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RESEARCH ARTICLE

Pollinator facilitation between florally contrasting congeners scales up to regional co-occurrence patterns

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Abstract

1. Plant–plant facilitation is pervasive in nature and can have community-wide consequences directly through amelioration of abiotic stress or indirectly through shared mutualists. Despite being widely demonstrated within local communities, indirect facilitation via pollinators varies in its impact on plant fitness and has rarely been tested for its role in structuring communities at larger spatial scales.
2. We hypothesized that pollinator facilitation among closely related but florally contrasting plant species can enhance the probability of their regional co-occurrence. We tested for local pollinator facilitation with field observations and common garden experiments between two *Bidens* spp. (Asteraceae) with contrasting flowers. Whereas *B. cernua* has a showy sunflower-like inflorescence (radiate inflorescence), *B. frondosa* has evolutionarily lost its ray florets (discoid inflorescence) and is comparatively inconspicuous in visual display. We also broadly sampled (co-)occurrence patterns of these and other *Bidens* spp. across New York State (USA).
3. The presence of showy *B. cernua* increased floral visitation to discoid *B. frondosa* in mixed natural populations and common garden experiments, but only increased seed set of *B. frondosa* in natural populations. We found little evidence for a cost of pollinator facilitation for the facilitating species *B. cernua*. Both species showed enhanced seed set from conspecific pollen supplementation but no cost of heterospecific pollen deposition, suggesting an overall benefit of increased pollinator visitation.
4. Across New York State, *B. cernua* and *B. frondosa* co-occurred more often than expected by chance. Moreover, frequent co-occurrence between radiate and discoid *Bidens* was general across multiple species in the genus. Despite the overall pattern of *Bidens* spp. to spatially disaggregate, likely due to competition, radiate *Bidens* species strongly aggregated with discoid *Bidens* species more often than expected.
5. *Synthesis*. Plants with a showy floral display conferred pollinator facilitation to a congener that lost that display, and display trait contrast predicted species co-occurrence across the landscape. Our study underscores the potential for positive interactions to reduce competitive displacement among close relatives and impact species distributions. We propose the novel hypothesis that congener

facilitation may be a general ecological mechanism that serves to compensate for the evolutionary loss of an adaptive trait.

KEYWORDS

Asteraceae, co-occurrence, determinants of plant community diversity and structure, facilitation, floral neighborhood, floral traits, Pollinator-mediated interactions

1 | INTRODUCTION

Facilitation—the positive interaction where one species benefits another through altering their shared environment—has received considerable attention in the last two decades and is now widely recognized as an important process structuring community composition and function (Bronstein, 2015; McIntire & Fajardo, 2014). In mixed-species plant communities, facilitative interactions between heterospecific neighbours can be mediated by pollinators, with cascading consequences through the plant community over time (Bertness & Callaway, 1994; Braun & Lortie, 2019). By indirectly enhancing pollinator visits to plants, neighbours can promote the persistence of rare species (Feldman et al., 2004; Ghazoul, 2006), support a more diverse and abundant pollinator assemblage (Losapio et al., 2021; Waser & Real, 1979; Wei et al., 2021) and enhance the resilience of both pollinator and plant communities in response to local species extinction (Bain et al., 2022; Verdú & Valiente-Banuet, 2008). There is indeed a growing body of theoretical and empirical understanding of multiple mechanisms of pollinator facilitation (Braun & Lortie, 2019; Laverty, 1992; McIntire & Fajardo, 2014; Moeller & Geber, 2005; Ogilvie & Thomson, 2016) and its potential consequences for plant fitness and community structure (Bouman et al., 2017; Mesgaran et al., 2017).

Pollinator facilitation can take place via multiple non-mutually exclusive mechanisms through space and time. These mechanisms make distinct predictions about the resulting consequences for species coexistence, and some of these theoretical predictions have been tested empirically. The most often evoked mechanism is 'magnet' flowers, where conspicuous species attract an abundance of pollinators that spill over to less conspicuous neighbours (Laverty, 1992; Moeller & Geber, 2005; Wassink & Caruso, 2013). Because the pollinator visits transferred from the facilitator to the facilitated species are definitionally in excess of what the facilitator needs for reproduction, the fitness of the facilitator species may not be affected by co-occurring facilitated species. Due to the fitness benefits of increased pollinator visits, the facilitated species tends to co-occur more frequently with the neighbouring species than predicted by chance (modelled in Gilpin et al., 2019; Johnson et al., 2003; Molina-Montenegro et al., 2008). In a second mechanism of pollinator facilitation, co-blooming flowers present a collective bouquet that is more attractive than any one species in isolation. In this scenario, every co-occurring species benefits from other co-blooming species; therefore, in theory, all species should co-occur with each other more frequently than predicted by chance (Wong et al., 2023). Finally, facilitation may not require spatial co-occurrence: sequentially flowering species can provision resources for pollinators and ensure sustained pollination service over non-overlapping blooming periods (Grab et al., 2017; Ogilvie & Thomson, 2016). Such temporal facilitation can leave little to no discernible spatial pattern with relation to flowering at a single time point, as seen in both natural (Ferrero et al., 2013) and experimentally grown mixed communities (Ferrero et al., 2013; Grab et al., 2017).

Given the diversity of pollinator facilitation mechanisms and the varying predictions each makes for community interactions and species co-distributions, a current goal in plant ecology is to identify floral or community characteristics that predict the likelihood and strengths of facilitation (Braun & Lortie, 2019; E-Vojtkó et al., 2020). However, it has been a difficult challenge to infer facilitation from community composition (Verdú et al., 2021). The long-held view of negative frequency dependence of pollinator visitation predicts that rare species are more likely to benefit from increased community-level display (Feldman et al., 2004; Rathcke & Jules, 1993), yet this tendency is modified by the strength of inter- and intra-specific competition as well as the degree of pollinator specialization (Bergamo, Streher, Wolowski, et al., 2020; Bergamo, Streher, Traveset, et al., 2020). Others have sought to identify floral traits that would predict facilitation (E-Vojtkó et al., 2020). While some work reported that flowers with similar floral colours are more likely to facilitate each other's pollination (Bergamo, Streher, Wolowski, et al., 2020), others found the opposite pattern (Ha et al., 2021). To date, generality in the drivers of facilitative interactions remains elusive.

The difficulty of predicting pollinator facilitation from easily measurable community or plant traits necessitates direct observations of pollinator activity as evidence of facilitation. Even when this has been done (Bergamo et al., 2022; Bergamo, Streher, Wolowski, et al., 2020), it is unclear whether such facilitation impacts plant community structure at larger scales. Past efforts aimed at scaling up the impact of plant–plant facilitation to landscape-level co-occurrence have been mostly limited to direct facilitative processes like the amelioration of abiotic stress (Berdugo et al., 2019; Soliveres et al., 2015). In these systems, instead of empirically measuring the alleviation of water or light stress, researchers used satellite images to infer facilitation. The same inference methods cannot be as easily drawn in systems of indirect facilitation through pollinators. Generalizing the consequences of pollinator-mediated effects to patterns of co-occurrence at larger scales thus requires spatially commensurate evidence for facilitation, a challenging undertaking that has not been previously reported.

