Int. J. Plant Sci. 180(9):974–986. 2019.
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1058-5893/2019/18009-0006$15.00 DOI: 10.1086/705607

DIFFERENCES IN FLOWERING PHENOLOGY ARE LIKELY NOT THE PRODUCT OF COMPETITION FOR POLLINATION IN *CLARKIA* COMMUNITIES

Katherine E. Eisen,[1,]* Diane R. Campbell,† Elizabeth Richards,* and Monica A. Geber*

*Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York 14853, USA; and †Department of Ecology and Evolutionary Biology, University of California, Irvine, California 92697, USA

Guest Editor: Johanne Brunet

Premise of research. Staggered flowering phenologies among co-occurring species have often been interpreted as the product of competition for pollination, but interspecific flowering time differences could result from facilitative, neutral, or competitive interactions. The consequences of interspecific differences in flowering time may vary with the density and species composition of a community.

Methodology. To determine whether staggered flowering times are adaptive in communities of *Clarkia* (Onagraceae) in the Kern River Canyon (Kern County, CA), we used potted plants to manipulate the flowering time of two species of *Clarkia* (*C. speciosa* and *C. xantiana*) that flower later than two other species of *Clarkia*. To determine whether the consequences of flowering time differences change with community context, we conducted this experiment at three types of communities that contained either zero *Clarkia* species (blank communities), the early-flowering species, or the early-flowering species and one late-flowering focal species (mixed communities).

Pivotal results. *Clarkia speciosa* set an equivalent amount of seeds across all community types and both flowering periods. In contrast, seed set of *C. xantiana* was higher during the early-flowering period in all community types. Pollinator visitation to *C. speciosa* was highest in early-flowering *Clarkia* communities, while visitation to *C. xantiana* did not vary across flowering periods or community types. Across communities and flowering periods, seed set of *C. xantiana* was positively correlated with site floral density.

Conclusions. Flowering later is not adaptive for *C. xantiana*, while flowering time may have no effect on the reproductive success of *C. speciosa*. These patterns indicate that later flowering in both species is likely not a result of interspecific competition for pollinators and may result from non-pollinator-mediated selection. In addition, our results indicate that the density of a community can affect the ecological consequences of a flowering strategy and, by extension, the evolution of flowering phenology.

Keywords: facilitation, community context, density, flowering time, pollinator visitation.

Online enhancements: appendix tables.

Introduction

One mechanism that can facilitate the co-occurrence of ecologically similar species is resource partitioning, wherein species experience less competition because they use different portions of the available resources in an environment (Hutchinson 1959; Macarthur and Levins 1967; Schoener 1974). A potential example of resource partitioning that has been studied (e.g., Robertson 1895) and debated for more than a century (Rathcke and Lacey 1985; Feinsinger 1987; Ollerton and Lack 1992; Fox and Kelly 1993; Ishii and Higashi 2001; Elzinga et al. 2007) occurs when a community of flowering plant species exhibits staggered flowering phenologies. The most commonly invoked explanation for staggered or asynchronous flowering times is that they minimize competition for pollination (reviewed in Rathcke and Lacey 1985; Fenner 1998), which can take the form of direct competition for pollinator visitation, or heterospecific pollen transfer (Pleasants 1980; Feinsinger 1987; Devaux and Lande 2009).

Despite continued interest in the competition for pollination hypothesis, there are two key issues with its prevalence. The first issue relates to other potential explanations for staggered flowering times. For instance, staggered flowering times could also result from sequential mutualism, where a later flowering species benefits from visitation by pollinators that previously visited earlier flowering species (Waser and Real 1979; Geber and Moeller 2006; Kudo 2006; Ogilvie and Thomson 2016). In addition, aggregated flowering times are not always maladaptive. Overlap in flowering may be beneficial if pollinator fidelity

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[1] Author for correspondence; email: kee39@cornell.edu.

Manuscript received January 2019; revised manuscript received May 2019; electronically published September 30, 2019.

is high (McGuire 1993; Kudo 2006), if plants partition pollinators by placing pollen on different parts of pollinators' bodies (Macior 1971; Brown and Kodric-Brown 1979; Botes et al. 2008; Huang and Shi 2013) or by releasing pollen at different times of the day (Stone et al. 1998), or if the benefits of a higher visitation rate outweigh the costs of heterospecific pollen transfer (Schemske 1981; Thomson 1982; Ashton et al. 1988; Gross et al. 2000). Beyond interactions with pollinators or plants that share pollinators, other agents of selection that may influence flowering phenology include abiotic factors, herbivores, and fruit dispersers (Rathcke and Lacey 1985; Brody 1997; Kudo 2006; Elzinga et al. 2007). Alternatively, variation in phenology across a community could be random (Gleeson 1981; Rabinowitz et al. 1981; Rathcke and Lacey 1985), neutral (Ollerton and Lack 1992), or shaped by phylogenetic constraints (Kochmer and Handel 1986; Johnson 1993; Wright and Calderon 1995; Madeira and Fernandes 1999; Ollerton and Diaz 1999; Lobo et al. 2003). While the pattern of staggered flowering times has been frequently interpreted as the product of competition for pollination, the type of interaction occurring between two species cannot be predicted from their flowering times alone (Thomson 1982) due to the number of processes that can generate staggered flowering times (e.g., phylogeny, random chance, non-pollinator-mediated selection).

The second issue with the prevalence of the competition hypothesis concerns the extent of the evidence for competition as a driver of staggered flowering times. While many empirical studies have inferred competition to be an important driver of community flowering patterns (Mosquin 1971; Heinrich 1975; Heithaus et al. 1975; Pleasants 1980; Lack 1982; Gross and Werner 1983; Armbruster and Herzig 1984; Armbruster 1986; Rathcke 1988; De Jong and Klinkhamer 1991; Ramsey 1995; Gross 1996; Lobo et al. 2003; Aizen and Vázquez 2006; Botes et al. 2008; Landry 2013) and different forms of competition can lead to staggered flowering patterns in a theoretical study (Devaux and Lande 2009), few studies have tested these inferences with manipulative experiments. Of the five published manipulative studies, two found evidence for competition via elevated heterospecific pollen transfer among coflowering plants (Waser 1978; Campbell 1985), two found no effect of flowering time on reproductive success (Armbruster and McGuire 1991; McGuire and Armbruster 1991), and one found evidence for both competitive and facilitative interactions (Ha and Ivey 2017). The sparse amount of direct evidence for the role of competition indicates that further manipulative experiments are needed to improve our understanding of this common feature of plant communities.

The fitness consequences of co-occurring with a coflowering species are likely to be context dependent, given that community context can affect the relationship between a trait and fitness (Geber and Moeller 2006; Sletvold and Ågren 2014). Properties of flowering plant communities that can affect pollinator visitation and plant reproductive success include species richness and heterospecific plant density, which can be positively correlated (Thomson 1978, 1981, 1982) or negatively correlated (Thomson 1982; Brown et al. 2002; Bell et al. 2005; Flanagan et al. 2009) with the reproductive success of a focal species, although the strength of these effects varies (e.g., Feinsinger et al. 1986; Caruso 1999; Wirth et al. 2011). In addition, change in floral density of co-occurring plant species over the course of a flowering season can alter pollinators' foraging preferences (Waser 1978; Campbell and Motten 1985; De Jong and Klinkhamer 1991; Ramsey 1995), such that flowering time may have indirect effects on reproductive success that are mediated by changes in plant density or by changes in pollinator preference. However, only a small number of studies have investigated how species' densities and phenologies interact to affect reproductive success (Kephart 1983; McKinney and Goodell 2011; Ha and Ivey 2017).

Communities of *Clarkia* in the southern foothills of the Sierra Nevada (California) provide an excellent system for testing how species interactions may affect the ecological consequences of flowering time for two reasons. First, the four outcrossing species of *Clarkia* that co-occur in the region flower later (May–June) than most other plants in the region (Lewis and Lewis 1955; MacSwain et al. 1973; Moeller 2004); species from other genera in the region tend to flower from February to April in response to winter rain (K. E. Eisen, M. A. Geber, personal observations). Second, all four species are primarily pollinated by solitary bees, some of which are specialists on the genus (MacSwain et al. 1973; Moeller 2006; Singh 2014). As a result, we expect that the critical species interactions for *Clarkia* in this region are either intraspecific interactions or interspecific interactions with congeneric species.

To examine whether flowering time affected plant reproductive success and how this relationship was affected by the community context, we manipulated the flowering time of the two naturally late-flowering *Clarkia* species (*C. speciosa* and *C. xantiana*) in three different types of plant communities. During both the early- and the late-flowering periods, we placed experimental arrays of potted plants at replicates of three types of communities, which enabled us to separate the effects of flowering time from the effects of co-occurring with congeners and with conspecifics. The three community types were (1) communities that contained no *Clarkia* naturally (blank sites), (2) communities that contained only the early-flowering species (early species only sites), and (3) communities that contained the early-flowering species and the late-flowering focal species that was added to the site (mixed sites). We used this design, along with measurements of pollinator visitation rate and local plant density, to address three questions about the adaptive nature of flowering time differences and whether these effects vary with community context: (Q1) Is reproductive success affected by flowering time, community type, or an interaction between these factors? (Q2) Does pollinator visitation rate or site floral density vary across community types or flowering periods? (Q3) Across community types and flowering periods, is reproductive success affected by pollinator visitation rate, site floral density, or an interaction between these factors?

