Interactions during growth eclipse interactions during flowering for determining plant fecundity in pollinator-sharing annual plants

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Abstract

Species interactions are foundational to ecological theory, but studies often reduce the complex nature of species interactions. In plant ecology, the result is that interactions during vegetative growth and flowering are considered separately, though both can affect fecundity. Here we use a system of annual flowering plants in the genus *Clarkia* to ask how interactions during flowering and growth contribute to plant interactions, and if pollinator behaviors explain apparent patterns in plant interactions during flowering. We measure seed success and fecundity of *Clarkia* focal plants in experimental interaction plots with the effect of pollinators experimentally removed or retained. We also observe pollinator behaviors in the plots and experimental arrays. During flowering, pollinators significantly changed the effect of *Clarkia* interactions on seed success in 31% of species interactions, and these changes corresponded to pollinator behaviors. Whole-plant fecundity, however, did not depend on interactions between *Clarkia*; instead, non-*Clarkia* forbs that grew earlier in the season limited fecundity, constituting a priority effect during vegetative growth. Our study shows that interactions during vegetative growth can preclude the effect of pollinator-mediated interactions on fecundity by limiting potential reproductive output, and that simultaneously studying different modes of interaction allows for understanding the contingency of ecological outcomes.

Introduction

Species interactions are foundational to the vast majority of ecological theory, including theories of the niche, population persistence, community network theory, density dependence, and coexistence theory. Despite outsize reliance on species interactions to explain natural patterns, however, the multifaceted nature of interactions can go unexamined in the literature (Bimler et al. 2018, Chesson 2018, Godoy et al. 2018, Bartomeus et al. 2021). In particular, studies suggesting a causal link between pollinator sharing and plant fecundity use proxies for pollination success but not whole-plant seed set, thus overlooking interactions over the course of growth in determining fecundity (Benadi and Pauw 2018, Opedal & Hegland 2019). On the other hand, studies suggesting a causal link between plant interactions over the course of growth typically overlook the importance of interactions during pollination and reproduction for fecundity (Chesson 2018, e.g., but see Lanuza et al. 2018). A natural step toward resolving this apparent discrepancy in approaches, and in bringing the multi-trophic complexity of plant interactions to bear in our theories of plant-pollinator systems, is to determine the components of natural history that might contribute to the net interaction between species, and the extent to which each component of the interaction actually determines plant performance (fecundity) (cf. Godoy et al. 2018).

Interactions between plants embedded in plant-pollinator networks can be broken down into two components: interactions over the course of vegetative growth that result from using resources like water, nitrogen, and sunlight, and interactions over the course of reproduction that result from pollinator sharing (Figure 1, Panel A). The net effect of growing together is thus a consequence of what transpires between plants over the course of both of these phases, despite the fact that they are rarely considered simultaneously. In the absence of pollinator sharing, plant interactions during vegetative growth -- be they positive, negative, or inconsequential -- should explain variation in performance (e.g. survival, fecundity) and thus

population persistence (Figure 1, Panel B). However, almost 90% of flowering plants are animal pollinated (Ollerton et al. 2011), and pollinator sharing is a widespread phenomenon in plant communities globally (Morales & Traveset 2008). As such, it is imperative to design studies that accommodate interactions during growth and pollination to understand and explain plant fecundity and understand population persistence (Bartomeus et al. 2021).

In flowering plant communities, pollinators have the potential to change the strength or direction of plant interactions by making them either more or less competitive, or more or less facilitative. The particular effect of pollinators on plant interactions depends on how pollinators behave while foraging, as well as the composition of the pollinator community. First, pollinator sharing can introduce or increase competition between plants. Two foraging behaviors in particular, preference and constancy, determine successful conspecific (compatible) pollen transfer. Preference is important because it represents a pollinator's choice to visit one plant species over others when all are available (Figure 1, Panel C). Preference can introduce competition by affecting the quantity of conspecific pollen that plants receive, where seed set declines with declining pollinator preference (Pauw 2012, Song & Feldman 2014, Benadi 2015). Constancy is the tendency of pollinators to visit one species of plant in a foraging bout (Figure 1, Panel D). If pollinators are inconstant, then they can introduce incompatible, heterospecific pollen to co-flowering plants, a form of reproductive interference between plants that decreases seed set. Literature reviews have shown that heterospecific pollen transfer, a result of inconstant foraging (for example), is not only widespread globally, but can have a large effect on individual plant fecundity (Morales & Traveset 2008, Arceo-Gómez et al. 2016, Arceo-Gómez et al. 2019, Moreira-Hernández & Muchhala 2019). Second, pollinator sharing may also have a facilitative effect on a plant interaction by either alleviating a competitive interaction or amplifying a positive interaction that has occurred during growth. Co-flowering plants have the potential to attract more pollinators than when growing alone; for example, high plant density may result in high

competition over growth, but during flowering high floral densities in the same areas can increase pollinator visitation rates and thus pollination service, a facilitative phenomenon known as joint attraction (Figure 1, Panel E; Kunin and Iwasa 1996, Moeller 2004, Feldman et al. 2004, Bizecki Robson 2013). The potential for such facilitation, however, should be contingent on low interspecific pollen transfer, and thus high pollinator constancy. Third and finally, understanding the composition of the pollinator community is critical in establishing the role of pollinators in plant interactions, because different pollinator taxa are likely to exhibit differences in pollination efficiency based on their behaviors (Waser et al. 1996; e.g. Eckhart et al. 2006, Barrios et al. 2016). Therefore, the effect of one plant species on another's successful pollination can greatly depend on the specific pollinator species makeup of the community.

Though recent observational work corroborates that pollinators can affect flowering plant seed set and flowering plant interactions (Lanuza et al. 2018, Bergamo et al. 2020), no experimental study has quantified the contribution of pollinator sharing to the net effect of plant interactions over growth and reproduction, nor demonstrated the link between interactions during reproduction and pollinator foraging behavior. In this work, we do both in a system of four sympatric and co-flowering winter annuals in the genus *Clarkia* (Onagraceae). These species share bee pollinators specialized on the genus rather than any one species, and commonly co-occur throughout their range of overlap, suggesting that they interact considerably over both growth and reproduction (MacSwain, Raven, & Thorp 1973; Moeller 2005; Eisen and Geber 2018). Furthermore, these *Clarkia* flower late in the season after almost all other annual plants in the area have senesced, such that the main interaction they experience during flowering is brought on by sharing pollinators with each other (MacSwain, Raven, & Thorp 1973).

In this work, we investigate the separate and combined effects of plant-plant interactions over growth and reproduction (via shared pollinators) among four species of *Clarkia*. To do so, we

use a combination of pairwise interaction plots with experimentally-sown *Clarkia* and experimental pollen supplementation. In the pairwise interaction plots, *Clarkia* interact both during growth and reproduction, with interactions during growth affecting plant size, and hence reproductive potential, and interactions via shared pollinators during flowering affecting successful pollination and seed set. The experimental pollen supplementation removes the effect of pollinator interactions on final seed set, allowing the effect of interactions during growth to be separated from the effect of interactions vias pollinators. We next investigate the link between pollinator behavior and *Clarkia* interactions during flowering using pollinator observations in our experimental interaction plots, and experimental floral arrays, to measure pollinator preference, constancy, and visitation rate in response to floral density.

We predict that increasing background *Clarkia* density in plots will change the fecundity of focal *Clarkia* plants sown into plots, independent of the effects of pollinators – i.e. *Clarkia* interactions over the course of growth will affect total potential fecundity, absent the contribution of pollinators. If sharing pollinators also contributes to the strength and direction of plant interactions, then pollinators will render *Clarkia* interactions either more competitive or facilitative -- i.e. pollinator-mediated *Clarkia* interactions over the course of flowering will also affect the probability of seed set and total realized fecundity. Finally, the way pollinators change *Clarkia* interactions should correspond to their foraging behavior. If interactions over reproduction are competitive, then we predict pollinators will either be inconstant, exhibit strong preferences for certain plant species, or both, because such behaviors result in heterospecific pollen transfer or lower pollen receipt by less-preferred plants. If interactions over reproduction are facilitative, then we predict pollinators will exhibit joint attraction and constant foraging.