Here, we test whether local-scale pollinator facilitation can scale up to regional patterns of species co-occurrence. We focus on a pair of native annual plants, *Bidens frondosa* L. and *B. cernua* L. (Asteraceae). *B. cernua* has a radiate, sunflower-like inflorescence with the petal-like ray florets, while *B. frondosa* has a discoid inflorescence lacking ray florets (Figure 1a). In Asteraceae, the inflorescence (capitulum) functions as a single floral unit where the sterile or pistillate ray florets substantially enhance the attractiveness of radiate species, increase pollination success and promote outcrossing (Andersson, 2001; Cerca et al., 2019; Kim et al., 2008). We observed that this congener pair, and *Bidens* spp. more generally, often bloom in intermixed populations at the end of the growing season in their native range of eastern North America. Inspired by our observations of *Bidens* distributions and the known pollinator-attracting function of ray florets, we hypothesized that if pollinator facilitation between species of contrasting (radiate vs. discoid) floral forms substantially increases seed set repeatedly across populations, it should also increase the frequency of landscape-level co-occurrence. We predicted that *B. frondosa* and other discoid *Bidens* receive more pollinator visits and set more seeds when intermixed with *B. cernua* or other radiate *Bidens*. We also predict that strong local facilitative interactions may predict more frequent co-occurrence between discoid and radiate *Bidens* species broadly across the landscape, in a manner that is distinct from co-occurrence patterns generated by shared habitat preferences. With a combination of field observations, common garden and growth chamber experiments, as well as broad sampling across New York state (USA), we specifically addressed the following questions:

1. Does co-occurrence with radiate *B. cernua* promote pollinator facilitation to discoid *B. frondosa*?
2. Do *B. frondosa* and *B. cernua* benefit from outcrossing or suffer from heterospecific pollen interference, and does change in pollinator visitation due to the presence of neighbouring congeners impact seed set of either *B. frondosa* or *B. cernua*?
3. Can local pollinator facilitation between florally contrasting *Bidens* explain co-occurrence patterns among *Bidens* spp. across the landscape?

2 | MATERIALS AND METHODS

2.1 | Study system

North American *Bidens* L. (Asteraceae) contains multiple species with either (1) radiate capitula (e.g. *B. cernua*, *B. laevis and B. aristosa*) with showy, yellow rays or (2) discoid capitula (e.g. *B. frondosa*, *B. connata*, *B. tripartita*) with button-like inflorescences (Figure 1a). In general, there is limited information on the reproductive biology and natural history of these species, except for a few studies on their tropical and oceanic congeners (Grombone-Guaratini et al., 2004; Knope et al., 2020; Steele, 1992). There is currently inadequate molecular phylogenetic information of this temperate group to resolve the relationship between species included in this study (but see Knope et al., 2020 for a subset of *Bidens* species in our study).

FIGURE 1 Study species. (a) (left to right) *B. frondosa*, B. *connata*, *B. cernua* and *B. laevis*. (b) Examples of two mixed communities of co-occurring *B. frondosa* and *B. cernua* included in the study.

2.2 | Floral visitation to *Bidens*

To test whether radiate congeners facilitate floral visitation to *B. frondosa*, we identified 10 populations of either just *B. frondosa* or just *B. cernua* (= single-species populations), and 7 mixed sites where the two species co-occur without other *Bidens* species (= mixed populations Figure 1b, Figure S1a). Mixed populations contained stable (persistent across at least 2 years, authors' observations), sizable (>30 individuals) and well-mixed (Figure 1b) populations of the two species at roughly equal densities (Figure S1b), spaced at least 5 km apart from the nearest site (Figure S1a). The sites did not have any other co-flowering plants at the time of our observations, and they did not differ significantly in air and ground temperature or surface soil pH at the time of observation (Figure S1c,d). We marked 15 individuals of each species (30 individuals total in mixed populations) that were evenly spread out throughout a 3 m × 5 m area in the centre of a population and observed floral visitations to those 15 individuals at each site for 1 h between 10:00 AM and 02:00 PM on sunny, clear days from 24 August 2021 to 16 October 2021. Each site was observed on 2 days and for 2 h total. Visitation was recorded at the plant level per insect, that is the same insect visiting the same plant multiple times counted as one visit. We did not collect any insect visitors and identified visitors to insect family or finer taxa in the field. Because the variable we were interested in (single vs. mixed populations) is replicated at the population level, and because our pollinator visitation data were taken at the site level, we treated the mean of pollinator visits to 15 plants at each site as the unit of replication in analyses, totalling 10 replicates for monospecific populations per species and 7 replicates for mixed-species populations. We assessed our sampling completeness for pollinator richness and diversity for each community type with rarefaction analyses using 'iNEXT' (Hsieh et al., 2016) in R (R Core Team, 2024).

To test whether patterns of floral visitation in natural populations could be replicated in a more controlled environment, we set up 11 sites as common gardens (Table S1) in Tompkins County, New York in the following year (2022). These sites were selected to mimic habitats where *Bidens* naturally occur in isolation and with congeners and are absent of any other co-flowering plants at the time of the experiment. All experiments were done with permission on land overseen by the Natural Areas Program Cornell Botanic Gardens (Cornell University). We deliberately chose sites at least 5 km away from natural *Bidens* populations and other co-blooming plants at the time of pollinator observations. The common garden experiment controlled for two confounding factors in our natural observations. First, by pairing mixed populations and single-species populations at the same sites, we controlled for the potentially differing abiotic environments that may have made our mixed populations a more suitable habitat for both species. Second, by controlling for the density and spacing between plants within each site, we eliminated potential density-dependent impacts of *Bidens* or other species in natural populations. For each species, seeds were collected and pooled from the 17 natural populations (10 single-species and 7 mixed-species populations) where we made pollinator observations. We soaked seeds in 10% bleach for 20 mins, rinsed them with D.I. water three times and placed them in the dark at 4°C for 60 days before incubation in a growth chamber (25°C day/20°C night, 16 h daylight) to germinate. Seedlings were grown in 4-inch (1.07 L) pots in Lambert All-Purpose Growing Mix (A.M. Leonard Tool & Supply Co., USA) with a 16 h daylight regimen (24°C day/20°C night) for 2 weeks before being transplanted into common gardens. At each site, we set up one plot with 30 individuals of *B. frondosa* and a paired plot with 15 *B. frondosa* and 15 *B. cernua*. Plants were spaced 50 cm apart in each 2.5 m × 3 m plot, and paired plots were spaced roughly 5 m apart. Mixed-species plots were planted in a full checkerboard array such that each plant's immediate neighbouring plants were all heterospecific. We supplemented the plots with daily watering for the first month and never fertilized the plants. We lost five *B. frondosa* and one *B. cernua* to mammalian herbivory. Upon blooming (roughly 85 days post transfer into the field), we recorded floral visitors to 15 *B. frondosa* from mixed and *B. frondosa*-only plots each for 1 h at each plot between 10:00–14:00 on sunny, clear days from 20 August 2022 to 6 September 2022, resulting in 11 replicates each for *B. frondosa*-only populations and for mixed-species populations. We also recorded floral visitors to the 15 *B. cernua* plants in mixed plots, but because we did not have *B. cernua*-only plots in our common garden experiments, we do not report the data here.

