Community Ecology (2021) 22:309–317
https://doi.org/10.1007/s42974-021-00056-5

ORIGINAL ARTICLE

Indirect facilitation mediated by pollinators in intermountain prairie

Scott Debnam[1] · **Huixuan Liao**[2] · **Ragan M. Callaway**[1]

Received: 26 April 2021 / Accepted: 19 August 2021 / Published online: 8 September 2021

Abstract

Pollinators can drive indirect facilitative and competitive indirect interactions among plant species. Most work on indirect facilitation via pollinators has focused on "magnet species" which enhance the pollination success of their neighbors because they are disproportionately attractive. However, focusing on magnet species may overestimate the generality of indirect facilitation and underestimate the occurrence of indirect competition among plant species via pollinators. We used experimental arrangements that included three flowering native intermountain prairie species (*Achillea millefolium*, *Gaillardia aristata*, and *Linum lewisii*), all of which are similarly attractive to pollinators, to explore how variation in species richness and density affected pollinator visitation rates, diversity, and behavior. All three plant species experienced significant increases in pollinator visitation and the species richness of visiting pollinator communities when grown with another species that was in flower at the same time. This "diversity" effect was stronger than the effects of the total density of individual plants in flower in a plot. We also found an increase in visitation time, per flower, for solitary pollinator species in plots with two species in flower compared to plots with one plant species in flower. Social pollinator species did not increase visitation time in two-species plots. Finally, seed set by *Linum* was significantly greater in two-species than in one-species plots. Our results indicate that indirect facilitative interactions mediated by pollinators may be common in intermountain prairie plant communities and that such indirect interactions do not have to mediated by benefactor species that are strikingly more attractive than their beneficiaries.

Keywords Diversity · Facilitation · Indirect interactions · Pollination · Visitation rate

Introduction

Pollinators can drive positive indirect interactions when comingled plant species attract more pollinator species and visits than the same plant species would attract growing alone (Feldman, 2004; Lazaró et al., 2009; Braun and Lortie, 2019; Underwood et al., 2020). Indirect interactions among plants involving pollinators can also be competitive (Levin, 1970; Reader, 1975; Waser and Fugate, 1986; Underwood et al., 2020), with interspecific neighbors either reducing visitation in species-diverse mixtures or reducing "carry over," the amount of pollen reaching a second conspecific after a pollinator stops over at a different species. Such positive and negative indirect interactions are common because many pollinators are generalists (Goulson, 2003; Hingston and McQuillan, 1998) and prefer mixed diets. Furthermore, generalist pollinators are also disproportionately abundant relative to specialists (Fort et al., 2016; Vázquez and Aizen, 2003), which is important because their abundance can amplify their effects. For example, nearly a hundred plant species can provide floral resources to honey bee (*Apis mellifera*) colonies (Coffey and Breen, 1997), and globally, honey bees utilize nearly 40,000 different species (Crane, 1990). Hingston and McQuillan (1998) found that *Bombus* species in Tasmania visited over 66 plant species from 21 different plant families, and Macfarlane (1974) found that *Bombus* species visited 419 different plant species in New Zealand. In Brazil, Filho and Packer (2015) found that the bees in the *Megachilidae* family visited 112 different plant species.

Most work on indirect facilitation mediated by pollinators has focused on "magnet species" (Braun and Lortie, 2019).

✉ Scott Debnam
scott.debnam@umontana.edu

[1] Division of Biological Sciences and the Institute on Ecosystems, University of Montana, Missoula, MT 59812, USA

[2] School of Life Sciences, Sun Yat-sen University, Guangzhou 510006, China

Magnet species are those in pollination webs that attract a highly disproportionately large number of pollinators and enhance the pollination success of their less attractive neighbors because their unusual attractiveness (i.e., Walther et al., 2008). This is due to flexible foraging strategies, in which insect pollinators switch from magnet species to other nearby flowering species. These switches may be influenced by patchy floral distribution, depletion of floral resources by other foragers, and low encounter rates of the magnet species (Goulson,1999, 1997). For example, *Podophyllum peltatum* (mayapple) produces no nectar, and Laverty and Plowright (1988) found that *Podophyllum* plants that were near *Pedicularis canadensis* (lousewort) produced more fruits and seeds than plants that were far from *Pedicularis*. This suggests that *Pedicularis* acted as a magnet for pollinators because of its showy flowers and nectar. Johnson et al. (2000) transplanted the non-nectar-producing orchid, *Anacamptis morio*, into patches of nectar-producing plants and found that visits to the orchid increased in the presence of the nectar-producing species. Master and Emery (2015) found a 240% increase in pollinator visitation to plots that contained the magnet *Ranunculus ficaria* compared to plots without *Ranunculus*. Clearly, exceptionally attractive plant species can indirectly facilitate other plant species that are pollinated by insects.

Magnet species may drive indirect facilitation, but focus on unusually attractive species might overestimate the generality of such positive effects in communities (Braun and Lortie (2019). In other words, might such indirect facilitative interactions function without magnet species? Can such indirect interactions be caused by mixtures of species that are similar in attractiveness? There is some evidence that such diversity-based facilitation may occur (see Braun and Lortie, 2019). Ghazoul (2006) found that pollinator visits to *Raphanus raphanistrum*, and subsequent seed production, increased when it co-occurred with *Hypericum perforatum* or *Solidago canadensis* instead of when *Raphanus* was alone. This suggests that interspecific facilitation involving pollinators may not require magnet species, but the attractiveness of *Hypericum* and *Solidago*, relative to *Raphanus*, was not measured. Lazaró et al. (2009) found that the diversity of plant species surrounding six different target species correlated with the composition of the pollinator community that visited the target, with visitation by uncommon pollinator species increasing with surrounding floral diversity. Thus, there is a growing, but limited, body of evidence, suggesting that indirect facilitation mediated by pollinators may be common even without the unusually strong effects of magnet species (Braun and Lortie, 2019).

