

Individual-based plant–pollinator networks are structured by phenotypic and microsite plant traits

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Abstract

1. The biotic and abiotic context of individual plants within animal-pollinated plant populations can influence pollinator foraging behaviour. Pollinator movements regulate pollen flow among plant individuals, and ultimately determine individual plant reproductive success. Yet the underlying drivers of this context dependency of interactions at the population level and their functional consequences for individuals remain poorly known.
2. Here we used a well-characterised population of *Halimium halimifolium* (Cistaceae), a Mediterranean shrub species, in combination with exponential random graph models (ERGMs) to evaluate how the intrapopulation variation in plant attributes configures individual-based plant–pollinator networks and determines their reproductive outcomes. Specifically, we assessed (a) how the intrinsic (i.e. phenotype and phenology) and extrinsic (i.e. microsite) plant attributes influenced the emerging configuration of the bipartite plant–pollinator network and the unipartite plant–plant network derived from pollinator sharing, and (b) how these plant attributes combined with the network topological position of individual plants affect their female fitness, measured as the total seed weight per plant.
3. We found that both intrinsic and extrinsic plant attributes contributed substantially to explain the configuration of both the bipartite and the unipartite pollination network. Besides the effects of plant attributes, the functional group to which pollinator species belonged was also important to determine the variance in plant–pollinator interaction odds, while the probability of plants to share more pollinator species was additionally influenced by the spatial distance between those plants. Furthermore, our results showed that these influences of plant attributes on network structure can be translated into functional outcomes at the plant individual level, with direct consequences for intrapopulation fitness variation.
4. *Synthesis*. This study builds towards a better understanding of the multiple drivers underlying the context dependency of plant–pollinator interactions and how they mediate the reproductive outputs of individual plants within a population. The application of our analytical framework allows a conceptual shift from descriptive to

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predictive research on the evolutionary and ecological processes that give rise to complex ecological networks at the population level.

KEYWORDS

Doñana, ecological networks, *Halimium halimifolium*, intraspecific variation, mutualism, plant fitness, plant–pollinator interactions

1 | INTRODUCTION

The foraging movements of pollinators influence how pollen transfer occurs among animal-pollinated plant individuals within a population (Morris et al., 1995), ultimately influencing their reproductive outputs. Within a generalist pollination system, a plant population is usually composed of individuals differing in their level of pollinator attraction, and therefore, the pollinators visiting a given plant are a subset of the pool of potential pollinators (Gómez et al., 2007; Herrera, 2005). These inter-individual differences in the pollinator assemblage of individual plants partially contribute to generate non-random patterns of pollen transfer events (Valverde, 2017), which may affect population dynamics and the local structuring of genetic diversity through a network of assortative mating events.

Individual plants within most populations differ in their phenotype and this variation among plants (e.g. in plant and flower size or flowering phenology) may cause differences in their pollination niche due to distinctive preferences by different pollinator guilds (Gómez et al., 2014). Therefore, individual plants displaying similar phenotypes are expected to interact with a similar pollinator assemblage, promoting mating events among those plants (Gómez et al., 2011). Furthermore, dissimilarities in phenological patterns among pollinator species may create temporal variation in pollinator availability, leading to differences in the pollinator assemblage interacting with plants diverging in flowering phenology (Fox, 2003; Primack, 1985). On one hand, individual plants with higher flowering synchrony within their population are expected to share pollinators with more conspecifics; but, on the other hand, they may also interact with fewer pollinators due to intraspecific competition. Thus, a higher flowering synchrony among conspecifics can influence the level of pollinator sharing and therefore, increase intrapopulation assortativity in mating (Weis, 2005).

Variation in the pollinator niche among individual plants may also be influenced by their spatial position in the population (Rodríguez-Rodríguez et al., 2017). The spatial position defines the ecological context of plants, such as the microtopographical conditions and the local plant community to which they are exposed (e.g. intraspecific and interspecific competition), generating different aspects of context dependency of interaction outcomes (Chamberlain et al., 2014). Because pollinator species may tend to forage in specific microsites, the fine-scale location of individual plants within a population is expected to affect their interactions with pollinators and consequently, the patterns of pollinator sharing among conspecific plants (Rodríguez-Rodríguez et al., 2015). Most plant–pollinator interaction studies do not address this spatial component, which might entail

important constraints given the fine-scale division of resources among insect pollinators in a plant population (Dupont et al., 2014) and the spatial heterogeneity in neighbourhood composition (Janovský et al., 2013).

Plant–pollinator communities have been widely studied during the last decades using bipartite interaction networks (Bascompte & Jordano, 2007), where pollinator species are connected to the plant species they visit. However, species-based networks overlook the existing intraspecific variation by pooling all the individuals in a single group (Dupont et al., 2014; Tur et al., 2015). In contrast to the community-level approach, individual-based networks can be used to unveil processes at the population level (e.g. Rodríguez-Rodríguez et al., 2017; Soares et al., 2021; Valverde et al., 2016) and convey a direct link to analyse demographic and evolutionary questions. In a bipartite, individual-based network within a plant population, pollinator species are connected to the individual plants they visit. When it is projected into a unipartite network, individual plants are visualised as nodes and the links connecting those nodes depict the level of pollinator sharing, which may serve as a proxy of mating probabilities (Fortuna et al., 2008). Thus, the unipartite network generated with this procedure is undirected, in contrast with real pollen-transfer networks. This undirected unipartite network allows us to elucidate how interactions and hence, potential mating events, are structured within a plant population.

Because intrapopulation variation in phenotype, phenology and microsite may determine how individual plants interact with pollinators, it is expected to also affect the relative position of those plants within the unipartite network. While there are clear hypotheses suggesting that plants occupying central positions may benefit from a higher level of pollinator sharing with conspecifics, increasing the probability of mating events and hence their reproductive success (Gómez & Perfectti, 2012; Soares et al., 2021), it is not trivial how to translate network topologies into functional implications. Recently developed exponential random graph models (ERGMs) allow us to evaluate how plant attributes influence the configuration of complex networks, advancing their study from descriptive metrics into a more cohesive predictive framework (Harris, 2014). Such analyses are useful to test hypotheses about processes that shape networks by modelling the probability of interaction establishment as a function of the characteristics of individuals (nodes) and the value of other links within the network (Snijders et al., 2010). ERGMs differ from traditionally used descriptive approaches in that it encourages and supports identifying underlying mechanisms that explain the whole structure of the network. Although this analytical tool has been widely used in social network studies in recent years, it

has rarely been considered for ecological network analysis (but see Miguel et al., 2018).

Here we aim to investigate how the intrapopulation variation in intrinsic (i.e. phenotype and phenology) and extrinsic (i.e. microsite) plant attributes shapes the structure of individual plant–pollinator networks and influences their functional outcomes (Figure 1). To address this question, we recorded individual plant–pollinator interactions in a population of the Mediterranean shrub *Halimium halimifolium* (Cistaceae). First, we assessed how the intrinsic and extrinsic plant attributes influenced the emerging configuration of the bipartite plant–pollinator network and the unipartite plant–plant network derived from pollinator sharing. Second, to evaluate how this association between plant attributes and network structure translates into functional outcomes, we analysed how individual female plant fitness (i.e. the total seed weight per plant) was affected by the combination of plant attributes and the topological position of individual plants within the pollination network.