Methods

System

Clarkia is a genus of outcrossing and generally self-compatible winter annual plants which germinate in late winter and grow over the course of the spring. The four species of *Clarkia* in this study (*C. cylindrica* ssp. *clavicarpa* (Jeps.) Lewis & Lewis*, C. speciosa* ssp. *polyantha* Lewis & Lewis*, C. unguiculata* Lindl.*, C. xantiana* ssp. *xantiana* A. Gray, family Onagraceae) are sympatric in the southernmost portion of the Sierra Nevada mountain range in the Kern River Canyon (KRC; Kern County, California). *Clarkia* species co-occur in communities of varying congeneric composition (from one to four *Clarkia* species), in low-elevation grassland, chaparral, and oak woodlands. In the KRC, *Clarkia* begin to flower in early May, and flowering lasts until mid- to late June. All four species overlap in flowering time for about two weeks in late May, and share a group of bee pollinators specialized on the genus rather than any one species (MacSwain, Raven, & Thorp, 1973, Singh 2013). Research has shown that at least one species, *C. xantiana*, has higher seed set when it grows in multi-species *Clarkia* communities than at sites where it occurs alone, and that this effect is explained by increased visitation from shared pollinators at multi-species sites (Moeller 2004).

In this work, we use two different experiments to understand how pollinator-mediated interactions contribute to the net interactions between *Clarkia*. First, we use an *in-situ* common garden experiment to estimate the strength of *Clarkia* interactions over growth and flowering, as well as estimate pollinator preference for *Clarkia* species. This is described in the 'Pairwise Interaction Plots' sections below. Because pollinator constancy was impossible to estimate in pairwise interaction plots due to their low species richness, we use experimental arrays of flowering plants to estimate pollinator constancy ('Pollinator Arrays' sections below).

Experimental Design

Pairwise Interaction Plots

Interactions over growth and flowering

To determine the net effects of *Clarkia* growing and flowering together, we used an experimental design closely modeled after work done to estimate competitive interactions in annual plant communities (Godoy & Levine 2014; Godoy et al. 2014; Kraft et al. 2015; Wainwright et al. 2019). In short, seeds of one *Clarkia* species were sown into a plot as a competitive background, and then seeds of the same and different *Clarkia* species were sown at low densities as monitored focal plants. This allowed us to estimate the effect of increasing sown seed density of background *Clarkia* on focal plant fecundity.

Realized total plant fecundity is a function of both how many ovules a plant produces, which is determined during growth and represents a plant's maximum potential fecundity, and the success of converting those ovules to seeds, which is determined during flowering/pollination. In our experiment, both of these phases are potentially determined by the density and identity of background sown *Clarkia*. To isolate the contribution of interactions over flowering to the net (combined growth and pollination) interactions of *Clarkia*, we added conspecific pollen to one flower on each focal plant. This manipulation allowed us to compare seed production in fruits with additional pollen and without additional pollen. The fruits that receive additional pollen as flowers do not rely on pollinators for successful maximum seed set, so the difference in seed production between these two pollination treatments is a direct quantification of the contribution of pollinator-mediated interactions to realized focal plant fecundity. In addition, seed production in the pollen-supplemented fruits can be interpreted as seed production in the absence of the interactions mediated by pollinators, and therefore an estimate of how maximum potential fecundity is a function of interactions over *Clarkia* growth.

In late June through early July 2016, we set up 160, 1X1 meter experimental plots in a community where all four species naturally occur in the Kern River Canyon (35°31'45N,

118°39'36W; Area = 0.57ha). We arranged plots in blocks of four, where plots were separated by ~1/4 meters, and blocks were separated by ~1/2 meter. We cleared all plots of all *Clarkia* to prevent confounding natural seed rain into the plots. We left the non-*Clarkia* plants in place. *Clarkia* seed was collected at various sites in the Kern River Canyon at the end of the 2016 growing season, after plants had senesced and fruits were just about to dehisce; this seed was used in the sowing of the experiment. We extracted seeds using a hand deawner (Hoffman Manufacturing, Inc, Fogelsville PA, USA) to break down the fruits, and a seed blower to clean the seed.

We sowed the collected seed into experimental plots in October 2016. Each block was haphazardly assigned a background *Clarkia* species, and each plot within the block was haphazardly assigned one of five seeding densities (0, 0.04, 0.16, 0.64, and 2.56 g/m^2). Background seeding densities were chosen based on previous estimates of naturally occurring seed production at the field site (James, unpublished data). In total, our design yielded 20 background species X density treatments, with eight plot replicates per treatment.

Twenty focal seeds were sown into one of four designated locations (one for each species) into each of the 160 plots. These locations were delimited using 2.5cm radius cabone craft rings (CSS Industries, Inc., PA, USA) secured in the ground with two 3.8cm fence staples.

In the spring of 2017, we pruned the focal seedlings in the cabone rings to one focal *Clarkia* plant. To prevent bias in selecting a focal seedling, we designated whatever seedling was closest to the center of the ring as the focal plant and weeded the rest. In this same period, we counted the number of background *Clarkia* that had germinated and the number of non-target grasses and forbs growing within a 5cm radius from the focal seedling. We also weeded any germinated, non-target *Clarkia* in the background of all plots.

During the two-week flowering phase in late May 2017, we haphazardly chose one flower on each focal plant to be the 'no pollen addition' or control fruit and receive no additional pollen, and another to be the 'pollen addition' fruit, receiving additional conspecific pollen. This was done for all focal plants with ≥ 2 flowers. To control for any potential differences in the environment to which paired flowers were exposed, we chose pairs of flowers that were open and in a similar reproductive stage on the focal plant. To add conspecific pollen to the pollen addition flowers, we harvested anthers from *Clarkia* before 8am from naturally-occurring *Clarkia* plants growing nearby, before pollinators begin foraging for the day. This pollen was applied to freshly opened and receptive stigmas on the selected flower on each focal plant immediately after harvesting the pollen.

Focal fruits were collected at the end of the growing season, after the focal plant had senesced but before its fruit capsules had dehisced. At the time of fruit collection, we counted the number of mature fruits on all focal plants and collected the total above ground biomass of *Clarkia* growing in all plot backgrounds. The number of seeds, aborted seeds, and ovules of each treatment fruit were counted and recorded.

Pollinator visitation in the interaction plots

During the co-flowering period in 2017, we observed bee visitation behavior in the pairwise interaction plots to quantify pollinator preferences and joint attraction. Due to time limitation in the season and the fact that some plots did not have surviving focal plants, not all $1m^2$ plots were observed; however, at least one plot from each block was observed over the course of co-flowering. Observations occurred in ten-minute periods. Once a bee entered a plot and visited a flower, one person tracked and called the bee's visits to flowers in the plot while another person recorded the information. The tracker identified the bee to either species or genus (when

species identification was impossible). After each observation period, we counted and recorded the number of open flowers of each species in the observed plot.

Pollinator Arrays to assess constancy

We assembled cut-stem arrays of the four *Clarkia* species to observe pollinator behavior during the 2015 and 2016 *Clarkia* growing seasons. To do so, we cleared a 5 x 5m patch of all *Clarkia* in the middle of the experimental site. The array site was prepared in late April before *Clarkia* plants had started flowering. We cleared the array site of all naturally-occurring *Clarkia* plants and constructed a grid with nodes at every 0.5m increment for a total of 100 nodes to place cut *Clarkia* stems. We buried a floral water pick at each node to fill with water and hold *Clarkia* stems.

The data we present in this work are a subset from a larger experiment to observe pollinator foraging behaviors. Here, each array treatment consists of one of four densities (in 2015: 10, 20, 40, or 100 plants; in 2016: 12, 24, 64, or 100 *Clarkia* stems) comprised of an equal number of cut stems for all four species of *Clarkia.* This design allowed us to observe pollinator constancy across a range of plant densities, holding diversity relatively constant. Because different bee species forage at different times of day (Hart & Eckhart 2010), we ran most treatments in the morning and afternoon on different days: one array run in the morning, and one array run in the afternoon. For each array run, we gathered *Clarkia* stems before 8am to assemble in the grid. We arranged *Clarkia* stems in the grid according to a randomly-generated map of a particular treatment, where locations in the grid were either left ‘blank’ or received one *Clarkia* stem of a prescribed *Clarkia* species depending on the treatment density.

During the array runs, we identified and monitored bees as they entered and foraged in arrays. When a bee entered the array and landed on a flower, one person called out the grid location of

the flower/bee, identified the bee to species or genus, and tracked the bee's movements until it left the array, while another person recorded. At the end of each array run, we gathered and disposed of wilted *Clarkia* stems. Rarely, we re-used stems if they were visibly in 'good-shape' (i.e., turgid petals and leaves), though never for more than two runs. Array treatments lasted 40 or 60 minutes; many treatments in 2016 were stopped at 40 minutes due to wilting. We did not run the experiment on days when the predicted peak temperature was below 21°C or wind was stronger than a light breeze.

Statistical Analysis

All calculations and statistical analyses were performed in R (R version 3.5.2, R Core Team, 2018).