Other plant community attributes, such as plant species density, can also have strong effects on pollinator visitation, and these can be stronger than the effects of species richness (Borges et al., 2003; Dauber et al., 2010; Hegland and Boeke, 2006; Sih and Baltus, 1987; Munoz and Cavieres, 2008) and alter the effects of species richness (Braun and Lortie, 2019). For example, Jennersten (1988) compared the pollination success of *Dianthus deltoides* in small fragmented populations to that in larger continuous populations. *Dianthus* flowers received fewer visits from pollinators in small populations than in large populations and seed set was much lower. In small populations experimentally pollinated flowers substantially increased seed set, but this did not occur in large populations. Platt et al. (1974) experimentally manipulated population densities of *Astragalus canadensis* and found that seed production was higher for high-density populations than low-density populations, and attributed this to pollination success and host detection by the pollinators. Host density clearly affects pollinator visitation, but we know little about the relative importance of host population density versus host community richness.

In order to explore the effects of floral richness in the context of the effects of flowering plant density and different degrees of inherent attractiveness, we used small-scale experimental arrangements of native intermountain prairie species to explore how variation in species richness and density affected pollinator visitation rates, diversity, and behavior. We asked the following questions: (1) Do flowering species attract more pollinator visits when planted with other flowering species? (2) Do two-species mixtures attract more visits, more diverse pollinator species, and longer residence times than single species? And, (3) do two-species mixtures produce higher seed productivity per mature inflorescence (seed head) than single species?

Methods

Study system

Our study was conducted in a common garden at Fort Missoula, Missoula Montana (N 46.84278 and W-114.05806) during May and June 2015 (see Liao et al., 2015). We used 10 perennial species that commonly occur in grasslands in the northern Rocky Mountains to create native plant assemblages. These were five grasses (*Festuca idahoensis*, *Koeleria macrantha*, *Poa secunda*, *Pseudoroegneria spicata*, and *Stipa comata*) and five forbs (*Achillea millefolium*, *Artemisia frigida*, *Gaillardia aristata*, *Geranium viscosisimum*, and *Linum lewisii*). The grasses did not provide resources to pollinators but their presence provided a realistic environment for pollinators to forage in. The five forb species increased our chances of getting more than one species flowering at the same time in plots. In February 2013, we grew plants from field-collected seeds in 50-ml pots filled with 50% sand and 50% potting soil in a greenhouse at University of Montana, Missoula, USA. Three months later, seedlings were transplanted into randomly arranged 0.8 × 1.0

m^2 plots in the common garden, which would be defined as "small-grained" by Braun and Lortie (2019). The distance between plots was 30 cm. We established monocultures for each individual species ($n = 4$ per species) and polycultures with all 10 species ($n = 10$) for a total of 50 plots. In each monoculture, twenty native plant seedlings were evenly planted in a 4 × 5 grid, with plants 20 cm from each other in each direction. For 10-species assemblages, two seedlings per species were planted and the positions of the seedlings were randomly located in the 4 × 5 grid of plants with the same spacing between neighboring individuals as that in monocultures.

To reduce nearby alternatives for pollinators and to increase the overall attractiveness of our common garden experiment, the flowers of all other flowering species within ≈ 20 m of the plots were continuously removed during the experiment. We watered the plots each evening during our sampling period. Only *Achillea*, *Gaillardia*, and *Linum* flowered during the experiment, and they each attracted substantial numbers of insect pollinators.

Data collection

We conducted five-minute observations of some combination of 43 different plots on 10 different days between June 02, 2015, and June 26, 2015, depending on what plants were flowering, for a total of 180 observations. Our total observation time (900 min) was similar to that reported in other studies (e.g., Muñoz and Cavieres, 2008; Lara-Romero et al., 2019; Albor et al., 2019), and sampling times per plot ranged from 10 to 50 total minutes with a mean of 22 min. The number of days sampled is included in our statistical model. For sampling, we chose the period of time during which flowering was common enough to find both one-species and two-species plots on the same day. Sampling was conducted only on days that were conducive to insect flight; with no sampling on days that were cooler than 12.8 °C or that were excessively windy (> 5.8 m/s). Plots were predominantly (80%) sampled on days that were sunny (8 of the 10 days) with temperatures ranging between 15.6 and 28.9 °C. The average sampling temperature was 25.6 °C. Our sampling was opportunistic as the species in flower in particular plots on a given sampling day varied substantially over the sampling period. Because of this natural variation, our sampling intensity per plot varied among the 43 plots, with the average number of sample days for a plot being 4.5 days, but ranging from 2 (a total of 10 min) to 10 (a total of 50 min) observation days per plot. No plot was sampled more than once per day. Observations were made between 0900 h and 1100. In each plot, we recorded the density of individual plants of each species in bloom. Over the 5-min observation period, all visits to each plant species in flower in the plot by all pollinators were recorded, which is by far the most common metric in such studies (Braun and Lortie, 2019). Landing on a flower was considered a visit. We recorded visits only when an insect landed on a flower in the plot. We also recorded the duration of visits when the density of pollinators was low enough to allow us to focus on a single insect. The exotic *A. mellifera* (honey bee) was identified to species, but otherwise pollinators were identified to either genus or family (Online Appendix, Fig. 1). This allowed us to measure the number of visits and some degree of the taxonomic richness of the pollinator community in each five-minute observation period. Taxonomic richness was defined as the number of different pollinator taxa that visited each plot in a given five-minute observational period.

We randomly collected 12 seed heads (mature inflorescences) from one randomly sampled *Linum* plant from each plot in which *Linum* occurred on June 29, 2015. These plots were classified as one-species and two-species plots. The seed heads were allowed to dry for 72 h, and then seeds were separated from the seed head. We counted the seeds in each of 12 seed heads from each *Linum* plant using a Konus dissecting scope (Model #5424).