We made the following predictions for each of these questions: (Q1) These species flower during the late-flowering period in nature, such that we expected greater reproductive success during the late-flowering period across all community types. Because greater reproductive success during the late-flowering period could be due to the abiotic environment, we used three types of communities in the study to distinguish between the effects of the abiotic environment and species interactions on reproductive success. An interaction between flowering time and the species composition of the experimental community could be driven by relatively stronger interspecific competition or interspecific facilitation with congeners, as well as by intraspecific competition or facilitation, depending on the magnitude and direction of the changes between the flowering periods and across the community types (fig. 1). (Q2) Because communities in our experiment with naturally occurring *Clarkia* contained either the early-flowering species only or the early-flowering species and one late-flowering species, we expected greater floral density during the early-flowering period. We also expected community types with greater floral density to be more attractive to pollinators. (Q3) Because pollinators are essential for reproductive success in these *Clarkia* species, we expected greater reproductive success with greater pollinator visitation rate. Local heterospecific plant density could have a positive effect (facilitation) or a negative effect (competition) on reproductive success.

Methods

Study system. Communities of *Clarkia* species (Onagraceae) provide an ideal system for testing whether differences in flowering time minimize competition and promote species co-occurrence. While none of the ~40 endemic winter annual plant species in the genus have identical ranges in the western United States, multiple species often occur in sympatry; a community may contain as many as six *Clarkia* species (Lewis 1953). All species of *Clarkia* are annuals, and these communities persist in the same location for long periods—30 to 40 yr or more (Lewis 1953; K. E. Eisen, M. A. Geber, personal observations)—creating an opportunity for species interactions to affect the selective environment (Thompson 2005). Within

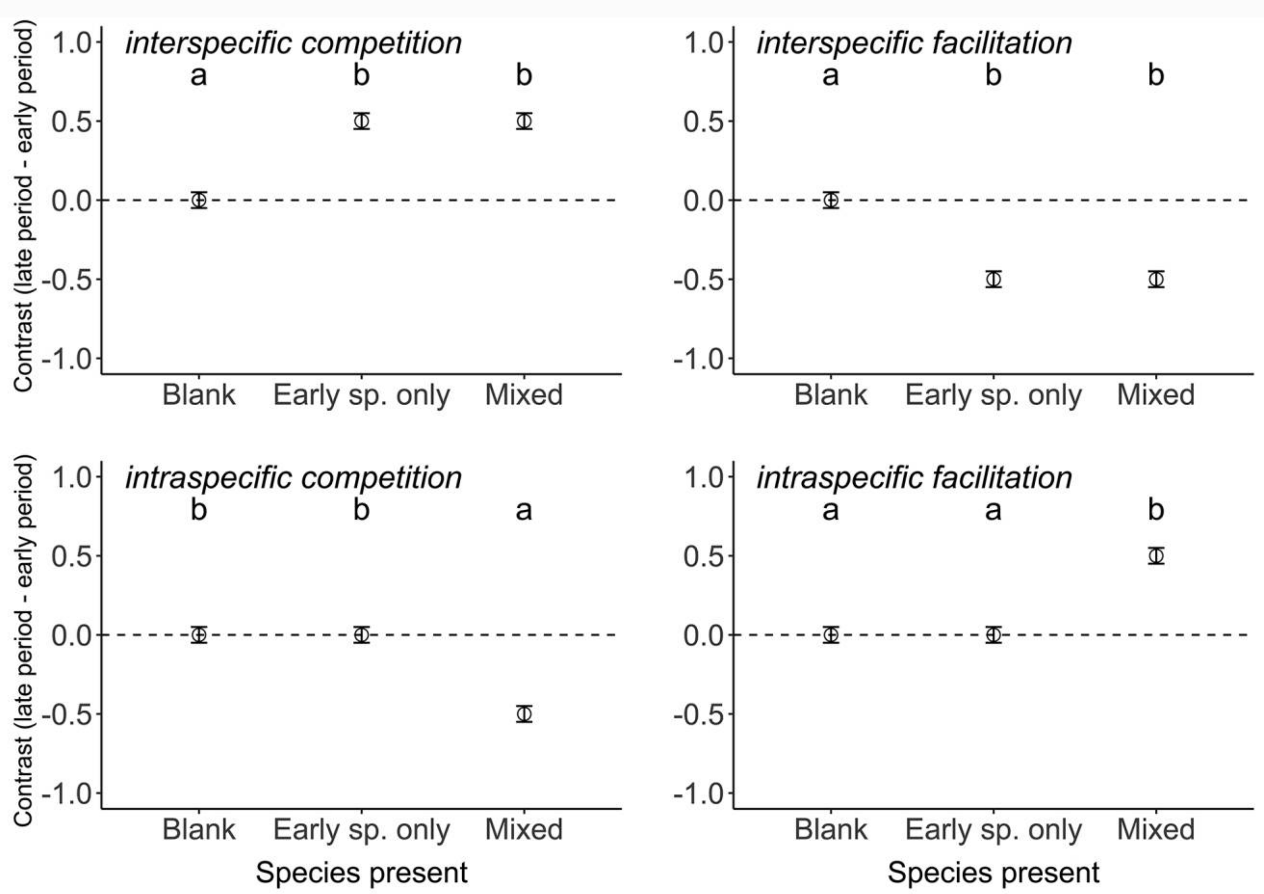

Fig. 1 Graphical representations of the expected results of our experiments under four different types of ecological interactions. Within each panel, the community or communities with the larger absolute values of the contrast comparing seed set between the late-flowering period and the early-flowering period are indicated by *b*, while the community or communities with the smaller differences are indicated by *a*. If the experimental plants experience interspecific competition from the early-flowering species (which occur at both early species only and mixed communities), then there will be a positive contrast in seed set at those community types that will be larger than the contrast at blank communities. Conversely, if the experimental plants experience interspecific facilitation from these species, there will be a negative contrast in seed set between the flowering periods in communities that contain *Clarkia* relative to blank communities. If the experimental plants experience intraspecific competition from naturally occurring congeners at mixed communities during the late-flowering period, then there will be a larger negative contrast between the flowering periods in mixed communities relative to the other communities. Conversely, if the experimental plants experience intraspecific facilitation from naturally occurring congeners at mixed communities during the late-flowering period, then there will be a greater positive difference between the flowering periods in those communities relative to the other communities. Intraspecific interactions and interspecific interactions are not mutually exclusive, although those outcomes are not illustrated in this figure.

multispecies communities, all *Clarkia* species generally do not flower at the same time (Lewis 1961; Moeller 2004; Singh 2014), and some species exhibit variation in flowering times across their ranges that is not correlated with clinal variation in the abiotic environment (Lewis 1961; Jonas and Geber 1999).

In the southern Sierra Nevada (Kern River Canyon), communities contain up to four outcrossing *Clarkia* species (*C. unguiculata* Lindley, *C. cylindrica* ssp. *clavicarpa* W. Davis, *C. xantiana* ssp. *xantiana* A. Gray, and *C. speciosa* ssp. *polyantha* Harlan Lewis and M. Lewis). Hereafter we refer to each species without its subspecies designation (e.g., *C. xantiana* for *C. x. xantiana*). Multispecies communities are as common as single species communities in the region (Eisen and Geber 2018). The species provide pollen and nectar rewards for bee visitors and are not known to hybridize in the field (MacSwain et al. 1973). Any selfing in these species is pollinator mediated, because flowers are protandrous and herkogamous: eight anthers mature over 2 or 3 d before the stigma becomes receptive (Lewis 1953). Outcrossing rates range from 0.79 to 1.0 in *C. unguiculata* (an early-flowering species; Vasek 1965; Ivey et al. 2016) and from 0.59 to 0.85 in *C. xantiana* (a late-flowering focal species; Moeller et al. 2012; Ivey et al. 2016). The species vary in flowering period and floral orientation: *C. cylindrica* (bowl-shaped flower) and *C. unguiculata* (open-faced flower) flower in early–mid May, while *C. speciosa* (bowl-shaped flower) and *C. xantiana* (open-faced flower) flower in early–mid June (Moeller 2004; Singh 2014). Most other flowering plants commonly observed in the Kern River Canyon flower in the late winter or early spring (February–April), including *Collinsia heterophylla*, *Eschscholzia californica*, and *Lupinus bicolor*, among many other species. Previous work has confirmed that *Clarkia* in the Kern River Canyon share pollinators (MacSwain et al. 1973; Moeller 2006; Singh 2014), which include generalist (polylectic) bees and 10 pollen specialists (oligolectic bees) from four families (Andrenidae, Apidae, Megachilidae, and Melittidae; MacSwain et al. 1973; Moeller 2005).

