Flowering overlap and floral trait similarity help explain the structure of pollination network

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RESEARCH ARTICLE

Flowering overlap and floral trait similarity help explain the structure of pollination networks

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Abstract

1. Co-flowering communities are usually characterized by high plant generalization but knowledge of the underlying factors leading to high levels of generalization and pollinator sharing, and how these may contribute to network structure is still limited.
2. Flowering phenology and floral trait similarity are considered among the most important factors determining plant generalization and pollinator sharing. However, these have been evaluated independently even though they can act in concert with each other. Moreover, the importance of flowering phenology and floral similarity, via their effects on plant generalization, in the structure of plant–pollinator networks has been scarcely studied. Here, we aim to evaluate the effect of flowering phenology and floral similarity in mediating the degree of pollinator sharing and plant generalization in two coastal communities and uncover their importance as drivers of plant–pollinator network structure.
3. We recorded flower production per species, as well as the identity and frequency of floral visitors along the entire flowering season. We estimated the degree of flowering overlap, the degree of floral similarity (using floral traits associated with size and colour) and the degree of pollinator sharing among plant species within both communities.
4. Structural equation models (SEM) showed a positive effect of flowering overlap on pollinator sharing and plant generalization. Pollinator sharing and plant generalization positively affected network nestedness. Furthermore, SEM showed a direct positive effect of flowering overlap on network modularity. The SEM analyses also revealed a significant interaction effect of floral similarity and flowering overlap on pollinator sharing, with consequences for network nestedness in one community.
5. *Synthesis*. Our results highlight the importance of integrating multiple axes of differentiation such as flowering phenology and floral similarity into our understanding of the drivers of plant–pollinator network structure.

KEYWORDS
betweenness centrality, coastal communities, co-flowering, flowering length, flowering phenology, plant generalization, pollinator sharing

[Correction added on 1 July 2022, after first online publication: The synthesis of the paper (point 5 of the abstract) has been reinstated.]

1 | INTRODUCTION

Pollination network studies have mostly focused on evaluating patterns and causes of plant–pollinator interaction structure (e.g. Bascompte & Jordano, 2007; Petanidou et al., 2008; Vázquez et al., 2009) to understand the drivers and consequences of spatio-temporal changes in network structure (e.g. CaraDonna et al., 2014; Peralta et al., 2020; Vázquez et al., 2009; Watts et al., 2016). Among the most important determinants of network structure is the morphological and phenological match between pairs of interacting plant and pollinator species (Peralta et al., 2020; Stang et al., 2007; Vázquez et al., 2009; Vizentin-Bugoni et al., 2014). For instance, a recent study showed that the phenological overlap between plants and pollinators determines the identity, frequency and the success and stability of these interactions (Peralta et al., 2020). However, there may be other factors that can contribute to plant–pollinator network structure that have received less attention. Specifically, the level of plant generalization with respect to floral visitors (i.e. the number of pollinator species associated with a single plant; plant generalization hereafter) and the degree of pollinator sharing with other plant species may influence patterns of network nestedeness and modularity, two main descriptors of plant–pollinator network structure (Petanidou et al., 2008; Valdovinos & Marsland, 2021). Nevertheless, the factors that influence the degree of plant generalization and pollinator sharing among co-flowering species and how these may affect overall plant–pollinator network structure have been little studied (but see Albor et al., 2020; Bergamo et al., 2017; Carvalheiro et al., 2014; Gibson et al., 2012).

Here, we present, and test, a causal framework that integrates the direct and indirect effects of floral trait similarity and flowering overlap on plant–pollinator network structure (Figure 1). Floral trait similarity has been considered a key factor mediating the degree of pollinator sharing among plant species (Bergamo et al., 2020; Fornoff et al., 2017; Ghazoul, 2006; Sargent & Ackerly, 2008). For instance, it is expected that greater floral trait similarity among species will increase pollinator sharing (Figure 1b), since pollinators respond to similar sensory stimuli (e.g. Faegri & Van der Pijl, 1979; Gibson et al., 2012; Ha et al., 2020; Herrera, 2020a; Sargent & Ackerly, 2008). Thus, plant species with greater floral trait similarity to other species in the community can be expected to have a larger contribution to plant generalization (Figure 1b) in plant–pollination networks (i.e. nested structure). Plant generalization and pollinator sharing are, in turn, expected to contribute positively to network nestedness and negatively to network modularity (Figure 1c; Olesen et al., 2007; Vázquez et al., 2009). Hence, high floral trait similarity would have an indirect positive effect on network nestedness and a negative one on modularity (Figure 1c).