Data analysis

We calculated the mean number of visits (calibrated by the sampling effort for each plot) of all pollinators to each species when flowering alone, and compared this to the mean number of visits to each species when flowering with one of the other two species. These means were tested with one way ANOVAs followed by Tukey post hoc tests. We measured the number of visits by all pollinator taxa to a plot during each of the five-minute observation periods (a plot was never sampled more than once per day) and tested the means of these between all one-species and two-species plots with an ANOVA with the number of species in flower (1 vs. 2) as a fixed variable, the density of all plants in flower as a covariate, and number of observation periods (days) that the plot was sampled as a covariate. We also recorded the number of different pollinator taxa that visited a plot during each of the five-minute observation periods (one per day) and tested the means of these between all one-species and two-species plots with the same ANOVA model. We recorded the mean duration of visits for as many pollinators as possible in one-species and two-species plots and divided these into two datasets: one for *A. mellifera* and *Bombus* species, and one for all other species, and tested these in separate ANOVAs with the same factors as above. This approach separated the social species from the solitary species. The rationale for this is that individuals of social species might forage differently than individuals of solitary species based on resource needs, individual learning, and the sharing of resource information possessed by social bees (Heinrich, 1976; Nieh et al., 2003; Dornhaus, 2006; Williams and Tepedino, 2003). The total pollinator taxa richness levels in one-species and two-species plots were also tested with the same ANOVA model. We compared the number of seeds per mature seed heads for *Linum* between one-species and two-species plots using an ANOVA with flowering species richness in plots as a fixed factor with seed head nested within plot as a random factor.

Results

Facilitation among plants

Each of the three plant species showed significant increases in average number of pollinator visits when grown with another species (Fig. 1). When grown in monoculture, *Linum* received an average of 1.6 ± 0.2 visits per sampling period, but when grown in plots with either *Achillea* or *Gallardia,* the visitation rate to *Linum* increased to 3.0 ± 0.8 and 3.9 ± 0.7 visits, respectively, per sampling period ($F_{\text{species combination}} = 9.62$; $P = 0.001$; Tukey for *Linum* alone vs. *Linum* with *Achillea* $P = 0.021$; Tukey for *Linum* alone vs. *Linum* with *Gallardia* $P = 0.001$). We could not compare the effect of *Achillea* on *Gallardia* because of low sample size, but *Gallardia* was visited an average of 2.6 ± 0.4 times when growing without another species in flower, versus 4.4 ± 0.5 times when growing with *Linum* in flower, an increase of 69% ($F_{\text{species combination}} = 7.53$; $P = 0.015$). Likewise, we could not measure the effects of *Gallardia* on *Achillea* because of low sample size, but *Achillea* received an average of 1.0 ± 0.6 pollinator visits during each observational period when growing alone, versus an average of 4.7 ± 0.3 pollinator visits when growing in plots with *Linum* in flower, an increase of 3.7 times the rate when growing alone ($F_{\text{species combination}} = 14.83$; $P = 0.004$). Our sample size for plots with *Achillea* and *Linum* together was very low, ($n = 3$), but each of these was sampled an average of five times over the flowering season.

For pollinators measured at the plot level, two-species plots affected pollinators differently than single-species plots, when all species combinations were combined. Two-species plots experienced a 66% increase in average visits over single-species plots (Fig. 2, Table 1). Neither the total density of plants in flower nor the number of observation days were correlated with the average number of visits per observation period (Table 1). Mean pollinator richness was 84% greater in two-species plots than in one-species plots, and neither the total density of plants in flower nor the number of observation days were correlated with average pollinator richness per observation period (Fig. 2, Table 1). Total pollinator richness across the entire sampling period was 67% higher in two-species plots than in one-species plots, and not surprisingly, total pollinator richness was affected by the number of observation days a plot received (Fig. 2, Table 1). Again total pollinator richness did not correspond with total flower density (Table 1).

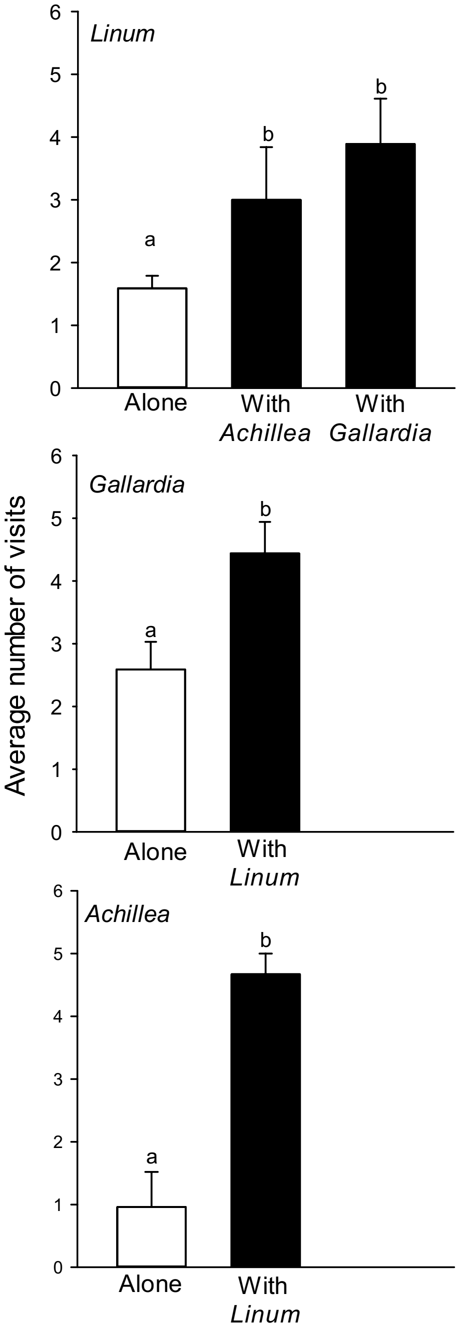

Fig. 1 Mean (± 1 SE) number of pollinator visitors to *Linum lewisii, Gaillardia aristida*, and *Achillea millefolium* when grown alone and with another flower species. Different letters indicate significant differences between means (see Table 1)

Seed set in *Linum* varied from 0 to 10 seeds per seed head with an average of 4.8 seeds per seed head across all plots combined. The average number of *Linum* seeds per seed head was 34% greater in two-species plots than in one-species plots (Fig. 3; $F_{\text{species richness}} = 15.13$; $P < 0.0001$).