Interactions during growth and reproduction

We used two different analyses to understand the effects of pollinators on *Clarkia* interactions. First, we used generalized linear mixed effects models with a binomial error distribution to determine what variables or combination of variables best explained the probability of successful seed set in focal fruits. To do so, we first counted the number of fertilized seeds, aborted seeds, and unfertilized ovules in the control and pollen-supplemented fruits harvested from the focal plants. The sum of these three values represents the total potential fecundity of a fruit. We then built a set of candidate models to explain variation in seed set success using four fixed effects – the pollination treatment, the focal *Clarkia* species identity, the background *Clarkia* species identity, and the biomass of background *Clarkia* in the plot. We did not include non-*Clarkia* grasses or forbs in this analysis because only *Clarkia* were flowering/releasing pollen during the experiment, and therefore would not affect the pollination interactions of *Clarkia*. We also used one random effect, the identity of the plant, in all models. We defined 'success' as fertilized, unaborted seeds in the fruit, and 'failure' as everything else (ovules and

aborted seeds). We fit the data to all candidate models using the lme4 package (Bates et al. 2015). We then calculated the AICc of each candidate model, which we used to score model fit; the model with the lowest AICc score is the best-fit model that we used for ecological inference. The most complex model we used included an interaction of all four fixed effects, and represents our prediction that successful seed set depends on the density-dependent effect of the background *Clarkia* on the focal *Clarkia*, and varies according to pollination treatment.

After identifying the best-fit model, we used estimated marginal means to determine the predicted density-dependent effect of background *Clarkia* on focal *Clarkia*, with and without pollen addition (package emmeans, Lenth 2019). Here, the effect of pollinators on the interaction is the change in the density-dependent effect of background *Clarkia* on focal *Clarkia* seed set between the two pollination treatments (pollen supplementation and no pollen supplementation). If pollinators change the strength or direction of the interaction, then the effect of increasing background *Clarkia* biomass will be significantly different between the two pollination treatments. We also tested if the estimated density-dependent effect of background *Clarkia* on focal *Clarkia* was significantly different from zero for both pollination treatments. This was to examine if and when pairwise *Clarkia* interactions were significantly different from neutral (no effect of increasing density). Finally, we estimated pollen limitation to successful seed set of each *Clarkia* species. To do so, we compared the probability of successful seed set according to pollination treatment for each species, averaged across all background treatments. If species exhibit pollen limitation to successful seed set, then there will be a significant difference between pollination treatments.

The second analysis was to determine what variables best explained the total reproductive output of focal plants in the interaction plots. Whereas the analysis described above is concerned with the probability of seed set, this analysis is concerned with the total realized

fecundity of focal plants- that is, accounting for variation in fruit production, which itself may be a function of the effects of background *Clarkia* density on focal *Clarkia* growth. We again used generalized linear mixed effects models with a Poisson error distribution to model total estimated reproductive output under two different scenarios: pollen addition (where pollinators do not introduce changes in *Clarkia* interactions) and no pollen addition (where pollinators can change *Clarkia* interactions). We included an observation-level random effect in these models to account for overdispersion in the data. Total realized fecundity of the focal plant was estimated for the two treatments (pollen addition and no pollen addition) by taking the product of the number of fruits on the focal plant, the average potential fecundity of the two treatment fruits we collected (i.e. the ovule+fertilized seed+aborted seed number), and the proportion of successful seeds in the supplemented fruit and the un-supplemented fruit.

We built candidate models using six potential fixed effects: pollination treatment, background *Clarkia* identity, focal *Clarkia* identity, background *Clarkia* biomass, and the number of forbs and grasses in the 5cm radius ring around focal *Clarkia* seedlings. We used two independent random effects: plant identity and (as mentioned) observation. The most complex candidate model included an interaction between the pollination treatment, background *Clarkia* identity, focal *Clarkia* identity, and background *Clarkia* biomass, as well as the additive effects of forb and grasses. This candidate model represented our prediction that full plant seed production depends on the density-dependent effect of the background *Clarkia* on the focal *Clarkia*, which is modified by the activity of pollinators. Forb and grass counts were centered and standardized to improve model performance. As before, we used AICc to score model fit, and used the model with the lowest AICc score for ecological inference. With the best-fit model, we used the Wald test to determine the significance of the predictors on full-plant fecundity.

Pollinator preference in the interaction plots

To quantify pollinator preference, we used plant-pollinator observations to build an interaction network using the R package bipartite (Dormann et al. 2008). In the network, we only included the first visit of each pollinator to a plot. This was because subsequent movements were confounded by the experimental design: each plot was dominated by one background species, and as such, subsequent movements within a plot were likely to be visits to the background species, irrespective of pollinator preference (in the observation periods, visits to focal plants against a background of a common species were rare). We first estimated d', or network specialization, of the three most common pollinator taxa we observed visiting the plots (Blüthgen et al. 2006). Higher values of d' indicate higher values of pollinator specialization within the network, which we interpret as taxon-level pollinator preferences for different *Clarkia*. We only included the three most common pollinator taxa because all other pollinators accounted less than 2% of the sample (Table S1). Next, we used a chi-squared test to determine if net visitation to *Clarkia* species deviated significantly from the null expectation of evenly-distributed visits among plants. If a certain *Clarkia* species is preferred by the pollinator community overall, then we would observe higher frequency of visitation to that species than under the null expectation of random visitation.

Pollinator constancy in the experimental arrays

To understand the potential for pollinator (in)constancy to affect pairwise interactions between species, we built a 4x4 matrix for each array run, where rows represent the *Clarkia* species first visited by a pollinator, and columns represent the species visited next in a sequence of two sequential moves. On-diagonal entries in the matrix thus represent pollinator movements to the same species of *Clarkia*, and off-diagonal movements between different species. We divided the sum of all movements in arrays by the sum of all inconstant movements to quantify the proportion of movements that were inconstant, i.e. the proportion of movements that might lead to incompatible pollen transfer in *Clarkia*. We also tabulated the number of inconstant

movements between each pair of *Clarkia* species and conducted a chi-squared test to determine which pairs of species are at higher risk for incompatible pollen transfer. For this test, we separated the pairs of species by the direction of the transition: for example, inconstant movements from *C. cylindrica* to *C. speciosa* were considered separately from inconstant movements from *C. speciosa* to *C. cylindrica.*

Joint attraction in the pairwise interaction plots

We used a linear model of visitation rate (visits per minute) and plotwise floral abundance to determine the potential for joint attraction in the pairwise interaction plots. Floral abundance from each array was log-transformed in the linear regression. If plant patches exhibit joint attraction, then visitation rate should increase as a function of plotwise floral abundance.

Results

The effect of interactions over growth and flowering on seed production

We collected 371 fruits from 232 focal *Clarkia* plants in the pairwise interaction plots. The uneven number of fruits collected was due to fruit loss caused by abortion and herbivory. We found that the best-fit model of the probability of successful seed set included an interaction of focal *Clarkia* species identity, background *Clarkia* species identity, background *Clarkia* biomass, and pollination treatment (Table S2). In other words, the best fit model of the probability of seed set depended on the species-specific, density-dependent effect of background *Clarkia* on focal *Clarkia*, and this effect was modified by pollinators.

Pollinators significantly changed the density-dependent effect of background *Clarkia* on focal *Clarkia* seed success in 31% of the interactions (five of 16 interactions; Figure 2, Table 1). In three of these interactions, the density-dependent effect was more competitive when the effect of pollinators was included (no pollen addition treatment) than when the effect of pollinators was

removed (pollen addition treatment). In other words, pollinators introduced a competitive effect of the background *Clarkia* on focal *Clarkia* for the following three background/focal species combinations: *C. unguiculata/C. xantiana; C. xantiana/C. unguiculata;* and *C. cylindrica/C. xantiana*. Conversely, in the other two cases, the density-dependent effect of the background was more positive with the effect of pollinators than without; that is, pollinators introduced a facilitative effect of the background on focal *Clarkia* in *C. speciosa/C. cylindrica* and *C. speciosa/C. speciosa* background/focal combinations.

Only two of the 32 density-dependent effects of background *Clarkia* density on the probability of focal *Clarkia* seed set were significantly different from zero. One was the competitive effect of *C. unguiculata* on *C. xantiana* in the pollen addition treatment ($z = -2.49$, $p = 0.01$), and the other was the competitive effect of *C. cylindrica* on *C. xantiana* in the no pollen addition treatment ($z = -4.89$, $p < 0.001$) (Figure 2).

Finally, the average pollen limitation to successful seed set varied by focal species. The effect of the pollen addition treatment compared to the no additional pollen treatment was negligible in *C. speciosa,* indicating that pollination service did not limit seed production for this species. Additional pollen increased the probability of successful seed set in *C. xantiana, C. cylindrica,* and *C. unguiculata*, in that order. This indicates that pollination service limited seed production in these three species, but to varying degrees (Figure 3).