2 | MATERIALS AND METHODS

2.1 | Study site

The study was performed in Doñana National Park (37°07'52.2"N 6°31'40.9"W, 12 m a.s.l.) within a 1.2 ha area bounded on its four sides by a stream, pine forests and semi-natural grasslands. Doñana National Park is located on the Atlantic coast of southwestern Spain, in an area with a Mediterranean-type climate where the vegetation is composed mainly of sclerophyllous shrublands. *Halimium*

halimifolium (Cistaceae) is a Mediterranean shrub that occupies the slopes of stabilised sand dunes (Díaz-Barradas & García-Novo, 1987) and usually blooms in late spring (May–June; Herrera, 1988) when all other co-occurring plant species have finished their flowering season. The study site is largely dominated by this plant species, which represents nearly 60% of the total vegetation cover. Although other plant species are also present in our study area (Figure S2), *H. halimifolium* was the only species in flower during the study period. Hence, we did not consider competition or facilitation for pollinators among the different plant species. Each *H. halimifolium* plant can produce up to 1,000 hermaphrodite yellow flowers (Figure S1) at once and flower opening occurs synchronously each day in the population. Flowers usually exhibit a conspicuous dark brown spot at the base of each petal, being the presence and size of these spots highly variable among individuals within populations (Figure S1). Although these dark spots have not yet been proven to act as floral guides in *H. halimifolium*, this kind of petal marks is widely recognised to enhance pollinator attraction in multiple plant species from a wide range of families (de Jager et al., 2017). As this plant species is self-incompatible and cannot reproduce asexually, cross-pollination promoted by insect visitation is necessary to complete seed production and allow population persistence (Talavera et al., 1997).

2.2 | Sampling

We conducted surveys to record pollinator visitations in the study site during the peak flowering period of *H. halimifolium* (25 days between May and June 2019). Prior to data collection, all individual

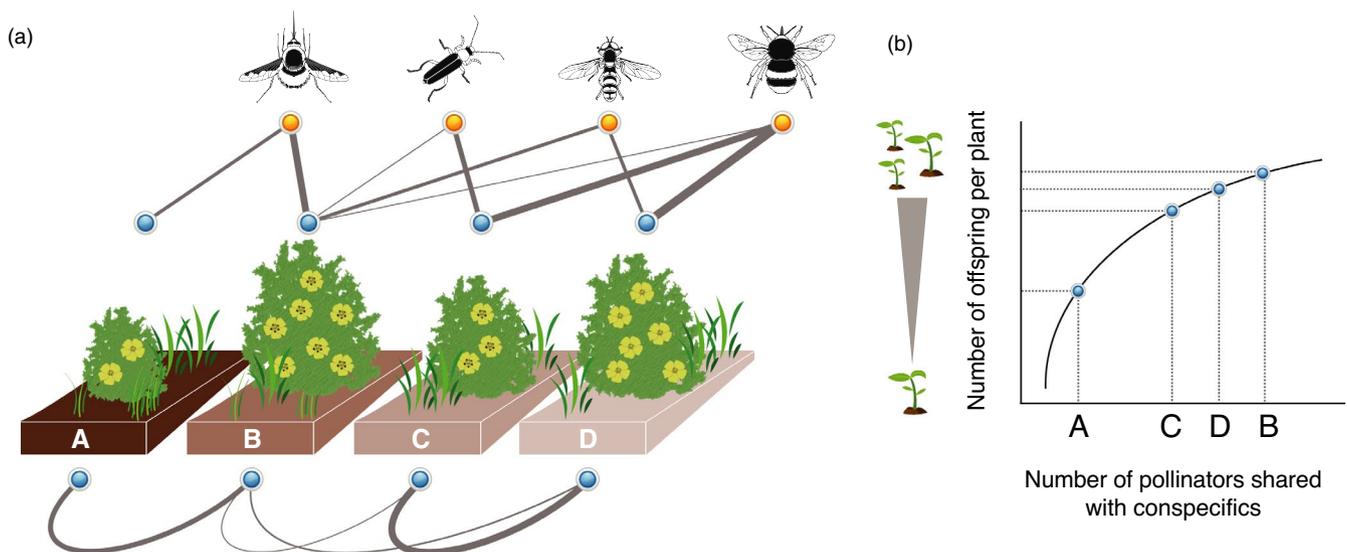


FIGURE 1 Conceptual diagram illustrating the relationship between the bipartite and the unipartite individual plant–pollinator networks (a) and its consequences for plant reproductive success (b). We use a minor, simplified, set of plant traits to illustrate that individual plants differ in phenotypic traits (e.g. size, number of flowers and presence of flower guides) and microsite characteristics (e.g. different ground colour tones). (a) Links in the bipartite network represent the number of visits from each pollinator species to each individual plant (top), while links in the unipartite network depict the number of pollinator visits shared between each individual plant pair (bottom). (b) The number of offspring per individual plant is expected to increase with the number of pollinator visits shared with other individual plants, as it increases the chances of being involved in pollen transfer and, eventually, in mating events. Pollinator icons were obtained from www.divulgar.net

plants of the population (160 individuals) were labelled. Interactions with pollinator species were recorded in 60 of those individuals, which were selected using a stratified random sampling where both isolated and aggregated plants were well represented (Figure S3). Along the study period, we performed four 30-min surveys on each individual plant using video cameras (GoPro HERO7, GoPro Inc.). Therefore, each of the 60 labelled plants was surveyed for 120 min across the flowering season, and thus, the entire survey lasted 7,200 min. Prior to each of these four surveys per individual plant, we recorded the total number of open flowers. To avoid within-day temporal bias in the pollinator assemblage sampling, these four surveys per plant were carried out at different times during the time period with open flowers (8:30 to 13:30), spanned out across four different sampling days. This sampling period encompasses the time of the day where the maximum activity of flower visitors to *H. halimifolium* occurs (Talavera et al., 1997). We assessed the completeness of sampling effort by calculating Chao asymptotic estimators (see Appendix S1 and Figure S4). Video cameras were placed approximately 30 cm away from the plant in each survey and therefore the number of flowers in view [35.21 ± 5.40 (mean \pm SE)] depended on the flower abundance of those plants. To capture the variability in pollinator visits associated with the heterogeneous distribution of flowers within plants, cameras were set up at varying heights in each of the four surveys (range 20 to 180 cm tall).

