CHARLES C. SHERROD LIBRARY
EAST TENNESSEE STATE UNIVERSITY

ILLiad Delivery Cover Sheet

To provide the fastest service, many documents are delivered to you automatically without staff intervention. If this item has missing or illegible pages, please let us know. We will obtain a better copy for you.

Email: libloan@etsu.edu

This article will be available in your ILLiad account for 30 days from the date of delivery.

Please be sure to download it to your computer.

NOTICE CONCERNING COPYRIGHT RESTRICTIONS

The copyright law of the United States (Title 17, United States Code) governs the making of photocopies or other reproductions of copyrighted material.

Under certain conditions specified in the law, libraries and archives are authorized to furnish a photocopy or other reproduction. One of the specified conditions is that the photocopy reproduction is not to be "used for any purpose other than private study, scholarship, or research." If a user makes a request for, or later uses, a photocopy or reproduction for purposes in excess of "fair use", that user may be liable for copyright infringement.

This institution reserves the right to refuse to accept a copying order if, in its judgment, fulfillment of the order would involve violation of copyright law.

Rapid #: -19364797

CROSS REF ID: **515152**

LENDER: **MVS :: Main Library**

BORROWER: **TET :: Charles C. Sherrod Library**

TYPE: Article CC:CCG

JOURNAL TITLE: Functional ecology

USER JOURNAL TITLE: Functional ecology. Functional ecology.

ARTICLE TITLE: Flower colour and flowering phenology mediate plant–pollinator interaction assembly in a diverse co flowering community

ARTICLE AUTHOR: Albor, Cristopher

VOLUME: https://doi.org/10.1

ISSUE:

MONTH: 07

YEAR: 2022

PAGES: -

ISSN: 0269-8463

OCLC #: 45446903

Processed by RapidX: 8/5/2022 6:48:47 AM

Received: 18 February 2022 | Accepted: 5 July 2022

DOI: 10.1111/1365-2435.14142

Functional Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Flower colour and flowering phenology mediate plant–pollinator interaction assembly in a diverse co-flowering community

Cristopher Albor[1] | **Tia-Lynn Ashman**[2] | **Amber Stanley**[2,3] | **Carlos Martel**[3] | **Gerardo Arceo-Gómez**[3]

[1]Department of Biological Sciences, University of Calgary, Calgary, AB, Canada

[2]Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA, USA

[3]Department of Biological Sciences, East Tennessee State University, Johnson City, TN, USA

Correspondence
Gerardo Arceo-Gómez
Email: gomezg@etsu.edu

Present address
Carlos Martel, Royal Botanical Gardens at Kew, London, UK

Handling Editor: Oscar Godoy

Abstract

1. Uncovering the role of competition and facilitation in community assembly is central for developing a predictive understanding of the forces that organize biodiversity. Standard trait-based approaches however rely on detection of only one assembly mechanism (competition or facilitation) along a single trait even though pollinator-mediated plant–plant interactions can be structured along multiple phenotypic, phenological and ecological traits.
2. We evaluated plant species distribution along multiple phenotypic and ecological traits (flower colour, flowering time, pollinator sharing) and described an entire co-flowering community as a set of modules with unique patterns of assembly, to test predictions regarding the relative contribution of competition and facilitation to the assembly of a diverse co-flowering community.
3. We show a modular pattern of flower colour assembly. Flower colour modules differ in their spectral reflectance patterns including colour hue and saturation. Within modules, however, species are differentially assembled along phenological and ecological traits (pollinator sharing) depending on the main pollinator group visiting plant species within each module. Results suggest different trait assembly patterns within individual trait-modules in the same co-flowering community and that different trait-patterns can result from the same type of ecological interaction.
4. This study reveals empirical evidence of community assembly along multiple axes of trait differentiation and raises caution when interpreting assembly patterns based on a single trait.

KEYWORDS
community assembly, competition, facilitation, floral colour, flowering time, modularity, pollination, trait network

1 | INTRODUCTION

Understanding the role of deterministic, neutral and historical processes in mediating the assembly of natural communities is a major goal in ecology and a topic of active research (Cavender-Bares et al., 2009; Clements, 1916; Diamond, 1975; Gleason, 1926; Götzenberger et al., 2012; Keddy, 1992; Ricklefs, 1987; Sargent & Ackerly, 2008; Tilman, 2004; Weiher et al., 1998). Within local communities, prevailing ecological theory suggests that biotic interactions within a trophic level can act as strong filters shaping species assembly (Cavender-Bares et al., 2009; Diamond, 1975; E-Vojtkó et al., 2020; Gómez et al., 2010; Götzenberger et al., 2012; Sargent & Ackerly, 2008; Valiente-Banuet & Verdú, 2007; Wilson, 1999). These interactions can be positive (e.g. facilitation) or negative (e.g. competition) and mediate the coexistence of plants (e.g. Sargent & Ackerly, 2008; Valiente-Banuet & Verdú, 2007; Wei et al., 2021) and animal species (e.g. Gómez et al., 2010; Ingram & Shurin, 2009). Nonetheless, the relative importance of competition versus facilitation in community assembly is an area of ongoing debate and still unknown in some systems (e.g. plant communities; Ashman et al., 2020; Götzenberger et al., 2012). This is mainly due to the difficulty of incorporating the intrinsic complexities of species-rich communities and the interactions within them (Ashman et al., 2020; Götzenberger et al., 2012; Hegland et al., 2009; Wei et al., 2021). This gap in knowledge has in turn hindered our ability to gain a more complete understanding of the ecological processes and underlying mechanisms that shape natural communities (Ashman et al., 2020; Götzenberger et al., 2012; Wolowski et al., 2017). Disentangling the role of competition and facilitation in community assembly is not only central for developing a predictive understanding of the processes that organize biodiversity, but it is also crucial for understanding how communities will respond to increasing human disturbances.

Pollinator-mediated interactions among plants can be key in shaping community assembly (de Jager et al., 2011; Sargent & Ackerly, 2008; Wei et al., 2021). For instance, floral traits such as colour, scent and quantity and quality of floral rewards determine how pollinators interact with flowers (e.g. Larue et al., Larue-Kontić & Junker, 2016; Yan et al., 2016), and can thus determine how plants interact with each other via pollinator attraction (Phillips et al., 2020; Sargent & Ackerly, 2008). However, in highly diverse plant communities, experimentally evaluating the direction of pollinator-mediated interactions (i.e. facilitation vs competition) between large numbers of plant species-pairs can be a daunting task (Mitchell et al., 2009). Hence, analytical approaches that evaluate phylogenetic and functional trait distributions have been widely used to uncover signals of pollinator-mediated competition and facilitation at the community level (e.g. de Jager et al., 2011; Kemp et al., 2019; McEwen & Vamosi, 2010; Sargent & Ackerly, 2008; Wolowski et al., 2017). Pollinator competition or facilitation have thus been inferred from the distribution of floral traits (e.g. flower colour) within a community (Sargent & Ackerly, 2008). For example, the functional clustering or aggregation of floral traits (compared with a random distribution) is interpreted as evidence of facilitation as the main force structuring co-flowering communities (de Jager et al., 2011; Sargent & Ackerly, 2008). This is because plants with high floral trait similarity amplify pollinator attraction and increase plant fitness compared with when they flower alone, hence promoting co-flowering. On the other hand, functional divergence or over-dispersion of floral traits is interpreted as evidence of pollinator competition (McEwen & Vamosi, 2010; Sargent & Ackerly, 2008). Floral trait over-dispersion leads to pollinator use differentiation and increases plant fitness in the presence of competition, thus allowing plants to co-flower (Sargent & Ackerly, 2008; Wei et al., 2021). However, pollinator competition and facilitation are not mutually exclusive (e.g. Bergamo et al., 2018; Tur et al., 2016), and it is unlikely that only one or the other is singly responsible for determining the structure of entire co-flowering communities.

The current reliance on solo-acting community assembly mechanisms (competition or facilitation) can be augmented by the use of trait-based approaches that evaluate species distribution along a single axis of trait differentiation (e.g. flower colour; McEwen & Vamosi, 2010; de Jager et al., 2011; Kemp et al., 2019; LeCroy et al., 2021). However, this is inadequate because pollinator-mediated plant–plant interactions are likely shaped by multiple phenotypic, phenological and ecological traits. For instance, species can be clustered in flower colour space but diverge in flowering time [first (blue) panel in Figure 1; Albor et al., 2020; Bergamo et al., 2018; Waser, 1978; Waser & Real, 1979]. From the perspective of flower colour alone such a pattern would be interpreted as pollinator facilitation even though plants do not flower at the same time and is unlikely they interact via pollinators (e.g. Albor et al., 2020; Bergamo et al., 2018), except in the still seldom documented case of sequential facilitation (see Braun & Lortie, 2019; Waser & Real, 1979). In fact, divergence in flowering phenology (i.e. flowering time) would likely suggest pollinator competition plays a larger role than facilitation (e.g. Aizen & Vázquez, 2006; Waser, 1978). Indeed, in a recent study, Albor et al. (2020) found that floral trait similarity is significantly higher when plant species overlap in flower time compared with when they do not. This result suggests that pollinator competition and facilitation may lead to species distribution along phenotypic and phenological axes, respectively (Figure 1a). Pollinator competition, for instance, can also be evidenced by high floral trait divergence among species with high flowering overlap [third (grey) panel in Figure 1; Albor et al., 2020]. Thus, studies that integrate trait distribution patterns along multiple traits are necessary to reveal the relative importance of pollinator competition and facilitation in mediating the assembly of natural plant communities.