Which floral resources pollinators exploit, however, also depends on their temporal availability (Kudo, 2006; Primack, 1985; Rathcke & Lacey, 1985). Thus, variation in the degree flowering overlap between plant species will also affect their degree of pollinator sharing (e.g. Weis, 2005; Wolowski et al., 2017). For instance, species with long flowering phenology (Arceo-Gómez et al., 2018) may increase the degree of pollinator sharing and plant generalization in plant–pollinator networks (Figure 1b), hence contributing to a more nested structure (Figure 1c). In contrast, species with low flowering overlap and low pollinator sharing may contribute to higher modularity (specialization) in plant–pollinator networks (Figure 1c; Biella et al., 2017; Hinton & Peters, 2021). Thus, the degree of pollinator sharing is constrained by both, flowering overlap and floral trait similarity, wherein species with long flowering phenology and high floral similarity are expected to have higher levels of pollinator sharing compared to other species (Albor et al., 2020; Arceo-Gómez et al., 2018). For instance, Lázaro et al. (2020) found a negative relationship between flowering length and species-level specialization within a network. Current evidence also suggests that invasive species with floral traits similar to those of native species could more readily integrate into native plant–pollinator networks (reviewed by Parra-Tabla & Arceo-Gómez, 2021). It is also possible that the effect of flowering overlap and floral trait similarity on network structure may depend on each other (i.e. interaction effect; Figure 1a) in a way that both would be required to maximize pollinator sharing. On the contrary, only one (floral similarity or flowering overlap) could be sufficient to achieve a 'maximum'

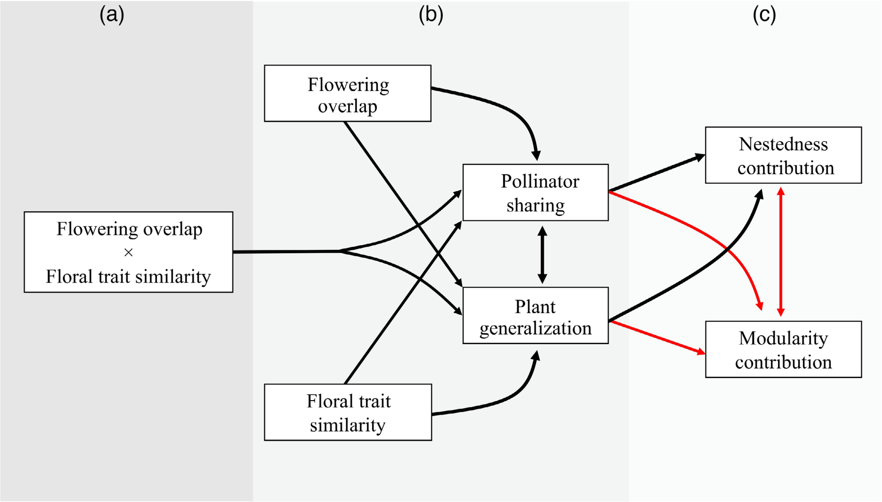

FIGURE 1 Structure of causal correlations proposed for the effects of flowering overlap, floral trait similarity, on plant generalization and pollinator sharing, and of these four variables in the structure of the plant–pollinator networks. Black colour and red colour lines show expected positive and negative effects, respectively.

level of pollinator sharing (e.g. high flowering overlap but low floral trait similarity). However, to our knowledge, how the degree of flower trait similarity and flowering overlap interact to affect nestedness and modularity in plant–pollinator networks remain largely unknown (but see Bergamo et al., 2017; Carvalheiro et al., 2014; Olesen et al., 2007). We evaluated the predictions associated with our proposed casual framework (Figure 1) in two distinct coastal co-flowering communities in the Yucatan Peninsula (Figure 2).

2 | MATERIALS AND METHODS

2.1 | Study area

We tested our causal framework using two adjacent coastal communities, one with distinct sand dune vegetation and a scrubland characterized by medium-height shrubs (Figure 2). These two communities are located near the town of Telchac (21° 20′11.7″N–89° 20′12.5″W; 0 to 8 m a.s.l.) in the Yucatan Peninsula, Mexico. The climate is hot and dry, with an annual temperature of 26°C, a seasonal rain pattern, and an average annual rainfall of 760 mm (Orellana et al., 2009). The sand dune community is located between the coastline and the beach area and is 10–15 m wide. The vegetation grows on a mobile sandy substrate, and is characterized by low height, <1 m to a maximum of 1.5 m (Figure 2a). This community is mainly composed of herbaceous species such as *Cakile edentula* and *Bidens pilosa*, *Ipomea pres-capre* and *Sesuvium portulacastrum* and some shrub species such as *Scaevola plumeri* and *Tournefortia gnaphalodes* (Parra-Tabla et al., 2018). The scrubland is located away from the coastline (approx. 10–20 m), the sand is fixed and the vegetation reaches a higher height (2–5 m; Figure 2b). This community is composed of herbaceous species such as *Euphorbia mesembryanthemifolia*, *Croton punctatus*, *Metastelma schlechtendalii* and *Canavalia rosea*, and shrub species such as *Pithecellobium keyense* and *Bonellia macrocarpa* (Campos-Navarrete et al., 2013; Parra-Tabla et al., 2018).

While some plant species grow in both communities (see Table S1), they differ significantly in plant species composition, although not in floral visitor composition (PERMANOVA: $F_{1,18} = 4.29$, $p < 0.005$ and $F_{1,18} = 1.35$, $p > 0.05$, respectively). Generalist plant–pollinator interactions are predominant in both communities (Campos-Navarrete et al., 2013; Parra-Tabla et al., 2019) and floral visitation rates do not differ between the two (0.23 ± 0.17, and 0.12 ± 0.07, mean of visits/flower ±*SD*; sand dune and coastal scrubland, respectively, $t = 0.05$, $p > 0.5$). However, in the sand dune, floral visits are typically shorter than in the scrubland, which can lead to differences in conspecific pollen loads on stigmas (Parra-Tabla et al., 2021).