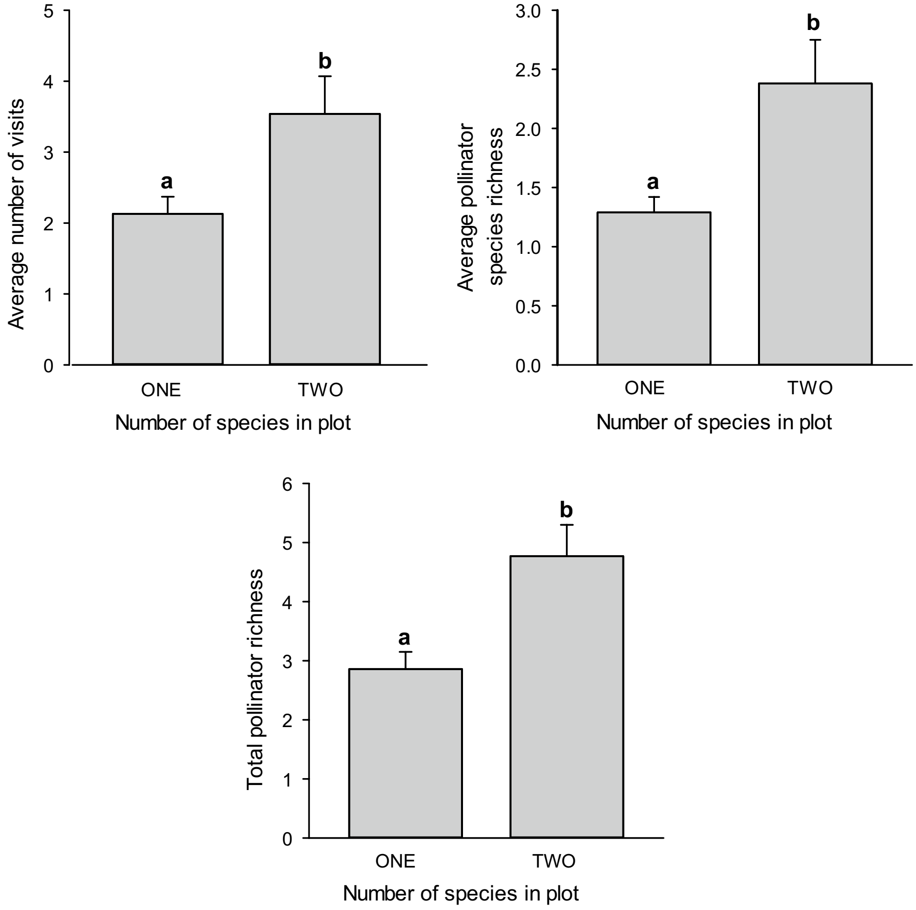

Fig. 2 Means (±1 SE) for **a** number of visits, **b** average pollinator species richness, and **c** total pollinator species richness in plots with one species in flower versus plots with two species in flower. Different letters indicate significant differences (see Table 1)

Table 1 Results for ANOVAs for the average number of visits for all pollinator taxa per each five-minute observation period of a given plot, the mean pollinator species richness attracted during each observation period, and the total pollinator species richness over all observations

Source	Average visits			Mean pollinator richness			Total pollinator richness		
	df	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*
Species richness	1	**8.633**	**0.006**	**1**	**13.26**	**0.001**	**1**	**14.56**	**< 0.001**
Plant density	1	0.311	0.582	1	0.002	0.965	1	0.515	0.477
Number days sampled	1	0.750	0.392	1	0.002	0.870	**1**	**4.402**	**0.042**
Error	40			40			40		

Species richness is the number of forbs in flower in a plot and was used as a fixed factor. Plant density is the number of flowering individuals in a plot and was used as a covariate. Days sampled is the number of days on which a plot was sampled and was used as a covariate.

Bold values represent significant effects ($P \leq 0.05$). There were no significant interactions between species richness and either covariate for any of the dependent variables

Pollinator community

We observed a total of eleven different pollinator taxa, that we could identify without destructive sampling, in our plots including the families Halictidae, Diptera, Vespidae, and Lepidoptera, the genera *Megachile, Osmia, Hylaeus, Ceratina, Melissodes, Nomada, and Bombus*, and the species *Apis mellifera.* Pollinators from Halictidae and Diptera, *Megachile*, and *A. mellifera* accounted for 86.1% of the visits (Online Appendix, Fig. 1).

As a group, *A. mellifera* and *Bombus* spp. (the two eusocial taxa, and the only two taxa that were exotic or with exotic species) showed no difference in visit duration between treatments (Fig. 4, Table 2). However, the group of all other pollinator taxa combined (all solitary natives) showed a 94% increase in visit duration in two-species plots (Fig. 4, Table 2). Visit duration showed no significant relationship with either flowering plant density or sampling intensity per plot (Table 2).