Here we integrate multi-trait phenotypes with the use of network analyses to help uncover the more complex nature of community assembly processes described above, where different mechanisms (Figure 1a) may act on a different subset of species in the community. Specifically, networks based on trait distances can reveal modular patterns of community structure along one floral trait (e.g. flower colour; Figure 1b). Modularity in trait-networks reflects the grouping of species based on trait distances, where some species are more similar to each other in trait-space (within modules)

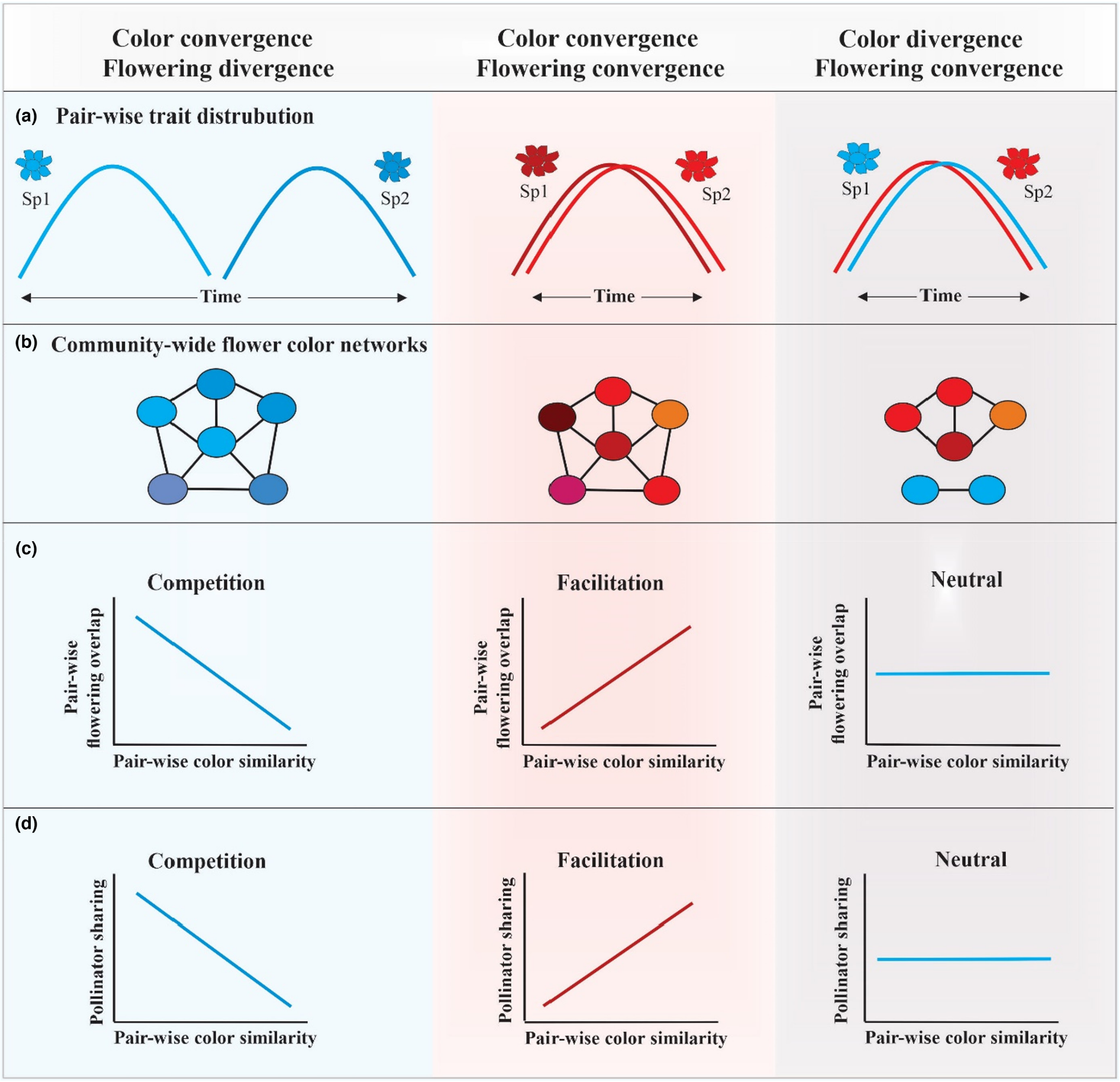

FIGURE 1 (a) Predicted flowering time and floral colour distribution patterns resulting from pollinator-mediated facilitative and competitive interactions between plant species-pairs in co-flowering communities. Similar colours reflect similarity in floral phenotypes (flower colour) and curves represent flower abundances across time. The first (blue) panel shows trait clustering of floral colour but over-dispersion in flowering time suggesting pollinator-mediated competitive interactions between plant species. The second (red) panel shows clustering of floral colour and flowering time suggesting pollinator-mediated facilitative interactions. The third (grey) panel shows over-dispersion in floral colour and clustering in flowering time suggesting niche differentiation as a result of pollinator-mediated competitive interactions. (b) Expected community-wide floral colour-networks constructed using flower colour distances between plant species (1-Euclidean distance); floral-colour modules reflect groups of plant species that are more similar to each other in flower colour space compared with species in other modules. Nodes (circles) represent plant species, the colour of the circles reflects different flower colours and the lines reflect the extent of flower colour similarity between species-pairs (c) expected relationship between flower-colour similarity and flowering overlap among species (within a trait-module) under the different competitive and facilitative scenarios. (d) Expected relationship between flower-colour similarity and pollinator use overlap (degree of pollinator sharing) among species (within a trait-module) under the different competitive and facilitative scenarios associated with specific patterns of flower colour and flowering time assembly.

compared with species in other groups (i.e. among modules; also see Kantsa et al., 2017; Albor et al., 2020; also see Olesen et al., 2007; Dupont & Olesen, 2009). While traditional null model approaches that rely on solo-acting assembly mechanisms reveal single patterns of flower colour distribution (i.e. all species are clustered or over-dispersed; de Jager et al., 2011; McEwen & Vamosi, 2010), trait-networks can reveal the existence of multiple trait-modules, each reflecting a distinct pattern of floral trait grouping [Kantsa et al., 2017; see third (grey) panel in Figure 1b]. This approach has thus the potential to reveal more realistic patterns of trait assembly since it is unlikely that all species in a community will either overlap or diverge in trait space (e.g. flower colour). In fact, most plant communities contain a wide diversity of flower colours associated with different pollinator groups (e.g. Ishii et al., 2019; Kemp et al., 2019), and with varying levels of similarity that may be better described via trait-network modularity (Figure 1b; Kantsa et al., 2017, 2018). This approach has been previously used to uncover the importance of modularity in floral scent (Kantsa et al., 2017, 2018) and flowering time (Albor et al., 2020) in structuring plant-pollinator interactions at the level of the entire community. However, to our knowledge, no study has used this approach to evaluate the drivers of pollinator-mediated plant interactions within individual trait-modules and to evaluate if multiple drivers (e.g. competition and facilitation) may operate within the same community. For instance, the study by Albor et al. (2020) revealed that, on average, floral trait similarity is higher for species within than between co-flowering modules, hence suggesting that only pollinator-mediated facilitation operates within all trait-modules. However, it is possible that competition and facilitation may occur simultaneously within different trait-modules. Thus, it is conceivable that not one (e.g. Albor et al., 2020), but all three assembly mechanisms and their underlying trait distribution patterns (Figure 1), operate within a single co-flowering community. However, to our knowledge, such a tantalizing possibility remains unexplored.

For instance, species distribution patterns along phenological (e.g. flowering overlap) and ecological axes (e.g. pollinator sharing) can be explored to reveal signals of pollinator competition and facilitation within individual floral trait-modules. In this sense, we can expect that if pollinator-mediated competition is the dominant force then increasing flower colour similarity between species within a module should decrease the intensity of flowering overlap [first (blue) panel in Figure 1c] and pollinator sharing (blue panel in Figure 1d) in order to minimize competition. On the contrary, if pollinator-mediated facilitation is the dominant process, then increasing flower colour similarity between species within a module should lead to increasing flowering overlap [second (red) panel in Figure 1c] and pollinator sharing (red panel in Figure 1d). Finally, in instances where trait over-dispersion (driven by pollinator competition) is sufficient to enhance co-flowering then we would not expect a relationship between flowering overlap and trait-distance [third (grey) panel in Figure 1c]. This because in this scenario (grey panel in Figure 1) co-flowering would be solely maintained by flower colour/niche differences that minimize pollinator competition (e.g. pollinator specialization). Thus, pollinator sharing is not expected to be high due to strong flower colour differentiation [third (grey) panel in Figure 1d]. However, if phenotypic similarity does occur between some species, it may increase pollinator sharing due to their high flowering overlap. This theoretical framework would not only allow the detection of multiple assembly mechanisms acting simultaneously but will also allow us to uncover the specific species involved in facilitative versus competitive interactions within highly diverse plant communities.

Here we evaluated distribution patterns of flower colour, flowering time and pollinator sharing using the above theoretical framework (Figure 1), and study an entire plant community by characterizing it as a set of multiple modules (based on flower colour differences), each with potentially unique patterns of assembly. We do this to further test the associated predictions regarding the role of competition and facilitation in the assembly of a diverse co-flowering community in northern California (Figure 1). Specifically we ask, (a) is co-flowering community assembly driven by pollinator competition, facilitation or both mechanisms acting simultaneously? and (b) is co-flowering assembly mediated by species distribution along one or multiple ecological and/or phenotypic axes (floral colour, flowering phenology, pollinator sharing)? Because shared evolutionary history can also drive patterns of flowering phenology (Rafferty & Nabity, 2017) and floral trait assembly (Ibanez et al., 2016; Shrestha et al., 2014), we also evaluated the role of phylogenetic relatedness in mediating the patterns observed (Webb, 2000; Webb et al., 2002).