2.3 | Estimating lifetime reproductive success of *Bidens*

We tested whether congener pollinator facilitation confers benefits of enhanced viable seed set to *B. frondosa* or entails costs to *B. cernua* for both the natural population study and the common garden experiment. Because both species exhibit parthenocarpy, or the development of fruit without fertilization, we estimated the number of viable seeds as a proxy for reproductive success, instead of more popular but potentially misleading proxies, such as the total number or mass of seeds. We estimated viable seed set for *B. frondosa* by directly examining its seed content, and for *B. cernua* by recording the germination rate. We chose different metrics of seed viability due to their distinct seed characteristics, and we describe our justifications and method for each species separately below.

For *B. frondosa*, we counted the number of capitula of each plant, weighed the mass of all the seeds produced, and randomly selected 50 seeds from the total seed set and weighed the mass of those 50 seeds. We then made a small incision width-wise across each of the 50 seeds. If a seed contains an ivory-coloured embryo inside, it was properly fertilized and was counted as viable. We recorded the percentage of viable seeds out of 50. Then, we inferred the total number of viable seeds per plant by the formula (total seed mass (g)/(mass of 50 seeds (g) /50)) × % of viable seeds. For *B. cernua*, it was logistically difficult to assess seed content as we did for *B. frondosa* because of their small seed size. Instead, we germinated the 50 randomly chosen seeds from each *B. cernua* plant by the same germination protocol as described above. We inferred the total number of germinated seeds per plant by (total seed mass (g)/(mass of 50 seeds (g)/50))×% of filled seeds. We did not measure the germination rate for every population of *B. frondosa* due to experimental constraints, as *B. frondosa* requires double the amount of stratification time than *B. cernua*. The germination rate for *B. frondosa* for the common garden experiments (above) and the growth chamber tests on the extent of autonomous selfing (below) showed that our examination of seed contents yielded similar rates of seed viability as actual germination rates for *B. frondosa* seeds. Replication in statistical analyses of viable seed set was the same as that for pollinator visitation.

2.4 | Extent of autonomous selfing and heterospecific pollen interference of *B. frondosa* and *B. cernua*

We conducted a growth chamber experiment to test whether outcrossing increases seed set for either *B. frondosa* or *B. cernua* and whether either species suffers heterospecific pollen interference from the other species. We pooled seeds from the same 17 natural populations for each species, germinated and grew them with the same protocol for the common garden experiment. We watered plants by completely saturating the pot every other day and did not fertilize. When the disc florets have fully displayed their anther and stigma, we applied one of four treatments to all capitula on a plant: (1) pooled conspecific pollen, (2) pooled heterospecific pollen (*B. frondosa* received *B. cernua* pollen, and vice versa), (3) self-pollen from the same capitulum or (4) no manipulation (control). Pooled conspecific and heterospecific pollen came from around 15 donor plants grown from seeds collected from the same 17 natural populations. The conspecific pollen treatment mimicked outcrossing; the heterospecific pollen treatments mimicked pollen interference from heterospecific plants; aided pollination from the same capitulum mimicked aided selfing by a pollinator carrying no external pollen; and the control treatment mimicked selfing without any floral visitation. We did not include an emasculation treatment because it was logistically impossible to emasculate all flowers within the highly condensed Asteraceae capitulum. The first three treatments were applied with a soft paintbrush once a day over 3 days. Each treatment had 15 replicate plants for each species, and we conducted the same experiment twice (total *n* = 30 for each treatment) and the experimental block was included as a fixed effect in statistical analyses.

2.5 | Data analysis

When analysing floral visitation data and lifetime reproductive success, we asked: (1) Does co-occurrence (a) increase pollinator visitation or viable seed set for *B. frondosa*, and (b) decrease either metric for *B. cernua*? Because these a priori questions were guided by known functions of rays, we performed pairwise comparisons between community types for *B. frondosa* and *B. cernua* separately. Because pollinator visitation data for *B. frondosa* and *B. cernua* in mixed natural populations came from the same populations, we could not perform the more omnibus two-way ANOVA F-test. Thus, for natural populations, we conducted Welch's *t*-tests to account for unequal variances between groups. For the common garden experiment, we conducted paired *t*-tests to account for non-independence between paired plots. To test whether co-occurrence caused shifts in pollinator community composition, we performed pairwise PERMANOVA on Bray–Curtis distance matrices of pollinator community with the 'adonis2' function in vegan 2.6–10 (Oksanen et al., 2025). Due to non-independence between data for *B. frondosa* and *B. cernua* from the same mixed population sites, we reported results after correcting for six pairwise comparisons with a Benjamini–Hochberg correction (see Results for specific comparisons). To test whether habitat conditions predicted either visitation or seed set in natural populations, we included total population size, temperature and pH separately as an additive covariate (pollination or seed set ~ community type + covariate). None of the covariates were statistically significant, so we report results from pairwise comparisons only. All statistical analyses were conducted in R 4.1.0 (R Core Team, 2024) and data visualized by ggplot2 3.4.0 (Wickham, 2016).

2.6 | Patterns of congener co-occurrences in New York State

We sampled occurrences of *Bidens* across New York State to test whether co-occurrence patterns could be predicted by the presence or absence of ray florets in neighbouring congeners. While both *B. frondosa* and *B. cernua* are weedy and have been introduced to the Western United States, east Asia and Europe, our sampling scale covered the centre of the native distribution of *B. cernua*, the less widely occurring of the two species. The region also encompasses the entire range of distributions for most other rare temperate North American *Bidens*. This choice of the overall spatial scale enables us to draw species-level inferences for the less weedy species. We made three independent sampling efforts (Figure S2): First, we largely followed the Hudson River and conducted a 295 km latitudinal transect (Plattsburg, NY to Nyack Beach State Park, NY) over 7–10 October 2022. The river provides an effective seed dispersal corridor and is where most public records of relatively rare *Bidens* species were located on iNaturalist.org (accessed July 2022). We then conducted a 345 km longitudinal transect (Dunkirk, NY to Hudson, NY) over 14–16 and 21–22 October. Our sampling was entirely observational on public land and did not require fieldwork permits. We supplemented these transects with observations centred around Tompkins County during the same time. We delimited each of the 27 natural populations where we observed pollinator visitation by a similar size (roughly 15 m^2). When the area with *Bidens* was more expansive, we roughly sampled a 3 m × 5 m area are in the centre of the population; when the populations grew along waterways, we sampled <15 m along both sides of the creek. Many populations were smaller than 15 m^2 and we sampled all plants at those sites. Any two sites were at least 5 km apart from each other. Because pollinator facilitation is a plant–plant level or community-level interaction, our choice of spacing between sites ensures each site as an independent replicate for the test of our hypotheses. In total, we observed *Bidens* at 147 out of a total of 198 sites. We focused our sampling efforts on *B. frondosa* and *B. cernua*, and another locally abundant discoid species *B. connata*. We also observed multiple unidentified radiate individuals and discoid individuals that were missing essential identifying characters. To prevent rare occurrences from biasing analyses, we grouped these rare species into either 'other radiate spp.' or 'other discoid spp.' category (Table S2).