The best-fit model for full-plant fecundity included the additive fixed effects of (1) pollination treatment and (2) the number of forbs surrounding the focal plant when it was a seedling (Table S1). In other words, the full-plant fecundity of focal *Clarkia* plants was best predicted by the effect that non-*Clarkia* forbs had on focal plants over the course of growth, and wholesale pollen limitation in *Clarkia* during flowering (Figure 4). Full-plant fecundity strongly declined with

increasing forbs (-0.77 ± 0.15 SE log unit decrease; Wald p-value < 0.001), and was significantly higher in the pollen addition treatment relative to the no pollen addition treatment (1.17 ± 0.20 SE log unit increase; Wald p-value < 0.001).

Pollinator foraging behaviors

Preference and joint attraction in the interaction plots

We performed 209, 10-minute observation periods and observed 446 pollinators in the *Clarkia* interaction plots in 2017. The three most abundant pollinator visitors, in order of abundance, were *Diadasia angusticeps* (Apidae), *Hesperapis regularis* (Mellitidae), and *Lasioglossum sp.* (Halictidae) bees, which made up more than 99% of the total observed pollinators (Table S1). The preference of these three pollinators varied, where *D. anguisticeps* exhibited the most specialized behavior, visiting *Clarkia speciosa* to the near exclusion of the other *Clarkia* (d' = 0.79), followed by *H. regularis* (d'=0.33), and *Lasioglossum sp.* (d'=17), both of which visited all four *Clarkia*, but most commonly *C. xantiana* and *C. cylindrica* (Figure 5, Panel A).

Overall visitation to the different *Clarkia* was significantly different from the null expectation that visitation to each species is proportional to their frequency in the network ($\chi^2(3)=64.4$; $p<0.001$). The residuals of the chi-squared analysis indicate strong overall pollinator preference for *C. speciosa* and *C. xantiana* (Pearson residuals = 3.7 and 3.4, respectively), weak avoidance of *C. cylindrica* (Pearson residual = -1.08), and strong avoidance of *C. unguiculata* (Pearson residual = -6.1).

Pollinator constancy in the experimental arrays

We performed 17 array runs with all four *Clarkia* species, observing 664 pollinator movements from 418 bees across 2015 and 2016. Of the 664 movements, only 100 (15%) were between

different plant species (and thus inconstant) movements. This indicates that *Clarkia* pollinators are by and large constant foragers, even when equally exposed to all four *Clarkia* species.

Of the inconstant movements between species, some transitions between species pairs were more common than others, indicating that certain species pairs were at higher risk for interspecific pollen transfer than others. Interspecific movements were significantly different from the null expectation of being evenly divided among species pairs ($\chi^2(11)=69.4$; $p<0.001$). The species pairs where switching occurred more frequently than the null expectation were (1) *C. xantiana* and *C. unguiculata,* and (2) *C. xantiana* and *C. cylindrica*; and, for each pair, switching was common in both directions (.e.g, X to U and U to X). Altogether, switches involving these two pairs of *Clarkia* accounted for more than 60% of inconstant movements in the dataset (Figure 5, Panel C).

Pollinator Joint Attraction

Finally, pollinator visitation rate (in visits per minute) increased with log floral abundance in the interaction plots, indicating joint attraction (ß=0.27, Wald's p-value<0.001; Figure 5, Panel C).

Discussion

Theories in ecology necessarily reduce complexity to generate testable hypotheses of how the natural world works. In community ecology, species interactions are the building blocks of theories of community functioning and species persistence. Often, studies focus on single aspects of species' life histories, such as interactions over growth or pollination, but not both. This can lead to overlooking the multiplex nature of species interactions and overly simplistic predictions about plant community functioning (Bartomeus et al. 2021). In this study we do our best to reconcile that plant interactions during both vegetative growth and flowering can affect interactions between co-flowering plant species in a system of four pollinator-sharing *Clarkia*

species. We experimentally addressed this in two parts: first, we grew *Clarkia* species together and used hand pollination to determine the contribution of interactions over pollination to the density-dependent effect of growing together for: (1) the probability of successful seed set and (2) the total seed set of focal plants. Second, we investigated pollinator behaviors to determine how the effect of species interactions we observed over pollination may be linked to patterns of pollinator choice and movement.

The effect of pollinator-mediated interactions on potential fecundity

We find that the contribution of pollinator-mediated interactions during flowering to the realized fecundity of plants is, above all, contingent on what transpires over growth. Whereas the probability of successful seed set depended on pollinator-mediated *Clarkia* interactions (discussed below), the realized fecundity of focal plants was best explained by only two variables: the number of non-*Clarkia* forbs surrounding seedlings during growth, and pollination treatment. We interpret this result to mean that the competitive effect of non-*Clarkia* forbs was much more important in determining the realized fecundity of focal plants than any effect of *Clarkia* density during growth or flowering. In particular, this result suggests that the competitive effect exerted by non-*Clarkia* forbs on *Clarkia* seedlings during growth limited total potential fecundity, and that this interaction overwhelmed the effects of interactions during flowering (which can only limit the proportion of successful seeds out of total potential fecundity). Because *Clarkia* are among the last to flower in the growing season in the region, this may be evidence for a priority effect – e.g. non-*Clarkia* forbs draw down resources earlier in the season, thus limiting the resources available later in the season when *Clarkia* plants grow and flower. This result is consistent with other studies demonstrating that differences in phenology can tip the balance of species interactions in annual plant systems (Godoy and Levine 2014): for example, early-season plants can prevent the establishment or limit reproduction of late-season plants due to resource draw down (specifically Nitrogen; Hooper & Dukes 2010, Mooney et al. 1986).

Despite not finding support for a significant effect of pollinator-mediated interactions on realized plant fecundity, we still found evidence of strong pollen limitation to reproduction: realized full-plant fecundity was higher in pollen-supplemented scenarios compared to no supplemental pollen scenarios (Figure 4). However, this effect did not vary among species, suggesting that differences in pollen limitation to successful seed set (at the fruit scale) were not great enough among *Clarkia* species to materialize in species-specific differences in how pollen limitation affected whole plant realized fecundity. Previous experimental work in other flowering plant systems suggests that as pollinators become scarcer, pollinator-mediated competition increases (Lázaro, Lundgren, and Totgren 2014; Ye et al., 2014). Taking the results of these studies and the present study together, we suspect that pollinator abundance was high enough that pairwise, pollinator-mediated interactions between plants did not bear on realized fecundity in our experiment. Further, it is likely that the extent to which pollinator-mediated effects on realized plant fecundity are a function of pollinator abundance, and as such may vary from year to year.

Pollinator-mediated interactions correspond to foraging behavior and affect the probability of successful seed set

The results at the scale of entire plants differ from results at the scale of fruits, where the probability of seed set was governed by the density and identity of *Clarkia* surrounding a focal plant. Significant shifts in species interactions between pollination treatments were apparent in five of the 16 pairwise species interactions; put another way, pollinators changed the positive, negative, or neutral effect of background *Clarkia* density on the probability of seed set. A few patterns stand out from this analysis. First, the *Clarkia* pairs that exhibited density-dependent interactions significantly different than zero (*C. cylindrica* background/*C. xantiana* focal, and *C. unguiculata* background/*C. xantiana* focal; Figure 2) shared pollinators (Figure 5, Panel A), and

represented the two species pairs that pollinators switched between most often (Figure 5, Panel B). Therefore, incompatible pollen transfer from pollinator sharing likely affects the probability of successful seed set. Second, the only species that exhibited a significant intraspecific pollinator-mediated interaction was *C. speciosa,* which does not share pollinators to a great extent with the other three species (Figure 5, Panel A), and experienced lower rates of inconstant visitation (Figure 5, Panel B). In this instance, increasing conspecific density trended toward competition when the effect of pollinators was removed (i.e. there was a negative effect of background density on seed set in the pollen addition treatment), but trended toward facilitation when the effect of pollinators was retained (i.e. there was a positive effect of background density on seed set in the no pollen addition treatment). This suggests that joint attraction of specialized pollinators (carrying compatible pollen) has the potential to introduce positive density-dependence in conspecific stands of flowering plants. Third and finally, the effect of *C. speciosa* backgrounds on *C. cylindrica* seed set trended towards facilitative without the effect of pollinators, but became less so with effect of pollinators; in this case, pollinators introduced a competitive effect that dampened *C. speciosa* facilitation of *C. cylindrica*. Because these two species do not share pollinators (Figure 4 Panel A), and there is rarely switching between the two (Figure 4 Panel C), the competitive effect from pollinators is likely due to low pollinator service to *C. cylindrica* when surrounded by *C. speciosa* (Table 1).