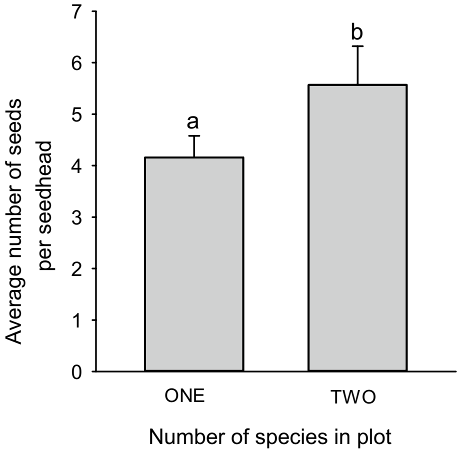

Fig. 3 Mean (± 1 SE) for number of seeds per *Linum lewisii* seed head in plots with *Linum* alone versus *Linum* with another flowering species. Different letters indicate significant differences at $P < 0.05$

Discussion

Our most salient finding was that, when visitation was measured to each species, three native intermountain prairie plant species experienced indirect facilitative interactions mediated by pollinators when any two of the three species were grown together. This facilitation was not mediated by an obvious magnet species because visitation per plant was not substantially different among any of the plant species. When flowering alone, *Linum* received 1.51 insect visitors per plant, *Gallardia* received 1.47 insect visitors per plant, and *Achillea* received 1.35 insect visitors per plant. Furthermore, the least visited species when alone, *Achillea*, significantly increased visitation to *Gaillardia*. All plant species experienced increased pollinator visitation when grown with another species regardless of the identity of the other species. Correspondingly, *Linum* plants produced more seeds per flower head when growing with either *Achillea* or *Gaillardia* than when alone in plots. Thus, our results support the idea that the diversity of flowering species in local patches, at a very fine grain (Braun and Lortie, 2019), can be important to

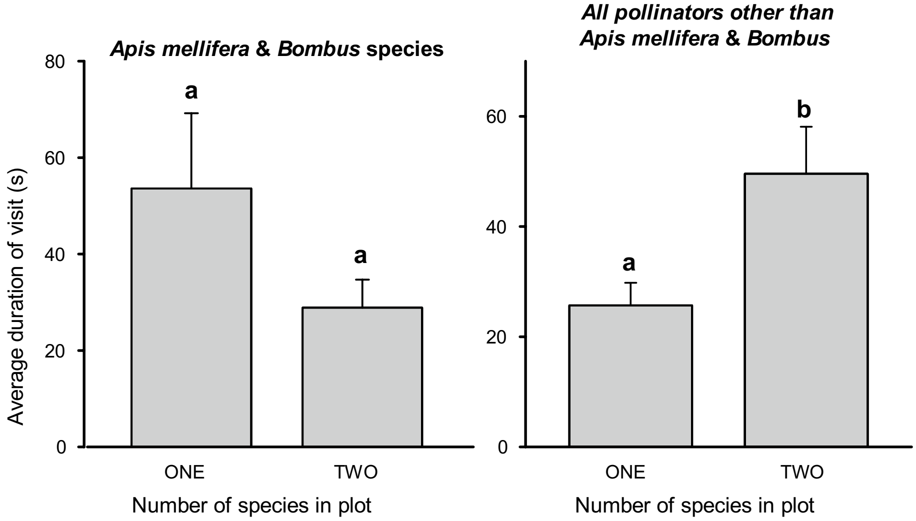

Fig. 4 Mean (± 1 SE) pollinator visitation, or "visit duration" for plots with one flowering species versus plots with two flowering species. Pollinators are separated into **a** social insects, *Apis mellifera* and *Bombus* species, and **b** and nonsocial species. Different letters indicate significant differences (see Table 2)

Table 2 Results for ANOVAs for the mean duration of visit for *Apis mellifera* and *Bombus* species averaged over all observation periods for each plot, and the mean duration of visit for all other pollinator species averaged over all observation periods for each plot

Source	Mean duration of visit Apis and Bombus			Mean duration of visit all others		
	df	*F*	*P*	*df*	*F*	*P*
Species richness	1	2.237	0.157	**1**	**5.767**	**0.025**
Plant density	1	0.225	0.643	1	0.453	0.508
Number days sampled	1	0.307	0.588	1	0.000	0.997
Error	18			26		

Species richness is the number of forbs in flower in a plot and was used as a fixed factor. Plant density is the number of flowering individuals in a plot and was used as a covariate. Days sampled is the number of days on which a plot was sampled and was used as a covariate.

Bold values represent significant effects ($P \leq 0.05$). Species richness is the number of forbs in flower in a plot and was used as a fixed factor. Plant density is the number of flowering individuals in a plot and was used as a covariate. Days sampled is the number of days on which a plot was sampled and was used as a covariate. Bold values represent significant effects ($P \leq 0.05$)

plant–pollinator interactions in ways that others have found for magnet species (Molina-Montenegro et al., 2008; Laverty, 1992; Johnson et al., 2000). This played out when visitation was measured at the whole-plot level, as plots with two species in flower received more visitations than plots with one species.

Not only did plant species increase visitation rates and seed set for each other, flowering species in pairs had positive effects on the pollinator community as well, when visitation was measured on a plot basis. Two-species plots increased the average pollinator diversity in a daily observation period, and the total pollinator diversity measured over the course of the experiment. Native pollinator species also increased the duration of visit in two-species plots. This may be important as wild native pollinators have been found to play a crucial role in agricultural seed set independently of the effects of managed pollinators (Garibaldi et al., 2013).

It is important to note that our small plots were only 30 cm apart, and although these distances are small, such a scale is a reasonable estimate of natural scales for flower patches. However, scale can have strong effects on the indirect effects of pollinators on plant interactions (see Albrecht et al., 2016), and depending on the mechanism, our small scale may increase the potential to show facilitation among plant species via pollinators. If complimentary attraction was important, a diverse patch very close to a monoculture patch might much more easily entice a monoculture's pollinators than a diverse patch that is far away, simply because they are more easily detected. Thus, as distances increase among patches of different diversities, the facilitative relationship we found may be likely to wane (see review by Braun and Lortie (2019). Floral density, as opposed to our measurements of plant density, can also affect the balance of indirect facilitation mediated by pollinators (Underwood et al., 2020). Pollinator visitation rates should increase with floral density until flowers exceed the ability of pollinators to visit them—'saturation', which can drive shifts from indirect facilitation to competition among flowering plants (Rathcke, 1983). Importantly, the ambient density of pollinators can determine when facilitation shifts to competition with floral density (Ye et al., 2013).