To quantify co-occurrence, we calculated the checkerboard scores (C-score, Stone & Roberts, 1990). For species pair *i* and *j*, C-score (C_{ij}) is defined as $C_{ij}=(r_i-S_{ij})\times(r_j-S_{ij})$ where r_i, r_j are the respective numbers of occurrence of species *i* and *j*, and S_{ij} is the number of co-occurrences of *i* and *j*. C-scores of *M* groups ($M>2$) are calculated by $C=M\ \Sigma_{j=i}\ \Sigma_{i<j}\ (C_{ij}/P)$, where *P* is the total number of two-species pair for *M* species ($P=M\times(M-1)/2$). We then bootstrapped 10,000 times over the observed occurrences for each species and compared the resulting null distribution of C-scores. The bootstrapping was done by codes modified from EcoSimR 1.0 (Gotelli & Ellison, 2013). If the observed C-score laid outside the 95% confidence interval (CI) of simulated C-scores, co-occurrence was not random. High C-scores suggest less frequent co-occurrence than expected by chance (disaggregated), and low C-scores indicate more frequent co-occurrence (aggregated). We report the percentile value (P) of where the observed C-score fell over the simulated C-score distribution, and Standardized Effect Size (SES), which is a standardized deviate that can be compared between different simulations (Stone & Roberts, 1990). Large positive SES values (>2.0) suggest disaggregation and low negative SES values (< −2.0) suggest aggregation. Significant aggregation or disaggregation SES values in comparisons among three or more groups indicate at least one group aggregates or disaggregates with at least another group. In total, we made six comparisons to answer three questions. First, we measured co-occurrence (1) between the two focal species, *B. frondosa* and *B. cernua* and (2) between the two contrasting floral forms, radiate and discoid, to test whether divergence in floral form correlates with aggregation between them. We then measured co-occurrence (3) among three discoid groups (*B. frondosa*, *B. connata* and other discoid spp.) and (4) between two radiate groups (*B. cernua* and other radiate spp.) to test whether congeners with shared floral forms disaggregate. Finally, we compared (5) among all five species categories (*B. frondosa*, *B. cernua*, *B. connata*, other radiate spp. and other discoid spp.) and (6) among three locally abundant species (*B. frondosa*, *B. cernua* and *B. connata*) to test for genus-level co-occurrence patterns when disregarding floral morphology.

We recognize that frequent co-occurrence can also be driven by shared habitat preference, but if so, co-occurrence frequency among all *Bidens* species, regardless of floral form, should also be aggregative. If co-occurrence is driven more by floral contrast-mediated pollinator facilitation and less by abiotic habitat preference, only species pairs with contrasting floral forms should co-occur more frequently than expected, and other species pairs of the same floral forms (e.g. different discoid species) should co-occur randomly or even disaggregate. For example, if a discoid species (e.g. *B. frondosa*) co-occurs frequently with a radiate species (e.g. *B. cernua*) due to shared habitat preference, and another discoid species (e.g. *B. connata*) also co-occurs frequently with the radiate species due to shared habitat preference, then—by the transitive nature of similarity- the two discoid species should share similar habitats as well, and should also co-occur with each other more often than expected. More broadly speaking, if shared habitat preference is driving co-occurrence between radiate and discoid *Bidens*, then radiate *Bidens* should also co-occur frequently with each other, as do discoid *Bidens* species. In contrast, if co-occurrence between radiate and discoid *Bidens* is driven by their contrasting floral form, then species with similar floral forms should co-occur as expected by chance (or less).

3 | RESULTS

3.1 | Co-occurrence with radiate *B. cernua* increased pollinator visitation to discoid *B. frondosa*

We detected strong pollinator facilitation for *B. frondosa* co-occurring with *B. cernua*, both in natural populations and in common gardens (Figure 2). In total, we found floral visitors from 11 insect families in natural populations, and all were shared between *B. frondosa* and *B. cernua* (Figure S5). In natural populations, *B. frondosa* received nearly 60% more insect visits when coexisting with *B. cernua* than in isolated populations (Figure 2a; Welch's $t=3.397$, $df=12$, $p=0.005$). Increased pollinator visits to *B. frondosa* did not come at an apparent cost to visits to *B. cernua*, as pollinator visitation rates were not different between single versus mixed plots (Welch's $t=-1.638$, $df=13$, $p=0.124$). Mixed-species populations were comprised of 44% (±14%) *B. frondosa*. Pollinator visitation was unaffected by total plant population size, temperature, soil pH or *B. frondosa* density in mixed populations (Figure S1 and Table S3). In common gardens, we found the same facilitative effect: *B. frondosa* in mixed plots received ~33% more visitation than that in monospecific plots (Figure 2b paired $t=-2.9147$, $df=10$, $p=0.015$).

Bidens spp. co-occurrence was associated with changes in compositions of floral visitors to both *B. frondosa*, but not *B. cernua*. In natural populations, *B. frondosa*'s floral visitor communities in *B. frondosa*-only populations were significantly different from those to *B. frondosa* in mixed-species populations (PERMANOVA: pseudo $F_{1,15}=2.4561$, adjusted $p=0.025$). Pollinator communities to *B. cernua* in different community types were not different (single vs. mixed populations: pseudo $F_{1,15}=1.4145$, adjusted $p=0.215$). Composition of insect visitors to *B. cernua* and *B. frondosa* in mixed populations was not different from each other ($F_{1,15}=0.6071$, adjusted $p=0.728$), suggesting the same pollinator communities did not show measurable preference between the two species in mixed populations. Pollinator communities in mixed populations (total visits to both species combined) were significantly different from those that visited *B. frondosa*-only populations (pseudo $F_{1,15}=6.2231$, adjusted $p=0.016$), but not from those to *B. cernua*