Video recordings were processed to annotate the identity of pollinator morphospecies visiting all the flowers in view and the number of times they interacted with those flowers (i.e. frequency of interactions). Pollinators were considered as all those insects landing on the flower and touching its reproductive structures. To facilitate pollinators' identification, a single representative specimen of each pollinator morphospecies present in the study site was captured in the field when possible, identified and vouchered at Estación Biológica de Doñana. Out of all pollinator morphospecies, 12 were identified at the species level, seven at the genus level, and only two at the family level. Independent surveys in our study area show that only one to three species with very similar morphology and behaviour occur within each of the lumped genera or families (Table S3). Besides, for the pollinator genera that performed most of the interactions, that is, *Lasioglossum* spp. (Hymenoptera: Halictidae), *Dasypoda* spp. (Hymenoptera: Melittidae) and *Mylabris* spp. (Coleoptera: Meloidae), only one species was identified with these independent surveys. For simplicity, we refer to these pollinator morphospecies as species hereafter.

In order to characterise the plant–pollinator interaction assemblage, we first constructed a weighted bipartite network linking each individual plant with the pollinator species visiting its flowers. This individual-based network was built by creating an adjacency matrix A , where elements a_{ij} represent the number of interactions between the pollinator species i and the individual plant j . The number of interactions was calculated as the total number of times a pollinator species visited any flower of a given plant, and hence interaction data were analysed as the total number of visits. Second, to depict the pattern of shared pollinator species among plants, we generated

the unipartite projection of matrix A by calculating the number of interactions shared by any two individual plants. The unipartite projection of matrix A for the P plants contains the parallel minimum of the observed interactions between two individual plants, so that the level of pollinator sharing is driven by the lowest communality in interactions with pollinator species. In this unipartite network, two individual plants are linked if they share at least one interaction with the same pollinator species. Hence, individual plants are not connected by plant-to-plant movements of individual pollinators, but by shared pollinator species. We assumed that sharing pollinator species is a surrogate indicator of the potential for effective pollen transfer among plants, given that most pollinators belonging to the same species have similar foraging behaviour (Fenster et al., 2004; Gómez & Perfectti, 2012). Thus, pollinator individuals from the same species are likely to show the same visitation patterns with individual plants. Two plants that are strongly connected in the unipartite network, and thus share most pollinators, will be more likely to be involved in mutual pollen transfer, and a potential mating event, than two plants with very different pollinators, connected by a weaker link. We thus considered the link weights estimated in this way as a proxy for the probability of mating events mediated by a given pollinator species (see Gómez et al., 2011; Rodríguez-Rodríguez et al., 2015).

2.3 | Plant attributes and fitness estimation

We obtained a set of intrinsic and extrinsic attributes for each surveyed individual plant, but we exclusively retained in the analysis those which were not redundant after testing for multicollinearity using VIF factors (threshold = 2, VIF R package, Lin, 2012; for information about the excluded plant attributes see Appendix S1). The extrinsic attributes selected included microsite traits related to microtopographical conditions and competition for abiotic factors, which largely influence both pollinator visitation and the availability of abiotic resources to complete fruit production: (a) cover (m^2) of intraspecific and interspecific neighbours in a 1 and 2 m radius, (b) distance to the stream, (c) distance to the habitat edge and (d) distance to the nearest tree (m). Intrinsic attributes comprised phenotypic and phenological traits associated with the ability of plants to attract pollinators: (a) maximum plant height (m), (b) total number of flowers during the flowering peak, (c) corolla diameter, that is, flower size (mm), (d) flower guide size (mm) and (e) flowering synchrony calculated by modifying the index by Marquis (1988) (Appendix S1). The specific biological predictions for the effects of these intrinsic and extrinsic variables on the bipartite and unipartite networks and the female plant fitness can be found in Table S1. Extrinsic variables and plant size were estimated using aerial images, an orthomosaic and a 3D surface model obtained with the performance of drone flights in the study population (see Appendix S1 for detailed methods of spatial data acquisition).

To quantify the female reproductive success per individual plant, we first calculated the fruit set as the proportion of flowers setting fruit. To do this, we collected 10 inflorescences per plant and

counted the total number of flower buds produced initially and the number of fruits at the end of the season. Second, we sampled five fully developed fruits and counted the number of seeds per fruit to obtain the average seed production per fruit in each plant, and also measured the average seed mass with a precision scale. An overall female reproductive success ('fitness' hereafter) per plant was estimated by weighing the total number of seeds per plant by seed mass (Appendix S1).

2.4 | Statistical analyses

2.4.1 | Ecological correlates of the bipartite plant-pollinator network structure

To analyse the ecological variables producing the overall structure of the individual-based pollination networks we built ERGMs (Lusher et al., 2013). An ERGM is a true generative statistical model of network structure and characteristics (i.e. it allows us to describe how data are generated in terms of probability): Node traits and local structural properties can be used to predict properties of the entire network (e.g. diameter, degree distribution, etc.). The probability of a given network, which can be re-expressed in terms of the conditional log-odds of a single link between two nodes, is modelled as a function of terms that represent network, node or link features. The ERGM design is analogous to a classical generalised linear model (GLM) and implements a Markov chain Monte Carlo maximum likelihood parameter estimation. The use of these models for weighted networks allows us to test hypotheses about the underlying mechanisms shaping networks by modelling how the number of links (here interactions between a pollinator species and an individual plant or the number of pollinator species shared among individual plants) is affected by specific predictor variables. These predictor variables can be node-based, dyadic and local structural covariates. Node-based covariates model how node attributes affect the number of links they establish (e.g. plant size). Dyadic covariates explain differences in link values between two nodes as outcomes of other kinds of relationships between those nodes (i.e. link attributes, e.g., spatial distance between plants). Structural covariates, also called 'network statistics', describe aspects of network topology that are expected to affect link formation, being the total number of link weights the most basic structural term in weighted ERGMs. Local link configurations (e.g. motifs, Milo et al., 2002) that are hypothesised to occur more often or less often than expected by chance can be also included as structural covariates. Yet we focused only on the total number of link weights as the unique local structural predictor. The structural term representing the total number of link weights mentioned above, referred to as 'sum' in ERGMs, models the general propensity of nodes to be connected to other nodes, and it is equivalent to having an intercept within a GLM. Therefore, this framework allows us to account for the fact that link values can be dependent on the values of neighbouring links or some other aspect of network topology, directly dealing with the nonindependence related to this.

The simplest ERGM controls for endogenous effects originated only from the pattern of links among nodes under a given reference distribution and hence, this model only incorporates structural covariates (Morris et al., 2008). However, the number of links between two nodes is expected to depend not only on the distribution of links joining two nodes, but also on exogenous effects of node and link attributes. A key choice in estimating weighted ERGMs is the selection of a reference distribution, which specifies a process underlying the count data before ERGM predictor terms are added. Because our plant-pollinator networks are based on counts of interactions, we used a Poisson structure, which effectively captures the underlying link distribution. The underlying Poisson distribution of the weighted ERGM allows the interpretation of the coefficients as the increase or decrease in the number of times that each plant-pollinator pair interacts (logged).

