FACILITATIVE INTERACTIONS AMONG PLANTS VIA SHARED POLLINATORS

DAVID A. MOELLER[1]

Department of Ecology and Evolutionary Biology, Corson Hall, Cornell University, Ithaca, New York 14853 USA

Abstract. Outcrossing in plants is influenced by the availability of pollinators and compatible mates, both of which may be modified by the population and community context in which plant–pollinator interactions occur. Although indirect interactions among plants through shared pollinators are often expected to be competitive, pollinator sharing may be beneficial when plant species jointly attract or maintain populations of pollinators. In this study, I tested the hypothesis that pollinator-sharing congeners facilitate reproduction in a focal taxon, *Clarkia xantiana* ssp. *xantiana*, and that positive interactions are most pronounced in small and sparse populations. Population surveys revealed that *C. x. xantiana* frequently coexists with pollinator-sharing congeners except at the periphery of its range. Populations varied extensively in size and density, with small populations more likely associated with pollinator-sharing congeners; conversely, populations occurring alone were more likely large. Flowering schedules in *Clarkia* communities ranged from segregated to aggregated. Although there was not strong evidence of character displacement, modes in flowering time were often staggered among *Clarkia* species resulting in a protracted flowering season within plant communities. Studies of bee pollinator availability in 17 populations and pollen limitation to reproduction in 39 replicate populations revealed that populations occurring with multiple congeners had high pollinator availability and low pollen limitation of reproduction compared to populations occurring alone. Population size was inversely related to pollen limitation but did not affect pollinator availability, suggesting that Allee effects were caused by mate limitation. Intraspecific interactions were also positive at a fine spatial scale where pollen deposition increased with the density of closely neighboring conspecifics across 11 populations. Overall, inter- and intraspecific interactions through shared pollinators were generally facilitative, suggesting that population viability and the coexistence of ecologically similar *Clarkia* species may be promoted by positive reproductive interactions.

Key words: Allee effects; density dependence; facilitation; indirect effects; Onagraceae; plant–pollinator interactions; pollen limitation; pollination; population size; positive interactions; solitary bees.

INTRODUCTION

Understanding the mechanisms of coexistence of ecologically similar species has been a challenging problem for ecologists (Hutchinson 1961). The underlying assumption for most models of coexistence is that competition for limiting resources is the dominant force regulating diversity (Tilman and Pacala 1993, Palmer 1994). A growing number of studies on plant communities, however, provide evidence that plant–plant interactions may vary from competitive to facilitative (Callaway 1995). While competitive interactions constrain the realized niche to some subset of the fundamental niche, facilitative interactions can serve to expand the realized niche, thereby allowing species to maintain population growth in areas where they could not exist alone (Higashi 1993, Bruno et al. 2003).

Most examples of positive interactions between plants involve direct interactions where one species ameliorates the physical or resource environment of another species (e.g., Bertness and Callaway 1994, Callaway et al. 2002). Indirect positive interactions are well known from trophic cascades (Wootton 1994), but remain poorly understood for species within trophic levels. In plants, indirect positive interactions may occur through a chain of competitive interactions (Miller 1994), through associational defense of co-occurring plants against natural enemies (Tahvanainen and Root 1972, Hamback et al. 2000), and through pollinator sharing. Animal-mediated interactions among plants differ from direct interactions in that animals are likely to extend the spatial scale over which plants interact.

The role of shared pollinators in structuring plant communities has been the focus of much study (reviewed in Palmer et al. 2003). In particular, competition for pollinator service (exploitation competition) and competition through interspecific pollen transfer (interference competition) have been suggested as important organizing forces shaping plant communities

[1] Present address: Department of Plant Biology, University of Minnesota, 1445 Gortner Avenue, St. Paul, Minnesota 55108 USA. E-mail: moell021@umn.edu

(Robertson 1895, Rathcke 1983, Waser 1983, Campbell 1985). Competitive interactions may influence patterns of community structure either through the ecological process of species sorting, where competitive exclusion eliminates inferior competitors from communities, or through the evolution of character displacement, where directional selection drives the divergence of traits mediating plant–pollinator interactions. It follows that coexistence may occur when plants partition pollinator services through segregated flowering times, pollen presentation schedules, or pollen placement on pollinators (e.g., Armbruster et al. 1994).