There are at least four potential mechanisms for the indirect facilitation by pollinators we documented (see Braun and Lortie, 2019). First, it has been argued that convergent floral traits might promote facilitation via increased pollination among plant species (Rathcke, 1983; Schemske, 1981). This assumes that flower morphology has converged to the point that pollinators no longer distinguish between the species. This mechanism is unlikely to be important in our system because the three different plant species had very different floral characteristics.

Competitor-free space is a second mechanism for facilitation that occurs when pollinators move from a preferred floral resource to a less preferred resource upon the arrival of a superior competitor (Ghazoul, 2006). When this happens, the less preferred flowering species receives more pollinator visits. Many researchers have observed displacement of pollinators from flowers by other pollinators (Goulson, 2003; Johnson and Hubbell, 1974; Nagamitsu and Inoue, 1997), but this scenario is poorly studied and we observed very little displacement of initial pollinators by late comers.

Third, complimentary attraction promotes facilitation when each flowering plant species attracts a different group of pollinators. Thus, two or more species together will attract more visits than either of the species alone (Moeller, 2004; Rathcke, 1988). Flowering species in our plots attracted specific pollinators with differing degrees of success. For example, *Gaillardia* was very attractive to *A. mellifera*, attracting 56% of all honey bees observed. In contrast, *Achillea* accounted for only 7% of *A. mellifera* visits. Sweat bees and flies visited *Achillea* with regularity (24% and 25% of the observed sweat bees and flies, respectively). Thus, a plot that contained *Gaillardia* and *Achillea* would be likely to attract a richer total group of pollinators than single species. This may, in turn result in greater pollination success for both species if the pollinators move more frequently to nearby conspecifics. This is a likely mechanism for our patterns.

The fourth possible mechanistic explanation for indirect facilitation such as we observed, and a second more likely mechanism for our patterns, is resource complementarity. Resource complementarity occurs when different species within a plant community provide unique sets of resources. Thus, a pollinator that visits different species obtains a wider set of resources required for survival and reproduction. This differs from complimentary attraction in that the pollinator visitor is returning to flowers with known nutritional value rather than selecting flowers based on plant attractants such as color, shape, or scent. Pollinator choice due to resource complementarity may occur because different plant species produce different amino acids and carbohydrate mixtures in their pollen and nectar (Petanidou et al., 2006; Szczêsna, 2006). Insect pollinators that feed on a mixed diet have increased longevity and brood productivity than those deprived of diversity in their diet. Honey bees, for example, require 10 amino acids to complete brood development (De Groot, 1953). Herbert et al. (1970) showed that nurse bees fed only dandelion pollen (*Taraxacum officinale*) failed to rear brood; however, once dandelion pollen was supplemented with the missing amino acids, full brood development occurred. Alaux et al. (2010) found that *A. mellifera* colonies that fed on a mixed diet showed an increase in immunocompetence compared to colonies that fed on monocultures. Mevi-Schütz and Erhardthad (2005) found similar results for butterflies. Thus, for many insects, resources from many plant species may be necessary to meet life history requirements. There has been no studies of the amino acids content of the nectar or pollen for the species that we used. However, Petanidou et al. (2006) reported evidence that species in the Asteraceae family do not provide all of the amino acids needed for honey bee brood development. Crane (1975) and Galetto and Bernadello (2003) found that species in the Asteraceae and Linaceae produce very low sugar ratios in their nectar. Thus, the individual species that we tested may not provide either enough sugar or amino acids for the optimal performance of pollinators, and thus, mixed diets may be crucial.

In summary, we found evidence for indirect facilitation among three species and no evidence for competition for pollinators. Such facilitation may provide more complete suite of plant-supplied resources to pollinators. Furthermore, our results are consistent with a number of studies (see review by van der Plas, 2019), indicating that plant species diversity increases the overall species richness and diversity of the insect pollinator community.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s42974-021-00056-5.

Acknowledgements We are grateful for assistance from Amber and Isabella Maccarone, and their unfailing support of SD and this research. This research was made possible by the generous donations of John and Dian Adams whose love of insect pollinators is surpassed only by their support of me and this research. RMC acknowledges support from NSF EPSCoR Track-1 EPS-1101342 (INSTEP 3) and NSF EPSCoR Cooperative Agreement OIA-1757351.

Authors' contributions SD conceived of and developed the project, SD and RMC collected data, HL developed the common gardens and conducted statistics, and SD and RMC wrote the paper.

Funding John and Diane Adams donations; NSF EPSCoR Track-1 EPS-1101342 (INSTEP 3); NSF EPSCoR Cooperative Agreement OIA-1757351.

Availability of data and material Data will be available at https://www.mtnsfepscor.org/.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Consent to participate Not applicable.

Consent for publication Not applicable.

Ethical approval Not applicable.

References

Alaux, C., Ducloz, F., Crauser, D., & Le Conte, T. (2010). Diet effects on honeybee immunocompetence. tp://rsbl.royalsocietypublishing.org/content/early/2010/01/18/rsbl.2009.0986.short.

Albor, C., García-Franco, J. G., Parra-Tabla, V., Díaz-Castelazo, C., & Arceo-Gómez, G. (2019). Taxonomic and functional diversity of the co-flowering community differentially affect Cakile edentula pollination at different spatial scales. *Journal of Ecology, 107*, 2167–2181. https://doi.org/10.1111/1365-2745.13183

Albrecht, M., Ramis, M. R., & Traveset, A. (2016). Pollinator-mediated impacts of alien invasive plantson the pollination of native plants: The role of spatial scale and distinct behaviour among pollinator guilds. *Biological Invasions, 18*, 1801–1812. https://doi.org/10.1007/s10530-016-1121-6

Borges, R. M., Gowda, V., & Zacharias, M. (2003). Butterfly pollination and high-contrast visual signalsin a low-density distylous plant. *Oecologia, 136*, 571–573. https://doi.org/10.1007/s00442-003-1336-y

Braun, J., & Lortie, C. J. (2019). Finding the bees knees: A conceptual framework and systematicreview of the mechanisms of pollinator-mediated facilitation. *Perspectives in Plant Ecology, Evolution and Systematics, 36*, 33–40. https://doi.org/10.1016/j.ppees.2018.12.003

Coffey, M. F., & Breen, J. (1997). Seasonal variation in pollen and nectar sources of honey beesin Ireland. *Journal of Apicultural Research, 36*, 63–76.