2 | MATERIALS AND METHODS

2.1 | Study site

The study was conducted in a diverse serpentine seep co-flowering community at the McLaughlin Natural Reserve in northern California, USA (38°51′41.4″N, 122°23′54.8″W; banana slug site in Koski et al., 2015; Wei et al., 2021). This reserve is part of the University of California Natural Reserve System, which provided permission to conduct the study. The plant community at the time of flower colour data collection (summer, May–June 2018) was composed of 39 annual and perennial insect-pollinated plant species (Table S1) growing embedded within a matrix of grassland and shrubland (medium size shrubs and bushes). Species number at these seeps however has been observed to vary spatially and temporally (Arceo-Gómez et al., 2018; Koski et al., 2015; LeCroy et al., 2021; Wei et al., 2021). Previous studies have also shown a high level of direct (via pollen transfer e.g. Arceo-Gómez et al., 2016) and indirect (via pollinator sharing) plant–plant interactions in these communities (e.g. Koski et al., 2015; Wei et al., 2021), which can shape the distribution of floral colour and flowering time (Arceo-Gómez et al., 2018; LeCroy et al., 2021; Sargent & Ackerly, 2008). The floral visitor community is primarily composed of bees but it also includes flies, butterflies and beetles among other insects (Koski et al., 2015; Wei et al., 2021). Flowering typically takes place within a short period of time (between May and July) when the seeps remain wet (Alonso et al., 2017; Arceo-Gómez et al., 2018). This short flowering period also limits the effect of environmental variation (temperature and photoperiod) in the timing and duration of flowering and increases the importance of biotic interactions in structuring co-flowering communities (Elzinga et al., 2007).

2.2 | Flower colour

We chose floral colour because it is considered an important trait mediating pollinator preference and shaping the structure of co-flowering communities (e.g. Kantsa et al., 2017; van der Kooi et al., 2016). Here, we measured floral reflectance spectra (340–700 nm) from the dominant corolla colour in five flowers per species with a handheld field spectrometer (StellarNet Inc.). Floral reflectance spectra were collected for all 39 plant species present at the site in the summer (May–June) of 2018 (Figure S1). Because hymenopterans (i.e. bees) are the most abundant floral visitors at the study site (Koski et al., 2015; Wei et al., 2021) we further used this data to model flower colour in the trichromatic colour-hexagon of the Hymenoptera vision model which considers the excitation of three types of photoreceptors (green, blue, and UV; Chittka, 1992). Bee colour hexagon and chromatic colour components (hue and saturation) were estimated using the R package PAVO (Maia et al., 2013) considering standard green as the background and D65 'standard daylight'. Colour hue (tonality/primary colour) is measured as a circular angle (i.e. hue angle: 0–360°) leading to six bee colour categories (blue, blue-green, green, UV, UV-blue, and UV-green; Kelber & Osorio, 2010; van der Kooi et al., 2019), whereas colour saturation (spectral purity) represents the spectral purity of colour (without grey and white light; Kelber & Osorio, 2010; van der Kooi et al., 2019).

2.3 | Flower colour similarity network

We constructed a flower colour network based on the level of flower colour similarity (using untransformed floral reflectance spectra) as a link between plant species-pairs (Figure 1d; also see Kantsa et al., 2017). Floral reflectance shows the intensity of reflected light by flowers (i.e. the observed colour) provided in relative proportions (i.e. 0% means that the flowers do not reflect any light in a specific wavelength, whereas 100% indicates full reflection). To construct a flower colour network, we estimated Gower's pairwise distances (Gower, 1971) between each plant species pair using the floral reflectance matrix (340 to 700 nm; e.g. Albor et al., 2020). Gower's distance has been shown to perform well with continuous data such as with flower colour distances (Gower, 1971; Laliberté & Legendre, 2010). Gower's distance (1 − average dissimilarity) thus represents the degree of flower colour similarity between two plant species (Albor et al., 2020; Gower, 1971). Species-pairs with colour distances lower than 0.2 were considered as 'identical' (colour distance equal to zero) in colour as insects, particularly Hymenoptera, often discriminate colours above this threshold (Chittka et al., 2001; de Jager et al., 2011). With this colour similarity matrix (Gower's distance) we constructed a undirected colour similarity network using Gephi 9.1 (Albor et al., 2020; Arceo-Gómez et al., 2018; Bastian et al., 2009; Fang & Huang, 2013). We then estimated network modularity (Q) to identify groups of species with higher flower colour similarity compared with other species in the community using the BIPARTITE package in R and the algorithm 'QuanBiMo' (Dormann & Strauss, 2014). Network modularity ranges from 0 (no modularity) to 1 (complete modularity; Dormann & Strauss, 2014). The significance of network modularity was evaluated using a null model approach to compare observed modularity with expectations derived from 1,000 randomly constructed networks (using the same observed colour distance values) using the 'r2dtable' algorithm and the 'nullmodel' function in the BIPARTITE package in R (Dormann & Strauss, 2014; also see Albor et al., 2020). We standardized modularity by calculating the Z-score of Q as: $ZQ = (Q_{\text{observed}} - Q_{\text{null}})/SDQ_{\text{null}}$. The Z-score measures the number of standard deviations that observed network modularity (Q) deviates from average modularity in 1,000 random networks. Networks were considered significantly modular when Z-cores values were ≥2 since their observed modularity is at least two standard deviations higher than expected from random networks with the same marginal totals (Albor et al., 2020; Dormann & Strauss, 2014).

2.4 | Flowering overlap

Flowering overlap data were obtained from Arceo-Gómez et al. (2018), which were collected by establishing 13 1 × 3 m plots at the study site in 2016. Plots were distributed approximately every five meters along the seep, but plots were added when necessary to include low abundance (rare) species not initially captured within plots. Thus, all insect-pollinated species were included in at least one plot and more abundant species were represented across multiple plots (Arceo-Gómez et al., 2018). With this approach the number and location of the plots reflected the presence and abundance of each insect-pollinated species in the seep (see Arceo-Gómez et al., 2018). Plant identity and number of open flowers for each species within the plots were recorded every 5 days between the beginning of May until June for a total of nine surveys (Arceo-Gómez et al., 2018). To estimate the intensity of flowering overlap between plant species-pairs the number of open flowers for each plant species, at each time interval, was used to estimate co-flowering overlap using the Schoener's index (SI) of niche overlap (Albor et al., 2020; Arceo-Gómez et al., 2018; Forrest et al., 2010; Schoener, 1970). From this index, $SI = 1 - ½\, \Sigma k|p_{ik} - p_{jk}|$, p_{ik} and p_{jk} represent the proportion of flowering by species 'i' and 'j', respectively, on day 'k' (Arceo-Gómez et al., 2018; Forrest et al., 2010). SI ranges from 0 (no overlap in flowering) to 1 (complete flowering overlap; Forrest et al., 2010; Arceo-Gómez et al., 2018; Albor et al., 2020).

2.5 | Floral visitor use overlap

Data on insect visitation (i.e. floral visitor) to each plant species at the study site was obtained from Wei et al. (2021) where it was recorded in 2 years (2016–2017) by surveying the site between 08:00–17:00 hr once every week for 9 weeks during peak flowering season (late April–June). Insect visitation to individual plant species was recorded simultaneously by three people by collecting all floral visitors with a sweep net when they were observed contacting floral reproductive structures (stamen or pistil). Lepidopterans were preserved dry and all other insects were preserved in 100% ethanol in a −20°C freezer until processed (Wei et al., 2021). Specimens were identified by specialists to the lowest taxonomical level possible and vouchers are kept at the Carnegie Museum of Natural History (Pittsburgh, PA; see Supplementary Material in Wei et al., 2021). From this raw data we estimated the amount of floral visitor sharing between plant species-pairs using Gower's pairwise distances (Gower, 1971) based on the number of visits by each insect species to each plant species (Albor et al., 2020). Floral visitor sharing (1 − average dissimilarity) thus represents the degree of similarity in the floral visitor community between two plant species (Albor et al., 2020; Gower, 1971). Floral visitors were classified into five taxonomic groups, that is, bees, beetles, lepidopterans, flies and wasps (Koski et al., 2015; Wei et al., 2021). These pollination groups reflect differences in their sensory systems (e.g. perception of colour), foraging behaviour (e.g. social vs. solitary), and taxonomic affinities, all of which have been shown to influence pollination dynamics (Koski et al., 2015).

2.6 | Phylogenetic relatedness

We reconstructed the phylogenetic relationships among the 39 species in the community using the 'phylo.maker' function implemented in R package V.PhyloMaker (Jin & Qian, 2019). Specifically, we used the updated mega-tree of vascular plants 'GBOTB.extended.tre' (Smith & Brown, 2018). We also used *V.PhyloMaker* 'scenario 3' to add missing species (11 species) to the phylogeny as polytomies within their parental clades and adjusted the branch lengths using the BLADJ function (Webb et al., 2008). To estimate species' phylogenetic relatedness, we computed pairwise phylogenetic distances between all plant species-pairs in the phylogeny (Webb et al., 2002). We obtained phylogenetic distances among all co-flowering species using the function cophenetic.phylo in the R package APE (Paradis et al., 2004; Figure S2).