We first fitted a Poisson-reference ERGM with the structure of the bipartite plant-pollinator network as the response variable, the sum of the link weights as a structural covariate (i.e. endogenous effect), and the intrinsic and extrinsic attributes of individual plants as node-based covariates (i.e. exogenous effects). The power of ERGMs is that we can also incorporate into the model pollinator node-based attributes that can influence the odds of establishing a link, in this case, the pollinator functional group (see Table S2 for pollinator classification into functional groups). In this ERGM, the expected number of interactions between pollinator species and individual plants in the network is modelled as a random variable with a Poisson distribution. By associating the structure of the bipartite network to specific plant attributes we aimed to assess the contribution of each predictor variable of plant and pollinator attributes to the overall plant-pollinator network configuration.

2.4.2 | Ecological correlates of the unipartite plant-plant network structure

To assess the association between plant attributes and the unipartite network structure depicting the overall patterns of pollinator sharing among conspecifics, we performed a second Poisson-reference ERGM. We modelled the structure of the unipartite plant-plant network as a function of the sum of the link weights as a structural covariate, and the dissimilarity in intrinsic and extrinsic plant attributes between individuals as node-based covariates. For each plant attribute, the dissimilarity is explicitly measured by the model as the absolute difference in two plants' values for that attribute. By doing so, we aimed to investigate whether individual plants with similar plant attributes shared more pollinator species, potentially leading to assortative mating events. We would expect that the higher the trait similarity among two plants, the greater their probability to share pollinator species. As a consequence of optimal foraging strategies of pollinators (Pasquaretta et al., 2017), they tend to move at short distances and thus, closer plants are more likely to share more pollinators than further plants and generate assortative matings. To account for this spatial effect, in this ERGM we also included

a matrix with the spatial distance between individual plants as a dyadic covariate.

After performing both ERGMs, we compared the relative contribution of extrinsic and intrinsic plant attributes to explain link weights (i.e. number of interactions established) by expressing each predictor estimate as a percentage of the total sum of the absolute values of the estimates. All predictor variables were standardised to allow meaningful comparisons among them in relative importance. ERGMs were computed using `SAND` and `ERGM` R packages (Handcock et al., 2018; Kolaczyk & Csárdi, 2017).

2.4.3 | Functional consequences

After assessing how extrinsic and intrinsic plant attributes shape the structure of the plant–pollinator networks, we evaluated how these influences translate into functional outcomes. The effects of plant attributes on plant fitness were tested using a GLM with a quasibinomial error distribution. We included the normalised plant fitness, which indicates how the fitness of a given individual departs from the population mean, as the response variable and the same extrinsic and intrinsic plant attributes as above as predictors. To account for the topological position of individual plants in the network, we estimated their centrality (Freeman, 1978) as a surrogate of the topological position of each individual. Centrality measures how well connected a given individual is with the rest of the co-occurring conspecifics owing to sharing pollinator species, and therefore its potential role as a pollen source and/or receiver. We assumed that a higher fraction of shared pollinator species reveals a higher potential for pollen transfer among two plants relative to other plant pairs with different pollinators. We estimated closeness centrality from the unipartite weighted network using the `BIPARTITE` R package (Dormann et al., 2008). Closeness centrality is positively related to the shortest number of direct and indirect interactions between one node and all other nodes in the network (shortest paths; Freeman, 1978). In the context of this study, closeness is based on the reachability of an individual plant within the network, indicating how well pollen originating from a focal plant can reach any other plant or how well conspecifics' pollen can reach this focal plant. By including both plant attributes and closeness centrality as predictor variables in the GLM, we accounted for both the network-mediated effects and the external influences of plant attributes on fitness.

Prior to model fitting, we tested for spatial autocorrelation of plant fitness and intrinsic plant attributes with Moran's I (`SPDEP` R package; Bivand & Wong, 2018). The relative contribution of both intrinsic and extrinsic plant attributes and plant centrality to explaining variation in fitness was assessed using the `RELAIMPO` R package (Grömping, 2006). This package uses the fitted linear model explained above with fitness as the response variable and intrinsic and extrinsic plant attributes as predictor variables and estimates the R^2 contribution of those variables to explaining variation in fitness averaged over resampled orderings among regressors.

All analyses were performed using R software version 3.5.3 (R Core Team, 2019).

3 | RESULTS

We counted a total of 33,262 flowers from all surveyed individual plants [554.37 ± 108.64 (mean \pm SE) per individual plant] across the study period. We recorded 2,774 interactions between 60 individual *H. halimifolium* plants and 21 pollinator species (Table S2). Most interactions were performed by *Lasioglossum* spp. (42.11%), *Dasyglossa* spp. (18.78%), *Apis mellifera* (13.27%) (Hymenoptera) and *Mylabris* spp. (11.46%) (Coleoptera). The level of pollinator sharing (i.e. the number of visits by shared pollinator species) of each individual plant with conspecifics was 530.00 ± 56.73 (mean \pm SE), while each individual plant shared pollinator species with 47.23 ± 1.36 conspecifics in the population. We observed substantial variation among individual plants in both extrinsic and intrinsic attributes (Table S4). The number of unique pairwise links between individual plants and pollinator species in the bipartite network was $L(y) = 208$ (Figure 2a), while the number of unique pairwise links among individual plants sharing pollinator species in the unipartite projection of the network was $L(y) = 1,478$ (Figure 2b).

3.1 | Ecological correlates of the bipartite plant–pollinator network structure

We found a 'sum' effect in the ERGM fitted with the bipartite network as the response variable (Table 1), indicating that the probability of observing this network configuration was partially influenced by the total number of interactions among individual plants and pollinator species. However, additional variables (i.e. exogenous), such as plant attributes, were needed to explain the observed structure of the network.

The model coefficients for exogenous variables (Table 1) represent the effects of plant or pollinator attributes on the likelihood of any plant–pollinator pair to increase the number of interactions. They indicate the expected change in the logged number of interactions between any plant–pollinator pair increasing (or decreasing) as a function of a given one-unit change in a specific plant or pollinator attribute. For example, our model showed that increasing the number of flowers in plants increased the odds of interacting with more pollinator species by a factor of $\exp(0.259) = 1.295$, or nearly 30% (Table 1). Flower guide size increased the odds of plants to interact with more pollinator species, while these odds decreased with plant height and flowering synchrony. The direction of the effects of both intraspecific and interspecific neighbourhood cover on plant–pollinator interaction probability depended on the spatial scale considered (1 vs. 2 m radius). The effect of the cover of intraspecific neighbours was positive within a 1 m radius and negative within a 2 m radius. Meanwhile, the effect of the cover of interspecific neighbours was negative within

