	-
Mutualists	0.076 \pm 0.079	0.96	0.341 ^{NS}	20.73
Antagonists	-0.491 \pm 0.087	-5.66	< 0.001***	68.85
Interaction MxA	-0.296 \pm 0.136	-2.18	< 0.05*	10.42

Table S1B. Species and taxa. See Appendix S1.

Regression coefficients	Estimate \pm s.e.	t value	P value	% Effect
Intercept	-0.295 \pm 0.068	-4.35	< 0.001***	-
<i>P. canariensis</i>	0.119 \pm 0.069	1.73	0.086	10.97
<i>C. teneriffae</i>	0.198 \pm 0.072	2.76	0.007**	17.22
<i>G. galloti</i>	0.131 \pm 0.076	1.72	0.089	6.95
Floral herbivores	-0.301 \pm 0.075	-4.01	< 0.001***	39.83
Nectar larcenists	-0.166 \pm 0.076	-2.17	0.032*	9.67
Predispersal seed predators	-0.151 \pm 0.076	-1.99	0.049*	15.36

Table S2. Average values (\pm s.d.) of interaction strengths with different types of mutualists and antagonists according to interaction typologies.

Interaction typology	Mutualists		Antagonists	
	Species	Interaction strength	Taxa	Interaction strength
	<i>P. canariensis</i>	0.079 ± 0.0066	Florivores	0 ± 0
	<i>C. caeruleus</i>	0.014 ± 0.0020	Nectar larcenists	0 ± 0
	<i>G. galloti</i>	0 ± 0	Seed predators	0 ± 0
	<i>P. canariensis</i>	0 ± 0	Florivores	0.1309 ± 0.1562
	<i>C. caeruleus</i>	0 ± 0	Nectar larcenists	0.0045 ± 0.0167
	<i>G. galloti</i>	0 ± 0	Seed predators	0.1255 ± 0.1911
	<i>P. canariensis</i>	0.0019 ± 0.0014	Florivores	0.0638 ± 0.0697
	<i>C. caeruleus</i>	0.0001 ± 0.0002	Nectar larcenists	0.0232 ± 0.0152
	<i>G. galloti</i>	0.003 ± 0.005	Seed predators	0.0268 ± 0.0461
	<i>P. canariensis</i>	0.0089 ± 0.0056	Florivores	0.0493 ± 0.0537
	<i>C. caeruleus</i>	0.0005 ± 0.0011	Nectar larcenists	0.0049 ± 0.0140
	<i>G. galloti</i>	0.0005 ± 0.0017	Seed predators	0.0390 ± 0.0557
	<i>P. canariensis</i>	0.0018 ± 0.0012	Florivores	0.3132 ± 0.1674
	<i>C. caeruleus</i>	0.0003 ± 0.0006	Nectar larcenists	0.0273 ± 0.0645
	<i>G. galloti</i>	0.0003 ± 0.0006	Seed predators	0.1191 ± 0.1351
	<i>P. canariensis</i>	0.0089 ± 0.0102	Florivores	0.2553 ± 0.1829
	<i>C. caeruleus</i>	0.0003 ± 0.0006	Nectar larcenists	0.0087 ± 0.0180
	<i>G. galloti</i>	0.0001 ± 0.0003	Seed predators	0.1219 ± 0.1297

APPENDIX S6. Relationship between the centrality of plants in the mating network and female reproductive success (FRS)

Table S1. Summary of the linear regression model (GLM) showing the effects of plant centrality, patch identity and standardized (z scores) plant traits on FRS. Plant centrality was estimated in terms of closeness (see *Methods: Mating consequences of interaction typologies* in the article). Code for statistical significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

	Estimate \pm s.e.	<i>t</i> value	<i>P</i> value	
Intercept	-1.099 \pm 0.306	-3.60	< 0.001	***
Closeness	0.368 \pm 0.095	3.88	< 0.001	***
Plant height	-0.174 \pm 0.084	-2.08	0.041	*
Nectar sugar reward	0.069 \pm 0.043	0.93	0.35	
Flowering synchrony	-0.055 \pm 0.089	-0.62	0.54	
Conspecific neighbourhood	0.101 \pm 0.094	1.07	0.28	
Distance to nearest tree	-0.188 \pm 0.086	-2.19	0.031	*
Patch	0.561 \pm 0.206	2.73	0.007	**

Table S2. Significance of fixed effects by means of likelihood ratio tests. We compared the full model with six regressors (full model) and without the effects on FRS of plant centrality, plant traits, and the identity of the replicate patch. d.f., degrees of freedom. Code for statistical significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

	d.f.	Deviance	<i>P</i> value
Full model	116	21.62	-
Model without closeness	110	-2.120	< 0.001 ***
Model without plant height	110	-0.598	0.037 *
Model without nectar sugar reward	110	-0.119	0.35
Model without flowering synchrony	110	-0.053	0.54
Model without conspecific neighbourhood	110	-0.159	0.28
Model without distance to nearest tree	110	-0.668	0.028 *
Model without Patch	110	-1.030	0.006 **

APPENDIX S7. Comparison of plant characteristics among interaction typologies depending on their closeness centrality

Methods

We tested for differences between interaction typologies with high ('Strong M – Weak A', 'Strong M – Strong A', labelled as 'high') and low closeness centrality ('Only M', 'Weak M – Weak A', 'Weak M – Strong A', 'Only A', labelled as 'low') in (a) plant height, (b) nectar sugar reward, (c) flowering synchrony, (d) conspecific neighbourhood, and (e) plant microhabitat by generalized linear regression (GLM). In each model, we included the respective plant trait as the response variable and plant-animal interaction typology as the explanatory variable. We used Gaussian family and identity link function for all plant traits, except for conspecific neighbourhood (quasipoisson family, log link function). Response variables were logarithmic (plant height, nectar sugar reward), quadratic (plant microhabitat), and arcsine (flowering synchrony) transformed when necessary.

Results

Plants with high centrality were taller ($t = -2.85$, $P < 0.01$) and less synchronized with their co-flowering conspecifics ($t = 3.87$, $P < 0.001$) compared to less central plants. However, both groups were similar in the rest of plant traits ($P > 0.05$ in all cases) (see figure below; dots and lines represent mean \pm SE of plant traits, respectively).

Fig. S1.