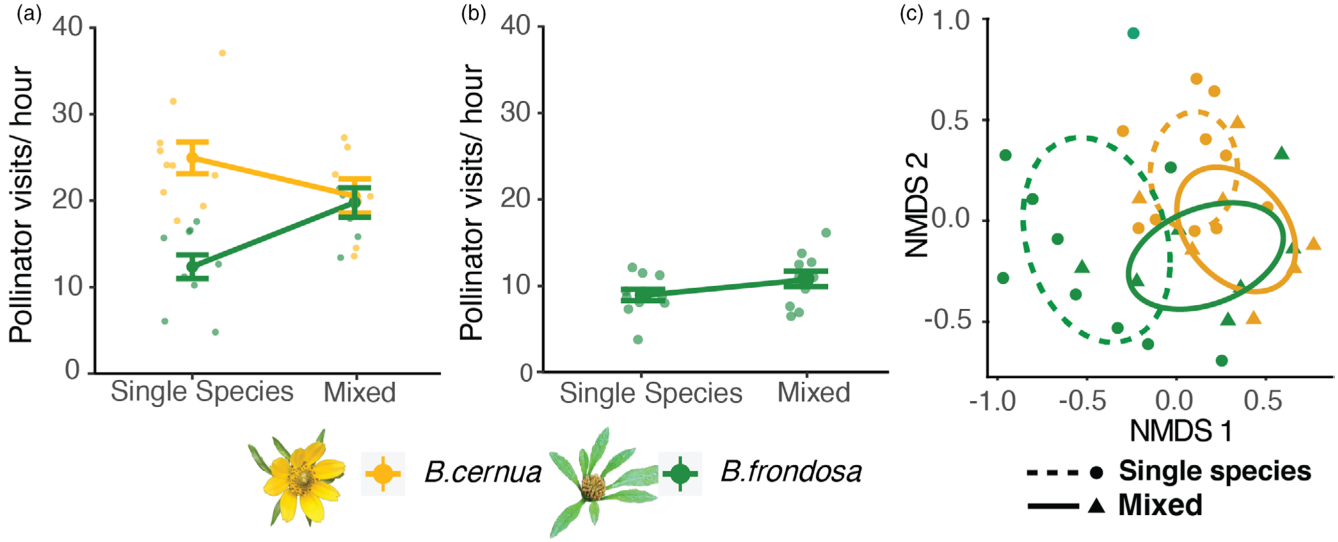

FIGURE 2 Co-occurrence with *B. cernua* increased pollinator visitation to *B. frondosa* in (a) natural populations and (b) common gardens. Individual points represent population averages; shown are means ±1 standard error. (c) Multivariate representation of the composition of insect floral visitors to *Bidens* by plant species and community type. Individual points represent population averages and ovals represent 95% confidence ellipses of group centroids.

populations (pseudo $F_{1,15}=0.086$, adjusted $p=0.242$). This pattern suggests that *B. cernua* was the main attractant in mixed populations and acted as 'magnet flowers' for *B. frondosa*. Our sampling yielded near-complete coverage of pollinator richness and diversity for both species in both community types (Figure S3).

Insect visitors were primarily comprised of *Vespidae* and *Cantharidae*, together comprising 57% of all visits and driving most of the shift in floral visitor community composition (Figures S5 and S6). Specifically, co-occurrence increased *Vespidae* visitation to *B. frondosa* by over 530% (Welch's $t=3.858$, $\mathrm{df}=8$, $p=0.004$) without significantly reducing their visits to *B. cernua* (Welch's $t=-0.325$, $\mathrm{df}=14$, $p=0.750$). Visits by *Cantharidae* spp. to *B. frondosa* increased by 21% in mixed populations (Welch's $t=0.820$, $\mathrm{df}=13$, $p=0.426$), and decreased by 22% to *B. cernua* (Welch's $t=-1.092$, $\mathrm{df}=13$, $p=0.295$), albeit both changes being non-significant. Floral visitor community composition also differed between community types in the common garden experiment (Figure S6B, pairwise PERMANOVA contrast: pseudo $F_{1,20}=1.649$, $p=0.027$). Co-occurrence with *B. cernua* did not change the overall Shannon-Wiener diversity index of floral visitor communities to *B. frondosa* (paired *t*-test, $t=-1.590$, $\mathrm{df}=10$, $p=0.143$), but did marginally increase *Vespidae* visits alone (paired *t*-test, $t=1.854$, $\mathrm{df}=10$, $p=0.093$).

3.2 | Co-occurrence with *B. cernua* increased seed set of *B. frondosa* in natural populations

Co-occurrence with *B. cernua* increased the number of filled seeds per plant for *B. frondosa* by 96% (Welch's $t=-2.313$, $\mathrm{df}=6.537$, $p=0.056$, Figure 3a). The number of filled seeds of *B. cernua* did not significantly decrease in mixed populations in a pairwise comparison (Welch's $t=0.749$, $\mathrm{df}=13.111$, $p=0.468$).

None of the environmental covariates measured significantly explained the component of fitness we measured (Table S3). Community type did not affect the inflorescence densities for *B. frondosa* (Welch's $t=1.841$, $\mathrm{df}=10.558$, $p=0.0939$, Figure S3a) or *B. cernua* (Welch's $t=1.287$, $\mathrm{df}=13.634$, $p=0.220$, Figure S3b). In common gardens, viable seed set of *B. frondosa* did not differ between paired monospecific plots and mixed plots with *B. cernua* (paired *t*-test: $p=0.650$, Figure 3b).

3.3 | *B. frondosa* and *B. cernua* benefit from conspecific pollen supplementation

To address the potential of increased pollinator visitation to impact seed set, we tested whether *B. frondosa* or *B. cernua* benefited from outcrossing and whether either species suffered from pollen interference. Although overall differences between pollen supplementation treatments were marginal (Figure 4; pollination treatment: $F_{3,231}=2.572$, $p=0.055$; species × pollination treatment: $F_{3,231}=0.355$, $p=0.785$), application of conspecific pollen increased the number of germinated seeds of *B. cernua* by 23% (Welch's $t=-2.322$, $\mathrm{df}=46.383$, $p=0.025$) and the number of filled seeds of *B. frondosa* by 37% (Welch's $t=-3.1834$, $\mathrm{df}=48.486$, $p=0.003$). Congeneric pollen application and self-pollen treatments did not change either species' reproductive success as estimated by seed set compared with the unmanipulated controls (Figure 4). We conclude that both *B. frondosa* and *B. cernua* benefit from conspecific pollen supplementation in terms of increased viable seed set. Given the absence of heterospecific pollen interference, increased pollinator visitation in the wild, even in mixed populations, likely contributes to the increased seed set for *B. frondosa* we observed.