Whereas five pairwise interactions were significantly different between pollination treatments, only two of these effects were significantly different from zero. The greatest change between the two pollination treatments was in plots where the background species was *C. unguiculata* and the focal species was *C. xantiana*. In this interaction, the significantly competitive effect of *C. unguiculata* density on *C. xantiana* ovule production during growth was neutralized when including the effect of pollinators. To wit, pollinators acted as a facilitative force and ‘rescued’ *C. xantiana* from the otherwise competitive effect of increasing *C. unguiculata* density. This result

may be explained by two pollinator behaviors we observed: first, joint attraction, where increasing *Clarkia* density in the plot attracted more pollinators overall, and second, that pollinators preferred *C. xantiana* much more than they did *C. unguiculata*, resulting in *C. xantiana* receiving a disproportionate amount of pollinator visits. The other species interaction significantly different from zero was that of *C. cylindrica* on *C. xantiana*, where the effect of *C. cylindrica* density on focal *C. xantiana* seed set shifted from neutral without the effects of pollinators, to significantly competitive when the effects of pollinators were retained – that is, pollinators introduced a competitive effect of *C. cylindrica* on *C. xantiana*. We suspect this can be explained simply by incompatible pollen transfer between plants from inconstant, highly-shared pollinators. That being said, in these two species pairs, the fact that pollinators alleviated competition in one case but exacerbated competition in another could alternatively be explained by potential differences in how different species tolerate incompatible pollen. For example, previous work has shown that flowering plants, including *Clarkia*, exhibit species-specific sensitivity or tolerance to heterospecific pollens (Arceo-Gómez 2016, Arceo-Gómez et al. 2019); it is possible that *C. xantiana* tolerates *C. unguiculata* pollen better than it does *C. cylindrica* pollen, resulting in the differences in pollinator-mediated interactions. Future work could investigate the extent to which pollinator foraging versus variation in heterospecific pollen tolerance influence susceptibility to incompatible pollen transfer.

Finally, pollen limitation to successful seed set varied according to species. On average, additional pollen did not affect the success of seeds in the fruits of *C. speciosa*, suggesting that the pollination service to this species was high enough that additional pollen was (on average) inconsequential for successful seed set. The behaviors of pollinators explain this result well: high pollinator preference and low pollinator overlap (and therefore likely little heterospecific pollen transfer) resulted in no effect of the experimental addition of pollen to *C. speciosa* flowers' seed set. In contrast, additional pollen increased the average success of seeds in the

three other species: *C. xantiana* experienced a mild boost in seed success with additional pollen, *C. cylindrica* a slightly higher boost, and *C. unguiculata* saw the greatest difference between additional pollen and no additional pollen treatments. This is again explained by pollinator behaviors, where the pollen limitation to successful seed set increased in order of pollinator preference.

The importance of studying multiple life history stages to understand plant interactions and fecundity

Studying different stages of the life history permits us a deeper understanding of how context-dependency plays out in plant interactions and plant communities. Our approach of studying the interactions of *Clarkia* species without removing the background of other grasses and forbs was revealing of the ecology of the system: if we had taken a more traditional approach of studying *Clarkia* pairwise interactions out of the context of the rest of the annual plant community (by weeding, for example), we may have come to the conclusion that interactions over pollination are strong drivers of *Clarkia* interaction dynamics because it would have been impossible to detect the priority effect introduced by non-*Clarkia* forbs. To investigate how variable community context could change the importance of interactions over growth versus flowering, this work could be extended by using models to compare population persistence or coexistence outcomes in neighborhoods that are dominated by non-*Clarkia* plants (where growth interactions and priority effects may take precedence in determining fecundity) versus neighborhoods comprising exclusively *Clarkia* plants (where pollinator-mediated interactions and interference competition might be more important for fecundity).

Finally, though we have studied both growth and pollination aspects of life history in order to understand how they work together to determine fecundity, the larger tasks of identifying population and community-level ramifications of species interactions remains. Incorporating

germination rates and rates of seed survival in the seed bank, as well as a dynamic understanding of both priority effects and pollinator population variation through time, could be relevant for understanding the role of species interactions in population persistence. In the future, studies should investigate the sensitivity of population growth rates to these variables, as well as how coexistence dynamics could change according to variation in neighborhood composition.

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Literature Cited

Arceo-Gómez, G., Raguso, R.A., and Geber, M.A. 2016. Can Plants Evolve Tolerance Mechanisms to Heterospecific Pollen Effects? An Experimental Test of the Adaptive Potential in Clarkia Species. Oikos 125: 718–25.

Arceo-Gómez, G., Schroeder, A., Albor, C., Ashman, T.L., Knight, T.M., Bennett, J.M., Suarez, B., and Parra-Tabla, V. 2019. Global Geographic Patterns of Heterospecific Pollen Receipt Help Uncover Potential Ecological and Evolutionary Impacts across Plant Communities Worldwide. Scientific Reports 9.

Barrios, B., Pena, S.R., Salas, A., and Koptur, S. 2016. Butterflies Visit More Frequently, but Bees Are Better Pollinators: The Importance of Mouthpart Dimensions in Effective Pollen Removal and Deposition. AoB PLANTS.

Bartomeus, I., Saavedra, S., Rohr, R.P., Godoy, O. 2021. Experimental Evidence of the Importance of Multitrophic Sturcture for Species Persistence. Proceedings of the National Academy of Sciences, 118: e2023872118.

Bates, D., Maechler, M., Bolker, B., Walker, S. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 671: 1-48.

Benadi G. 2015. Requirements For Plant Coexistence Through Pollination Niche Partitioning. Proceedings of the Royal Society B 282:20150117.

Benadi, G., and Pauw, A. 2018. Frequency Dependence of Pollinator Visitation Rates Suggests That Pollination Niches Can Allow Plant Species Coexistence. Journal of Ecology 106: 1892–1901.

Bergamo, P.J., Streher, N.S., Traveset, A., Wolowski, M., and Sazima, M. 2020. Pollination Outcomes Reveal Negative Density-Dependence Coupled with Interspecific Facilitation among Plants. Ecology Letters.

Bimler, M. D., Stouffer, D., Lai, H. R., and Mayfield, M.M. 2018. Accurate Predictions of Coexistence in Natural Systems Require the Inclusion of Facilitative Interactions and Environmental Dependency. Journal of Ecology 106: 1839–52.

Bizecki Robson, D. 2013. An Assessment of the Potential for Pollination Facilitation of a Rare Plant by Common Plants: Symphyotrichum sericeum (Asteraceae) as a Case Study. Botany 91: 34–42.

Blüthgen, N., Menzel, F., and Blüthgen, N. 2006. Measuring Specialization in Species Interaction Networks. BMC Ecology 6.

Chesson, P. 2018. Updates on Mechanisms of Maintenance of Species Diversity. Journal of Ecology 106: 1773–94.

Dormann, C.F., Fruend, J., Bluethgen, N. & Gruber B. 2009. Indices, graphs and null models: analyzing bipartite ecological networks. The Open Ecology Journal, 2: 7-24.

Eckhart, V., Rushing, N.S., Hart G.M., and Hansen, J.D. 2006. Frequency-Dependent Pollinator Foraging in Polymorphic Clarkia Xantiana Ssp. Xantiana Populations: Implications for Flower Colour Evolution and Pollinator Interactions. Oikos 112: 412–21.

Eisen, K.E., and Geber, M.A. 2018. Ecological Sorting and Character Displacement Contribute to the Structure of Communities of Clarkia Species. Journal of Evolutionary Biology 31: 1440–58.

Feldman, T.S., Morris, W.F. and Wilson, W.G. 2004. When Can Two Plant Species Facilitate Each Other ’s Pollination? Oikos 105:197–207.

Godoy, O., and Levine, J.M. 2014. Phenology Effects on Invasion Success: Insights from Coupling Field Experiments to Coexistence Theory. Ecology 95: 726–36.

Godoy, O., Bartomeus, I., Rohr, R.P., and Saavedra,S. 2018. Towards the Integration of Niche and Network Theories. Trends in Ecology and Evolution 33:287–300.

Hart-Fredeluces, G. & Eckhart, V. 2010. Ecological Separation in Foraging Schedule And Food Type Between Pollinators Of The California Wildflower, Clarkia xantiana ssp. xantiana. Journal of Pollination Ecology 2.

Hooper, D.U., and Dukes, J.S. 2010. Functional Composition Controls Invasion Success in a California Serpentine Grassland. Journal of Ecology 98: 764–77.

Kharouba, H. M., Ehrlén, J., Gelman, A., Bolmgren, K., Allen, J.M., Travers, S.E., and Wolkovich, E.M. 2018. Global Shifts in the Phenological Synchrony of Species Interactions over Recent Decades. Proceedings of the National Academy of Sciences of the United States of America 115: 5211–16.

Kunin, W., and Iwasa, Y. 1996. Pollinator Foraging Strategies in Mixed Floral Arrays: Density Effects and Floral Constancy. Theoretical Population Biology 49: 232–63.