To determine the completeness of our vegetation sampling (i.e. plant species richness), we constructed rarefaction curves and calculated Hill numbers ($q = 0$, see Chao et al., 2014), using the iNEXT package (Hsieh et al., 2016) in R 3.6.3 software. Rarefaction curves were constructed with 500 randomizations and 95% confidence intervals. Results showed that for both communities the sampling effort was adequate, covering 94.5% and 85.3% of plant species richness in the dune and scrubland communities, respectively (Figure S1).

FIGURE 2 Study sites, sand dune (a) and coastal scrubland (b) communities in Telchac, Yucatan, Mexico.

2.2 | Flowering phenology and pollinators activity

Ten plots of 10 × 2 m separated by 5 m were established parallel to the coastline in the two communities. In each community, 10 censuses on each plot were carried out recording the number of open flowers for each species. The censuses were carried out every 8–10 days from August to December 2019. This period encompasses the rainy season during which the vast majority of plant species in both communities are in bloom (Campos-Navarrete et al., 2013; Parra-Tabla et al., 2019).

To record flower visitors' identity and activity, two observation rounds (8:30 am and 10:30 am) were conducted within the plots during each visit to a community. The greatest activity of diurnal flower visitors occurs between 08:00 am and 12:00 (Campos-Navarrete et al., 2013; Parra-Tabla et al., 2019). The observation time per plot was 10 min and was carried out by the same group of people at a distance of 1 m around the plot. Visits were only recorded when contact between the insect and the reproductive structures of the flowers was observed. The low vegetation height in both communities and the low plant density allowed us to observe all interactions between plants and flower visitors within each plot (Figure 2). Flower visitors were identified at the species or morphospecies level with the support of field identification guides previously elaborated for these communities (Campos-Navarrete et al., 2013; Parra-Tabla et al., 2019). Previous studies have showed that this sampling protocol adequately reflects the abundance and diversity of plant–flower interactions and the richness of interactions in these communities while minimizing disturbance of flower visitor activity (Campos-Navarrete et al., 2013; Parra-Tabla et al., 2019). To test the completeness of our flower visitor's sampling and of each plant–floral visitor network (i.e. observed numbers of unique plant–floral visitor interactions), we followed the same procedure described above for plant species richness. In the case of interaction richness, we estimated the percentage of interaction richness detected in our sampling by dividing the observed by the estimated number of pairwise interactions (Parra-Tabla et al., 2019). For insect richness, we sampled 95.2% and 95.5% of all insects visiting flowers in the dune and scrubland communities, respectively (Figure S2a). For interaction richness, we sampled 91.8% and 84.7% of all unique plant–flower visitor interactions in the sand dune and scrubland communities, respectively (Figure S2b). The main groups of pollinators in both sites were Hymenoptera, Diptera and Lepidoptera (Table S2). No permission was needed for fieldwork.

2.3 | Floral trait similarity

We estimated species floral trait similarity in each community using the following traits: flower length, the diameter of the corolla, the opening of the corolla tube and flower colour. The first three traits were measured with a calliper (±0.1 mm) in 1–5 flowers per plant in at least five plants per species. The length of the flower (i.e. flower size) is associated with pollinator attraction (Faegri & Van der Pijl, 1979; Zhao et al., 2016), and corolla tube opening restricts pollinators' access to flower rewards and has thus been associated with the level of specialization (Caruso, 2000). Although floral symmetry has been associated with the level of plant generalization (e.g. Lázaro & Totland, 2014; Neal et al., 1998), in our study system only 3–4 species have bilateral symmetry in the dune and scrubland, respectively. Thus, this was not included as ca. 10% of species in both communities have radial symmetry. Flower colour, which is also associated with pollinator attraction (Hirota et al., 2012; Spaethe et al., 2001), was measured by analysing floral reflectance spectra (300–700 nm) of the dominant corolla colour in 1–3 flowers per species, with a spectrophotometer (StellarNet INC) and a Tungsten Halogen lamp as an artificial light source. Reflectance measurements were taken in a room with natural light conditions following user specifications of StellarNet INC company (StellarNet, 2019). With this data, we estimated flower colour using chromatic coordinates (x and y) of the Hymenoptera vision model, based on *Apis mellifera* (Chittka, 1992; Chittka & Raine, 2006). Hymenoptera are the most abundant floral visitors in the studied communities (Albor et al., 2019; Campos-Navarrete et al., 2013; Parra-Tabla et al., 2019). The estimation of the hexagonal colour vision model was done with the package PAVO in R 3.6.3 software (R Development Core Team, 2020; see Figure S3). To calculate floral trait similarity among plant species from each community, a matrix of traits was constructed using the average value of each functional trait (i.e. flower length, full corolla diameter, corolla tube opening and colour) for each species. Then, trait distances between species pairs of species and the average similarity of species floral traits (for all traits) were calculated using Gower's pair distance (1 − average dissimilarity). Gower's distance was used because it is appropriate when the descriptors are not dimensionally homogeneous (Gower, 1971). The Gower distance index is restricted between values of 0 and 1, in which values close to 1 indicate high similarity and values close to 0 indicate low similarity. The combined use of morphological and visual traits used here allows for a strong evaluation of flower preference by pollinators (Albor et al., 2020). It is also possible that each floral character independently affects pollinator attraction and pollination success (see Kingsolver et al., 2001; Lázaro et al., 2008). To test for this, we further correlated each character independently with our dependent variables (degree of pollinator sharing and plant generalization) but we did not find a significant correlation in any case ($p > 0.05$ for all, see Table S3).