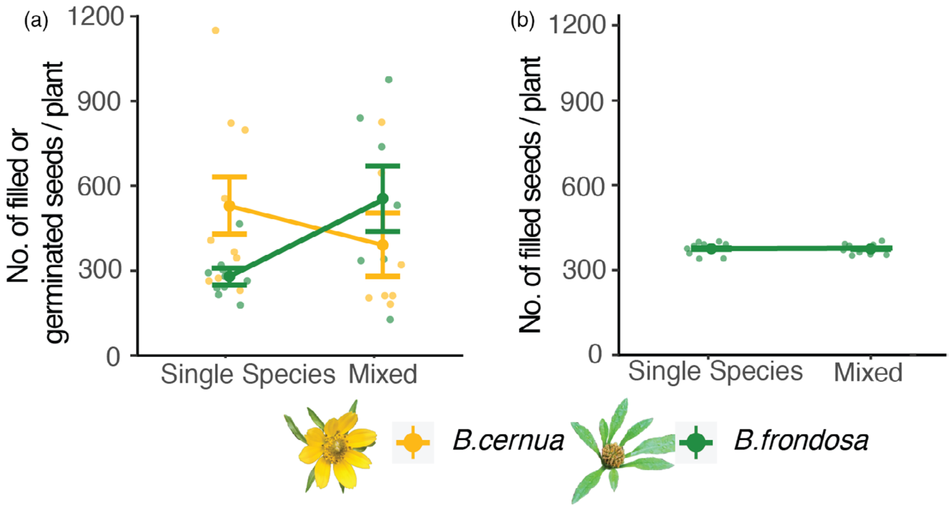

FIGURE 3 Co-occurrence with *B. cernua* (a) increased viable seed set for *B. frondosa* in natural populations but not (b) in common gardens. Individual points represent population averages; shown are means ±1 standard error.

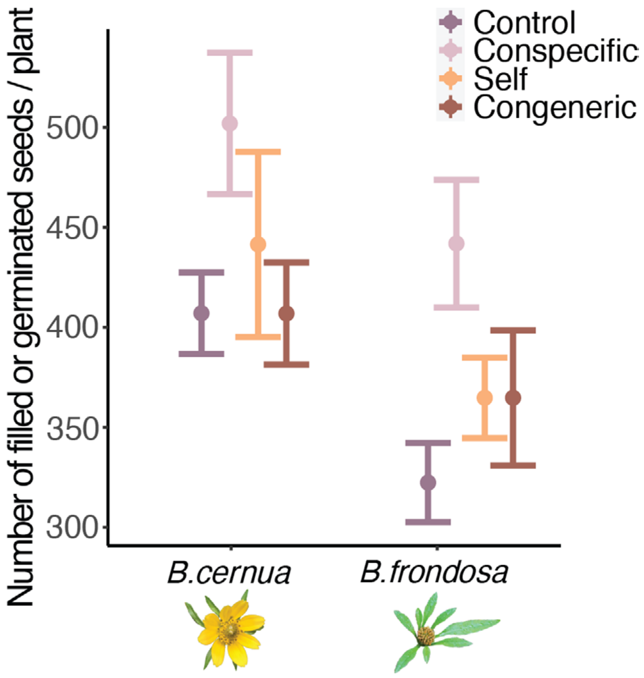

FIGURE 4 Application of conspecific pollen yielded higher female viable seed set in both *B. cernua* and *B. frondosa* compared with controls; application of self-pollen or congeneric pollen had little effect. Shown are means ±1 standard error.

3.4 | Floral trait divergence explains aggregation of *Bidens* congeners

As we detected strong pollinator-mediated facilitation between *B. frondosa* and *B. cernua* across multiple natural populations, we would expect that they may co-occur more frequently than expected, and congener pairs with similarly contrasting floral form may also co-occur in an aggregative pattern. As we've reasoned in the Methods, even though we did not exhaustively characterize habitat attributes for different *Bidens* species, we reasoned that co-occurrence due to shared habitat preference would generate different co-occurrence patterns than if contrasting floral form is driving co-occurrence. Across 147 sites with at least one *Bidens* spp., we found *B. frondosa* in 73 populations and *B. cernua* in 87 populations (Figure 5, Tables S2 and S4). We observed another locally abundant discoid species *B. connata* at 30 sites. Overall, 111 populations had discoid *Bidens* and 107 populations had radiate *Bidens*, including 4 rare *Bidens* species (two radiate and two discoid) that were grouped as 'other radiate *Bidens* spp.' and 'other discoid *Bidens* spp.' in our analyses.

B. frondosa strongly aggregated with *B. cernua* more than expected by chance (Figure 5a, Standardized Effect Size [SES] = −1.6987, lower-tail $p=0.032$, Table S4). More generally, all discoid *Bidens* spp. tended to aggregate with radiate congeners (Figure 5b, SES = −2.2308, lower-tail $p=0.005$), but randomly with other discoid congeners (Figure 5c, SES = −1.054, lower-tail $p=0.117$). All radiate *Bidens* spp. disaggregated from other radiate *Bidens* (Figure 5d, SES = 1.4732, upper-tail $p=0.086$). Overall, five groupings of *Bidens* spp. (*B. frondosa*, *B. cernua*, *B. connata*, other radiate *Bidens* spp. and other discoid *Bidens* spp.) disaggregated when treated as equivalent (Figure 5e, SES = 11.143, upper-tail $p<0.001$). After removing the rare species, the three most abundant species (*B. frondosa*, *B. cernua* and *B. connata*) were found to aggregate (Figure 5f, SES = 3.84, upper-tail $p=0.047$).

4 | DISCUSSION

Our study advances the current literature by showing that contrasting floral traits can not only confer pollinator-mediated facilitation, but also correlate with community composition across the landscape. We directly observed pollinator facilitation and confirmed its fitness impact on the facilitated *B. frondosa*. We further found that the underlying floral display contrast broadly explained congener co-occurrence across the landscape and was associated with a species co-distribution pattern opposite to that expected from shared habitat preferences or competition. Although coexisting congeners