Experimental design. Our experiment tested the effects of staggered flowering times on plant reproductive success. We grew two species of *Clarkia* (*C. speciosa* and *C. xantiana*) from seed in pots over the course of 3 mo to yield plants with a range of flowering times. We used these potted plants to conduct our experiment at three community types: no natural *Clarkia* species present, early-flowering *Clarkia* species only, and early and focal *Clarkia* species. We used two or three sites (replicates) for each community type (see table 1). The experiment was conducted at two flowering times (early and late) within each community type for each of the two focal species. As such, the experiment had 3 community types × 2 flowering period × 2 focal species × 2 or 3 sites per community type. During each flowering period, we estimated local plant density in the communities that contained *Clarkia* naturally (see table 1), conducted pollinator observation sessions, and counted the proportion of seeds produced by focal plants to determine how flowering time affects plant reproductive success.

Table 1

Sites Utilized in the Experiment for Each Focal Species

Focal species, community type	Site name	Latitude (°N)	Longitude (°W)	Early period			Late period		
				Dates	N_{fruit}	N_{pos}	Dates	N_{fruit}	N_{pos}
C. speciosa:									
Mixed	CB 279	35.53141	−118.64174	May 14–21	30	2	June 5–12	30	2
Mixed	Site 30	35.52541	−118.66633	May 17–24	29	2	June 10–17	30	2
Mixed	Cattle Pens	35.52172	−118.66689	May 20–27	28	2	June 12–19	28	2
Early only	Summer Camp	35.52943	−118.64599	May 14–21	29	2	June 10–17	30	2
Early only	Cattle Gate	35.57702	−118.54050	May 17–24	26	2	June 5–12	30	2
Early only	Demo III	35.53165	−118.62193	May 20–27	30	2	June 12–19	30	2
Blank	Cattle Pens North	35.52412	−118.66865	May 14–21	30	2	June 10–17	27	2
Blank	OKCR 28.41	35.56626	−118.57543	May 17–21	0	2			
Blank	Pizza Place	35.56022	−118.58066	May 20–23	0	2			
Blank	Borel Jr.	35.59101	−118.51788				June 5–9	18	1
C. xantiana:									
Mixed	Half Circle Pullout	35.52854	−118.65968	May 11–18	30	2	June 4–11	30	2
Mixed	Valley of the Gods	35.54549	−118.61692	May 15–22	30	2	June 8–15	30	2
Mixed	Cow Flat	35.52583	−118.66035	May 19–26	30	2	June 11–18	30	2
Early only	CB 345	35.56420	−118.58661	May 11–18	30	2	June 4–11	30	2
Early only	Wet Corner	35.52539	−118.66446	May 19–26	30	2	June 8–14	0	0
Early only	Little Pine	35.57475	−118.54462	May 15–20	17	2			
Early only	OKCR 25.14	35.55145	−118.60160				June 11–18	30	2
Blank	CB 372	35.58005	−118.55179	May 12–19	29	2	June 4–11	30	2
Blank	Dent	35.54998	−118.61614	May 19–26	30	2	June 8–15	29	2
Blank	Flat Top Rock	35.57558	−118.55678	May 15–19	0	1			

Note. The community types were as follows: mixed communities contained the early-flowering *Clarkia* plus the focal species that was experimentally placed at the site, early only communities contained the early-flowering *Clarkia* only, and blank communities contained no *Clarkia*. Thirty plants were placed at each site during each period, such that N_{fruit} represents the number of plants that survived the experimental treatment and set one or more fruit(s). N_{pos} indicates the number of pollinator observation sessions conducted at each site during each experimental period.

Experimental setup. Seeds used for this experiment were collected from 11 sites in June and July of 2015; five of these 11 sites contained both species, resulting in eight collection sites per species (table A1; tables A1–A6 are available online). One to several fruits per plant were collected from 50 haphazardly chosen plants of each species at each site.

Seed germination and transplanting took place weekly between January 24 and March 27, 2016. Each week, we germinated between 100 and 400 seeds and planted between 50 and 350 seedlings in pots per species as detailed below. During each round of planting, we planted seedlings from each of the eight collection sites for each species. Seeds were placed on moist filter paper in a petri dish, wrapped in parafilm, and stratified at 5°C for 7 d. We then transplanted two or three seedlings into 656 mL Deepots (D40L, Stuewe and Sons, Tangent, OR) filled with Pro-Mix HP Mycorrhizae (Premier Tech Horticulture, Quakertown, PA). The plants were grown in randomized positions on benches in a fenced lathhouse at the University of California Irvine Greenhouse, where they were subject to local temperatures and precipitation events, which are fairly similar to field conditions. As a result, we watered plants sporadically as needed via misting, showering, or subirrigation. We thinned pots after 4–5 wk to contain one seedling and added eight prills of Osmocote flower and vegetable 14-14-14 fertilizer (Scotts, Marysville, OH).

On April 1–2, 2016, we transported ~2620 plants via truck from Irvine, California, to Lake Isabella, California. The remaining 360 plants were transported by car on April 10. In Lake Isabella, plants were maintained at ambient conditions in a fenced enclosure or in a portable greenhouse structure. This location was more than 5 km from the nearest populations of both focal species. We recorded the date of first flower for each plant. For both species, the mean ±1 SE number of days between the start of flowering and when a plant was used in the experiment was 5 ± 0.25 d.

Experimental treatments. The treatment periods ran from May 11 to May 27 (early period) and from June 4 to June 19 (late period; see table 1). While each treatment at each site lasted 1 wk, the treatment periods were longer than 1 wk across the three types of communities (table 1).

For each focal species, we conducted flowering time treatments at three community types: (1) blank communities, at which no *Clarkia* were present naturally; (2) early-flowering communities, which contained the two early-flowering species only; and (3) mixed flowering communities, which contained the two early-flowering species and the late-flowering species used as focal species (table 1). Flowering time treatments were replicated at two or three sites per community type for each focal species. Different sites were used for each of the two focal species. The goal was to use the same sites for early- and late-flowering treatments. In general, we used the same sites for both the early- and the late-flowering period treatments for a focal species. However, two sites used in the early-treatment period were not reused in the late treatment period because of significant herbivory by deer or cattle during the early-flowering period; we replaced these sites with other sites of the same community type (table 1). During the early period, two sites with *C. speciosa* and one site with *C. xantiana* were destroyed by cattle, and one *C. xantiana* site was destroyed by deer herbivory. During the late period, one *C. speciosa* site was destroyed by rabbit herbivory, and one *C. xantiana* site was destroyed by small mammals. These sites were excluded from the analyses during these flowering periods.

We set up two or three sites at a time (table 1). The sites that were set up on a given day contained the same focal species but differed in community type in order to distribute the replicates of community types across the 2-wk early-flowering period and the 2-wk late-flowering period. The day before plants were set out, we selected 30 plants per site from all available flowering plants of that species. Each plant included in the experiment had a minimum of three unopened buds at the start of the experimental period to ensure that plants would open new flowers during the weeklong experimental treatment. When selecting plants for each site, we distributed the plants that were flowering from each seed source site across the two or three treatment sites that were set up on the same day in order to minimize any spurious effects of the source site on plant reproductive success. As a result, each set of 30 plants that comprised an experimental array at a site during a flowering period contained plants from six to eight source sites, although the proportion of plants from each source site varied between arrays conducted during the early- and late-flowering periods (data not shown).

We recorded the total number of open flowers on each plant at the start of the experimental treatment. To mark which flowers on a plant would be in female phase during the experiment, we tied a piece of green embroidery floss around each stem above any female-phase flowers. (In *Clarkia*, flowering proceeds from the bottom of the stem toward the top, and flowers are in male phase for 2–3 d before they transition to female phase.) To ensure that sites received the same number of open flowers both within and across the treatment periods, we counted the total number of flowers open on all plants in each flowering treatment set. The mean ± 1 SE total number of open flowers for each *C. speciosa* treatment set was 80.6 ± 1.4, and the total number for *C. xantiana* was 119.8 ± 2.4; these values were determined by the first set of treatment plants for each focal species. If subsequent sets of treatment plants did not fall within this range, we either increased the number of flowers by swapping in plants with more open flowers or decreased the number of flowers by pinching off open flowers on some plants. We removed any fruits that were beginning to develop on all plants to promote increased investment in flower production.

At the start of the experimental period, we placed the 30 plants at a site into six Deepot racks (five plants per rack) in a cluster with no more than 1 m between each rack. All 30 experimental plants were placed in a single cluster at each site because *Clarkia* plants tend to occur at high densities (e.g., upward of 100 flowers per m^2; K. E. Eisen, unpublished data) and because pollinators may routinely avoid low-density patches (e.g., Kunin 1993). In the event that the main stem of a plant broke during transportation and handling, we replaced it with an alternate plant. We used bamboo poles to secure the racks to the hillsides, and we fenced the cluster of plants at each site using plastic deer fencing attached to bamboo poles. Each pot was set in a 9 fl. oz. clear plastic cup, which was filled with water. We refilled cups every 2 or 3 d.