Previous studies in the dune community have shown that the floral traits studied do not have a phylogenetic signal (Albor et al., 2020), indicating that floral trait similarity is not likely determined by shared evolutionary history. Similarly, no floral trait phylogenetic signal was observed in the scrubland community (Albor C. unpublished data). However, it is important to note that other floral traits important for pollinator attraction (e.g. nectar concentration or floral scents) have shown phylogenetic signal (Ornelas et al., 2007; Prieto-Benítez et al., 2016), and these should be considered in future studies.

2.4 | Flowering overlap

To estimate flowering overlap between plant species pairs, we calculated the niche overlap index of Schoener (SI; Schoener, 1970) as follows: $\mathrm{SI} = 1 - (1/2)\Sigma k \left| P_{ik} - P_{jk} \right|$, where P_{ik} and P_{jk} are the proportion of flowering species *i* and *j*, respectively, that occurred in the day k (Forrest et al., 2010). The SI index considers the intensity (flower density) and the frequency (number of samples) of flowering overlap between each pair of plant species. Therefore, species with a high SI overlap not only flower simultaneously for longer periods of time, but also with greater intensity (i.e. high flower density). However, as we were interested in evaluating the effect of overall flowering overlap on the degree of pollinator sharing and interaction strength, we further calculated the Betweenness centrality value (BC hereafter) for each plant species within a co-flowering network where links represent the degree of co-flowering overlap between each plant species pair (Albor et al., 2020; Arceo-Gómez et al., 2018). Co-flowering networks depict groups of plant species (i.e. co-flowering modules) that overlap more in their flowering phenology than other groups in the community (see Arceo-Gómez et al., 2018). In co-flowering networks, a high BC value allows identifying plant species that due to their high degree of flowering overlap with other species in the community can function as a 'bridge' for pollinators between non-overlapping flowering species (Arceo-Gómez et al., 2018). The BC was calculated as: $\sum_{s \neq v \neq t} \frac{\sigma_{st}(v)}{\sigma_{st}}$, where σ_{st} is the total number of shortest paths from species *s* to the species *t* and $\sigma_{st}(v)$ is the number of paths of *s* and *t* that cross through the species *v* (Brandes, 2001). Following Arceo-Gómez et al. (2018), we obtained the BC of each plant species constructing a weighted undirected co-flowering network for each community using Gephi, version 9.1 (Bastian et al., 2009), and the Schoener's flowering overlap index (described above).

2.5 | Plant–pollinator networks structure, nestedness and modularity contributions

To characterize plant–pollinator network structure, we constructed an interaction frequency matrix for each site using the number of times every floral visitor was observed visiting flowers of a particular plant species (Bascompte & Jordano, 2007). The interaction matrixes were used to construct plant–pollinator networks (Figure S4) and to estimate network metrics for each plant community using the BIPARTITE package in R (Dormann & Strauss, 2014; Oksanen et al., 2015). For each plant–pollinator network, we evaluated the significance of nestedness and modularity using null model analysis to compare observed nestedness and modularity values against expectations from 1000 randomly constructed networks using the *r2dtable* algorithm (function 'nullmodel' in bipartite; Dormann & Strauss, 2014). In both communities, network nestedness and modularity were significantly different from random: dune community (nestedness = 0.61, $Z = 19.1$, $p < 0.05$; modularity = 0.13, $Z = 87.9$; $p < 0.05$) and scrubland community (nestedness = 0.72, $Z = 24.4$, $p < 0.05$; modularity = 0.21, $Z = 152.6$; $p < 0.05$).

From the plant–pollinator interaction networks, the following species-level estimators were calculated: (a) plant generalization that was estimated using the *species interaction strength*; higher strength value indicates that more pollinator species depend on it (i.e. generalist species, see Nielsen & Totland, 2014; Watts et al., 2016); (b) *nestedness contribution*, which estimates the individual contribution of each plant species to the overall nested structure of the network (Saavedra et al., 2011); and (c) *modularity contribution*, which estimates the individual contribution of each plant species to overall network modularity (Guimerà et al., 2005); for this, we estimated the distribution of links within the modules (*z* values) which refers to the number of within-module connections (Guimerà et al., 2005). To take into account that the *z* value of each species may be correlated with the even distribution of links within and across modules (*c* values), thus decreasing their contribution to modularity (see Guimerà et al., 2005), we also calculated the *c* values and tested their correlation with *z* values in both communities. The results showed no significant correlation between *c* and *z* values in any community ($t = 1.05$, $p = 0.3$, and $t = 0.2$, $p = 0.8$, respectively). The *z* and *c* values were calculated using the *czvalues* function of the BIPARTITE package of R (Dormann et al., 2009). The interaction strength value and nestedness contribution were also estimated with the package BIPARTITE in R (Dormann et al., 2009).

2.6 | Pollinator sharing

The degree of pollinator sharing between pairs of plant species was estimated using the symmetric niche overlap index of Pianka (Pianka, 1973): $O_{jk} = \left(\sum P_{ij}P_{ik}\right) / \sqrt{\left(\sum P_{ij}2 / P_{ik}2\right)}$, in which O_{jk} represents the pollinator sharing between the plant species *j* and *k*; and P_{ij} and P_{ik} represent the number of floral visits realized by the pollinator *i* to the plant species *j* y *k*, respectively. The pollinator sharing for each plant was obtained by averaging over each unique species pair. This index considers the identity of the different pollinator taxa, as well as their relative frequency of visits. The Pianka index is constrained between values of 0 and 1, in which values close to 1 indicate high pollinator sharing and values close to 0 indicate low pollinator sharing.