Lanuza, J. B., Bartomeus, I. and Godoy, O. 2018. Opposing Effects of Floral Visitors and Soil Conditions on the Determinants of Competitive Outcomes Maintain Species Diversity in Heterogeneous Landscapes. Ecology Letters 21: 865–74.

Lázaro, A., Lundgren, R., and Totland, Ø. 2014. Experimental Reduction of Pollinator Visitation Modifies Plant–Plant Interactions for Pollination. Oikos 123: 1037–48.

Lenth, R. 2020. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.4.4. https://CRAN.R-project.org/package=emmeans

MacSwain, J. W., Raven, P. H. and Thorp, R. W. 1973. Comparative Behaviour Of Bees And Onagraceae. IV. Clarkia bees of the western United States. University of Calif. Publ. Entomol. 1:80.

Moeller, D.A. 2004. Facilitative Interactions among Plants via Shared Pollinators. Ecology 85: 3289–3301.

Moeller, D.A. 2005. Pollinator Community Structure And Sources Of Spatial Variation In Plant-Pollinator Interactions In Clarkia xantiana ssp. xantiana. Oecologia 142: 28-37.

Mooney, H. A., Hobbs, R.J., Gorham, J., and Williams, K. 1986. Biomass Accumulation and Resource Utilization in Co-Occurring Grassland Annuals. Oecologia 70: 555–58.

Moreira-Hernández, J.I., and Muchhala, N. 2019. Importance of Pollinator Mediated Interspecific Pollen Transfer for Angiosperm Evolution. Annual Review of Ecology, Evolution, and Systematics.

Morales, C.L., and Traveset, A. 2008. Interspecific Pollen Transfer: Magnitude, Prevalence and Consequences for Plant Fitness, Critical Reviews in Plant Sciences, 27:221-238.

Ollerton, J., Winfree, R. and Tarrant, S. 2011. How Many Flowering Plants Are Pollinated by Animals? Oikos 120: 321–26.

Opedal, Ø.H., and Hegland, S.J. 2019. Using Hierarchical Joint Models to Study Reproductive Interactions in Plant Communities. Journal of Ecology 00 (October):1–11.

Pauw, A. 2012. Can pollination niches facilitate plant coexistence?. Trends in Ecology & Evolution 28.

Singh, I. 2013. Master's Thesis. Cornell University.

Waser, N.M., Chittka, L., Price, M.V., Williams, N.M., and Ollerton, J. 1996. Generalization in Pollination Systems, and Why It Matters. Ecology 77:1043–60.

Ye, Z.M., Dai, W.K., Jin, X.F., Gituru, R.W., Wang, Q.F., and Yang, C.F. 2014. Competition and Facilitation among Plants for Pollination: Can Pollinator Abundance Shift the Plant-Plant Interactions? Plant Ecology 215:3–13.

Zhiyuan, S. and Feldman, M.W. 2014. Adaptive Foraging Behaviour Of Individual Pollinators And The Coexistence Of Co-Flowering Plants. Proceedings of the Royal Society B 281: 20132437.

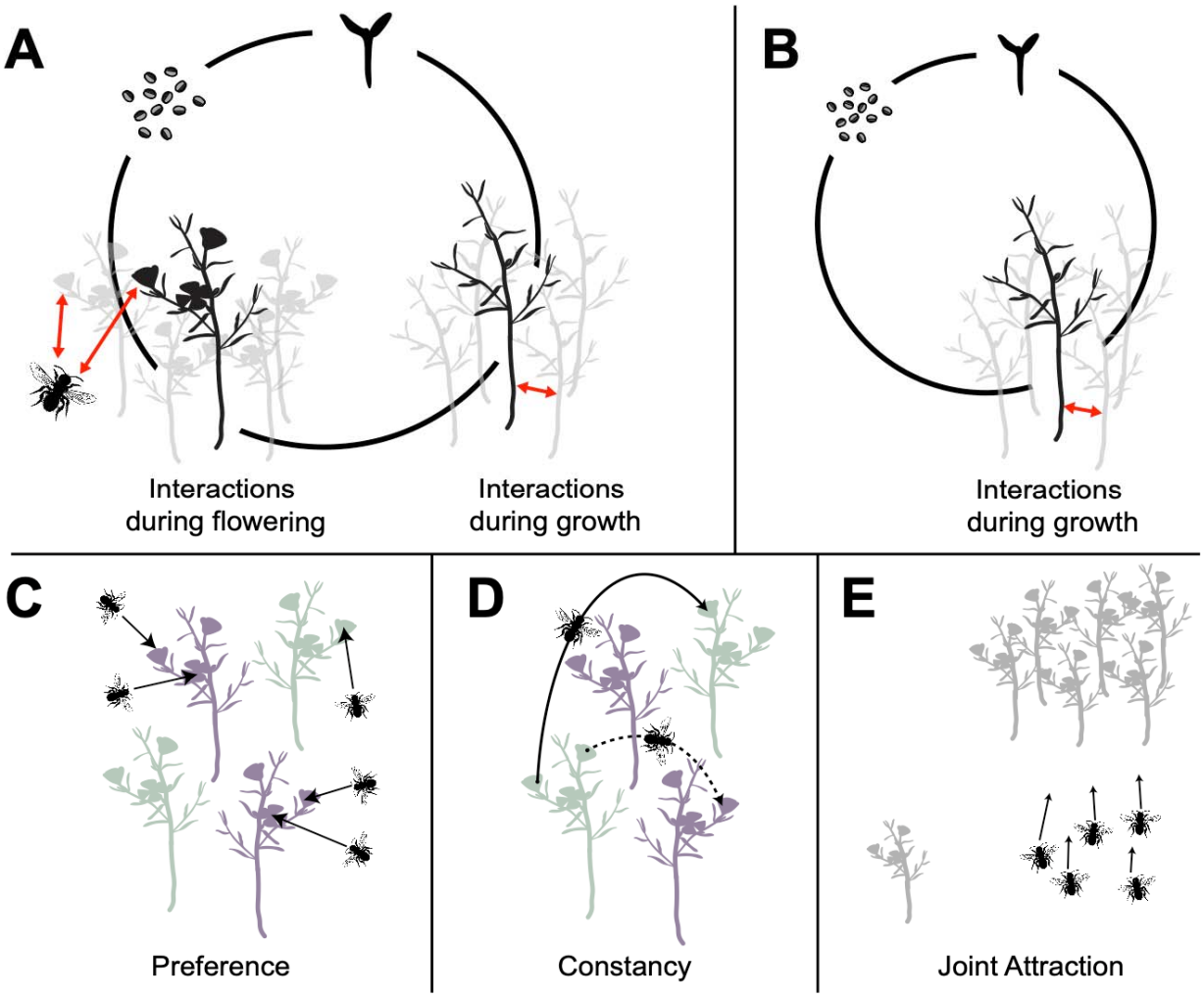

Figure 1. (A) Flowering plants can interact with each other during growth, which determines potential reproductive output, and flowering, which determines realized reproductive output (via pollination). (B) Models and tests often focus on how interactions during growth affect realized reproductive output without considering the effects of interactions during pollination. (C) Pollinator preference for one species over another affects the realized reproductive output of both species. (D) Pollinator constancy (solid line is a constant move; dashed line is an inconstant move) can affect the extent to which plants experience reproductive interference throughout heterospecific pollen. (E) Joint attraction of pollinators can be a positive effect of flowering plant co-occurrence.