In spite of an emphasis on competitive interactions via pollinators, studies have not consistently detected an effect of pollinator sharing on community structure (e.g., Feinsinger 1987, Murray et al. 1987, Armbruster and McGuire 1991). It is clear that in many plant communities flowering times overlap considerably, where multiple species share pollinators or abiotic pollen vectors (Smith-Ramírez et al. 1998, Gross et al. 2000). At the timescale of the flowering season, there is evidence for aggregated flowering schedules within taxonomic groups, which has been interpreted to be the result of phylogenetic constraints (Kochmer and Handel 1986, Johnson 1992, Wright and Calderon 1995). A relatively unexplored hypothesis to explain the coexistence of plant species is that pollinator availability and reproductive success for a given plant species may be enhanced by associated species that share pollinators. Several authors have outlined the potential for positive interactions (Macior 1971, Brown and Kodric-Brown 1979, Waser and Real 1979, Thomson 1981, Rathcke 1983), but evidence remains limited to systems where plant species providing no pollinator rewards benefit from close proximity to rewarding species (Laverty 1992, Johnson et al. 2003).

Reproductive interactions have generally been examined in the context of how pollinator sharing influences patterns of pollinator foraging within plant communities and in turn, its effects on visitation rates and interspecific pollen transfer. Although competitive interactions through pollinator sharing have been well characterized using this framework, facilitative interactions may often manifest at larger spatial scales because (1) highly mobile pollinators forage over broad areas and can select among patches of plants (Beekman and Ratnieks 2000) or (2) plant communities affect the population dynamics and persistence of less mobile pollinators (e.g., solitary bees, thrips), which are often distributed patchily over the landscape (Steffan-Dewenter and Tscharntke 1999). Likewise, attributes of plant populations may have similar impacts on the spatial distribution of pollinators and modify the importance (or nature) of interactions between co-flowering plant species. For example, Rathcke (1983) proposed that when plant density is high, conspecifics and heterospecifics may compete for a limited supply of pollinators; whereas, plant populations of low density or

small size may benefit from the presence of co-flowering species due to greater pollinator availability. Integrating community and population perspectives on reproductive ecology is increasingly important as it is now well known that plant population viability can be threatened by Allee effects, where mating success is limited due to small population size or low density (Sih and Baltus 1987, Aizen and Feinsinger 1994, Groom 1998, Hackney and McGraw 2001); however, the importance of pollinator-mediated facilitative interactions in mitigating Allee effects has not been investigated.

In this study, I examined the nature of intra- and interspecific interactions between plants in the genus *Clarkia* that share pollinators and overlap in flowering time. I focused on the reproductive ecology of a focal taxon, *Clarkia xantiana* ssp. *xantiana*, an annual plant endemic to southern California, USA. I assessed the potential importance of interactions between *C. x. xantiana* and pollinator-sharing congeners in space and time by examining spatial patterns of coexistence and temporal patterns of co-flowering across most of *C. x. xantiana*'s geographic range. I used hand-pollination experiments with *C. x. xantiana* to examine whether reproduction was pollen-limited and the potential causes of pollen limitation. The investigation was hierarchical in assessing the effects of the plant community (coexisting congeners) and population attributes (population size and mean population density) on the degree of pollen limitation, and at a finer scale, in examining the influence of local conspecific density (within 1 m^2) on pollen deposition to focal plants. The study was particularly aimed at testing the hypothesis that coexisting *Clarkia* species facilitate reproduction in *C. x. xantiana* and that facilitative effects are most important for small or sparse populations.

Study system

The genus *Clarkia* (Onagraceae) is ideal for studying community-level reproductive interactions because many species occur in sympatry, flower toward the end of spring after most other plant genera have flowered, and share bee pollinators (Lewis and Lewis 1955, MacSwain et al. 1973). Bee pollinators include at least 10 solitary bee species that specialize on *Clarkia* pollen for nest provisioning and rarely visit other co-flowering plant genera (MacSwain et al. 1973). *Clarkia* pollen specialists' scopae are composed of sparse, weakly branched hairs, which assist in collecting *Clarkia*'s large, clustered pollen grains (MacSwain et al. 1973). Although it is clear that *Clarkia* species share pollinators, hybridization is very rare due to strong postzygotic isolating mechanisms (Lewis and Lewis 1955).