2.7 | Hypotheses testing

We first used analysis of variance (ANOVA) to evaluate differences in flower colour properties (i.e. hue and saturation) between the observed modules in the flower colour network to confirm that these represent distinct colour modules. For this, species were categorized according to their module membership into module 'one' or 'two' (see results). We also use one-way ANOVA to evaluate differences in average flower colour similarity (Gower's distance) between plant species within each colour module. We did this first using the raw floral reflectance spectra (i.e. all insects) and then using colour distances exclusively based on the Hymenoptera vision model, which is the dominant floral visitor group in this community (Koski et al., 2015; Wei et al., 2021). To estimate colour distances in the Hymenoptera vision model, we used the function 'coldist' in the package PAVO in R (Maia et al., 2013), which calculates Euclidean colour distances. In this case smaller distances indicate higher flower colour similarity. We also use one-way ANOVAs to evaluate differences in the intensity of flowering overlap (SI Index) across all plant species-pairs between the two observed flower colour modules. Residuals for all models were normally distributed (Shapiro–Wilk test, $p > 0.05$). The F statistics and significance values were determined using the Anova function in the CAR package in R (Fox et al., 2012). We also evaluated if the overall amount of floral visitor sharing (Gower's distance) between species was different for plants species-pairs within each module. Because of the large percentage of zeros in this dataset, and to avoid overestimating pollinator specialization (i.e. zero Gower's distance) due to incomplete sampling, we ran two separate models. First, we ran a model as described above for flowering overlap with Gower's distance as the response variable and 'module' as the predictor variable but only using non-zero data. In addition, we used a zero-inflated beta regression with all the data (including zeros) using the GAMLSS package in R (Rigby & Stasinopoulos, 2005; Vaidya et al., 2018). Zero-inflated beta regression analyzes the data as a mixture of Bernoulli and beta distributions and simultaneously estimates two parameters. First, a binomial model to estimate the probability that two plants will not share a pollinator (Gower's distance = 0) and then a model accounting for this probability (i.e. expected value for the beta component; Rigby & Stasinopoulos, 2005; Vaidya et al., 2018).

We further used generalized linear models (GLMs) to evaluate if the number of observed flower visits by the three main floral visitor groups at the study site, that is, bees, flies and beetles (Koski et al., 2015; Wei et al., 2021), differed for plant species in flower colour module 'one' compared with those in module 'two'. A separate GLM was run for each visitor group with module as the independent variable and the number of observed visits as the response variable. GLMs were fitted using a Poisson distribution and identity link function. The Poisson distribution was used as it is often used with count data with values higher than zero (Crawley, 2012). The Poisson distribution also provided the best model fit while minimizing overdispersion. Statistical significance was determined using a Wald's chi-squared test (ANOVA function, CAR package; Fox et al., 2012).

We then fitted two GLMs per network module to evaluate the expected relationships between flower colour similarity (Gower's pairwise distance) and flowering overlap (Schoener's index based on species flower counts) and between flower colour similarity and flower visitor sharing (Gower's pairwise distance; see Figure 1c,d), which outcomes can help infer the three predicted community assembly scenarios and the underlying mechanisms (Figure 1a). These relationships were evaluated using all plant species-pairs within each of the two flower colour modules observed (see Results). GLMs were performed using a Gamma distribution and log link function. Gamma distribution is best used for continuous non-integer data such as the co-flowering index and flower colour similarity (Crawley, 2012). The Gamma distribution also provided the best model fit while minimizing overdispersion. A value of 0.1 was added to the flowering overlap index (SI) to eliminate zeros in the response variable and meet model assumptions (e.g. Lázaro et al., 2013). Finally, we used GLM to evaluate the potential influence of phylogenetic relatedness on flower colour similarity, flowering overlap and floral visitor sharing. Each relationship was tested independently within each flower colour module. GLMs were performed using a Gamma distribution and log link function. Statistical significance was determined using a Wald's chi-squared test (ANOVA function, CAR package; Fox et al., 2012). All GLMs were conducted using the 'glm' function in R STATS package version 4.05.

3 | RESULTS

The floral colour network was composed of 39 co-flowering species and showed a significant modular structure (Q = 0.05; Z-core = 3.75 and $p < 0.05$). Specifically, the network contained two modules of 18 (hereafter, module one) and 21 (hereafter, module two) plant species, respectively (Figure 2; Figure S3). The model of flower reflectance spectra using the trichromatic colour-hexagon of the Hymenoptera showed that plant species in module one predominantly stimulated the bee green photoreceptor while flower spectra of species in module two stimulated the blue photoreceptor (Figure 2; Figure S4). These two colour modules were also significantly different in their specific colour properties. Specifically, flower colour saturation was significantly higher in module one than module two ($F_{1,38}$ = 7.42, $p < 0.01$; Figure 3b), whereas colour tonality (i.e. hue angle) was significantly higher in module two than in module one ($F_{1,38}$ = 6.88, p = 0.01; Figure 3c). Average similarity in flower reflectance (raw reflectance spectra) across all plant species-pairs ranged from 0.01 to 0.79. The average flower reflectance similarity between plant species-pairs was significantly higher in module two (mean ± SE: 0.86 ± 0.01) than in module one (0.75 ± 0.01; $F_{1,362}$ = 28.27, $p < 0.001$; Figure 3a). Furthermore, the average flower colour distance between plant species-pairs based on the Hymenoptera vision model was smaller (i.e. higher colour similarity) in module two (mean ± SE: 10.45 ± 0.41) compared with module one (higher colour dissimilarity; 14.46 ± 0.71; $F_{1,362}$ = 27.02, $p < 0.001$). Average flowering overlap (co-flowering index) between species-pairs ranged from 0 to 0.92 but flowering overlap was not significantly different between module one (SI index: 0.32 ± 0.03) and module two (0.27 ± 0.03; $F_{1,176}$ = 3.09, $p > 0.05$).

From Wei et al. (2021) we recorded a subset of 1,161 individual insects belonging to 142 pollinator species (1 to 103 individuals per species) at the study site. Among the most abundant groups of floral visitors at our study site were bees (57%), flies (24%), beetles (10%) and lepidopterans (8%). The amount of pollinator sharing (1 − average dissimilarity) across all species-pairs ranged from 0 to 0.99 and ANOVA showed it was significantly higher in module two (mean ± SE: 0.92 ± 0.01) than in module one (0.87 ± 0.01; $F_{1,124}$ = 19.75, $p < 0.001$; Figure 3d). Results from the zero-inflated beta regression (including zeros) further confirmed that values of pollinator sharing were higher for species-pairs within module two compared with those in module one (t = 4.3, $p < 0.001$). The pollinator species composition pool was also different between flower colour modules. Specifically, the number of observed flower visits by bees was significantly higher in plants within module two compared with those in module one (χ^2 = 11.1, $p < 0.001$; Figure 3e). On the contrary, the number of observed flower visits by beetles was higher in module one than in module two (χ^2 = 20.8, $p < 0.001$; Figure 3f). No differences in the number of observed flower visits by flies were observed between module one (5.06 ± 2.34) and module two (5.51 ± 1.63; χ^2 = 0.3, p = 0.5).

Phylogenetic relatedness between plant species-pairs was not significantly related to their flower colour distance, intensity of flowering overlap (Schoener's index) or pollinator sharing (Gower's pairwise distances) for either module ($\chi^2 < 0.25$, $p > 0.05$ for all). We found a significant negative relation between flower colour similarity and flowering overlap for plant species in module two (χ^2 = 5.57, p = 0.01), but not in module one (χ^2 = 0.001, $p > 0.05$; Figure 4). Furthermore, pollinator sharing was positively related with flower colour similarity in module one (χ^2 = 5.38, p = 0.02), but not in module two (χ^2 = 0.18, $p > 0.05$; Figure 4).

4 | DISCUSSION

While most studies have relied on the distribution of a single floral trait to infer mechanisms of co-flowering community assembly (e.g. McEwen & Vamosi, 2010; de Jager et al., 2011; Kemp et al., 2019; but see Wolowski et al., 2017; Bergamo et al., 2020) our results show empirical evidence of assembly along multiple axes of trait differentiation (i.e. flower colour and flowering time), likely mediating patterns of co-flowering. Similar to other studies (e.g. de Jager et al., 2011; Kantsa et al., 2017, 2018; Kemp et al., 2019), we show that plants can be grouped based on flower colour similarities and differences. However, our approach revealed a more complex pattern than previous studies by uncovering a modular structure of flower colour assembly within the same community. Specifically, our results show that not all plant species follow the same flower colour distribution pattern (i.e. clustered or over-dispersed; McEwen & Vamosi, 2010; de Jager et al., 2011), but in turn species are organized in different flower colour-groups (modules), each with a distinct pattern of assembly. In this seep community, we found two plant groups (modules; Figures 2; Figure S3) with unique differences in flower colour reflectance spectra, hue, saturation and overall floral colour similarity (Figure 3a–c). This modularity in flower colour assembly could be the result of convergence and/or divergence patterns driven by floral visitors with different colour preferences. For instance, plants in module two seem to strongly attract visitation by bees, as this module was mainly composed of species with flowers perceived as bee-blue and bee UV-blue (i.e. floral spectra with low saturation and high hue angle; Supporting Information Figures S1 and S4), which are commonly associated with bee-pollinated species (e.g. Morawetz et al., 2013; Papiorek et al., 2013; Reverté et al., 2016). In fact, our results showed that the number of bee flower visits in module two