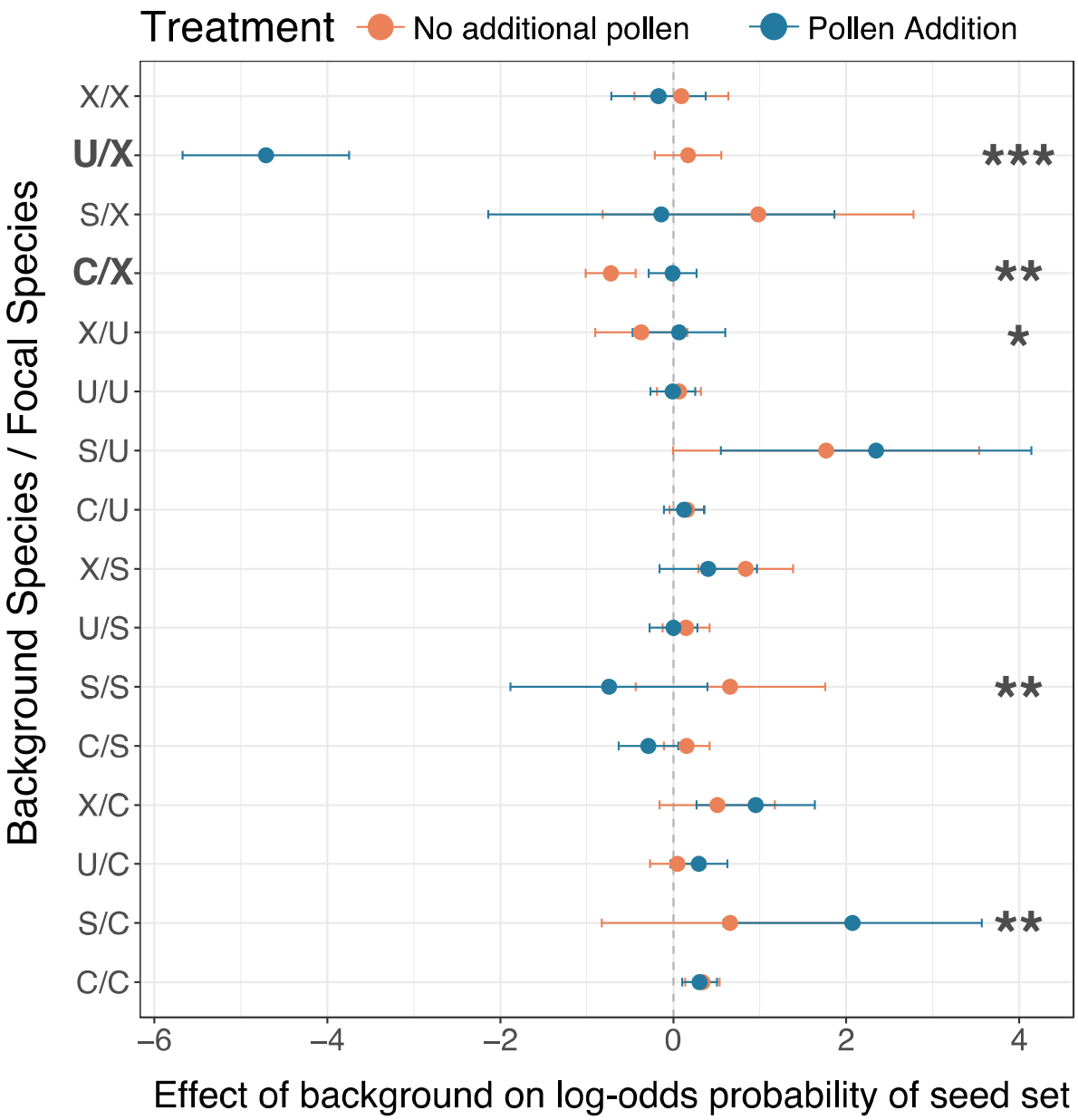
Treatment
No additional pollen
Pollen Addition
Background Species / Focal Species
X/X
U/X
S/X
C/X
X/U
U/U
S/U
C/U
X/S
U/S
S/S
C/S
X/C
U/C
S/C
C/C
***
**
*
**
**
−6
−4
−2
0
2
4
Effect of background on log-odds probability of seed set

Figure 2. The effect of increasing density of background *Clarkia* on the probability of an ovule becoming a successful seed in focal *Clarkia*. The effect (slope) varies according to species pairs and interactions over pollination. Each row is a different background/focal species combination. Points indicate the estimated effect of increasing background species' density on the probability of seed set for the focal species, and lines are standard errors. Negative values indicate the probability of seed set declines with increasing background density (a competitive effect of background *Clarkia*), whereas positive values mean that the probability of seed set increases with background density (there is a facilitative effect of background *Clarkia*). Letters stand for the first letter of the species epithet: C- *Clarkia cylindrica*; S- *C. speciosa*; U-*C. unguiculata*; and X- *C. xantiana*. Blue points are the treatment where the effect of pollinators is removed (pollen addition). Orange points are the treatment where the effect of pollinators is retained (no additional pollen). Bolded combinations are those that include an interaction between background density and pollination treatment that is significantly different from zero; stars indicate a significant effect of pollination treatment on the interaction (*, $p<0.05$; **, $p<0.01$; ***, $p<0.001$).

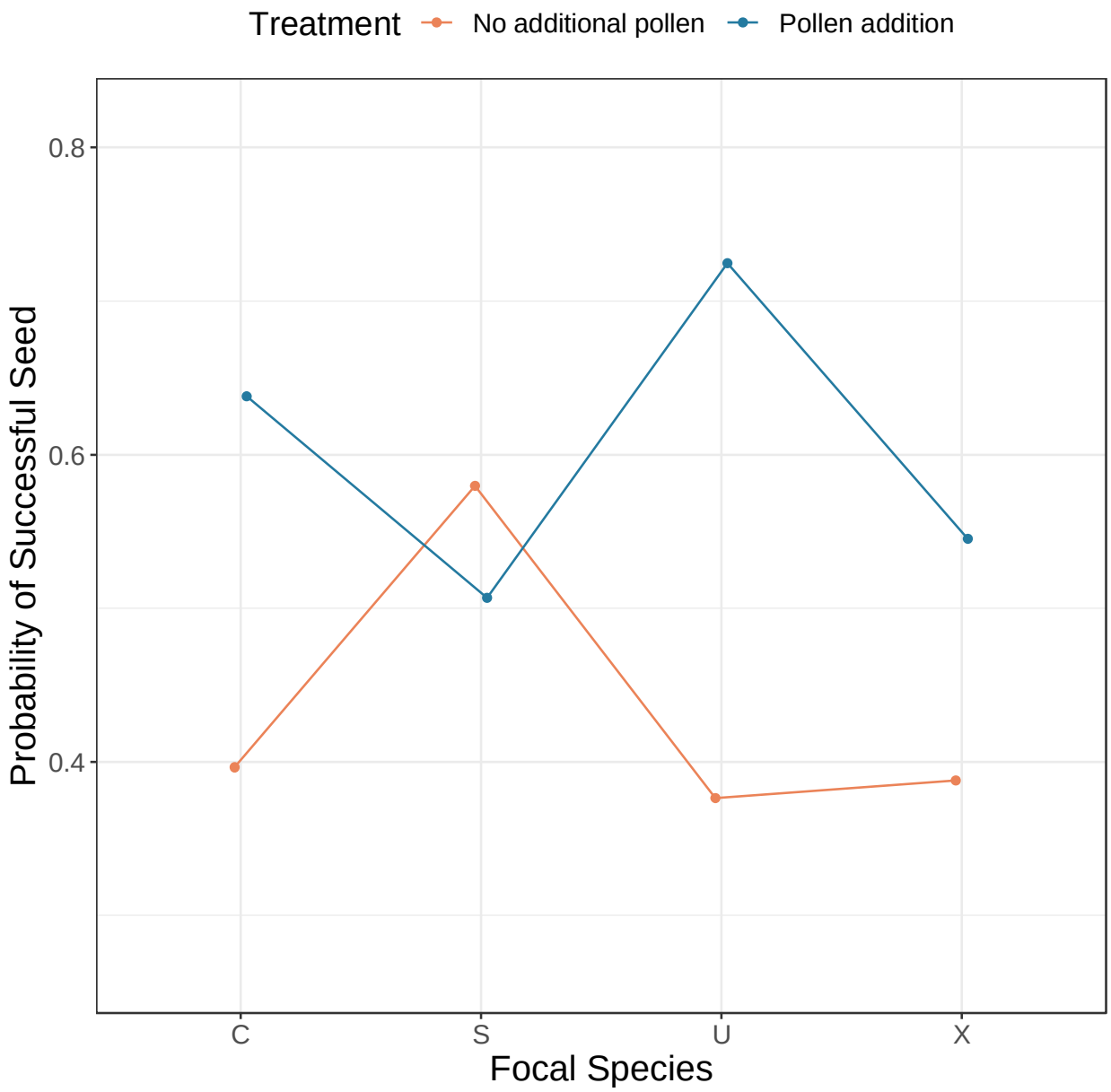

Figure 3. Species-specific probability of seed success in fruits for both pollination treatments. Points represent the estimated average across all background species treatments at the mean background *Clarkia* density. Bars represent the 95% confidence interval for each estimate.