Floral density and pollinator visitation rate. Within the first 1 or 2 d of each experimental period, we measured the density of naturally occurring *Clarkia* at each site by throwing quadrats along transects and counting the number of stems and open flowers of each species. We threw quadrats every 5 m along 6–13 transects (mean ± 1 SE = 10 ± 1 transects) that ran horizontally across the slope of each site. Because of differences in the shapes and sizes of the sites, the shortest transects were 10 m long and the longest were 125 m long. Transects were separated vertically (up or down the slope of the site) by 5 m at smaller sites and by 10 m at larger sites. This resulted in 46 quadrats at the smallest site and 246 quadrats at the largest site (mean ± 1 SE = 93 ± 16 quadrats).

To determine whether pollinator visitation changed across community types and flowering periods, we conducted two pollinator observation sessions on the experimental plants at each site that was not destroyed by herbivory (see table 1) during both the early- and late-flowering period. One session took place in the morning (0830–1200) and one in the afternoon (1230–1500); each session lasted 1 h. Two observers (K. E. Eisen and E. Richards) conducted each session. When visitation rates were low to moderate ($N = 51$ sessions), each observer watched 15 plants in the experimental cluster, and the observers shifted their positions every 15 min to reduce bias and observer fatigue. When visitation rates were high ($N = 11$ sessions), each observer watched 10 plants at a time, such that there were 10 out of the 30 total plants not being observed at any given time. During these sessions, the observers shifted their positions every 10 min to watch a different set of plants, which meant that each plant was watched for 40 min during the hour-long session. At the end of every session, we counted the total number of open flowers on the experimental plants.

At the end of each weeklong experimental treatment, we removed the plants from the field sites and transported them back to the fenced enclosure and portable greenhouse in Lake Isabella. Excluding those sites that were severely damaged by herbivory, the number of plants that survived to produce one or more mature fruits among the sets of 30 plants ranged from $N = 26$ to $N = 30$ (see N_{fruit} in table 1). To mark which flowers were exposed to pollinators during the experimental treatment, we applied green fabric paint to plants' stems just above the last senesced flower and recorded the number of flowers exposed. Plants were not reused in subsequent treatments and were maintained until they set fruit. When the fruits were mature, we counted the number of mature fruits and collected each mature fruit. The mean ± 1 SE fruits produced by *C. speciosa* plants was 5.68 ± 0.21 fruits per plant ($N = 412$ plants), and 13.83 ± 0.46 fruits per plant ($N = 407$ plants) for *C. xantiana*.

Data processing. We used the number of pollinator visits observed during a session and the number of open flowers to calculate a pollinator visitation rate per flower per hour. For the sessions where only two-thirds of the plants were watched at any given time due to high pollinator activity ($N = 11$; see above), we multiplied the number of observed visits by 1.5 and divided by the number of open flowers across all plants to calculate a pollinator visitation rate per flower per hour.

We used the percentage of ovules that set seeds per flower per plant as our measure of reproductive success for two reasons. First, incorporating the number of ovules into the calculation of reproductive success can provide insight into whether a plant is pollen limited and facilitates comparisons between fruits that may have produced different numbers of seeds because the fruits had different numbers of ovules. Second, our experimental plants produced more ovules during the early-flowering period, likely because plants were at a slightly earlier stage of development (results not shown) and ovaries of earlier flowers contain more ovules. As such, not incorporating ovules into our measure of reproductive success would overestimate the reproductive success of plants in the early treatment. To calculate the average percentage of ovules that set seeds per flower per plant, we counted the number of developed seeds, aborted seeds, and ovules in a maximum of seven fruits per plant. The average proportion of ovules that set seeds per fruit was calculated by dividing the average number of seeds (including developed and aborted seeds) produced by the sum of the average number of seeds and ovules. This proportion was then multiplied by the proportion of flowers that set fruits per plant (no. fruits divided by no. flowers) to obtain the average proportion of ovules that set seeds per flower per plant after correcting for fruit set. Data from each of the two focal species were analyzed separately.

Statistical analyses. All analyses were performed using R (R Core Team 2018). To determine whether reproductive success is affected by flowering time, community type, or an interaction between these factors (Q1), we used generalized linear mixed models (GLMM) using the lmer function in the lme4 package in R (Bates et al. 2015). The response variable was the average proportion of seeds per flower (described above). Two random effects were included in all models: the site where the experiment took place and the seed source site. We conducted a model selection procedure that compared the most complex model with all possible models with fewer terms. The fixed effects in our most complex model were community type (blank, early species only, and mixed), flowering period (early, late), and their interaction, and our least complex model contained only the two random effects described above. We compared Akaike information criterion (AIC) values across all models and conducted log-likelihood ratio tests to select the best model, which had the lowest AIC score and also a significant log-likelihood ratio test statistic for a comparison with at least one simpler model. We also used the r.squaredGLMM function in the MuMIn package in R (Bartoń 2019) to calculate marginal coefficients of determination (R^2_{GLMM}) for each model; these values represent the amount of variance explained by the fixed effects in each model. For the variables included in the best model, we calculated the estimated marginal means, which are the mean responses for each factor level adjusted for the other variables in the model, for the proportion of seeds set at each level of the flowering period and community type variables and estimated contrasts between flowering periods using the emmeans function in the emmeans R package (Lenth 2018); contrasts between the late- and early-flowering periods (calculated as late period–early period) at a community type ±1 SE are presented.

To determine whether pollinator visitation rate or site floral density varies across community types or flowering periods (Q2), we used site-level averages in pollinator visitation rate (visits per flower per hour) and site floral density (flowers per m^2). Each of these response variables was examined separately for each focal species using linear mixed models. We conducted model selection using the same methods outlined above. In these models there was only one random effect—the site where the experiment took place—because the data were site-level averages, and the source site data, which were collected on the plant level, could not be incorporated into the analyses. As described above, we used comparisons of AIC values and log-likelihood tests to select the best model and then used the estimated marginal means and contrasts across the factor or factors included in the best model to determine the effects of these factors; estimated marginal means ± 1 SE are presented. Across both flowering periods, higher pollinator visitation at sites with *Clarkia* would be consistent with facilitation, while lower pollinator visitation at sites with *Clarkia* would be consistent with competition. To determine whether pollinator visitation rate, site floral density, or their interaction affect seed set (Q3), we ran additional linear mixed models using the same model structures and model selection procedure used for Q1 (described above).

Results

Q1: Is reproductive success affected by flowering time, community type, or an interaction between these factors?

Clarkia speciosa. None of the models with fixed effects were a better fit than the model that included only random effects of source population and treatment site (fig. 2*A*; table A2).

Clarkia xantiana. The best model for the number of seeds per flower of *C. xantiana* was one that included a fixed effect of flowering period (Δ AIC = 2.27; $\chi^2 = 33.121$, df = 1, $P < 8.66 \times 10^{-9}$; table A2). The fixed effect of period explained ~9% of the total variation in seeds per flower (table A2). Seed set per flower was consistently higher during the early period relative to the late period at all community types (fig. 2*B*; table A3).

Q2: Does pollinator visitation rate or site floral density vary across community types or flowering periods?

Clarkia speciosa. For pollinator visitation rate to *C. speciosa*, the model that included a fixed effect of community type was better than the model that included only a random effect of treatment site (Δ AIC $= 3.297$; $\chi^2 = 7.296$, df $= 2$, $P = 0.026$; table A4). Pollinator visitation to *C. speciosa* was highest at early species only communities (2.697 ± 0.626 visits per flower per hour), which is consistent with facilitation between *C. speciosa* and the early-flowering species, although differences across community types were not significant (results not shown). For site floral density, none of the models that included fixed effects were better than the model that included only a random effect of treatment site (table A5).

Clarkia xantiana. For pollinator visitation rate to *C. xantiana*, none of the models with fixed effects were a significant improvement over the model that included only a random effect of treatment site (table A4). For site floral density, none of the models that included fixed effects were better than the model that included only a random effect of treatment site (table A5).

Q3: Across community types and flowering periods, is reproductive success affected by pollinator visitation rate, site floral density, or an interaction between these factors?

Clarkia speciosa. None of the models with fixed effects were a better fit than the model that included only random effects of source population and treatment site (table A6).