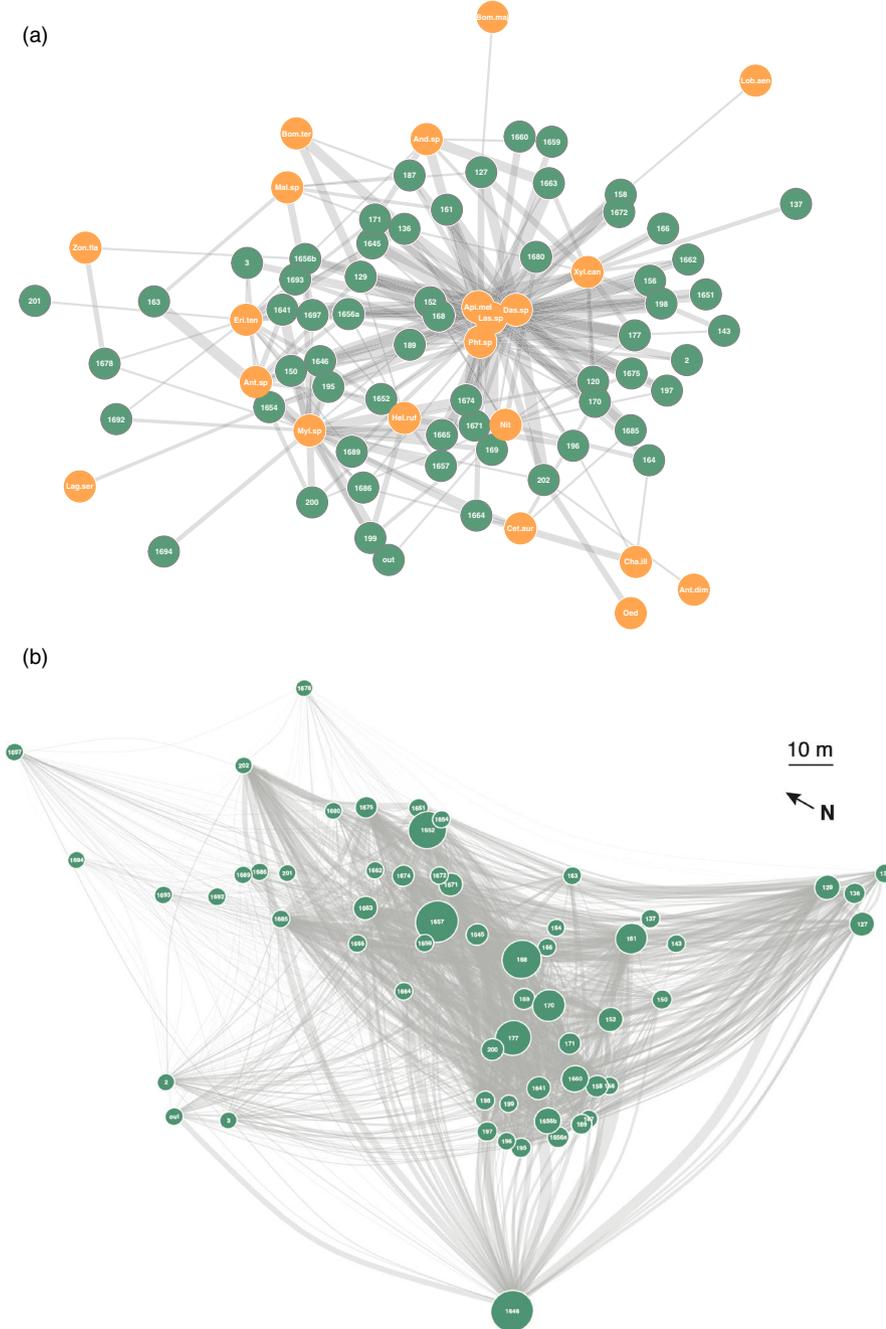


FIGURE 2 (a) Weighted bipartite network representing interactions between individual plants (green nodes) and pollinator species (orange nodes). The links between nodes depict flower visitation interactions while the width of the links refers to the strength of the interaction (i.e. number of interactions recorded). The layout of the network representation was created using an energy-minimisation algorithm. Pollinator species represent: And.sp - *Andrena* spp., Ant.dim - *Anthaxia dimidiata*, Ant.sp - *Anthrenus* spp., Api.mel - *Apis mellifera*, Bom.ter - *Bombus terrestris*, Bom.maj - *Bombylius major*, Cet.aur - *Cetonia aurata*, Cha.ill - *Chasmatoxerus illigeri*, Das.sp - *Dasygaster* spp., Eri.ten - *Eristalis tenax*, Hel.ruf - *Heliotaurus ruficollis*, Lag.ser - *Lagorina sericea*, Las.sp - *Lasioglossum* spp., Lob.aen - *Lobonyx aeneus*, Mal.sp - *Malthodes* spp., Myl.sp - *Mylabris* spp., Nit - Nitidulidae, Oed - Oedemeridae, Pht.sp - *Phthiria* spp., Xyl.can - *Xylocopa cantabrita*, Zon.flav - *Zonitis flava*. (b) Weighted unipartite network illustrating the pattern of shared pollinator species among *Halimium halimifolium* individual plants. Two individual plants are linked if they shared at least one pollinator species visiting their flowers. Link width is proportional to the number of interactions shared between two individual plants. Node size refers to the female plant fitness while node position indicates the spatial location (X–Y coordinates) of individual plants

a 1 m radius and positive within a 2 m radius (see Table 1 for specific effect sizes). The functional group to which pollinator species belonged also had a significant effect on link establishment. The odds of establishing more plant–pollinator interactions especially increased when pollinator species were medium- and small-sized bees, by a factor of $\exp(2.114) = 8.281$ and $\exp(3.480) = 32.460$ respectively.

Overall, intrinsic (i.e. phenotype and phenology) and extrinsic (i.e. microsite) plant attributes accounted for 9.54% and 8.01%, respectively, of the variation in plant–pollinator interaction odds, while the pollinator functional group explained 74.42% of this variation.

3.2 | Ecological correlates of the unipartite plant–plant network structure

The ‘sum’ effect was significant in the ERGM with the unipartite network as the response variable (Table 2). Thus, the number of interactions between a given pair of plants (i.e. number of pollinator visits shared) partially depended on the total number of interactions in the unipartite network. The odds of two plants to share more pollinator species were positively associated with the dissimilarity between those plants in flower size, total number of flowers, distance to stream and cover of interspecific neighbours in a radius of 2 m. These odds decreased with the dissimilarity in plant height, flower

TABLE 1 Summary of the exponential random graph model (ERGM) showing the effects of individual plant attributes and pollinator functional groups on the structure of the bipartite plant–pollinator network. The ‘sum’ effect assesses the influence of the plant–pollinator link weights’ distribution on the configuration of the bipartite network. Estimates of predictor variables with significant effects indicate the expected change, increasing or decreasing, in the logged number of plant–pollinator interactions given a one-unit change in that predictor variable. As the first pollinator functional group (beeflies) is used as a reference, the interpretation of the effects of the remaining groups is relative to beeflies. Significant values ($p < 0.05$) appear in boldface