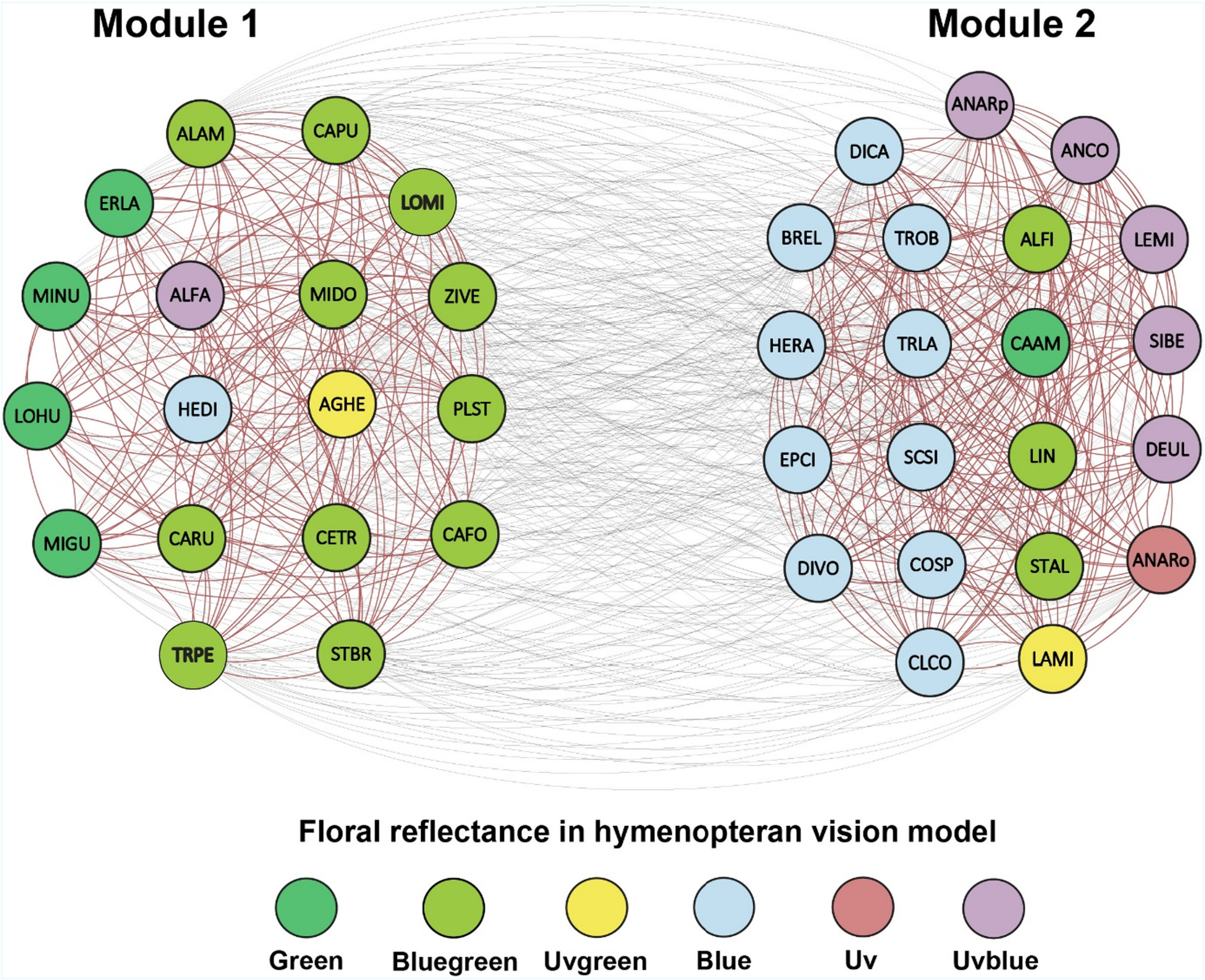

FIGURE 2 Flower colour network constructed based on the estimation of overall (untransformed) flower reflectance similarity (Gower's distance) among plant species showing two colour modules (a). Nodes (circles) represent plant species denoted by species codes (see Table S1 for full species names) and line width reflecting the amount (strength) of flower reflectance similarity between species-pairs. For illustrative purposes only the colour of the nodes represents the flower colour spectra based on the Hymenoptera vision model, which is the dominant floral visitor group in the community.

is approximately 30% higher than in module one (Figure 3e). Further analyses also showed that flower colour similarity was significantly higher for plant species-pairs within (mean ± *SE*: 0.62 ± 0.01) than between modules (0.58 ± 0.01; $F_{1,437} = 8.1$, $p < 0.0$; data not shown) supporting the existence of two distinct colour modules. Thus, differences in plant species composition within floral-colour modules likely reflect pollinator-specific floral colour preferences shaping community assembly (e.g. Ellis et al., 2021) beyond a single clustered or over-dispersed pattern. Studies that evaluate the existence of community assembly patterns that are not constrained to a single outcome (clustered vs over-dispersed) are hence paramount in fully uncovering the ecological mechanisms that shape communities in nature (e.g. Bergamo et al., 2020; Wolowski et al., 2017).

Our approach considering multiple traits also showed different patterns of assembly within individual flower colour-modules. Specifically, our results show plant species within colour-modules can be further structured with respect to flowering time. For instance, we found a negative correlation between flowering overlap and flower reflectance similarity within flower colour-module two. That is, within that module, the more similar in flower colour two species are the greater their divergence in flowering time. This is in line with our expectation of pollinator competition as the dominant organizing force [see first (blue) panel in Figure 1c]. The high level of flower colour similarity and pollinator sharing (Figure 3) within module two may thus be at least partially due to plant species' divergent structure in flowering phenology. Specifically, pollinators visit phenotypically similar plant species at different points in time during the season. It is important to note however, that this pattern of phenotypic similarity and staggered pollinator visitation may also be reflective of sequential facilitation (e.g. Waser, 1978) instead of

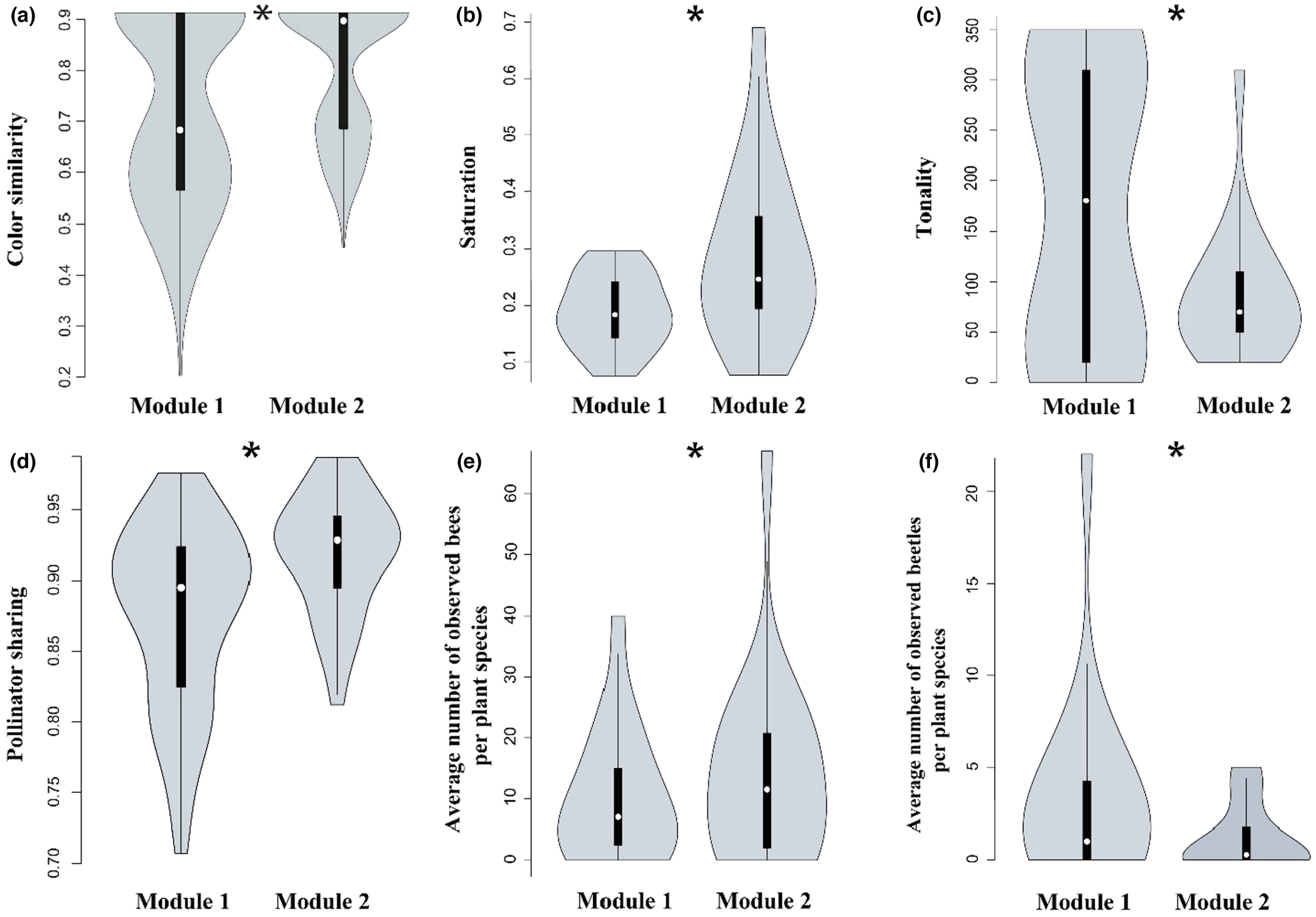

FIGURE 3 Density plot of differences (median ± quartile) in (a) overall flower colour similarity, (b) flower colour saturation, (c) colour tonality (hue angle) between the two observed modules. Differences in overall (d) pollinator sharing (Gower's distance) and number of observed flower visits by (e) bees and (f) beetles to plants in floral colour-module 'one' and module 'two' are also shown. All comparisons are significant at $*p < 0.05$. No differences in the number visits by flies were observed ($p > 0.5$).