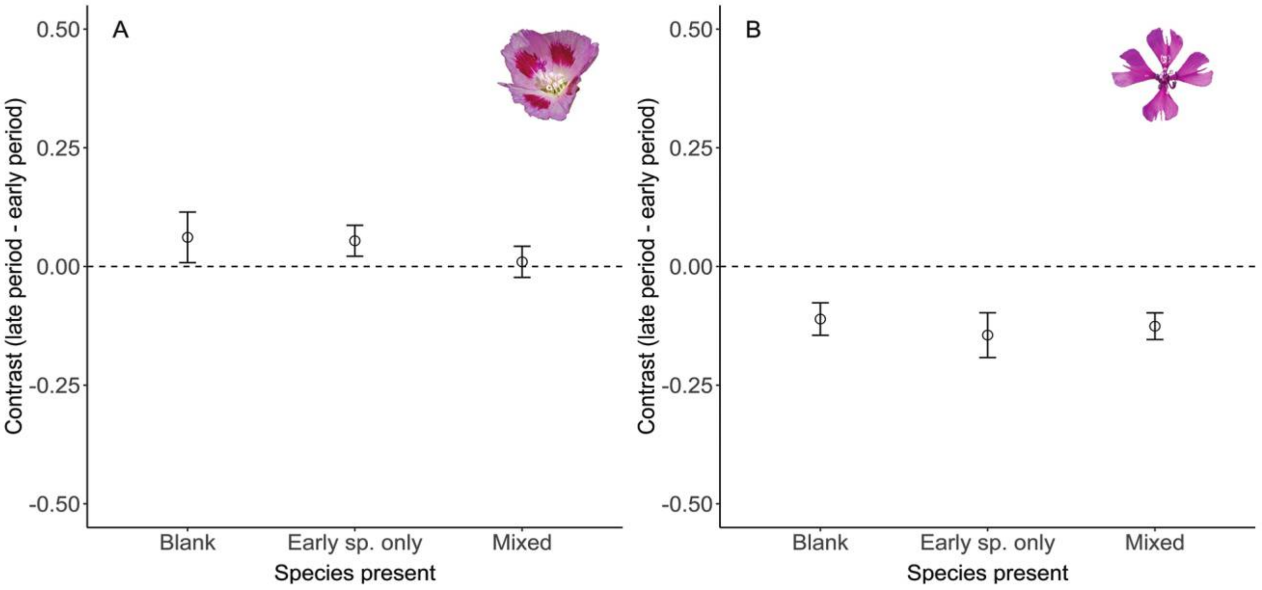

Fig. 2 The contrasts in seed set between the late- versus the early-flowering period in *Clarkia speciosa* (*A*) and *C. xantiana* (*B*) at the three community types (blank—no *Clarkia* present naturally, early sp. only—only the early-flowering species [*C. unguiculata* and *C. cylindrica*] present naturally, mixed—the two early-flowering species plus the late-flowering focal species present naturally). Circles are contrasts calculated as the estimated marginal mean from the late-flowering period minus the estimated marginal mean from the early-flowering period, and error bars are 1 SE. In *C. speciosa* (*A*), seed set did not differ across community types or flowering periods. In *C. xantiana* (*B*), plants in the early-flowering period produced ~25% more seeds than plants in the late-flowering period across all community types (negative contrasts indicate greater reproductive success during the early-flowering period).

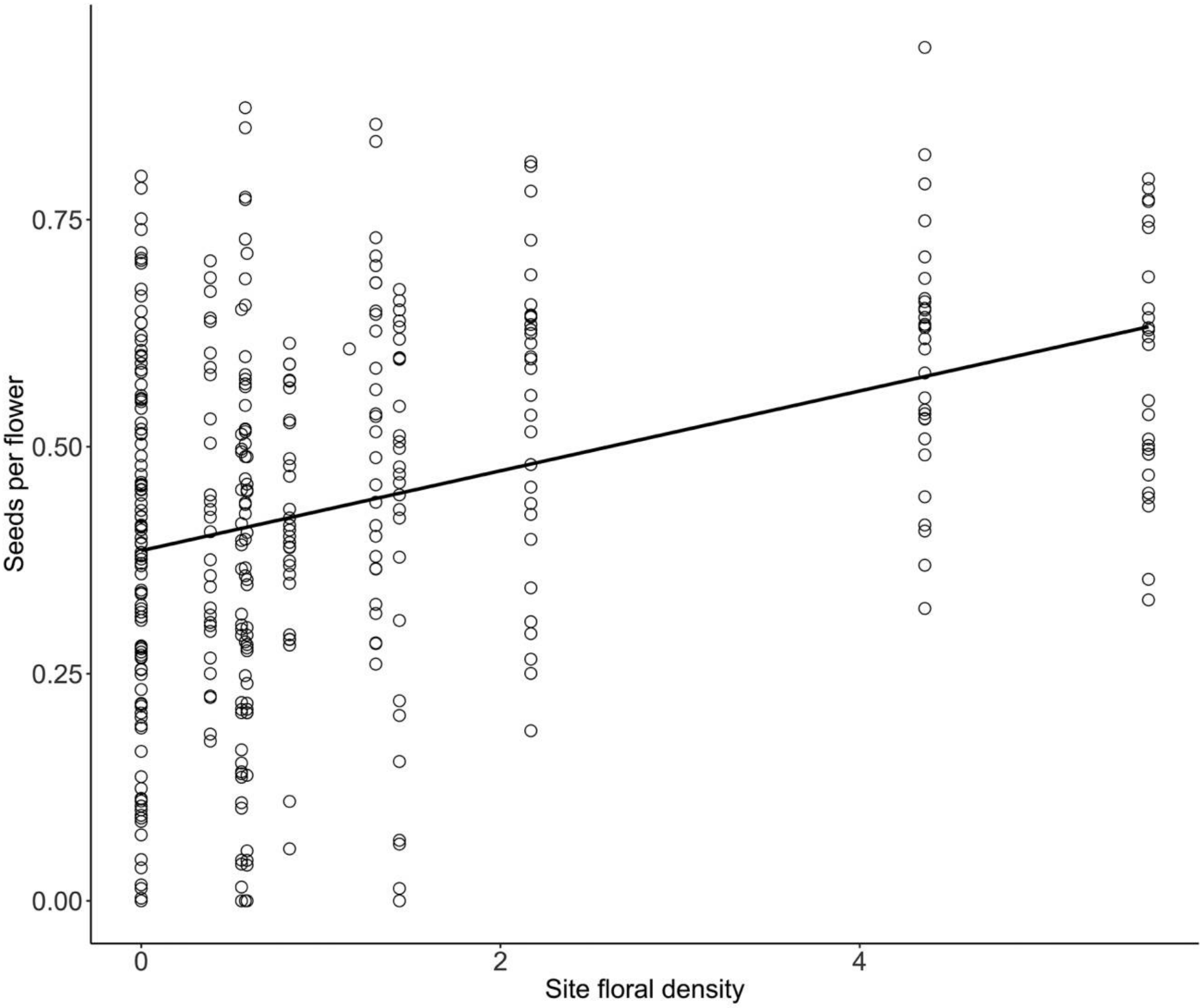

Fig. 3 Site floral density was positively correlated with seed set per flower in *Clarkia xantiana*.

***Clarkia xantiana*.** The best model for the number of seeds per flower of *C. xantiana* was one that included a fixed effect of site floral density (ΔAIC $= 7.27$; $\chi^2 = 9.279$, df $= 1$, $P = 0.002$; table A6). There was a positive relationship between site floral density and seed set per flower for *C. xantiana* (fig. 3).

Discussion

Our study sought to determine whether staggered flowering times are adaptive for two species of *Clarkia* that flower later than co-occurring congeners and whether the ecological interactions between species with staggered flowering times vary with community context. We observed equivalent seed set for *C. speciosa* across flowering periods and greater seed set for *C. xantiana* during the early-flowering period. These results suggest that flowering time may not affect the reproductive success of *C. speciosa* and that late flowering is not adaptive for *C. xantiana*. These patterns indicate that later flowering in both species is not likely to result from interspecific competition for pollination and may result from non-pollinator-mediated selection. In addition, we observed a significant effect of one community context factor, floral density, on the reproductive success of *C. xantiana*. Here we discuss what types of ecological interactions and evolutionary processes likely contribute to the observed patterns and what additional data would be needed to attribute these patterns to specific drivers.

Clarkia speciosa *Had Equivalent Seed Set across the Flowering Periods*

Across all communities, seed set of *C. speciosa* did not differ between the flowering periods (contrasts close to or overlapping zero; fig. 2*A*). These results for *C. speciosa* are similar to those of two studies of coblooming species in interior Alaska, which also found no effect of synchronous flowering on reproductive success (Armbruster and McGuire 1991; McGuire and Armbruster 1991). In *C. speciosa*, the observed similarity in reproductive success across the flowering periods could result from different types of species interactions in each flowering period. For instance, pollinator visitation rates to *C. speciosa* did not differ between the early- and late-flowering periods, but previous studies have documented that *Diadasia angusticeps*, an oligolectic bee that is primarily active late in the flowering season (Singh 2014; A. R. M. James, unpublished data), is the main pollinator of *C. speciosa* in the region. While this specialized relationship likely contributes to the reproductive success of *C. speciosa* during the late-flowering period, equivalent reproductive success during the early-flowering period could result from joint attraction of other pollinators that typically visit the early-flowering species. Joint pollinator attraction is one form of interspecific facilitation has been observed in a number of systems (Brown and Kodric-Brown 1979; Schemske 1981; Ashton et al. 1988; Gross et al. 2000), including communities of *C. xantiana* (Moeller 2004). Tracking visitation rates by specific bee species and estimating the single visit efficiency of these pollinators (Sahli and Conner 2007; Ne'Eman et al. 2010) would provide insight into whether different bee species could be equally effective pollinators of *C. speciosa* across the flowering periods (Rafferty and Ives 2012).