2.7 | Statistical analyses

To test the causal framework proposed (Figure 1), a structural equation model (SEM) was adjusted for each community using the package PIECEWISESEM in R (Lefcheck, 2016). The use of SEM models allows multiple hypotheses to be tested simultaneously and is a useful tool for quantifying direct and indirect effects by linking multiple variables into a single causal framework (Grace, 2006; Lefcheck, 2016). Additionally, this procedure allows detecting significant relationships between variables originally not considered within the proposed relationship structure.

The overall fit of the SEMs for each community was evaluated with Shipley's *d*-generalized separation test based on Fisher's *C* statistics (Shipley, 2009). Fisher's *C* statistic evaluates whether the data recorded in the field fit the causal hierarchical predictions proposed in the model and evaluates whether all possible explanatory variables are included (Shipley, 2009). To improve the fit of the SEMs, we include autocorrelation between variables at the same hierarchical level. In all cases, means ± *SD* are presented unless otherwise specified. All the R scripts used for data analyses are available in Appendix S1.

3 | RESULTS

We recorded 74,965 flowers belonging to 40 plant species (dune: 29,065 flowers of 28 species; shrub: 45,900 of 35 species) during the entire flowering period. In all, 42 species/morphospecies of pollinators and 23 species of visited plants were recorded in the dune community, and 48 and 25 in the scrubland community, respectively: Hymenoptera (dune: 3141 visits [73%], scrubland: 2309 visits [67%]), Diptera (dune: 625 visits [14.5%], scrubland: 687 visits [20%]) and Lepidoptera (dune: 536 visits [12.5%], scrubland: 442 visits [12.8%]; Table S2). Average interaction strength in the dune and in the scrubland community were similar (1.49 ± 2.16 and 1.37 ± 2.7, respectively), suggesting low plant generalization in both. However, we observed large variation in the level of generalization among plant species in both communities (Figure S5). For example, in the sand dune, species, such as *Melanthera nivea*, *Bidens pilosa* and *S. plumieri*, showed high plant generalization (7.63, 6.87 and 5.05, respectively) and in the scrubland community the species with high plant generalization were *M. nivea*, *Porophyllum punctatum* and *Lantana involucrata* (10.63, 9.36 and 8.53, respectively). In contrast, in the sand dune, the species with the lowest plant generalization were *Gomphrena serrata*, *Sesuvium portulacastrum* and *Varronea globosa* (0.01, 0.03 and 0.09, respectively), and in the scrubland community *C. punctatus*, *Acanthocereus tetragonus* and *Agave angustifolia* (0.02, 0.001 and 0.001, respectively; Suárez-Mariño et al., 2022).

In both communities, more than one-third of the pollinators were shared (0.32 ± 0.26 and 0.40 ± 0.10, sand dune community and scrubland community, respectively; Figure S5; Suárez-Mariño et al., 2022).

3.1 | Flowering overlap and floral trait similarity

Average BC score in the dune community was 1.78 ± 1.52 and in the coastal scrubland was 4.71 ± 4.94. However, we observed large variation in BC among plant species in both communities (Figure S5); for instance, in the sand dune, seven species did not overlap in flowering (e.g. *Commicarpus scandens*, *Sesuvium portulacastrum*) and others showed values over twice the average BC score (e.g. *B. pilosa*, *C. edentula*, *M. nivea* and *S. plumieri*; Suárez-Mariño et al., 2022). Similarly, in the scrubland 10 species that did not overlap in flowering at all (e.g. *Acanthocereus tetragonus*, *Pithecellobium keyense*) and others showed overlap values up to three times higher than the average BC score (e.g. *C. rosea*, *M. nivea*, *P. punctatum*, *Waltheria rotundifolia*; Figure S5; Suárez-Mariño et al., 2022). Overall floral similarity was similar between communities (0.75 ± 0.08 and 0.76 ± 0.08, dune and scrubland communities, respectively), suggesting high floral resemblance between plant species in both communities (Figure S5).

3.2 | Hypotheses testing: Structural equation models (SEM)

Fisher's *C* values indicated that the proposed SEMs models in both communities adequately represented the data and support the hierarchical structure proposed in the models (dune community: $C = 4.14$; $p = 0.12$ and scrubland community $C = 0.05$; $p = 0.97$). In both communities, SEM showed a significant positive effect of flowering overlap on plant generalization, but not on the degree of pollinator sharing (Figure 3b; Table 1). In contrast, floral trait similarity had no significant effect on either pollinator sharing or plant generalization in any community (Figure 3b; Table 1). Pollinator sharing and interaction strength showed a significant positive effect on nestedness contribution in both communities (Figure 3c; Table 1). Taken together, these results suggest that greater flowering overlap affects plant–pollinator network structure in both communities through its positive effects on plant generalization (Figure 3b). In addition, SEM analysis revealed a significant, but not previously considered, direct and positive effect of flowering overlap on network modularity in the sand dune community (Figure 3c; Table 1), suggesting that greater flowering overlap increases the number of species links within modules.