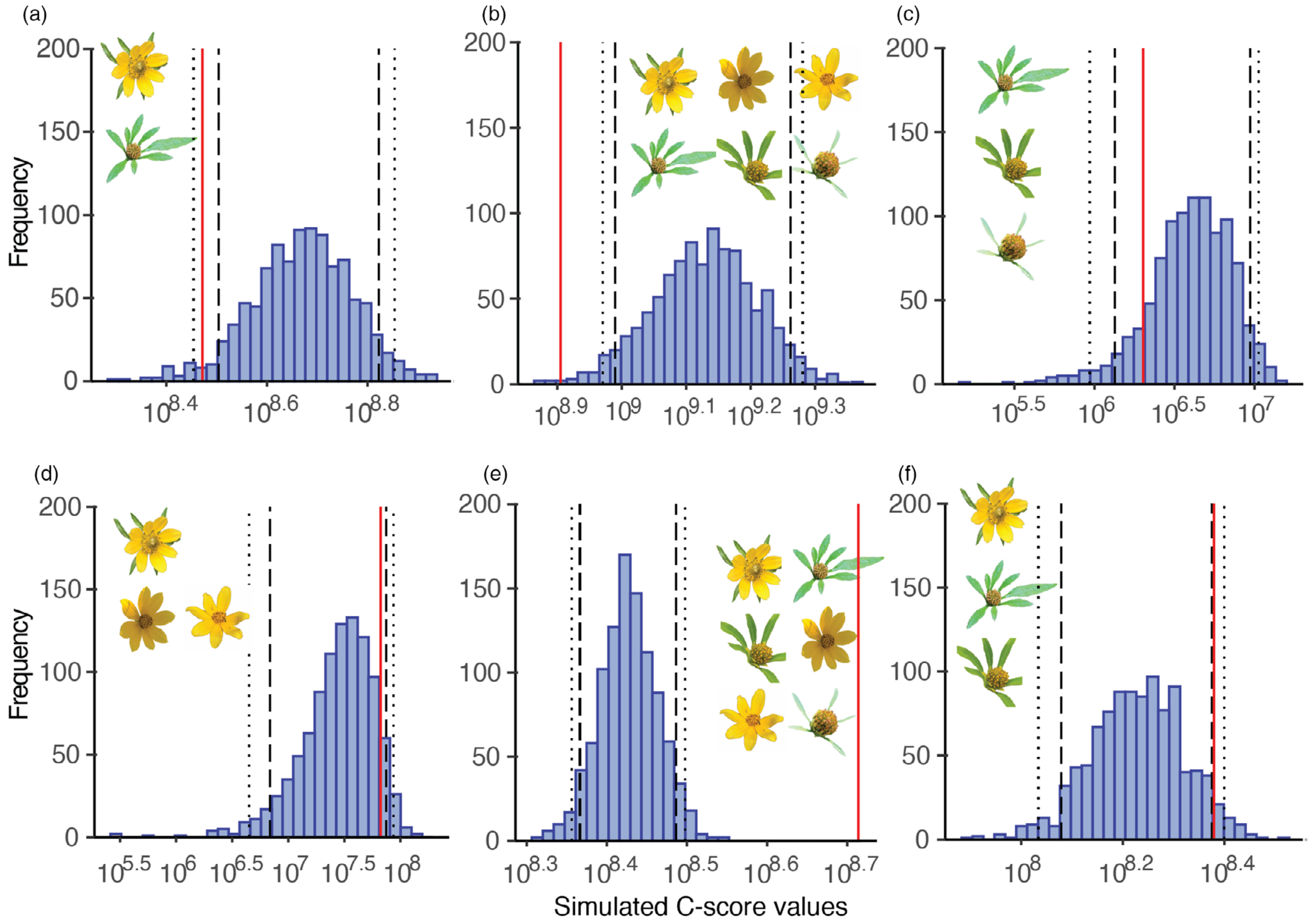

FIGURE 5 Floral trait divergence explains spatial aggregation of *Bidens* species across 147 natural populations. Histograms show the distribution of the simulated co-occurrence index (blue bars), the value for the observed data (red line), and the one-tailed (dashed line) and two-tailed (dotted line) 95% confidence interval of the estimated co-occurrence index. Panels depict co-occurrence between (a) *B. frondosa* and *B. cernua*, (b) discoid vs. radiate species (comparison between two groups) (c) among discoid species (*B. frondosa*, *B. connata* and other discoid spp.; three groups), (d) among radiate species. (*B. cernua* vs. other radiate spp.; two groups), (e) all five species categories (*B. frondosa*, *B. cernua*, *B. connata*, other radiate spp. and other discoid spp.; five groups) and (f) three most abundant species (*B. frondosa*, *B. cernua* and *B. connata*; three groups). Different rows of floral icons represent distinct groups used for each comparison, and floral icons in the same row are considered part of the same group for comparison, except for (e), where five groups encompassing seven species are being compared and six floral icons of the seven species (all except *B. discoidea*) are arranged for best visual arrangement.

often compete (Weber & Strauss, 2016), here we have shown that positive interactions may counter competition, especially among species with contrasting phenotypes.

In our focal species pair, we did not observe a measurable cost to the facilitator (showy *B. cernua*) or detect any congeneric pollen interference. We noted an average 20% decrease in viable seed set for *B. cernua*, which may disqualify it from being a true 'magnet' flower (see Introduction). However, beyond being statistically non-significant, this decrease in viable seed set is apparently not strong enough to drive disaggregation between *B. cernua* and *B. frondosa* (Figure 5a). Thus, what might appear as a weak 'magnet' flower or even an inferior competitor for pollinator visitation can have a 'magnet' effect across multiple communities. In natural mixed populations, pollinator visitation to *B. frondosa* and *B. cernua* was nearly identical (Figure 2a), suggesting that the visual function of *B. cernua's* rays is mainly to bring in pollinators from afar. Once insects are in a mixed-species population, those who visit pay equal amounts of visitation to both plant species (Figure 2a) and are largely overlapping in insect composition (Figure 2c), despite the contrasting visual display of the two species. Results from congener pollen application suggested a near absence of heterospecific pollen interference, despite the close phylogenetic relationship between *B. frondosa* and *B. cernua* (Knope et al., 2020) and general prediction of heterospecific pollen interference between closely related species (Ashman & Arceo-Gómez, 2013; Streher et al., 2020). The scale-dependent advantage of *B. cernua*'s rays coupled with the lack of congeneric pollen interference perhaps potentiated the pervasiveness of the two species' co-occurrence.

We found that congener co-occurrence increased viable seed production of *B. frondosa* only in natural populations, even though floral visitation to *B. frondosa* increased in mixed populations in both natural populations and common gardens, albeit to a smaller magnitude (60% increase in natural populations, 33% in common gardens). We note that viable seed set was nearly 25% higher in natural populations overall than in our common garden experiment, and the variance in viable seed set was much lower in the common gardens (Figure 3). The discrepancy in mean reproductive success between these two settings is most likely explained by the set-up of the common gardens. Natural populations have potentially persisted, if not locally adapted, to where they were for multiple generations, so those populations that have persisted in mixed or single-species populations might have been more responsive to their local abiotic and pollinator environment than they would be in a common garden among other plants. Mixing seed sources from different populations and planting them in replicated common gardens may have neutralized between-population divergence and obscured the effect on one aspect of fitness that we observed in the wild. Additionally, while patterns of pollinator visitation were similar between natural and experimental populations, the composition of visiting insect communities was different (Figures S5 and S6). Most noticeably, we found fewer Cantharids and more Reduviids in common gardens. While there are records of Cantharids and Vespids as successful pollinators for other plants (Baskin et al., 2000; Fateryga, 2010; Pérez-Hernández, 2018; Ward & Johnson, 2013), there are no such records for Reduviids. A discrepancy in pollination efficiency may have led to the lack of effect on seed set in the common gardens despite consistent differences in floral visitation.

4.1 | Alternative explanations of co-occurrence

Our study successfully scaled up effects at the local scale between individuals to patterns across populations. While we have experimentally demonstrated pollinator-mediated benefits in terms of viable seed set from co-occurrence, there are alternative hypotheses that may explain the landscape-level co-occurrence patterns we observed, such as shared habitat preference, co-dispersal or conserved traits explained by phylogenetic relatedness. We address each alternative hypothesis in turn.