| | Estimate \pm SE | z value | p |
|---|--------------------|---------|------------------|
| Sum | -0.963 \pm 0.149 | -6.472 | <0.001 |
| Intrinsic plant attributes | | | |
| Maximum height (m) | -0.144 \pm 0.033 | -4.375 | <0.001 |
| Flower guide size (mm) | 0.204 \pm 0.028 | 7.394 | <0.001 |
| Flower size (mm) | 0.021 \pm 0.032 | 0.674 | 0.500 |
| Total number of flowers | 0.259 \pm 0.023 | 11.297 | <0.001 |
| Flowering synchrony | -0.517 \pm 0.049 | -10.486 | <0.001 |
| Extrinsic plant attributes | | | |
| Distance to stream (m) | -0.073 \pm 0.055 | -1.325 | 0.185 |
| Distance to tree (m) | 0.006 \pm 0.035 | 0.169 | 0.866 |
| Distance to edge (m) | 0.02 \pm 0.045 | 0.455 | 0.649 |
| Cover of intraspecific neighbours in $r = 1$ m ²) | 0.215 \pm 0.051 | 4.202 | <0.001 |
| Cover of interspecific neighbours in $r = 1$ m ²) | -0.317 \pm 0.062 | -5.115 | <0.001 |
| Cover of intraspecific neighbours in $r = 2$ m ²) | -0.109 \pm 0.048 | -2.283 | <0.001 |
| Cover of interspecific neighbours in $r = 2$ m ²) | 0.221 \pm 0.041 | 5.426 | <0.001 |
| Pollinator functional group | | | |
| Hoverflies | 0.211 \pm 0.222 | 0.952 | 0.341 |
| Large bees | 0.223 \pm 0.179 | 1.247 | 0.212 |
| Large beetles | 1.482 \pm 0.145 | 10.208 | <0.001 |
| Medium-sized bees | 2.114 \pm 0.135 | 15.625 | <0.001 |
| Medium-sized beetles | -0.933 \pm 0.17 | -5.485 | <0.001 |
| Small bees | 3.480 \pm 0.137 | 25.364 | <0.001 |
| Small beetles | -0.484 \pm 0.196 | -2.472 | <0.001 |

guide size, flowering synchrony, distance to the nearest tree and cover of intra- and interspecific neighbours in an $r = 1$ m (Table 2).

We also found that the odds of pollinator sharing between plants decreased with the spatial distance between those plants by a factor of $\exp(1.790) = 5.989$. Intrinsic and extrinsic plant attributes explained 15.65 and 15.88%, respectively, of the variation in the odds

TABLE 2 Summary of the exponential random graph model (ERGM) showing the effects of individual plant attributes on the structure of the unipartite network derived from pollinator species sharing among conspecific plants. The ‘sum’ effect assesses the influence of the plant–plant link weights’ distribution on the configuration of the unipartite network. Estimates of predictor variables with significant effects indicate the expected change, increasing or decreasing, in the logged number of pollinator species shared given a one-unit change in that predictor variable. Significant values ($p < 0.05$) appear in boldface

| | Estimate \pm SE | z value | p |
|---|--------------------|---------|------------------|
| Sum | 3.005 \pm 0.028 | 108.984 | <0.001 |
| Intrinsic plant attributes | | | |
| Maximum height (m) | -0.119 \pm 0.012 | -10.132 | <0.001 |
| Flower guide size (mm) | -0.222 \pm 0.01 | -21.219 | <0.001 |
| Flower size (mm) | 0.138 \pm 0.011 | 12.335 | <0.001 |
| Total number of flowers | 0.134 \pm 0.006 | 20.620 | <0.001 |
| Flowering synchrony | -0.482 \pm 0.015 | -31.978 | <0.001 |
| Extrinsic plant attributes | | | |
| Distance to stream (m) | 0.197 \pm 0.037 | 5.265 | <0.001 |
| Distance to tree (m) | -0.047 \pm 0.013 | -3.645 | <0.001 |
| Distance to edge (m) | -0.025 \pm 0.013 | -1.855 | 0.064 |
| Cover of intraspecific neighbours in $r = 1$ m ²) | -0.112 \pm 0.014 | -8.116 | <0.001 |
| Cover of interspecific neighbours in $r = 1$ m ²) | -0.471 \pm 0.017 | -28.342 | <0.001 |
| Cover of intraspecific neighbours in $r = 2$ m ²) | 0.013 \pm 0.015 | 0.875 | 0.381 |
| Cover of interspecific neighbours in $r = 2$ m ²) | 0.246 \pm 0.01 | 24.184 | <0.001 |
| Spatial distance between plants (m) | -1.790 \pm 0.186 | -9.552 | <0.001 |

of pollinator sharing, while the spatial distance between individual plants accounted for 25.58% of this variation.

3.3 | Functional consequences

Plant fitness and intrinsic plant attributes were not spatially auto-correlated (Table S5). The GLM with individual plant fitness as the response variable revealed that the topological position of individual plants within the unipartite network (i.e. closeness centrality) was positively associated with plant fitness (Table 3; Figure 3a). We also found that individual plant fitness was associated with intrinsic and extrinsic plant attributes, after controlling for the network-mediated effects (Table 3). Interestingly, individual plant fitness increased with the total number of flowers and flowering synchrony (Figure 3b,c);

TABLE 3 Results of the generalised linear model (GLM) evaluating the effects of the network topological position and individual plant attributes on female plant fitness. The fitted GLM accounted for 84.81% of the variation. Fitness was estimated as the total number of seeds per individual weighted by the seed mass and normalised (See Materials and Methods: Plant attributes and fitness estimation). Significant values ($p < 0.05$) appear in boldface

| | Estimate \pm SE | t value | p |
|--|--------------------|---------|------------------|
| Intercept | -2.597 \pm 0.121 | -19.610 | <0.001 |
| Topological position | | | |
| Closeness | 0.767 \pm 0.215 | 3.576 | <0.001 |
| Intrinsic plant attributes | | | |
| Maximum height (m) | -0.232 \pm 0.157 | -1.478 | 0.142 |
| Flower guide size (mm) | 0.127 \pm 0.116 | 1.092 | 0.281 |
| Flower size (mm) | -0.103 \pm 0.131 | -0.783 | 0.437 |
| Total number of flowers | 1.501 \pm 0.162 | 9.271 | <0.001 |
| Flowering synchrony | 0.666 \pm 0.237 | 2.808 | 0.007 |
| Extrinsic plant attributes | | | |
| Distance to stream (m) | -0.577 \pm 0.219 | -2.639 | 0.011 |
| Distance to tree (m) | -0.252 \pm 0.171 | -1.474 | 0.147 |
| Distance to edge (m) | 0.077 \pm 0.221 | -0.349 | 0.729 |
| Cover of intraspecific neighbours in $r = 1$ m (m^2) | 0.259 \pm 0.207 | 1.2503 | 0.218 |
| Cover of interspecific neighbours in $r = 1$ m (m^2) | -0.059 \pm 0.206 | -0.286 | 0.776 |
| Cover of intraspecific neighbours in $r = 2$ m (m^2) | -0.469 \pm 0.192 | -2.447 | 0.018 |
| Cover of interspecific neighbours in $r = 2$ m (m^2) | -0.099 \pm 0.202 | -0.494 | 0.623 |

and decreased with distance to the stream and cover of intraspecific neighbours in $r = 2$ m (Table 3; Figure 3d,e).