Clarkia xantiana *Had Higher Seed Set When It Flowered Early*

Across all community types included in the experiment, *C. xantiana* set ~25% more seeds during the early-flowering period compared with the late-flowering period (negative contrasts indicate higher reproductive success during the early-flowering period; fig. 2*B*). This result was not consistent with the expectation that staggered flowering times in multispecies *Clarkia* communities are driven by competition for pollination among co-occurring species. Rather, *C. xantiana* may have experienced relatively stronger facilitation from the early-flowering species. Despite the pervasive expectation of competition for pollination, the presence of congeners can be facilitative if pollinators are more attracted to diverse communities (Thomson 1978) and exhibit sufficient constancy in foraging (Thomson 1982). *Clarkia xantiana* represents one of the best documented cases of facilitation due to increased pollinator visitation in multispecies communities (Moeller 2004). However, the significant contrast in reproductive success at blank communities suggests that the early period may provide abiotic conditions that promote greater reproductive success (e.g., De Jong and Klinkhamer 1991).

Later Flowering in Both Species Could Result from Ecological Specialization, Developmental Constraints, Trait Correlations, or Non-Pollinator-Mediated Selection

The neutral effect of flowering time on seed set in *C. speciosa* and the positive effect of earlier flowering on seed set in *C. xantiana* suggests that the late flowering observed in nature is largely determined by a factor other than the potential for competition with or facilitation from the early-flowering species. There are four possible explanations for later flowering time, which does have a genetic basis in *C. xantiana* (Gould et al. 2014). First, late flowering could result from ecological specialization on some pollinators, which can occur without the evolution of phenotypic specialization that would preclude effective pollination by other pollinators (Aigner 2006; Armbruster 2017). Pollination by multiple species or functional groups of pollinators without apparent fitness trade-offs occurs in a number of generalized systems, including *Dudleya greenei* (Aigner 2004), *Pontederia cordata* (Harder and Barrett 1993), *Erysimum* species (Gómez et al. 2014), and *Impatiens pallida* and *Erythronium grandifiorum* (Wilson and Thomson 1996). Second, late flowering could be due to a developmental constraint (Diggle 1999; Ehrlén 2015). For example, a species of orchid (*Catasetum viridiflavum*) in Panama does not flower in synchrony with its primary pollinator in part due to constraints from factors that affect vegetative growth (Zimmerman et al. 1989). A similar but weaker relationship was observed in an understory forest herb (*Lathyrus vernus*), in that conditions of vegetative growth restrict flowering time but plants with similar vegetative phenologies may vary in flowering phenology (Sola and Ehrlén 2007). Because both *C. xantiana* and *C. speciosa* grown from seed in a greenhouse environment have a longer development time than the early-flowering species (Eisen and Geber 2018), the length of their developmental periods may cause these species to flower later than the early-flowering species. Third, flowering time in the late-flowering species could result from a trait correlation if later flowering is correlated with a trait that is under strong selection (Ehrlén 2015). For instance, multivariate selection analyses of two populations of *Arabidopsis lyrata* indicated that selection on some phenological traits was primarily due to correlated selection on inflorescence number (Sandring et al. 2007). However, this type of correlated evolution may be unlikely in *C. xantiana* due to weak correlations between phenology and floral or vegetative traits (Dudley et al. 2007; Gould et al. 2014). Fourth, late flowering in *C. xantiana* or *C. speciosa* may be the product of selection from another agent, such as herbivores or seed predators (reviewed in Brody 1997; Ehrlén 2015). Selection from predispersal seed predators tends to favor later flowering (reviewed in Strauss and Whittall 2006; Elzinga et al. 2007), although earlier flowering may be more advantageous in this system due to the existence of other species that may provide forage for herbivores earlier in the spring. Abiotic factors could also serve as agents of selection on flowering time. While earlier flowering in annuals is thought to be adaptive in order to complete the life cycle before severe heat or drought stress (e.g., Levitt 1980) and could have contributed to higher seed set of *C. xantiana* during the early-flowering period, later flowering may be a product of dehydration avoidance, which is another potential strategy for coping with seasonal drought (Ludlow 1989).

Relationship between Site Floral Density and Seed Set Suggests C. xantiana *Experiences Facilitation from Co-occurring Congeners*

Across all community types and both flowering periods, we observed a positive effect of floral density on the proportion of seeds set by *C. xantiana*. While high heterospecific density is expected to lead to interspecific competition for pollination (Feinsinger 1987; Ghazoul 2006; Seifan et al. 2014), a positive relationship between total floral density and reproductive success has been observed in a number of systems where co-occurring species contribute to joint pollinator attraction or joint pollinator maintenance (Thomson 1981, 1982; Johnson et al. 2003; Liao et al. 2011; Ye et al. 2014), including previous studies of

C. xantiana (Moeller 2004; Moeller and Geber 2005) and other species in the genus (Ha and Ivey 2017). Facilitation mediated by joint pollinator attraction to patches with higher floral density is particularly likely for *C. xantiana* for several reasons. Previous studies have identified a positive relationship between intraspecific density and pollen deposition (Moeller 2004), increased visitation to *C. xantiana* in communities with co-occurring congeners (Moeller 2004; Moeller and Geber 2005), as well as significant overlap in the primary pollinators of *C. xantiana* and the two early-flowering species (Moeller 2005; Singh 2014; A. R. M. James, unpublished data). In addition, *C. xantiana* exhibits tolerance to heterospecific pollen transfer (Arceo-Gómez et al. 2016), which could cause the benefits of joint pollinator attraction or joint pollinator maintenance to outweigh any associated interference competition from heterospecific pollen transfer (Thomson 1982). Further work is needed to determine whether the early-flowering species also experience facilitation. These effects may not be reciprocal for the early-flowering species if pollinators display a preference for *C. xantiana* (Brown et al. 2002; Seifan et al. 2014; A. R. M. James, unpublished data) or if the early-flowering species are not tolerant of heterospecific pollen transfer (Bell et al. 2005; Flanagan et al. 2009).

Caveats

Our study had three limitations. First, because of the logistical challenges associated with manipulating flowering time in natural communities, we conducted our experiment at a small number of sites of each community type for each species ($N = 2$ or 3 sites during each flowering period). All previous studies have only manipulated flowering time at one site (Waser 1978; Campbell 1985; Armbruster and McGuire 1991; McGuire and Armbruster 1991). In addition, significant herbivory from cattle and deer further reduced our sample size in three instances (see table 1). Most notably, fruits were only collected from one blank site for *C. speciosa* during the early-flowering period. Second, our experimental design consisted of placing 30 potted plants in a cluster at each experimental site. We did this to maximize the signal of these experimental plants, since *Clarkia* often occur at high densities (K. E. Eisen, M. A. Geber, personal observations). However, this experimental design may have significantly decreased the potential for pollen or mate limitation among the experimental plants. Repeating the experiment with experimental plants in a number of smaller clusters within each site rather than one larger cluster may provide more insight into whether flowering time is adaptive in different neighborhood contexts. Third, due to the intensive nature of the experiment, we were only able to conduct two pollinator observation sessions during each treatment period at each site. While we avoided conducting observation sessions on cloudy or cool days, variation in climatic conditions, in addition to sampling error associated with small sample sizes, may have influenced our results. Further innovation in automated methods of conducting pollinator observations (e.g., Weinstein 2015) will improve our ability to quantify pollinator visitation.

Conclusions

Staggered flowering phenologies have been interpreted as the product of competition for pollination for more than a century, but our study suggests that flowering time differences may not be adaptive in *Clarkia* communities in the foothills of the southern Sierra Nevada. Other factors aside from competition, such as specialized interactions with pollinators, developmental constraints, and trait correlations likely contribute to the staggered flowering phenologies observed. In addition to supporting alternative hypotheses for the existence of staggered flowering times, our results provide indirect evidence of relatively stronger interspecific facilitation in these communities and indicate that flowering density can affect the ecological consequences of a flowering strategy and, by extension, the evolution of flowering time. While manipulating flowering time in the field remains logistically challenging, additional experimental studies that manipulate both flowering time and community context factors will contribute to our understanding of how floral trait evolution occurs in response to selection mediated by pollinators and other agents.

Acknowledgments

We thank D. A. Moeller for guidance and discussion of the experimental design and logistics. M. K. Gallagher and W. Yang provided assistance with plant care at the University of California, Irvine, and M. K. Gallagher, I. W. K. Hunter, J. Powers, and W. Recart provided assistance with transporting plants. J. Benning, N. Graham, L. Jacob, A. R. M. James, and G. Siegmund provided field assistance. The manuscript was improved by thoughtful comments from J. Brunet, K. D. Holmes, A. R. M. James, and G. Siegmund, and several anonymous reviewers. We thank Lynn Johnson and Erika Mudrak from the Cornell Statistical Consulting Unit for advice on statistical analyses. Funding for this work was provided by a Paul Fellowship for Study and Research in Absentia and awards from the Paul P. Feeny Graduate Student Research Fund and the Betty Miller Francis '47 Fund from the Cornell University Department of Ecology and Evolutionary Biology to K. E. Eisen, an Andrew W. Mellon Student Research Grant from the Cornell University College of Agricultural and Life Sciences to K. E. Eisen, and National Science Foundation grant DEB-1256288 to M. A. Geber.