The results suggest that the effect of floral trait similarity on pollinator sharing was site dependent. While in the scrubland community SEM revealed a significant interaction effect of flowering overlap and floral trait similarity on pollinator sharing, in the dune community floral trait similarity did not show a significant effect (Figure 3a,b; Table 1).

This result suggests that in the scrubland community species with high values of flowering overlap and high floral trait similarity have the highest levels of pollinator sharing, but suggests that pollinator sharing would be low even at high levels of flowering overlap if floral trait similarity among species is low (Figure 4). Because SEM showed a significant effect of pollinator sharing on nestedness contribution in this community, this interaction effect may also have an indirect effect on network nestedness (Figure 3c). Finally, the SEM revealed a negative correlation between nestedness and modularity contribution for both communities (Figure 3c; Table 1).

4 | DISCUSSION

Our results showed that flowering overlap affects the structure of plant–pollinator networks mainly via its effect on degree of plant generalization (i.e. the number of pollinator species associated with a single plant). Interestingly, the effect of floral trait similarity appeared to be contingent on the degree of flowering overlap, at least in one community. Overall, our results provide insights into the factors and potential underlying mechanisms that explain the structure of pollination networks, mainly through their effects on pollinator use by plants.

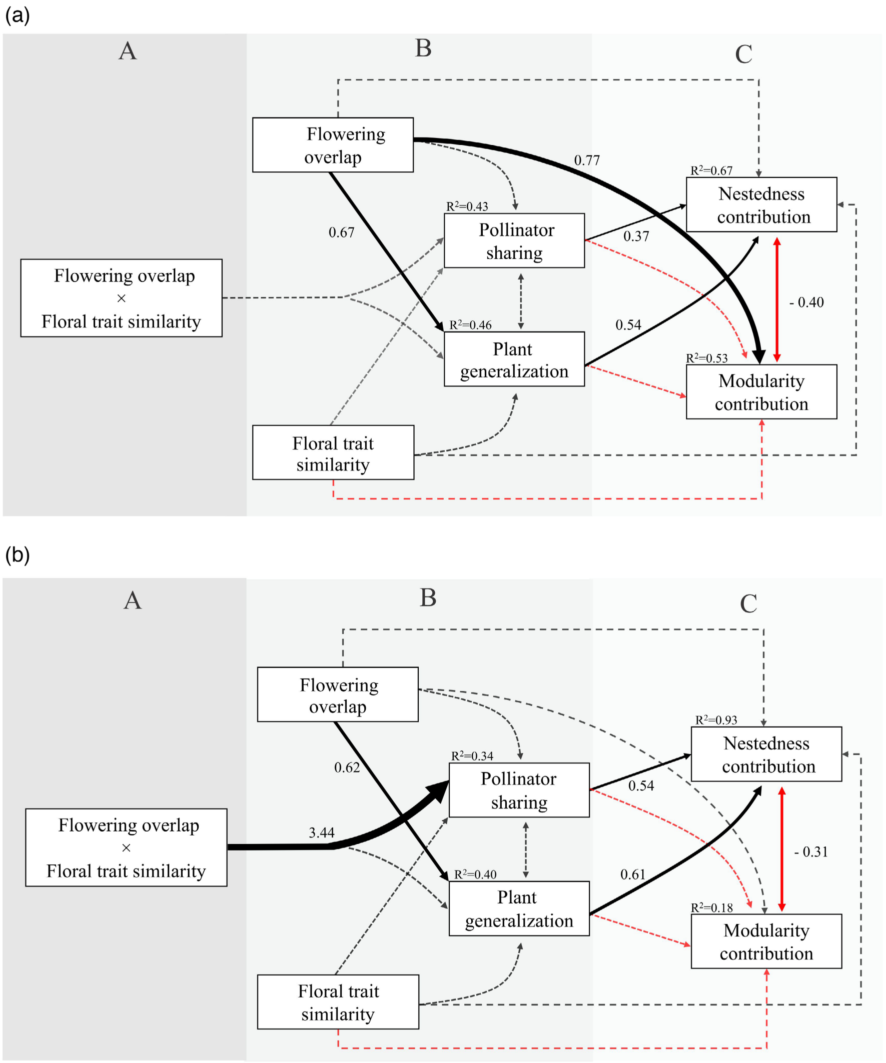

FIGURE 3 Results from structural equation models (SEMs) at the sand dune community (a) and the coastal scrubland community (b), for the effects of flowering overlap, floral trait similarity, plant generalization and pollinator sharing, and of these four variables in the structure of the plant–pollinator networks. The solid arrows show a significant relationship between the variables ($p \leq 0.05$). Non-significant routes ($p > 0.05$) are indicated by dashed lines. For significant effects, the values of the standardized regression coefficients are shown (values shown over the box). Black colour lines show positive effects and red colour lines negative effects.