Crane, E. (1975). *Honey. A comprehensive survey*. William Heinemann Ltd.

Crane, E. (1990). *Bees and beekeeping: Science*. William Heinemann Ltd.

Dauber, J., Biesmeijer, J. C., Gabriel, D., Kunin, W. E., Lamborn, E., Meyer, B., & Settele, J. (2010). Effects of patch size and density on flower visitation and seed set of wild plants: A Pan-European approach. *Journal of Ecology, 98*, 188–196. https://doi.org/10.1111/j.1365-2745.2009.01590.x

Filho, LC., & Packer, L. (2015). Revision of the Neotropical subgenera Coelioxys (Platycoelioxys) Mitchell and C. (Rhinocoelioxys) Mitchell (Hymenoptera; Megachilidae) with the description of one new species. *Zootaxa, 3941*(2), 151–203. https://doi.org/10.11646/zootaxa.3941.2.1

De Groot, A. P. (1953). Protein and amino acid requirements of the honeybee. *Physiologia Comparata Et Oecologia, 3*, 1–90.

Dornhaus, A., Klügl, F., Oechslein, C., Puppe, F., & Chittka, L. (2006). Benefits of recruitment in honey bees: Effects of ecology and colony size in an individual-based model. *Behavioral Ecology, 17*, 336–344. https://doi.org/10.1093/beheco/arj036

Feldman, T. S., Morris, W. F., & Wilson, W. G. (2004). When can two plant species facilitate each other's pollination? *Oikos, 105*, 197–207. https://doi.org/10.1111/j.0030-1299.2004.12845.x

Fort, H., Vázquez, D. P., & Lan, B. L. (2016). Abundance and generalisation in mutualistic networks: Solving the chicken-and-egg dilemma. *Ecology Letters, 19*, 4–11.

Galetto, L., & Bernardello, G. (2003). Nectar sugar composition in angiosperms from Chaco and Patagonia (Argentina): An animal visitor's matter? *Plant Systematics and Evolution, 238*, 69–86. https://doi.org/10.1007/s00606-002-0269-y

Garibaldi, L. A., Steffan-Dewenter, I., Winfree, R., Aizen, M. A., Bommarco, R., Cunningham, S. A., & Bartomeus, I. (2013). Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science, 339*, 1608–1611. https://doi.org/10.1126/science.1230200

Ghazoul, J. (2006). Floral diversity and the facilitation of pollination. *Journal of Ecology, 94*, 295–304.

Goulson, D., Ollerton, J., & Sluman, C. (1997). Foraging strategies in the small skipper butterfly, *Thymelicus flavus*: When to switch? *Animal Behaviour, 53*, 1009–1016.

Goulson, D. (1999). Foraging strategies of insects for gathering nectar and pollen, andimplications for plant ecology and evolution. *Perspectives in Plant Ecology, Evolution and Systematics, 2*, 185–209.

Goulson, D. (2003). Effects of introduced bees on native ecosystems. *Annual Review of Ecology, Evolution, and Systematics, 34*, 1–26.

Heinrich, B. (1976). Bumblebee foraging and the economics of sociality: How have bumblebeesevolved to use a large variety of flowers efficiently? *American Scientist, 64*, 384–395.

Hegland, S. J., & Boeke, L. (2006). Relationships between the density and diversity of floral resourcesand flower visitor activity in a temperate grassland community. *Ecological Entomology, 31*, 532–538. https://doi.org/10.1111/j.1365-2311.2006.00812.x

Herbert, E. W., Bickley, W. E., & Shimanuki, H. (1970). The brood-rearing capability of caged honeybees fed dandelion and mixed pollen diets. *Journal of Economic Entomology, 63*, 215–218.

Hingston, A. B., & McQuillan, P. B. (1998). Nectar robbing in *Epacris impressa* (Epacridaceae) by therecently introduced bumblebee *Bombus terrestris* (Apidae) in Tasmania. *Victorian Naturalist, 115*, 116–119.

Jennersten, O. L. A. (1988). Pollination in *Dianthus deltoides* (Caryophyllaceae): Effects of habitat fragmentation on visitation and seed set. *Conservation Biology, 2*, 359–366.

Johnson, L. K., & Hubbell, S. P. (1974). Aggression and competition among stingless bees: Field studies. *Ecology, 55*, 120–127. https://doi.org/10.2307/1934624

Johnson, S. D., Peter, C. I., Nilsson, L. A., & Ågren, J. (2000). Pollination success in a deceptive orchid is enhanced by co-occurring rewarding magnet plants. *Ecology, 84*, 2919–2927. https://doi.org/10.1890/02-0471

Lara-Romero, C., Seguí, J., Pérez-Delgado, A., Nogales, A., & Traveset, A. (2019). Beta diversity and specialization in plant–pollinator networks along an elevational gradient. *Journal of Biogeography, 46*, 1598–1610. https://doi.org/10.1111/jbi.13615

Laverty, T. M., & Plowright, R. C. (1988). Fruit and seed set in mayapple (*Podophyllum peltatum*): Influence of intraspecific factors and local enhancement near *Pedicularis canadensis*. *Canadian Journal of Botany, 66*, 173–178. https://doi.org/10.1139/b88-027

Laverty, T. M. (1992). Plant interactions for pollinator visits: A test of the magnet species effect. *Oecologia, 89*, 502–508.