Intrinsic plant attributes accounted for 50.64% of the variation in individual plant fitness, and extrinsic attributes explained 34.59% of this variation. Meanwhile, the topological position of individual plants within the network accounted for 14.78% of this variation.

4 | DISCUSSION

Our findings revealed how the individual variation in plant attributes existing in natural populations gives rise to the overall structural patterns of individual-based plant–pollinator networks and its functional implications. We found that intrinsic (i.e. phenotypic traits and flowering phenology) and extrinsic (i.e. microsite) plant attributes had comparable influences on structuring both, the plant–pollinator

bipartite network and the plant–plant unipartite network. Furthermore, our results also showed that network structure, and specifically the position of individual plants within this network, together with the direct effects of plant attributes, had considerable consequences for individual plant fitness. Overall, these findings suggest that the ability of individual plants to participate in shared interactions, and therefore to increase their reproductive success, may ultimately be determined by the intraspecific variation in microsite characteristics, phenotype and phenological traits.

4.1 | Ecological correlates of the bipartite plant–pollinator network structure

Variation in traits of both plant and animal partners is increasingly recognised as forces structuring ecological networks at the level of interactions among species (Bartomeus et al., 2016). Similarly, intraspecific trait variation can play an important role in shaping individual-based networks, yet this aspect remains virtually unexplored in the literature (Miguel et al., 2018). By using ERGMs we were able to further recognise specific plant attributes (individual phenotype, phenology and microsite) that shape the observed individual plant–pollinator network structure. We thus assessed the relative contribution of extrinsic and intrinsic plant attributes to explaining the odds of interactions to increase for individual plants.

Our findings showed that intraspecific trait variation in floral and vegetative phenotypes among plants influenced the establishment of interactions with pollinator species, which is in accordance with previous work (Dupont et al., 2014; Gómez & Perfectti, 2012; Weber & Kolb, 2013). We also demonstrated that this influence upscales to affect the structure of the individual-based pollination network. Specifically, we found that the probability of interacting with more pollinator species increased with the size of the flower guides, which is widely known to positively affect pollinator attraction (Waser, 1983). Although plant size is expected to increase plant attractiveness for pollinators, we found a negative effect of plant height on the probability to interact with pollinator species. This result is probably due to the non-uniform distribution of flowers in taller plants, as they usually have the highest flower density at the base of the plant.

Contrary to our expectations, the individual flowering synchrony influenced the structure of the network by decreasing the odds of individual plants to interact with pollinator species. This result may respond to the fact that a high abundance of flowers in the population can decrease the chance of a pollinator to visit a given individual plant, leading to the so-called 'dilution effect' (Holzschuh et al., 2011), especially in high-density stands. However, we found that the flowering synchrony of plants also increased their fitness. Our findings suggest that higher floral availability in the population can result in high pollen loads carried by pollinators, which can ultimately increase individual plant fitness. Another non-exclusive plausible explanation is that plants with higher synchrony can share pollinators with a larger set of conspecific plants, which may

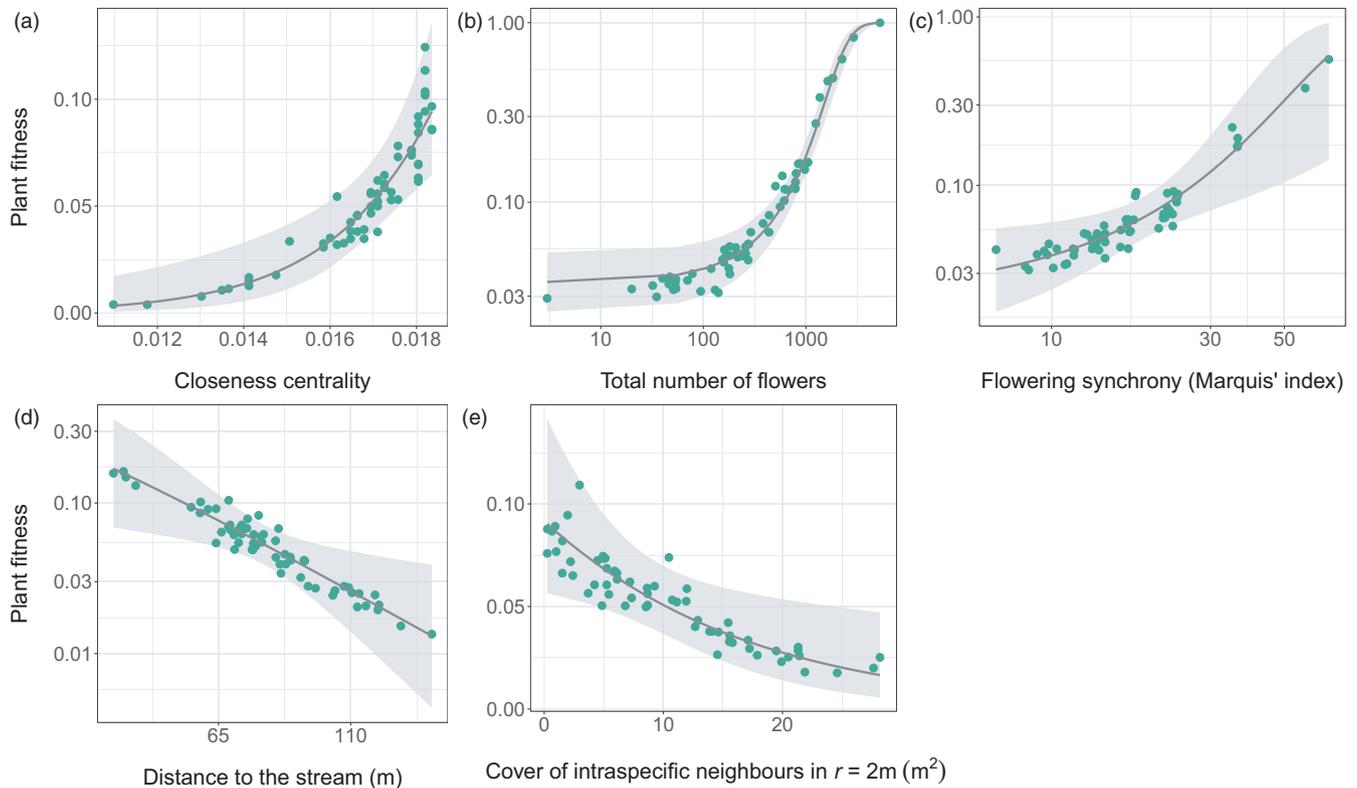


FIGURE 3 Partial residual plots showing the variability of female plant fitness of individual plants explained by (a) closeness centrality, (b) total number of flowers, (c) flowering synchrony, (d) distance to the stream and (e) cover of intraspecific neighbours in a 2 m radius, when controlling for the effects of the remaining variables included in the GLM. Points represent individual plants surveyed in the study population and the grey area indicates the 95% confidence interval for the fitted values. Axis scale differs among plots to enhance the visualisation of the data. Note log scale on both axes for the plots illustrating the effects of the total number of flowers (b), flowering synchrony (c) and distance to the stream (d)

increase their chances of receiving better quality pollen in comparison to asynchronous plants (Antonovics & Levin, 1980).