4.1 | Effect of flowering overlap on pollinator sharing, plant generalization and its consequences on plant–pollinator networks

Studies of flowering phenology in natural communities have a long history in ecology, and they have shown its importance for understanding patterns of pollinator use by plants and partitioning of floral resources by pollinators (e.g. Feinsinger, 1987; Rathcke & Lacey, 1985). However, the importance of phenological patterns in mediating the structure of entire plant–pollinator networks is less understood (but see Encinas-Viso et al., 2012; Lázaro et al., 2020; Vázquez et al., 2009). Here we show that the degree of flowering overlap can help elucidate the contribution of individual plant species to the structure of plant–pollinator networks via its effect on plant generalization. Our study showed that in both communities an increase in flowering overlap leads to a higher degree of plant generalization. These results are in line with similar studies that have shown a link between flowering phenology and specialization (or generalization) in animal-pollinated plants (e.g. Biella et al., 2017; Lázaro et al., 2020; Tur et al., 2013; Watts et al., 2016). For instance, in a diverse marshland, Lázaro et al. (2020) observed that an increase in flowering duration decreased the level of plant specialization and determined a plants' role in the network as core or peripheral species. Our results also highlight the potential role of interspecific variation in flowering phenology in mediating plant–pollinator network structure.

Our study further suggests that the degree of flowering overlap can indirectly influence the contribution of each plant species to the nested structure of plant–pollinator networks. This via its direct positive effect on plant generalization. For instance, in the sand dune and scrubland communities, species, such as *Bidens pilosa* and *Scaevola plumieri*, and *Melanthera nivea* and *Porophyllum punctatum*, respectively, showed the highest flowering overlap with all other species and also interacted with 20%–60% of the pollinator species present in these communities (Suárez-Mariño et al., 2022; Figure S5). Thus suggesting that these plant species can be key to maintaining the nested structure of plant–pollinator networks in the studied communities (Campos-Navarrete et al., 2013; Parra-Tabla et al., 2019; Suárez-Mariño et al., 2019; and see Arceo-Gómez et al., 2018; Martín González et al., 2010). Interestingly, our study also revealed a non-previously considered direct effect of flowering overlap on network modularity.

TABLE 1 Results of the structural equation model (SEM) for the coastal dune and coastal scrubland communities. Each dependent variable is shown numbered and in bold type with its respective predictor variables (see Figure 1). Standardized regression coefficients estimates (±*SE*) are shown. Significant effects (<0.05) are shown in bold type.

	Sand dune				Coastal scrubland			
Variables	Estimate	*SE*	*df*	*p*	Estimate	*SE*	*df*	*p*
1. Pollinator sharing								
Floral trait similarity	0.02	0.68	24	0.90	−0.28	0.95	31	0.27
Flowering overlap	0.83	0.36	24	0.69	−2.97	0.10	31	0.07
Floral trait similarity × Flowering overlap	−0.17	0.46	24	0.93	3.44	0.13	31	**<0.05**
2. Nestedness contribution								
Floral trait similarity	0.19	1.78	23	0.11	−0.01	0.77	30	0.80
Pollinator sharing	0.37	0.82	23	**<0.05**	0.54	0.21	30	**<0.001**
Flowering overlap	−0.06	0.15	23	0.70	0.004	0.01	30	0.94
Plant generalization	0.54	0.10	23	**<0.01**	0.61	0.02	30	**<0.001**
3. Modularity contribution								
Floral trait similarity	0.04	1.54	23	0.74	0.003	1.97	30	0.98
Pollinator sharing	0.04	0.71	23	0.81	0.29	0.55	30	0.13
Flowering overlap	0.77	0.13	23	**<0.01**	0.28	0.04	30	0.22
Plant generalization	−0.12	0.09	23	0.55	−0.15	0.07	30	0.47
Nestedness contribution	−0.40	—	28	**<0.05**	−0.31	—	35	**<0.05**
4. Interaction strength								
Flowering overlap	0.67	0.21	25	**<0.001**	0.62	0.07	32	**<0.001**
Floral trait similarity	0.02	3.58	25	0.87	0.25	4.39	32	0.07
Pollinator sharing	—	—	23	0.12	—	—	30	0.97

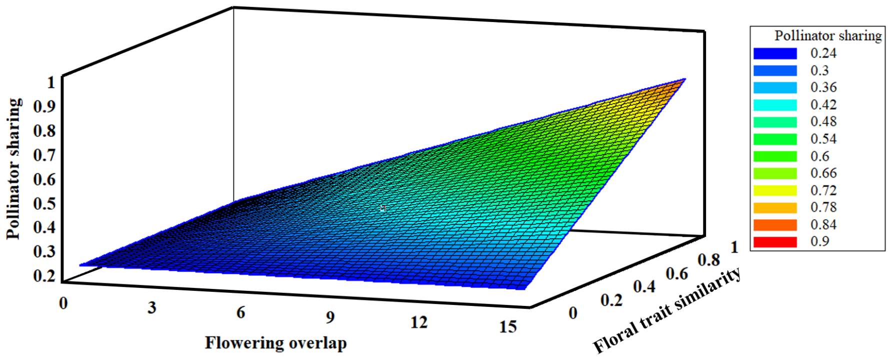

FIGURE 4 Surface plot of the interaction effect between flowering overlap and floral trait similarity on pollinator sharing in the scrubland community.

It is possible that the effect of flowering overlap on modularity is driven by the formation of co-flowering modules in which an increasing flowering overlap also increases the frequency of specialized interactions. This means that in the sand dune community some species can have high levels of flowering overlap and also be specialized. For instance, species as *Canavalia rosea* and *Croton punctatus* showed high levels of flowering overlap but were visited by less than 10% of the pollinator species (see Figure S5). This pattern could be due to increased competition for pollinators, which would lead to low pollinator sharing and more specialized plant–pollinator interactions (see Valdovinos & Marsland, 2021; Wei et al., 2021). The sand dune has been described as a community characterized by limited pollinator activity and high plant competition for pollinators (Albor et al., 2020; Parra-Tabla et al., 2019). Further studies should thus test whether low pollinator visits is a limiting factor for seed production, to fully establish the impact of competition for pollinators for the persistence of plant populations in this community.