Literature Cited

Aigner PA 2004 Floral specialization without trade-offs: optimal corolla flare in contrasting pollination environments. Ecology 85:2560–2569.

——— 2006 The evolution of specialized floral phenotypes in a fine-grained pollination environment. Pages 23–46 *in* NM Waser, J Ollerton, eds. Plant-pollinator interactions: from specialization to generalization. University of Chicago Press, Chicago.

Aizen MA, DP Vázquez 2006 Flowering phenologies of hummingbird plants from the temperate forest of southern South America: is there evidence of competitive displacement? Ecography 29:357–366.

Arceo-Gómez G, RA Raguso, MA Geber 2016 Can plants evolve tolerance mechanisms to heterospecific pollen effects? an experimental test of the adaptive potential in *Clarkia* species. Oikos 125:718–725.

Armbruster WS 1986 Reproductive interactions between sympatric *Dalechampia* species: are natural assemblages "random" or organized? Ecology 67:522–533.

——— 2017 The specialization continuum in pollination systems: diversity of concepts and implications for ecology, evolution and conservation. Funct Ecol 31:88–100.

Armbruster WS, AL Herzig 1984 Partitioning and sharing of pollinators by four sympatric species of *Dalechampia* (Euphorbiaceae) in Panama. Ann Mo Bot Gard 71:1–16.

Armbruster WS, AD McGuire 1991 Experimental assessment of reproductive interactions between sympatric *Aster* and *Erigeron* (Asteraceae) in interior Alaska. Am J Bot 78:1449–1457.

Ashton PS, TJ Givnish, S Appanah 1988 Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. Am Nat 132:44–66.

Bartoń K 2019 MuMIn: multi-model inference. R package version 1.43.6. https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf.

Bates D, M Mächler, BM Bolker, SC Walker 2015 Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48.

Bell JM, JD Karron, RJ Mitchell 2005 Interspecific competition for pollination lowers seed production and outcrossing in *Mimulus ringens*. Ecology 86:762–771.

Botes C, SD Johnson, RM Cowling 2008 Coexistence of succulent tree aloes: partitioning of bird pollinators by floral traits and flowering phenology. Oikos 117:875–882.

Brody AK 1997 Effects of pollinators, herbivores, and seed predators on flowering phenology. Ecology 78:1624–1631.

Brown BJ, RJ Mitchell, SA Graham 2002 Competition for pollination between an invasive species (purple loosestrife) and a native congener. Ecology 83:2328–2336.

Brown JH, A Kodric-Brown 1979 Convergence, competition, and mimicry in a temperate community of hummingbird-pollinated flowers. Ecology 60:1022–1035.

Campbell DR 1985 Pollinator sharing and seed set of *Stellaria pubera*: competition for pollination. Ecology 66:544–553.

Campbell DR, AF Motten 1985 The mechanism of competition for pollination between two forest herbs. Ecology 66:554–563.

Caruso CM 1999 Pollination of *Ipomopsis aggregata* (Polemoniaceae): effects of intra- vs. interspecific competition. Am J Bot 86:663–668.

De Jong TJ, PGL Klinkhamer 1991 Early flowering in *Cynoglossum officinale* L. constraint or adaptation? Funct Ecol 5:750–756.

Devaux C, R Lande 2009 Displacement of flowering phenologies among plant species by competition for generalist pollinators. J Evol Biol 22:1460–1470.

Diggle PK 1999 Heteroblasty and the evolution of flowering phenologies. Int J Plant Sci 160:S123–S134.

Dudley LS, SJ Mazer, P Galusky 2007 The joint evolution of mating system, floral traits and life history in *Clarkia* (Onagraceae): genetic constraints vs. independent evolution. J Evol Biol 20:2200–2218.

Ehrlén J 2015 Selection on flowering time in a life-cycle context. Oikos 124:92–101.

Eisen KE, MA Geber 2018 Ecological sorting and character displacement contribute to the structure of communities of *Clarkia* species. J Evol Biol 31:1440–1458.

Elzinga JA, A Atlan, A Biere, L Gigord, AE Weis, G Bernasconi 2007 Time after time: flowering phenology and biotic interactions. Trends Ecol Evol 22:432–439.

Feinsinger P 1987 Effects of plant species on each other's pollination: is community structure influenced? Trends Ecol Evol 2:123–126.

Feinsinger P, KG Murray, S Kinsman, WH Busby 1986 Floral neighborhood and pollination success in four hummingbird-pollinated cloud forest plant species. Ecology 67:449–464.

Fenner M 1998 The phenology of growth and reproduction in plants. Perspect Plant Ecol Evol Syst 1:78–91.

Flanagan R, RJ Mitchell, D Knutowski, JD Karron 2009 Interspecific pollinator movements reduce pollen deposition and seed production in *Mimulus ringens* (Phrymaceae). Am J Bot 96:809–815.

Fox GA, CK Kelly 1993 Plant phenology: selection and neutrality. Trends Ecol Evol 8:34–35.

Geber M, D Moeller 2006 Pollinator responses to plant communities and implications for reproductive character evolution. Pages 102–119 *in* SCH Barrett, LD Harder, eds. Ecology and evolution of flowers. Oxford University Press, New York.

Ghazoul J 2006 Floral diversity and the facilitation of pollination. J Ecol 94:295–304.

Gleeson SK 1981 Character displacement in flowering phenologies. Oecologia 51:294–295.

Gómez JM, F Perfectti, M Abdelaziz, J Lorite, AJ Muñoz-Pajares, J Valverde 2014 Evolution of pollination niches in a generalist plant clade. New Phytol 205:440–453.

Gould B, DA Moeller, VM Eckhart, P Tiffin, E Fabio, MA Geber 2014 Local adaptation and range boundary formation in response to complex environmental gradients across the geographical range of *Clarkia xantiana* ssp. *xantiana*. J Ecol 102:95–107.

Gross CL 1996 Is resource overlap disadvantageous to three sympatric legumes? Aust J Ecol 21:133–143.

Gross CL, DA Mackay, MA Whalen 2000 Aggregated flowering phenologies among three sympatric legumes: the degree of non-randomness and the effect of overlap on fruit set. Plant Ecol 148:13–21.

Gross RS, PA Werner 1983 Relationships among flowering phenology, insect visitors, and seed-set of individuals: experimental studies on four co-occurring species of goldenrod (*Solidago*: Compositae). Ecol Monogr 53:95–117.

Ha MK, CT Ivey 2017 Pollinator-mediated interactions in experimental arrays vary with neighbor identity. Am J Bot 104:252–260.

Harder LD, SCH Barrett 1993 Pollen removal from tristylous *Pontederia cordata*: effects of anther position and pollinator specialization. Ecology 74:1059–1072.

Heinrich B 1975 Bee flowers: a hypothesis on flower variety and blooming times. Evolution 29:325–334.

Heithaus ER, TH Fleming, PA Opler 1975 Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. Ecology 56:841–854.

Huang SQ, XQ Shi 2013 Floral isolation in *Pedicularis*: how do congeners with shared pollinators minimize reproductive interference? New Phytol 199:858–865.

Hutchinson GE 1959 Homage to Santa Rosalia or why are there so many kinds of animals? Am Nat 93:145–159.

Ishii R, M Higashi 2001 Coexistence induced by pollen limitation in flowering-plant species. Proc R Soc B Biol Sci 268:579–585.

Ivey CT, LS Dudley, AA Hove, SK Emms, SJ Mazer 2016 Outcrossing and photosynthetic rates vary independently within two *Clarkia* species: implications for the joint evolution of drought escape physiology and mating system. Ann Bot 118:897–905.

Johnson SD 1993 Climatic and phylogenetic determinants of flowering seasonality in the Cape Flora. J Ecol 81:567–572.

Johnson SD, CI Peter, LA Nilsson, J Agren 2003 Pollination success in a deceptive orchid is enhanced by co-occurring rewarding magnet plants. Ecology 84:2919–2927.

Jonas CS, MA Geber 1999 Variation among populations of *Clarkia unguiculata* (Onagraceae) along altitudinal and latitudinal gradients. Am J Bot 86:333–343.

Kephart SR 1983 The partitioning of pollinators among three species of *Asclepias*. Ecology 64:120–133.

Kochmer JP, SN Handel 1986 Constraints and competition in the evolution of flowering phenology. Ecol Monogr 56:303–325.

Kudo G 2006 Flowering phenologies of animal-pollinated plants: reproductive strategies and agents of selection. Pages 139–158 *in* SCH Barrett, LD Harder, eds. Ecology and evolution of flowers. Oxford University Press, New York.

Kunin WE 1993 Sex and the single mustard: population density and pollinator behavior effects on seed-set. Ecology 74:2145–2160.