pollinator competition. However, we feel this is less likely as there is still little evidence suggesting a high frequency of facilitative processes in the absence of co-flowering between species-pairs (Braun & Lortie, 2019), and its potential role in structuring entire co-flowering communities is thus virtually unknown. Nonetheless, our approach still provides an opportunity to formulate predictions and to design logistically feasible experiments to directly test these two opposite predictions (see below). Furthermore, as stated above, flower colour characteristics and visitation patterns observed in module two strongly suggest that plant species are more reliant on bee visitation compared with those in module one. Bees are not only the most abundant visitors at our study site (Wei et al., 2021) but they are also considered among the most efficient pollinators (e.g. Ballantyne et al., 2017; Hung et al., 2018). Thus, the level of phenotypic convergence (flower colour) required to attract this highly abundant/efficient group of insects may result in strong competition, which is minimized via flowering time divergence. This would also explain why the increasing amount of flower colour similarity necessary for bee pollination (e.g. de Jager et al., 2011; Bergamo et al., 2018) does not lead to a decrease in pollinator sharing as initially predicted under pollinator competition [first (blue) panel in Figure 1d]. Overall, our results suggest that the use of specific pollinator groups (and their associated sensory systems) may impose constraints in the axis of niche differentiation and assembly within a community. Interestingly, if we had only relied on flower colour similarity we would have concluded that pollinator facilitation is the main assembly force in the entire community (e.g. de Jager et al., 2011). For instance, results using traditional null model analyses with a larger species pool from multiple seeps at the natural reserve (48 species) revealed a significant clustered pattern in flower colour at our study site [observed mean pairwise distance (MPD) = 0.28, random MPD = 0.3, p = 0.05; also see LeCroy et al., 2021]. Thus, our approach raises caution in interpreting assembly patterns along a single trait (also see Wolowski et al., 2017).

In contrast, we did not find a significant relationship between flower colour similarity and flowering overlap for plant species within module one. However, overall flower colour similarity and pollinator sharing was significantly lower for this module (Figure 3). This suggests that a lower level of flower colour similarity among plant species in this module may be sufficient to reduce reproductive interference and allow co-flowering [third (grey) panel in Figure 1a]. The higher colour dissimilarity between plants in module one may be

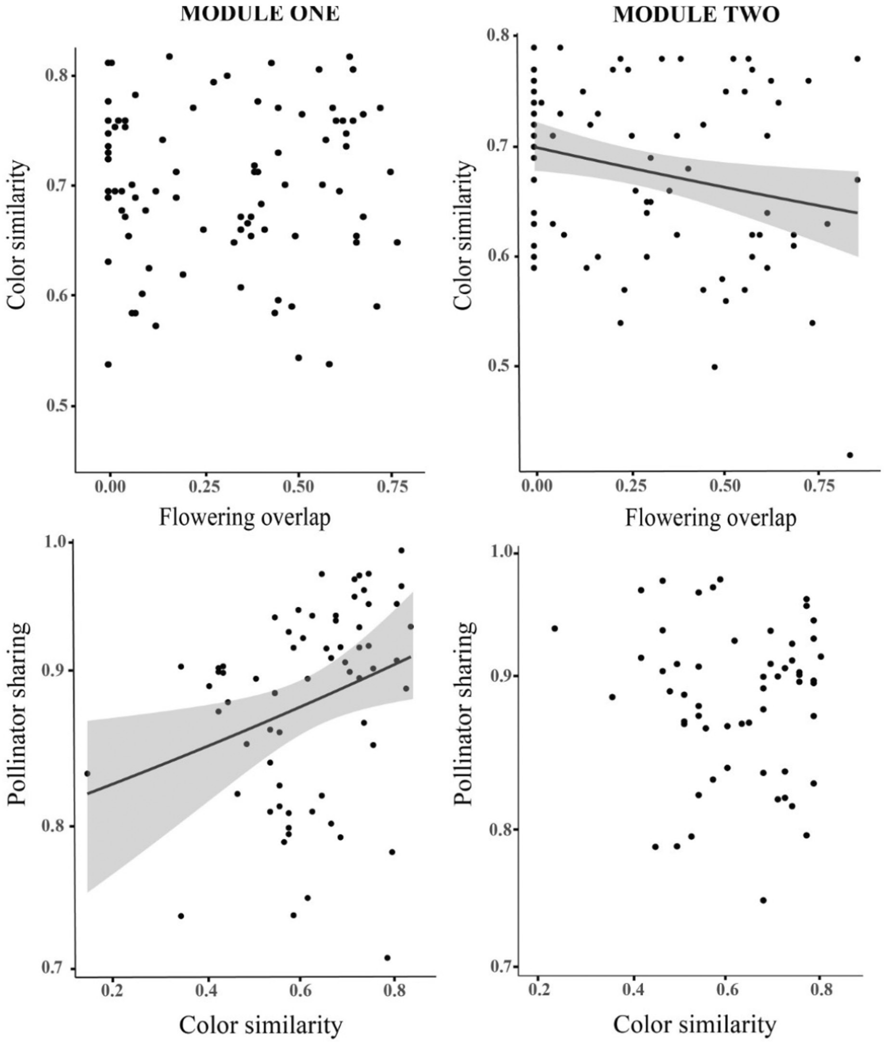

FIGURE 4 Results from generalized linear models evaluating the relationship between flower colour similarity with flowering overlap and pollinator sharing for each of the two network colour modules. Tests are based on predictions of trait associations supporting the action of pollinator-mediated competitive and facilitative processes (Figure 1). Only the relationships showing trend lines (±95%CI) are significant at $p < 0.05$.

the result of higher flower visitation by other insect groups such as beetles (e.g. generalist plant species), which may result in selective pressure for low floral colour similarity (or reduced pressure for high colour similarity). For instance, our results showed that flowers of plant species in this module received a higher proportion (~50%) of visits by beetles compared with species in module two (Figure 3f). However, because species in this module are not structured in flowering time (as in module two), an increase in flower colour similarity can lead to an increase in pollinator sharing. The higher dissimilarity in flower colour (compared with module two) and low pollinator sharing within module one also suggests pollinator competition is the main force mediating its structure, but with species assembled along a morphological (flower colour) rather than a phenological axis of differentiation (grey panel in Figure 1). Thus, our results show that different trait-structure patterns (Figure 1a) may result from the same type of ecological interaction within the same community depending on plant species' main pollinator groups (also see Wolowski et al., 2017). In a similar study, Bergamo et al. (2018) also showed that assembly patterns may vary depending on the main pollinator functional group. Interestingly, in that same study species with the strongest phenotypic similarity also had the highest amount of flowering overlap suggesting pollinator facilitation. The existence of multiple assembly patterns may only be revealed when evaluating patterns within different subsets of species (e.g. modules) in a community separately. For instance, when we only evaluated differences in pollinator sharing and flowering overlap for all species-pairs within-modules compared with those between-modules (thus ignoring within-individual trait patterns; e.g. Albor et al., 2020), no differences were observed ($F_{1,437} < 0.15$, $p > 0.05$; data not shown), presumably because different patterns (and mechanisms) operate within individual colour modules. It is also important to note the lack of a significant relationship between phylogenetic relatedness and patterns of flower colour similarity, flowering time and pollinator use overlap, suggesting that the assembly patterns observed here are largely driven by the action of plant-pollinator interactions and not due to shared evolutionary history (also see LeCroy et al., 2021). Other studies have also shown that phenotypic differentiation (e.g. flower colour) in sympatric plants can be mediated by plant-pollinator interactions even in closely related species (e.g. Grossenbacher & Stanton, 2014; Muchhala et al., 2014). Further supporting this result, we also found a weak phylogenetic signal for flower colour in this community ($\lambda = 0.05$; Figure S2).

Finally, it is important to emphasize that although evaluating trait distribution patterns to uncover signals of the role of competitive and facilitative interactions in the assembly of highly diverse communities is a valuable approach (de Jager et al., 2011; Kemp et al., 2019; McEwen & Vamosi, 2010; Sargent & Ackerly, 2008; Wolowski et al., 2017), the patterns observed would ideally be confirmed by experimentally evaluating the fitness effects of co-flowering. The role of traits such as floral colour and flowering time in mediating co-flowering assembly should also be tested experimentally and their importance evaluated compared with other traits such as floral size, scent, floral rewards and others that have also been shown to be important for pollinator attraction. These types of experimental approaches combined with the uncovering of community-wide patterns is key in order to fully tease apart the relative contribution of competition and facilitation to community assembly (e.g. sequential facilitation vs competition). In this sense, our analytical framework is also valuable in that it allows the detection of specific plant species involved in competitive versus facilitative interactions, based on trait and pollinator use relationships within individual trait-modules (Figure 1c–d), and to formulate explicit predictions that can be tested experimentally. For instance, by manipulating species' flowering time (e.g. in the greenhouse) and/or floral colour (e.g. Bischoff et al., 2015) and evaluate changes in competitive/facilitative interactions with other species within the module. Or by conducting standard pollinator competition experiments where pollination success (e.g. seed set) is evaluated in plant species-pairs flowering alone and in the presence of a competitor. Species-pair selection and predictions could be formulated based on the results of our posed framework instead of conducting experiments on all possible plant-species-pairs in a community. For instance, we could experimentally test the prediction of competition-driven flowering time divergence and assembly in *Delphinium uliginosum* (DEUL), *Brodeia elegans* (BREL), *Collinsia sparsifolia* (COSP), *Anthirrinun cornutum* (ANCO), all purple/blue flowers (in the human spectrum) in module two (Figure 2).