Lázaro, A., Lundgren, R., & Totland, O. (2009). Co-flowering neighbors influence the diversity and identity of pollinator groups visiting plant species. *Oikos, 118*, 691–702. https://doi.org/10.1111/j.1600-0706.2008.17168.x

Levin, D. A., & Anderson, W. W. (1970). Competition for pollinators between simultaneously flowering species. *The American Naturalist, 104*, 455–467. https://doi.org/10.1086/282680

Liao, H., Luo, W., Peng, S., & Callaway, R. M. (2015). Plant diversity, soil biota and resistance to exotic invasion. *Diversity and Distributions, 21*, 826–835. https://doi.org/10.1111/ddi.12319

Macfarlane, R. P. (1974). Ecology of Bombinae (Hymenoptera: Apidae) of Southern Ontario, with emphasis on their natural enemies and relationships with flowers. PhD, thesis, University of Guelph, Guelph, ON, Canada.

Masters, J. A., & Emery, S. M. (2015). The showy invasive plant *Ranunculus ficaria* facilitates pollinator activity, pollen deposition, but not always seed production for two native spring ephemeral plants. *Biological Invasions, 17*, 2329–2337. https://doi.org/10.1007/s10530-015-0878-3

Mevi-Schütz, J., & Erhardt, A. (2005). Amino acids in nectar enhance butterfly fecundity: A long-awaited link. *The American Naturalist, 165*, 411–419. https://doi.org/10.1086/429150

Moeller, D. A. (2004). Facilitative interactions among plants via shared pollinators. *Ecology, 85*, 3289–3301. https://doi.org/10.1890/03-0810

Molina-Montenegro, M. A., Badano, E. I., & Cavieres, L. A. (2008). Positive interactions among plantspecies for pollinator service: Assessing the 'magnet species' concept with invasive species. *Oikos, 117*, 1833–1839. https://doi.org/10.1111/j.0030-1299.2008.16896.x

Muñoz, A. A., & Cavieres, L. A. (2008). The presence of a showy invasive plant disrupts pollinatorservice and reproductive output in native alpine species only at high densities. *Journal of Ecology, 96*, 459–467. https://doi.org/10.1111/j.1365-2745.2008.01361.x

Nagamitsu, T., & Inoue, T. (1997). Aggressive foraging of social bees as a mechanism of floral resource partitioning in an Asian tropical rainforest. *Oecologia, 110*, 432–439.

Nieh, J. C., Contrera, F. A., Ramírez, S., & Imperatriz-Fonseca, V. L. (2003). Variation in the ability to communicate three-dimensional resource location by stingless bees from different habitats. *Animal Behaviour, 66*, 1129–1139. https://doi.org/10.1006/anbe.2003.2289

Petanidou, T., Van Laere, A., Ellis, W. N., & Smets, E. (2006). What shapes amino acid and sugarcomposition in Mediterranean floral nectars? *Oikos, 115*, 155–169. https://doi.org/10.1111/j.2006.0030-1299.14487.x

Platt, W. J., Hill, G. R., & Clark, S. (1974). Seed production in a prairie legume (*Astragalus canadensis* L.). *Oecologia, 17*, 55–63.

Rathcke, B. (1983). Competition and facilitation among plants for pollination. In L. Real (Ed.), *Pollination biology* (pp. 305–329). Academic Press Inc.

Rathcke, B. (1988). Interactions for pollination among coflowering shrubs. *Ecology, 69*, 446–457. https://doi.org/10.2307/1940443

Reader, R. J. (1975). Competitive relationships of some bog ericads for major insectpollinators. *Canadian Journal of Botany, 53*, 1300–1305. https://doi.org/10.1139/b75-156

Schemske, D. W. (1981). Floral convergence and pollinator sharing in two bee-pollinated tropical herbs. *Ecology, 62*, 946–954. https://doi.org/10.2307/1936993

Sih, A., & Baltus, M. S. (1987). Patch size, pollinator behavior, and pollinator limitation in catnip. *Ecology, 68*, 1679–1690. https://doi.org/10.2307/1939860

Szczêsna, T. (2006). Protein content and amino acid composition of bee-collected pollen from selected botanical origins. *Journal of Apicultural Science, 50*, 81–90.

Underwood, N., Hambäck, P. A., & Inoye, B. D. (2020). Pollinators, herbivores, and plant neighbourhood effects. *The Quarterly Review of Biology, 95*, 37–57.

van der Plas, F. (2019). Biodiversity and ecosystem functioning in naturally assembled communities. *Biological Reviews, 94*, 1220–1245. https://doi.org/10.1111/brv.12499

Vázquez, D. P., & Aizen, M. A. (2003). Null model analyses of specialization in plant–pollinator interactions. *Ecology, 84*, 2493–2501.

Walther, J. B., Van Der Heide, B., Kim, S.-Y., Westerman, D., & Tong, S. T. (2008). The role of friends' appearance and behavior on evaluations of individuals on Facebook: Are we known bythe company we keep? *Human Communication Research, 34*, 28–49.

Waser, N. M., & Fugate, M. L. (1986). Pollen precedence and stigma closure: A mechanism ofcompetition for pollination between *Delphinium nelsonii* and *Ipomopsis aggregata*. *Oecologia, 70*, 73–577. https://doi.org/10.1007/BF00379906

Williams, N. M., & Tepedino, V. J. (2003). Consistent mixing of near and distant resources in foragingbouts by the solitary mason bee Osmia lignaria. *Behavioral Ecology, 14*, 141–149. https://doi.org/10.1093/beheco/14.1.141

Ye, Z.-M., Dai, W.-K., Jin, X.-F., Gituru, R. W., Wang, Q. F., & Yang, C.-F. (2013). Competition and facilitation amongplants for pollination: Can pollinator abundance shift the plant–plant interactions? *Plant Ecology, 215*, 3–13.