First, co-occurrence could be driven by strong affiliation to the same microhabitat, rather than the facilitated species 'chasing' the facilitator species via indirect positive interactions. Nonetheless, results from our study suggest that habitat affiliation is likely not the predominant driver of co-occurrence. Our modelling of congener co-occurrence suggests that *Bidens* species were unlikely to co-occur with congener overall (Figure 5e). This pattern of disaggregation runs opposite to what we would predict if habitat preference was a strong and consistent driver of co-occurrence for the genus. Only when we distinguished *Bidens* species by radiate versus discoid floral form did we find strong aggregation of congeners. We also found random, rather than aggregative, co-occurrences among congeners of the same floral form (Figure 5c,d). Such occurrence patterns suggest mechanisms linked to contrasts in floral forms are outweighing disaggregating forces, such as competition.

Secondly, *Bidens* spp. may co-disperse and thus be found in the same populations. The barbed 'tickseeds' of *Bidens* spp. are thought to be primarily dispersed on mammalian fur and skin and certainly follow corridors along streamside habitats. However, if shared dispersal drives co-occurrence, we would again predict other *Bidens* spp. to aggregate with each other. On the contrary, we found *Bidens* spp. to disaggregate on average across the genus (Figure 5e). Similar to facultative co-dispersal by large frugivores in other systems (Albrecht et al., 2015; Camargo et al., 2022), co-dispersal likely acts as a *reinforcing* factor after the benefits of co-occurrence have been initiated.

Thirdly, pairwise facilitative effects tend to increase with phylogenetic distance (Montesinos-Navarro et al., 2017, 2019). Currently, there is no well-sampled phylogeny for *Bidens* spp. When such phylogenetic information becomes available, future work will more effectively test whether phylogenetic distance is a complementary explanatory factor of co-occurrence in this system, as has been shown in Florida oaks (Cavender-Bares et al., 2004), California annual herbs (Godoy et al., 2014) and California lilacs (Ackerly, 2004). In these systems, phylogenetically conserved traits have been shown to assemble into phylogenetically over-dispersed local communities. If *Bidens* follow the same pattern of assemblage, florally contrasting and facilitative congeners ought to be more distantly related to each other than either is to their florally similar congeners. Namely, all radiate *Bidens* are each other's closest relatives, as are discoid *Bidens*. Preliminary phylogenetic analysis by Knope et al., 2020 suggests at least two independent transitions from radiate to discoid capitula in *Bidens*, suggesting that multivariate trait or niche divergence, as is proxied by phylogenetic distance, is likely only a complementary explanation for the co-occurrence patterns we observed.

4.2 | Floral neighbourhood and (the loss of) floral display

Congruent with the recent finding that the magnitude of pollinator facilitation increases with floral dissimilarity (Ha et al., 2021), we detected strong facilitation in a system representing an extreme form of contrasting displays: presence versus absence of the main visual display organ. Loss of rays has occurred multiple times in Asteraceae and has been viewed as a cost-saving strategy during transition from outcrossing to selfing. However, records of self-incompatible or pollen-limited discoid Asteraceae abound (Baldwin, 2005; Cerca et al., 2019; Ferrer et al., 2009; Love et al., 2016). Because these repeated shifts towards discoid capitula were not always accompanied by shifts away from dependency on external pollination, we postulate that plants may employ alternative strategies to mitigate the loss of an ancestrally beneficial adaptation; namely, discoid Asteraceae may compensate for the reduced conspicuousness to pollinators due to the loss of rays.

Our study presents a case where congener facilitation serves as an ecological mechanism to compensate for the loss of an adaptive trait in a novel way. Looking beyond *Bidens* congeners, the loss of rays is associated with overlapping distributions of many radiate and discoid Asteraceae congeners like *Anacyclus* spp. (Cerca et al., 2019) and *Senecio* spp. (Andersson, 2008). More generally, the loss of visual advertisement, volatile attractants or floral rewards is prevalent across flowering plants. Florally divergent congener pairs across angiosperms thus provide systems to test whether contrasting or complementary floral display traits consistently mediate plant–plant interactions. Particularly when divergence in display occurred recently and contrasting congeners inhabit similar environments, facilitation may enable an inconspicuous species to become a persistent piggybacker of pollinator services generated by their conspicuous, closely related neighbours.

Floral display involves both advertisements that attract animals to come in contact with flowers, like that tested in this study, and rewards that provide an energetic benefit to pollinators for the visit. While our study is the first to our knowledge to explicitly test whether contrast in advertisement between congeners confers interspecific facilitation across spatial scales, much research has been conducted on reward, particularly in rewarding–rewardless floral mimicry pairs (Lichtenberg et al., 2020; Sakata et al., 2014). Rewardless orchid mimics often benefit from occurring in close vicinity to rewarding flowers in low densities, limiting pollinator learning of signal honesty and discernment of fine-scale floral phenotype (Jersáková et al., 2012; Johnson, 2000). Records of such tracking are rare outside of such highly specialized systems. A parallel body of literature on Batesian mimicry in animals has also stated that defence mimics should occur in sympatry with their models in a negative frequency-dependent manner (Finkbeiner et al., 2018; Pfennig et al., 2001; Ruxton & Schaefer, 2016). It would be a fruitful line of future research to test whether classical theories on density-dependent assemblage of reward or defence mimicry pairs can be extended to other axes of organismal display, such as the floral phenotypes studied here.

5 | CONCLUSION

We conclude that pollinator facilitation, conferred by contrast in floral display, has a strong impact on reproductive success in natural populations and explains population-level co-occurrence between *Bidens* congeners across the landscape. More generally, our findings suggest that broad community assembly patterns can potentially be distilled to discrete trait-mediated indirect plant–plant interactions. While our regional survey of co-occurrence patterns confirmed our predictions of the impact of local facilitative interactions through space, much remains to be studied if such interactions can impact community persistence or evolution through time. We speculate that floral neighbourhoods might ultimately shape natural selection, particularly on floral display traits, and local adaptation of the facilitator and facilitated species. Exploring these possibilities will bridge the gap between studies on plant–plant facilitation, community ecology and evolution.

AUTHOR CONTRIBUTIONS

Xuening Zhang and Anurag A. Agrawal conceived the study and wrote the manuscript. Xuening Zhang collected data and performed the analyses.

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CONFLICT OF INTEREST STATEMENT

We declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.70065.

DATA AVAILABILITY STATEMENT

All R codes and raw data are deposited in https://doi.org/10.6084/m9.figshare.24085077 (Zhang, 2023).

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SUPPORTING INFORMATION

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

Figure S1. Metadata for natural *Bidens* populations observed in this study.

Figure S2. Transect map for observed *Bidens* populations.

Figure S3. Number of inflorescences of *B. frondosa* and *B. cernua*, in natural populations and common gardens.

Figure S4. Rarefaction analysis of sampling coverage of pollinator richness.

Figure S5. Pollinator visitation data by taxonomic groups.

Figure S6. Shift in pollinator composition in common garden and pollinator visitation to *B. frondosa* by pollinator taxonomic group.

Table S1. Locations of common garden sites.

Table S2. Occurrences and co-occurrences of *Bidens* across 147 sampled sites.

Table S3. Statistical summary of environmental covariates in the analysis of pollinator visitations and fitness in natural populations.

Table S4. Checkboard score statistics.

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