Overall, our approach of characterizing the community as a set of multiple modules based on flower colour differences reveal evidence suggesting that multiple assembly patterns, driven by the same or different ecological mechanisms (competition vs. facilitation), can operate within the same co-flowering community. These more complex patterns of community assembly may only be revealed by simultaneously evaluating multiple axes of phenotypic (e.g. floral traits) and ecological differentiation (e.g. pollinator use), and thus we raise caution when interpreting assembly patterns along a single trait. We emphasize the need for more studies (also see Hegland et al., 2009; Wolowski et al., 2017) that evaluate the interplay between competition and facilitation, its importance in plant community assembly, and how these patterns may vary in space and time, to advance our understanding of the mechanisms that shape biodiversity in nature.

AUTHOR CONTRIBUTIONS

Cristopher Albor and Gerardo Arceo-Gomez conceptualize the ideas; Gerardo Arceo-Gomez, Tia-Lynn Ashman and Amber Stanley collected the data; Cristopher Albor, Amber Stanley and Carlos Martel analyse the data and produced the figures; C.A. and G.A.-G. wrote the first draft; all authors contributed with substantial revisions.

ACKNOWLEDGEMENTS

The authors than R. Kaczorowski and R. Hayes for their help collecting data in the field. We thank the directors of the McLaughlin Natural Reserve for logistical support during this study. This work was funded by the National Science Foundation grant DEB 1452386 to T.-L.A. and DEB 1931163 to G.A.-G.

CONFLICT OF INTEREST

The authors have no conflict of interest to report.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.2ngf1vhrb (Albor et al., 2022).

ORCID

Cristopher Albor https://orcid.org/0000-0002-9870-4094
Tia-Lynn Ashman https://orcid.org/0000-0002-9884-5954
Gerardo Arceo-Gómez https://orcid.org/0000-0003-3458-1600

REFERENCES

Aizen, M. A., & Vázquez, D. P. (2006). Flowering phenologies of hummingbird plants from the temperate forest of southern South America: Is there evidence of competitive displacement? *Ecography*, *29*, 357–366.

Albor, C., Arceo-Gómez, G., & Parra-Tabla, V. (2020). Integrating floral trait and flowering time distribution patterns help reveal a more dynamic nature of co-flowering community assembly processes. *Journal of Ecology*, *108*, 2221–2231.

Albor, C. Ashman, T. L., Stanley, A., Martel, C., & Arceo-Gómez, G. (2022). Data from: Flower color and flowering phenology mediate plant-pollinator interaction assembly in a diverse co-flowering community. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.2ngf1vhrb

Alonso, C., Arceo-Gómez, G., Meindl, G. A., Abdala-Roberts, L., Parra-Tabla, V., & Ashman, T.-L. (2017). Delimiting plant diversity that is functionally related via interactions with diurnal pollinators: An expanded use of rarefaction curves. *Flora: Morphology, Distribution, Functional Ecology of Plants*, *232*, 56–62.

Arceo-Gómez, G., Abdala-Roberts, L., Jankowiak, A., Kohler, C., Meindl, G. A., Navarro-Fernández, C. M., Parra-Tabla, V., Ashman, T.-L., & Alonso, C. (2016). Patterns of among- and within-species variation in heterospecific pollen receipt: The importance of ecological generalization. *American Journal of Botany*, *103*, 396–407.

Arceo-Gómez, G., Kaczorowski, R. L., & Ashman, T.-L. (2018). A network approach to understanding patterns of coflowering in diverse communities. *International Journal of Plant Sciences*, *179*, 569–582.

Ashman, T.-L., Alonso, C., Parra-Tabla, V., & Arceo-Gómez, G. (2020). Pollen on stigmas as proxies of pollinator competition and facilitation: Complexities, caveats and future directions. *Annals of Botany*, *125*, 1003–1012.

Ballantyne, G., Baldock, K. C. R., Rendell, L., & Willmer, P. G. (2017). Pollinator importance networks illustrate the crucial value of bees in a highly speciose plant community. *Scientific Reports*, *7*, 1–13.

Bastian, M., Heymann, S., & Jacomy, M. (2009). Gephi: An open source software for exploring and manipulating networks. *Proceedings of the International AAAI Conference on Web and Social Media*, *3*, 361–362.

Bergamo, P. J., Streher, N. S., Wolowski, M., & Sazima, M. (2020). Pollinator-mediated facilitation is associated with floral abundance, trait similarity and enhanced community-level fitness. *Journal of Ecology*, *108*, 1334–1346.

Bergamo, P. J., Wolowski, M., Maruyama, P. K., Vizentin-Bugoni, J., & Sazima, M. (2018). Trait patterns across space and time suggest an interplay of facilitation and competition acting on Neotropical hummingbird-pollinated plant communities. *Oikos*, *127*, 1690–1700.

Bischoff, M., Raguso, R. A., Jürgens, A., & Campbell, D. R. (2015). Context-dependent reproductive isolation mediated by floral scent and color. *Evolution*, *69*, 1–13.

Braun, J., & Lortie, C. J. (2019). Finding the bees knees: A conceptual framework and systematic review of the mechanisms of pollinator-mediated facilitation. *Perspectives in Plant Ecology, Evolution and Systematics*, *36*, 33–40.

Cavender-Bares, J., Kozak, K. H., Fine, P. V. A., & Kembel, S. W. (2009). The merging of community ecology and phylogenetic biology. *Ecology Letters*, *12*, 693–715.

Chittka, L. (1992). The colour hexagon: A chromaticity diagram based on photoreceptor excitations as a generalized representation of colour opponency. *Journal of Comparative Physiology A*, *170*, 533–543.

Chittka, L., Spaethe, J., Schmidt, A., & Hickelsberger, A. (2001). Adaptation, constraint, and chance in the evolution of flower color and pollinator color vision. In L. Chittka & J. D. Thomson (Eds.), *Cognitive ecology of pollination* (pp. 106–126). Cambridge University Press.

Clements, F. E. (1916). *Plant succession: An analysis of the development of vegetation*. Carnegie Institution of Washington.

Crawley, M. J. (2012). *The R book* (p. 16). John Wiley & Sons.

de Jager, M. L., Dreyer, L. L., & Ellis, A. G. (2011). Do pollinators influence the assembly of flower colours within plant communities? *Oecologia*, *166*, 543–553.

Diamond, J. M. (1975). Assebly of species communities. In M. L. Cody & J. M. Diamond (Eds.), *Ecology and evolution of communities* (pp. 342–444). Harvard University Press.

Dormann, C. F., & Strauss, R. (2014). A method for detecting modules in quantitative bipartite networks. *Methods in Ecology and Evolution*, *5*, 90–98.

Dupont, Y. L., & Olesen, J. M. (2009). Ecological modules and roles of species in heathland plant–insect flower visitor networks. *Journal of Animal Ecology*, *78*, 346–353.

Ellis, A. G., Anderson, B., & Kemp, J. E. (2021). Geographic mosaics of fly pollinators with divergent color preferences drive landscape-scale structuring of flower color in daisy communities. *Frontiers in Plant Science*, *12*, 617761.

Elzinga, J. A., Atlan, A., Biere, A., Gigord, L., Weis, A. E., & Bernasconi, G. (2007). Time after time: Flowering phenology and biotic interactions. *Trends in Ecology and Evolution*, *22*, 432–439.

E-Vojtkó, A., de Bello, F., Durka, W., Kühn, I., & Götzenberger, L. (2020). The neglected importance of floral traits in trait-based plant community assembly. *Journal of Vegetation Science*, *31*, 529–539.

Fang, Q., & Huang, S. Q. (2013). A directed network analysis of heterospecific pollen transfer in a biodiverse community. *Ecology*, *94*, 1176–1185.

Forrest, J., Inouye, D., & Thomson, J. (2010). Flowering phenology in subalpine communities: Does climate variation reshuffle species assemblages? *Ecology*, *91*, 431–440.

Fox, J., Weisberg, S., Adler, D., Bates, D., Baud-Bovy, G., Ellison, S., Firth, D., Friendly, M., Gorjanc, G., Graves, S., & Heiberger, R. (2012). *Package 'car'* (p. 16). R Foundation for Statistical Computing.

Gleason, H. A. (1926). The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club*, *53*, 7.

Gómez, J. P., Bravo, G. A., Brumfield, R. T., Tello, J. G., & Cadena, C. D. (2010). A phylogenetic approach to disentangling the role of competition and habitat filtering in community assembly of Neotropical forest birds. *Journal of Animal Ecology*, *79*, 1181–1192.

Götzenberger, L., de Bello, F., Bråthen, K. A., Davison, J., Dubuis, A., Guisan, A., Lepš, J., Lindborg, R., Moora, M., Pärtel, M., Pellissier, L., Pottier, J., Vittoz, P., Zobel, K., & Zobel, M. (2012). Ecological assembly rules in plant communities-approaches, patterns and prospects. *Biological Reviews*, *87*, 111–127.

Gower, J. C. (1971). A general coefficient of similarity and some of its properties. *Biometrics*, *27*, 857–871.

Grossenbacher, D. L., & Stanton, M. L. (2014). Pollinator-mediated competition influences selection for flower-color displacement in sympatric monkeyflowers. *American Journal of Botany*, *101*, 1915–1924.

Hegland, S. J., Grytnes, J. A., & Totland, Ø. (2009). The relative importance of positive and negative interactions for pollinator attraction in a plant community. *Ecological Research*, *24*, 929–936.