Although the effect of the microsite, especially neighbourhood composition and density, has previously been considered for plant–frugivore (e.g. Carlo, 2005; Guerra et al., 2017; Miguel et al., 2018; Morales et al., 2012) and plant–pollinator interactions (e.g. Delesalle & Mazer, 2002; Lázaro et al., 2009), it has rarely been included in network studies. Previous studies support the notion that the local microclimatic variation affects pollinator composition, activity and behaviour at flowers (Herrera, 1995; Potts et al., 2005). Our results expand these findings by suggesting that microsite influences extend to the overall structure of the pollination network at the plant population level, potentially affecting mating patterns. Specifically, we found that the direction of the effects of interspecific and intraspecific neighbours on the establishment of individual plant–pollinator interactions changed with the spatial scale (1 vs. 2 m radius). This result might indicate the existence of a facilitation–competition continuum dependent on the spatial distance to neighbours. As previously indicated, interspecific competition or facilitation for pollinators was not possible to occur in our study population because *H. halimifolium* was the only plant species flowering during the study period. However, the presence of interspecific neighbours may still affect individual plants' visitation patterns indirectly via competition.

These findings show that the effects of the plant microsite on the establishment of individual plant–pollinator interactions are as important as the effects of the phenotype or phenology.

In light of all of these results, the context dependency previously found in species-level networks (Poisot et al., 2015) appears also as an important driver of individual-based pollination networks, with direct consequences for plant fitness. Additionally, our results revealed that the functional group of pollinator species explained most of the variation in the odds of establishing more plant–pollinator interactions. This finding may be attributable to the fact that the visitation patterns of different pollinator functional groups are influenced by distinct plant attributes (Fenster et al., 2004). Thus, the inclusion of all pollinator groups in the analyses may mask the actual influences of plant attributes on the emerging structure of the network.

4.2 | Ecological correlates of the unipartite plant–plant network structure

ERGMs successfully evaluate how attributes of individual plants influence the odds of sharing pollinator species among them and hence, of being involved in reciprocal pollen transfer and mating events, enhancing their fitness. We found that for most plant

attributes, similar individual plants were likely to share more pollinator species, which may translate into potential assortative mating in the study plant population (Waser, 1983). Besides, the similarity in traits consistently associated with greater pollinator sharing showed larger effect sizes than the similarity in traits more associated with divergence in interacting pollinator species. These results also suggest that pollinator preferences for plant attributes are distinct among pollinator species even when foraging within a monospecific flowering stand, scaling up to affect the entire network configuration. It must be pointed out that the between-plant spatial distance was the variable that most influenced the structure of the unipartite network of pollinator sharing, highlighting the importance of accounting for the spatial component when studying plant–animal interactions (see also Dupont et al., 2014; Pasquaretta et al., 2017).

Our interpretations of the results outlined above provide evidence that distinct plant attributes operate in different ways when structuring bipartite and unipartite individual-based pollination networks. While most studies (e.g. Dupont et al., 2014; Stang et al., 2006) only account for the effects of individual or species traits on the establishment of plant–pollinator interactions, we suggest that taking into account the influence of those traits on the indirect interactions among plants, via shared pollinator species, is essential to better predict the functional consequences of plant–animal interactions.

4.3 | Functional consequences

The position of plant species in community-wide plant–pollinator networks is expected to affect the reproductive success of those plant species and ultimately the functioning of the whole plant community (Magrach et al., 2020). However, plant fitness measured at the species level is determined by the way individual plants within populations interact with pollinator species, besides the interspecific context in which these individual plants are found. By downscaling from plant communities to populations we can better predict the functional consequences of network configuration, as the pattern of shared pollinator species among individual plants may be translated into a pattern of mating to some extent (Gómez et al., 2011) and hence, links conceptually to demographic and evolutionary effects.

Our findings support the intuitive idea that individual plant fitness is positively associated with the level of pollinator sharing with other conspecific plants (i.e. with the closeness centrality of individual plants within the network). Beyond the network-mediated effects, fitness variation was also driven by differences in plant attributes related to flower abundance and microsite. Because we estimated plant fitness as the total number of seeds produced per plant, we expected the total number of flowers per plant to have a significant direct effect on fitness. Moreover, our results showed that the combination of the network topological position and both intrinsic and extrinsic plant attributes was accurate at predicting the reproductive outcomes of *H. halimifolium* plant–pollinator interactions. By contrast, previous work found that the plant topological role had a higher effect than plant attributes on plant fitness

(Gómez & Perfectti, 2012; Rodríguez-Rodríguez et al., 2017; Soares et al., 2021), but this could be strongly dependent on the spatial context and the species-specific characteristics.

The use of centrality measures is not as powerful as the ERGM approach to describe network topology; however, the ERGM design in its current form does not allow us to assess the fitness consequences of the overall network structure. While ERGMs offer real potential to test hypotheses about network configuration, developing an integrative modelling framework to improve our understanding of the linkage between network structure and functionality is still a current challenge in ecology.

Altogether, our findings indicate that the effect of both intrinsic and extrinsic plant attributes on structuring the pollination networks can ultimately determine differences in plant fitness, even at the scale of small populations. The emergence of the pattern of non-random, assortative mating events found may create a spatial genetic structure within the population as a result of the spatially restricted gene flow generated (Epperson, 1993). Our approach, bridging the complexity of the whole pollination network and its direct effects on among-individual fitness variation, would contribute to explaining the higher levels of genetic structure found in most animal-pollinated plant populations (Vekemans & Hardy, 2004), where the mobility and preferences of different pollinator groups may drive a high frequency of assortative mating events (Valverde, 2017).

5 | CONCLUSIONS

Our study opens up new analytical approaches to further understand how complex ecological networks are configured at the population level by disentangling the underlying drivers of the context dependency of interactions, that is, plant traits versus microhabitat attributes. Individual-based networks and ERGMs provide novel insights into how individual-plant variation in both intrinsic and extrinsic attributes predictably shifts the functional outcomes of mutualistic interactions. This close relationship between the inter-individual variation in plant attributes and their fitness might be especially relevant in habitats with patchiness in biotic and abiotic variables, which affect animal foraging behaviour within a plant population. Such a predictive framework has potential to move forward ecological network analyses from descriptive metrics to more powerful forecasting approaches. Therefore, the analytical tools we used would help to better assess how the pervasive context dependency of species interactions influences the evolutionary and ecological processes taking place within populations, and to predict the potential responses of these populations to environmental changes.

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AUTHORS' CONTRIBUTIONS

B.A.-C., I.B. and P.J. conceived the ideas and designed methodology; B.A.-C. collected the data, performed the analyses with the help of P.J. and I.B., and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data and R code for the analyses are available at the Zenodo Digital Repository (<https://doi.org/10.5281/zenodo.3756781>; Arroyo-Correa et al., 2020) and the GitHub repository (<https://github.com/BlancaAC>).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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