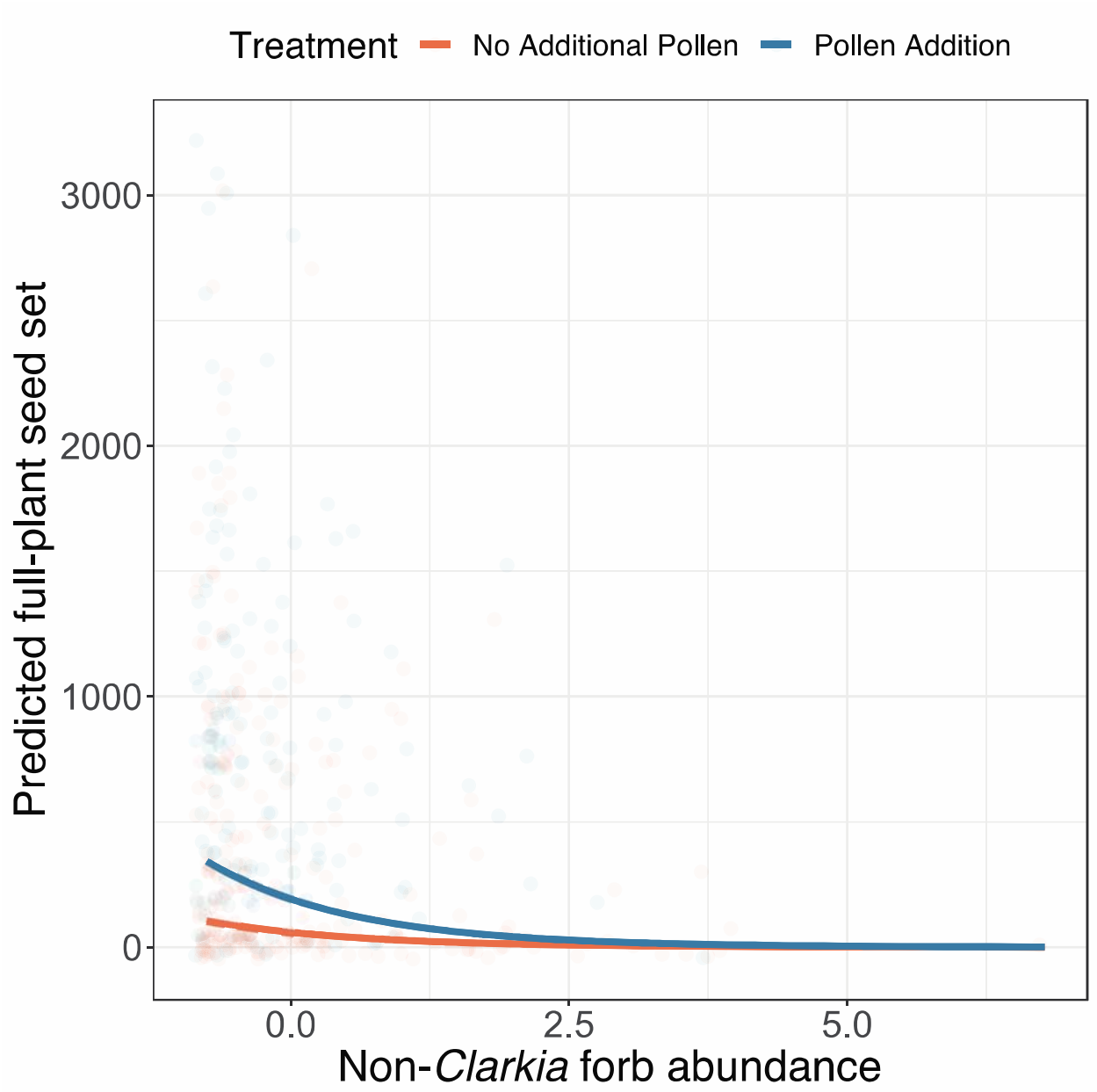

Figure 4. Predicted full-plant seed set as a function of pollination treatment and the number of non-*Clarkia* forbs surrounding the focal as a seedling.

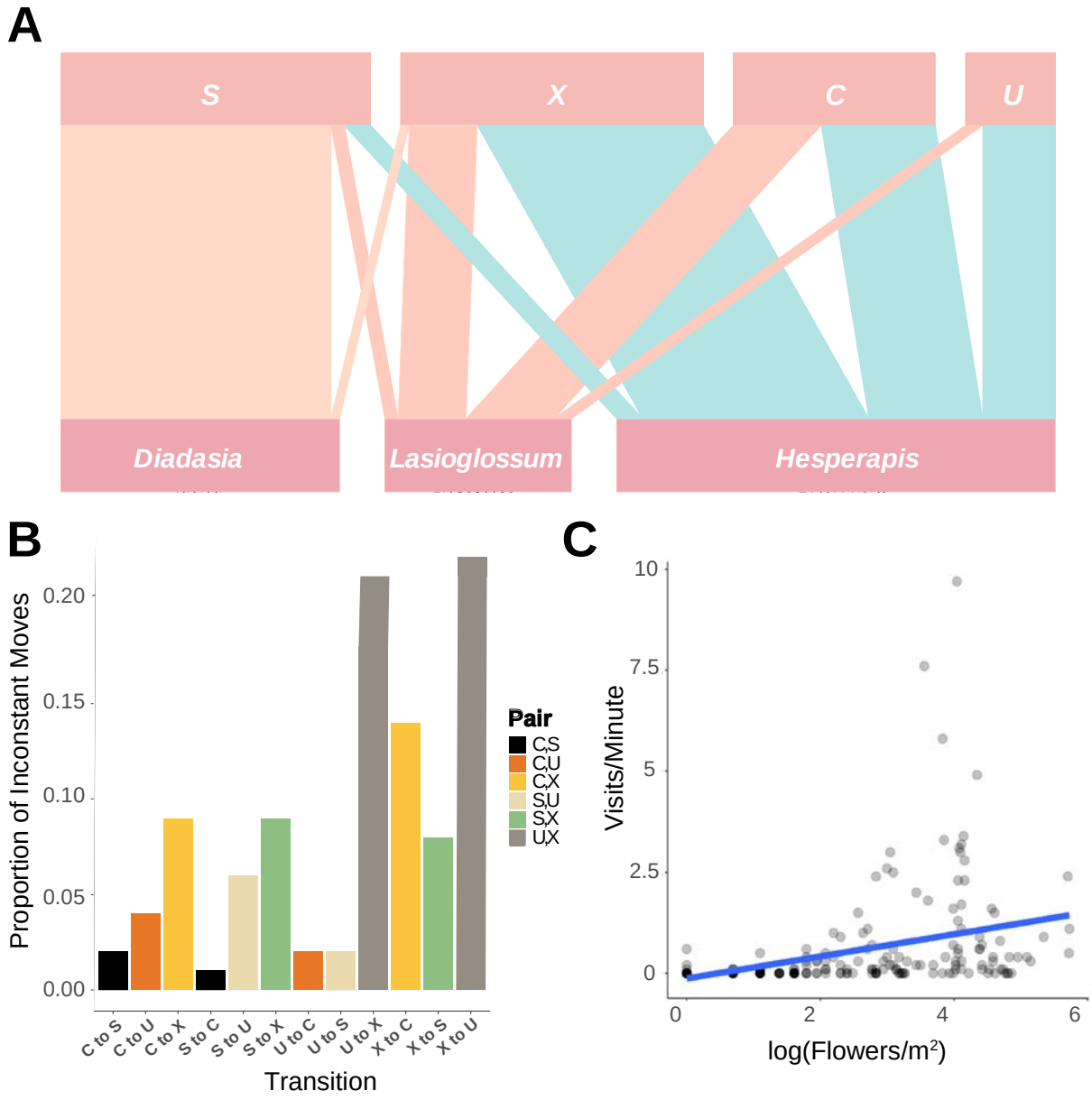

Figure 5. (A) The network of the plant and pollinator interactions observed during the pairwise interaction experiment. (B) The proportion of inconstant moves for each transition type between different *Clarkia*, colored by species pair, in the experimental array experiment. (C) Rate of visitation (visits per minute) as a function of floral abundance in the experimental array.

Table 1. The effect of pollinators on the log-odds probability of seed set in the interactions between Clarkia species (Figure 1), and the explanation of the change in terms of observed pollinator behaviors (Figure 3). Only statistically significant pairwise interactions are shown in this table.

Background	**Focal**	**Change in effect of background on focal ± SE (no additional pollen treatment effect – pollen addition treatment effect)**	**Interpretation**	**Behavioral Explanation**	**p-value**
Clarkia unguiculata (U)	*Clarkia xantiana* (X)	4.88 ± 0.93	Pollinators alleviate the competitive effect of U on X	Joint attraction to higher densities, but pollinator preference for *C. xantiana*	< 0.001 (***)
Clarkia cylindrica (C)	*Clarkia xantiana* (X)	-0.72 ± 0.21	Pollinators exacerbate the competitive effect of C on X	Incompatible pollen transfer	0.0011 (**)
Clarkia xantiana (X)	*Clarkia unguiculata* (U)	-0.44 ± 0.21	Pollinators exacerbate the competitive	Pollinator preference for *C. xantiana* and	0.039 (*)

			effect of X on U	incompatible pollen transfer	
Clarkia speciosa (S)	*Clarkia speciosa* (S)	1.40 ± 1.48	Pollinators alleviate the competitive effect of S on S	Pollinator attraction to higher densities	0.0091 (**)
Clarkia speciosa (S)	*Clarkia cylindrica* (C)	-1.41 ± 0.53	Pollinators reduce the facilitative effect of S on C	Low pollinator overlap and therefore low pollinator service to C	0.0073 (**)