Hung, K. L. J., Kingston, J. M., Albrecht, M., Holway, D. A., & Kohn, J. R. (2018). The worldwide importance of honey bees as pollinators in natural habitats. *Proceedings of the Royal Society B: Biological Sciences*, *285*, 2017–2140.

Ibanez, S., Arène, F., & Lavergne, S. (2016). How phylogeny shapes the taxonomic and functional structure of plant-insect networks. *Oecologia*, *180*, 989–1000.

Ingram, T., & Shurin, J. B. (2009). Trait-based assembly and phylogenetic structure in northeast Pacific rockfish assemblages. *Ecology*, *90*, 2444–2453.

Ishii, H. S., Kubota, M. X., Tsujimoto, S. G., & Kudo, G. (2019). Association between community assemblage of flower colours and pollinator fauna: A comparison between Japanese and New Zealand alpine plant communities. *Annals of Botany*, *123*(3), 533–541.

Jin, Y., & Qian, H. (2019). V.PhyloMaker: An R package that can generate very large phylogenies for vascular plants. *Ecography*, *42*, 1353–1359.

Kantsa, A., Raguso, R. A., Dyer, A. G., Olesen, J. M., Tscheulin, T., & Petanidou, T. (2018). Disentangling the role of floral sensory stimuli in pollination networks. *Nature Communications*, *9*, 1041.

Kantsa, A., Raguso, R. A., Dyer, A. G., Sgardelis, S. P., Olesen, J. M., & Petanidou, T. (2017). Community-wide integration of floral colour and scent in a Mediterranean scrubland. *Nature Ecology and Evolution*, *1*, 1502–1510.

Keddy, P. A. (1992). Assembly and response rules: Two goals for predictive community ecology. *Journal of Vegetation Science*, *3*, 157–164.

Kelber, A., & Osorio, D. (2010). From spectral information to animal colour vision: Experiments and concepts. *Proceedings of the Royal Society B: Biological Sciences*, *277*, 1617–1625.

Kemp, J. E., Bergh, N. G., Soares, M., & Ellis, A. G. (2019). Dominant pollinators drive non-random community assembly and shared flower colour patterns in daisy communities. *Annals of Botany*, *123*, 277–288.

Koski, M. H., Meindl, G. A., Arceo-Gómez, G., Wolowski, M., LeCroy, K. A., & Ashman, T.-L. (2015). Plant-flower visitor networks in a serpentine metacommunity: Assessing traits associated with keystone plant species. *Arthropod-Plant Interactions*, *9*, 9–21.

Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, *91*(1), 299–305.

Larue-Kontić, A.-A. C., & Junker, R. R. (2016). Inhibition of biochemical terpene pathways in *Achillea millefolium* flowers differently affects the behavior of bumblebees (*Bombus terrestris*) and flies (*Lucilia sericata*). *Journal of Pollination Ecology*, *18*, 31–35.

Lázaro, A., Jakobsson, A., & Totland, Ø. (2013). How do pollinator visitation rate and seed set relate to species' floral traits and community context? *Oecologia*, *173*, 881–893.

LeCroy, K. A., Arceo-Gómez, G., Koski, M. H., Morehouse, N. I., & Ashman, T.-L. (2021). Floral color properties of serpentine seep assemblages depend on community size and species richness. *Frontiers in Plant Science*, *11*, 2107.

Maia, R., Eliason, C. M., Bitton, P., Doucet, S. M., & Shawkey, M. D. (2013). *pavo* : An R package for the analysis, visualization and organization of spectral data. *Methods in Ecology and Evolution*, *4*, 906–913.

McEwen, J. R., & Vamosi, J. C. (2010). Floral colour versus phylogeny in structuring subalpine flowering communities. *Proceedings of the Royal Society B: Biological Sciences*, *277*, 2957–2965.

Mitchell, R. J., Flanagan, R. J., Brown, B. J., Waser, N. M., & Karron, J. D. (2009). New frontiers in competition for pollination. *Annals of Botany*, *103*, 1403–1413.

Morawetz, L., Svoboda, A., Spaethe, J., & Dyer, A. G. (2013). Blue colour preference in honeybees distracts visual attention for learning closed shapes. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, *199*, 817–827.

Muchhala, N., Johnsen, S., & Smith, S. D. (2014). Competition for hummingbird pollination shapes flower color variation in Andean Solanaceae. *Evolution*, *68*, 2275–2286.

Olesen, J. M., Bascompte, J., Dupont, Y. L., & Jordano, P. (2007). The modularity of pollination networks. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 19891–19896.

Papiorek, S., Rohde, K., & Lunau, K. (2013). Bees' subtle colour preferences: How bees respond to small changes in pigment concentration. *Naturwissenschaften*, *100*, 633–643.

Paradis, E., Claude, J., & Strimmer, K. (2004). APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, *20*, 289–290.

Phillips, R. D., Peakall, R., van der Niet, T., & Johnson, S. D. (2020). Niche perspectives on plant-pollinator interactions. *Trends in Plant Science*, *25*, 779–793.

Rafferty, N. E., & Nabity, P. D. (2017). A global test for phylogenetic signal in shifts in flowering time under climate change. *Journal of Ecology*, *105*, 627–633.

Reverté, S., Retana, J., Gómez, J. M., & Bosch, J. (2016). Pollinators show flower colour preferences but flowers with similar colours do not attract similar pollinators. *Annals of Botany*, *118*, 249–257.

Ricklefs, R. E. (1987). Community diversity: Relative roles of local and regional processes. *Science*, *235*, 167–171.

Rigby, R. A., & Stasinopoulos, D. M. (2005). Generalized additive models for location, scale and shape. *Journal of the Royal Statistical Society: Series C*, *54*, 507–554.

Sargent, R. D., & Ackerly, D. D. (2008). Plant-pollinator interactions and the assembly of plant communities. *Trends in Ecology & Evolution*, *23*, 123–130.

Schoener, T. W. (1970). Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology*, *51*, 408–418.

Shrestha, M., Dyer, A. G., Bhattarai, P., & Burd, M. (2014). Flower colour and phylogeny along an altitudinal gradient in the Himalayas of Nepal. *Journal of Ecology*, *102*, 126–135.

Smith, S. A., & Brown, J. W. (2018). Constructing a broadly inclusive seed plant phylogeny. *American Journal of Botany*, *105*, 302–314.

Tilman, D. (2004). Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences of the United States of America*, *101*, 10854–10861.

Tur, C., Sáez, A., Traveset, A., & Aizen, M. A. (2016). Evaluating the effects of pollinator-mediated interactions using pollen transfer networks: Evidence of widespread facilitation in south Andean plant communities. *Ecology Letters*, *19*, 576–586.

Vaidya, P., McDurmon, A., Mattoon, E., Keefe, M., Carley, L., Lee, C. R., Bingham, R., & Anderson, J. T. (2018). Ecological causes and consequences of flower color polymorphism in a self-pollinating plant (*Boechera stricta*). *New Phytologist*, *218*, 380–392.

Valiente-Banuet, A., & Verdú, M. (2007). Facilitation can increase the phylogenetic diversity of plant communities. *Ecology Letters*, *10*, 1029–1036.

van der Kooi, C. J., Dyer, A. G., Kevan, P. G., & Lunau, K. (2019). Functional significance of the optical properties of flowers for visual signalling. *Annals of Botany*, *123*, 263–276.

van der Kooi, C. J., Pen, I., Staal, M., Stavenga, D. G., & Elzenga, J. T. M. (2016). Competition for pollinators and intra-communal spectral dissimilarity of flowers. *Plant Biology*, *18*, 56–62.

Waser, N. M. (1978). Interspecific pollen transfer and competition between co-occurring plant species. *Oecologia*, *36*, 223–236.

Waser, N. M., & Real, L. A. (1979). Effective mutualism between sequentially flowering plant species. *Nature*, *281*, 670–672.

Webb, C. (2000). Exploring the phylogenetic structure of ecological communities: An example for rain forest trees. *The American Naturalist*, *156*, 145–155.

Webb, C. O., Ackerly, D. D., & Kembel, S. W. (2008). Phylocom: Software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics*, *24*(18). https://doi.org/10.1093/bioinformatics/btn358

Webb, C. O., Ackerly, D. D., McPeek, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, *33*, 475–505.

Wei, N., Russell, A. L., Jarrett, A. R., & Ashman, T.-L. (2021). Pollinators mediate floral microbial diversity and microbial network under agrochemical disturbance. *Molecular Ecology*, *30*, 2235–2247.

Weiher, E., Clarke, G. D. P., & Keddy, P. A. (1998). Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos*, *81*, 309–322.

Wilson, J. B. (1999). Assembly rules in plant communities. In E. Weiher & P. Keddy (Eds.), *Ecological assembly rules: Perspectives, advances, retreats* (pp. 130–164). Cambridge University Press.

Wolowski, M., Carvalheiro, L. G., & Freitas, L. (2017). Cambridge influence of plant–pollinator interactions on the assembly of plant and hummingbird communities. *Journal of Ecology*, *105*, 332–344.

Yan, J., Wang, G., Sui, Y., Wang, M., & Zhang, L. (2016). Pollinator responses to floral colour change, nectar, and scent promote reproductive fitness in *Quisqualis indica* (Combretaceae). *Scientific Reports*, *6*, 1–10.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Albor, C., Ashman, T-L, Stanley, A., Martel, C., & Arceo-Gómez, G. (2022). Flower colour and flowering phenology mediate plant–pollinator interaction assembly in a diverse co-flowering community. *Functional Ecology*, *00*, 1–13. https://doi.org/10.1111/1365-2435.14142