4.2 | Effect of floral trait similarity on pollinator sharing, plant generalization and its consequences on plant–pollinator networks

Our prediction regarding the effect of floral trait similarity on pollinator sharing and plant generalization was partially supported.

While in the sand dune community we did not observe an effect of floral trait similarity, in the scrubland community its effect was dependent on flowering overlap, suggesting a site-dependant effect of floral similarity on the structure of plant–pollinator networks.

A growing number of studies that have shown that an increase in floral trait similarity can lead to an increase in pollinator sharing (e.g. Albor et al., 2020; Carvalheiro et al., 2014; Ghazoul, 2006; Gibson et al., 2012; Sargent & Ackerly, 2008). For instance, Gibson et al. (2012) found that floral trait similarity between native and invasive plants predicts the degree of flower visitor overlap between them. However, the lack of a significant effect of flower trait similarity in the sand dune community may be because average trait similarity is already very high with low variability (sand dune community 0.75 ± 0.08). Interestingly, a study conducted in multiple dune communities in the same geographic area found no differences in floral trait similarity between species with greater flowering overlap (0.79 ± 0.14) compared to those with low phenological overlap (0.78 ± 0.23; Albor et al., 2020). This suggests that in these communities there is an already high floral trait similarity regardless of species phenological differences. In coastal ecosystems with harsh abiotic conditions (e.g. high temperatures, salt spray, winds), flowering plants typically experience low floral visitation rates (e.g. Campos-Navarrete et al., 2013; Parra-Tabla et al., 2019). In these type of environments, it would be expected that facilitative plant–plant interactions that increase pollinator attraction would be predominant, hence resulting in high floral similarity and high levels of pollinator sharing (see Albor et al., 2020; Bergamo et al., 2020; Sargent & Ackerly, 2008). Thus, it is possible that strong pollinator limitation in these ecosystems leads to high floral similarity that constrains or decreases pollinator responses to floral trait variation.

However, despite high floral trait similarity in the scrubland community (0.76 ± 0.08), we found a significant flowering overlap × floral trait similarity interaction on pollinator sharing. This result could have important implications in our understanding of the mechanisms that mediate the assembly of co-flowering communities. For instance, while high competition for pollinators may lead to low pollinator sharing and more specialized plant–pollinator interactions, facilitation may lead to high pollinator sharing and thus more generalized plant–pollinator interactions in co-flowering communities (Albor et al., 2020; Sargent & Ackerly, 2008; Valdovinos & Marsland, 2021; Wei et al., 2021). Thus, the contingent effect between flowering phenology and floral traits, further underlines the importance of not considering plant traits independently if we want to advance our understanding of the mechanisms mediating community assembly. In addition, future studies should also evaluate pollinator phenology and trait matching between floral and pollinator traits, as these factors can be important in explaining the temporal and spatial stability of pollination networks (see Bergamo et al., 2017; Peralta et al., 2020).

On the other hand, it is important to note that another factor that could mask single or combined effect of floral trait similarity, is that in both communities there is a high dominance of the introduced honey bee *Apis mellifera*, which can monopolize floral visits (63.2% and 48.4% of the total flower visits in the sand dune and in the scrubland community, respectively; Figure S4; Table S2) and interacts with a very high proportion of plant species (76.1% and 88% in the sand dune and in the scrubland community, respectively; Figure S4; Table S2). It is possible that the presence of this super-generalist species causes a rearrangement in the identity of plant–pollinator interactions (e.g. Herrera, 2020b; Magrach et al., 2017; Montero-Castaño & Vilà, 2017), potentially diluting the single or combined effects of floral trait similarity and flowering overlap (see Montero-Castaño & Vilà, 2017).

Finally, it is important to note that we observed some differences between the two plant communities suggesting that the effect of flowering overlap and floral trait similarity on the structure of plant–pollinator networks may be community dependent. Although this study was not designed to compare both communities, or to make inferences by vegetation type, it is worth pointing out that these communities differ in their composition of flowering species, but not in the composition of pollinator species. This underlines the importance of an explicit incorporation of flowering phenology as a driver of the structure of plant–pollinator networks. Furthermore, we observed an effect of floral similarity contingent on flowering overlap (in the scrubland community), underlying the importance of considering both factors to understand their individual or combined effect on the structure of plant–pollinator networks. Future studies should also consider comparisons between multiple communities as well as consider temporal changes in the composition of plant and pollinator communities (Albor et al., 2020; CaraDonna & Waser, 2020; Schwarz et al., 2020). This in order to more fully understand the underlying mechanisms shaping plant–pollinator networks.

AUTHORS' CONTRIBUTIONS

A.S.-M, V.P.-T. and G.A.-G. conceptualized the study; A.S.-M and C.A. collected and analysed the data; the manuscript was drafted by A.S.-M and V.P.-T. The final MS was edited by all the co-authors.

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CONFLICT OF INTEREST

The authors declares that there are no conflict of interest.

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