Lack AJ 1982 Competition for pollinators in the ecology of *Centaurea scabiosa* L. and *Centaurea nigra* L. I. Variation in flowering time. New Phytol 91:297–308.

Landry CL 2013 Pollinator-mediated competition between two coflowering Neotropical mangrove species, *Avicennia germinans* (Avicenniaceae) and *Laguncularia racemosa* (Combretaceae). Ann Bot 111:207–214.

Lenth R 2018 emmeans: estimated marginal means, aka least-squares means. R package version 1.3.0. https://rdrr.io/cran/emmeans/.

Levitt J 1980 Responses of plants to environmental stress. Academic Press, New York.

Lewis H 1953 The mechanism of evolution in the genus *Clarkia*. Evolution 7:1–20.

——— 1961 Experimental sympatric populations of *Clarkia*. Am Nat 95:155–168.

Lewis H, ME Lewis 1955 The genus *Clarkia*. Univ Calif Publ Bot 20:241–392.

Liao K, RW Gituru, YH Guo, QF Wang 2011 The presence of coflowering species facilitates reproductive success of *Pedicularis monbeigiana* (Orobanchaceae) through variation in bumble-bee foraging behaviour. Ann Bot 108:877–884.

Lobo JA, M Quesada, KE Stoner, EJ Fuchs, Y Herrerías-Diego, J Rojas, G Saborío 2003 Factors affecting phenological patterns of bombacaceous trees in seasonal forests in Costa Rica and Mexico. Am J Bot 90:1054–1063.

Ludlow MM 1989 Strategies in response to water stress. Pages 269–281 *in* K Kreeb, H Richter, T Hinkley, eds. Structural and functional responses to environmental stresses. SPB, The Hague.

Macarthur R, R Levins 1967 The limiting similarity, convergence, and divergence of coexisting species. Am Nat 101:377–385.

Macior LM 1971 Co-evolution of plants and animals: systematic insights from plant-insect interactions. Taxon 20:17–28.

MacSwain J, PH Raven, R Thorp 1973 Comparative behavior of bees and Onagraceae. IV. *Clarkia* bees of the western United States. Univ Calif Publ Entomol 70:1–80.

Madeira A, GW Fernandes 1999 Reproductive phenology of sympatric taxa of *Chamaecrista* (Leguminosae) in Serra do Cipó, Brazil. J Trop Ecol 15:463–479.

McGuire AD 1993 Interactions for pollination between two synchronously blooming *Hedysarum* species (Fabaceae) in Alaska. Am J Bot 80:147–152.

McGuire AD, WS Armbruster 1991 An experimental test for reproductive interactions between two sequentially blooming *Saxifraga* species (Saxifragaceae). Am J Bot 78:214–219.

McKinney AM, K Goodell 2011 Plant-pollinator interactions between an invasive and native plant vary between sites with different flowering phenology. Plant Ecol 212:1025–1035.

Moeller DA 2004 Facilitative interactions among plants via shared pollinators. Ecology 85:3289–3301.

——— 2005 Pollinator community structure and sources of spatial variation in plant-pollinator interactions in *Clarkia xantiana* ssp. *xantiana*. Oecologia 142:28–37.

——— 2006 Geographic structure of pollinator communities, reproductive assurance, and the evolution of self-pollination. Ecology 87:1510–1522.

Moeller DA, MA Geber 2005 Ecological context of the evolution of self-pollination in *Clarkia xantiana*: population size, plant communities, and reproductive assurance. Evolution 59:786–99.

Moeller DA, MA Geber, VM Eckhart, P Tiffin 2012 Reduced pollinator service and elevated pollen limitation at the geographic range limit of an annual plant. Ecology 93:1036–1048.

Mosquin T 1971 Competition for pollinators as a stimulus for the evolution of flowering time. Oikos 22:398–402.

Ne'Eman G, A Jürgens, L Newstrom-Lloyd, SG Potts, A Dafni 2010 A framework for comparing pollinator performance: effectiveness and efficiency. Biol Rev 85:435–451.

Ogilvie JE, JD Thomson 2016 Site fidelity by bees drives pollination facilitation in sequentially blooming plant species. Ecology 97:1442–1451.

Ollerton J, A Diaz 1999 Evidence for stabilising selection acting on flowering time in *Arum maculatum* (Araceae): the influence of phylogeny on adaptation. Oecologia 119:340–348.

Ollerton J, AJ Lack 1992 Flowering phenology: an example of relaxation of natural selection. Trends Ecol Evol 7:274–276.

Pleasants JM 1980 Competition for bumblebee pollinators in Rocky Mountain plant communities. Ecology 61:1446–1459.

R Core Team 2018 R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/.

Rabinowitz D, JK Rapp, VL Sork, BJ Rathcke, A Reese, JC Weaver, JK Rapp, GA Reese, JC Weaver 1981 Phenological properties of wind- and insect-pollinated prairie plants. Ecology 62:49–56.

Rafferty NE, AR Ives 2012 Pollinator effectiveness varies with experimental shifts in flowering time. Ecology 93:803–814.

Ramsey M 1995 Causes and consequences of seasonal variation in pollen limitation of seed production in *Blandfordia grandiflora* (Liliaceae). Oikos 73:49–58.

Rathcke B 1988 Interactions for pollination among coflowering shrubs. Ecology 69:446–457.

Rathcke B, EP Lacey 1985 Phenological patterns of terrestrial plants. Annu Rev Ecol Syst 16:179–214.

Robertson C 1895 The philosophy of flower seasons, and the phaenological relations of the entomophilous flora and the anthophilous insect fauna. Am Nat 29:97–117.

Sahli HF, JK Conner 2007 Visitation, effectiveness, and efficiency of 15 genera of visitors to wild radish, *Raphanus raphanistrum* (Brassicaceae). Am J Bot 94:203–209.

Sandring S, MA Riihimäki, O Savolainen, J Ågren 2007 Selection on flowering time and floral display in an alpine and a lowland population of *Arabidopsis lyrata*. J Evol Biol 20:558–567.

Schemske DW 1981 Floral convergence and pollinator sharing in two bee-pollinated tropical herbs. Ecology 62:946–954.

Schoener TW 1974 Resource partitioning in ecological communities. Science 185:27–39.

Seifan M, EM Hoch, S Hanoteaux, K Tielbörger 2014 The outcome of shared pollination services is affected by the density and spatial pattern of an attractive neighbour. J Ecol 102:953–962.

Singh I 2014 Pollination interaction networks between *Clarkia* (Onagraceae) species and their pollinators in the Southern Sierra Nevada, California. Cornell University, Ithaca, NY.

Sletvold N, J Ågren 2014 There is more to pollinator-mediated selection than pollen limitation. Evolution 68:1907–1918.

Sola AJ, J Ehrlén 2007 Vegetative phenology constrains the onset of flowering in the perennial herb *Lathyrus vernus*. J Ecol 95:208–216.

Stone GN, P Willmer, JA Rowe 1998 Partitioning of pollinators during flowering in an African *Acacia* community. Ecology 79:2808–2827.

Strauss SY, JB Whittall 2006 Non-pollinator agents of selection on floral traits. Pages 120–139 *in* SCH Barrett, LD Harder, eds. Ecology and evolution of flowers. Oxford University Press, New York.

Thomson JD 1978 Effects of stand composition on insect visitation in two-species mixtures of *Hieracium*. Am Midl Nat 100:431–440.

——— 1981 Spatial and temporal components of resource assessment by flower-feeding insects. J Anim Ecol 50:49–59.

——— 1982 Patterns of visitation by animal pollinators. Oikos 39: 241–250.

Thompson JN 2005 The geographic mosaic of coevolution. University of Chicago Press, Chicago.

Vasek FC 1965 Outcrossing in natural populations. II. *Clarkia unguiculata*. Evolution 19:152–156.

Waser NM 1978 Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. Ecology 59:934–944.

Waser NM, LA Real 1979 Effective mutualism between sequentially flowering plant species. Nature 281:670–672.

Weinstein BG 2015 MotionMeerkat: integrating motion video detection and ecological monitoring. Methods Ecol Evol 6:357–362.

Wilson P, JD Thomson 1996 How do flowers diverge? Pages 88–111 *in* DG Lloyd, SCH Barrett, eds. Floral biology: studies on floral evolution in animal-pollinated plants. Springer, Boston.

Wirth LR, NM Waser, R Graf, F Gugerli, U Landergott, A Erhardt, HP Linder, R Holderegger 2011 Effects of floral neighborhood on seed set and degree of outbreeding in a high-alpine cushion plant. Oecologia 167:427–434.

Wright SJ, O Calderon 1995 Phylogenetic patterns among tropical flowering phenologies. J Ecol 83:937–948.

Ye ZM, WK Dai, XF Jin, RW Gituru, QF Wang, CF Yang 2014 Competition and facilitation among plants for pollination: can pollinator abundance shift the plant-plant interactions? Plant Ecol 215:3–13.

Zimmerman JK, DW Roubik, JD Ackerman 1989 Asynchronous phenologies of a Neotropical orchid and its euglossine bee pollinator. Ecology 70:1192–1195.