In *Clarkia xantiana* ssp. *xantiana* A. Gray, outcrossing is promoted through protandry and herkogamy; there are no known facultative (delayed) self-pollination mechanisms (Eckhart and Geber 1999). Populations are discrete and occur primarily on exposed hillsides. *C. x. xantiana* is sympatric with three other
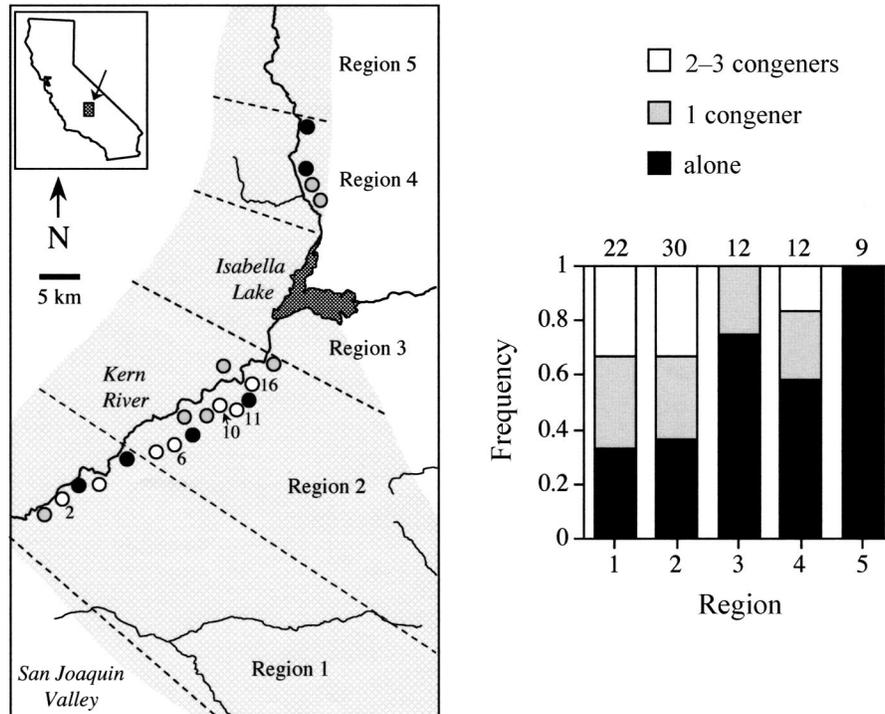
FIG. 1. Geographic range of *C. x. xantiana* covered in this study (gray shaded area). For the population survey, the range was divided into five regions (delineated by dashed lines) along a southwest to northeast environmental gradient. The right panel shows the frequency of coexistence between *C. x. xantiana* and congeners for 85 populations across the five regions. Bars show the proportion of populations in each region that coexist with no *Clarkia* species, one species, and 2–3 species. The number of populations per region is indicated above each bar. Populations included in studies of pollinator availability and pollen limitation are shown on the map and coded according to community type. Three-species communities for which null-model tests of flowering phenology were conducted are labeled by site number as in Fig. 2.

Clarkia taxa, all of which are outcrossing and provide pollen and nectar rewards for bee visitors: *C. cylindrica* ssp. *clavicarpa* W. Davis, *C. speciosa* ssp. *polyantha* Harlan Lewis and M. Lewis, and *C. unguiculata* Lindley. These species coexist over small spatial scales, overlap in bee pollinator communities (MacSwain et al. 1973), and specialist bees are the most abundant and reliable pollinators (Moeller, *in press*).

METHODS

Population survey of coexistence frequency

The frequency of coexistence of *C. x. xantiana* with outcrossing congeners was documented for all known *C. x. xantiana* populations in the southern Sierra Nevada, California, USA (Fig. 1). I recorded the presence or absence of the three outcrossing congeners for 85 *C. x. xantiana* populations. To assess geographic variation in the frequency of *Clarkia* species associations, the area covered in the survey was divided into five regions, which partition the major SW to NE gradient in precipitation and correspond with transitions in dominant vegetation. From SW to NE, *C. x. xantiana* occurs in the grasslands of the lower foothills (region 1), blue oak (*Quercus douglasii*) woodland of the mid to upper foothills (region 2), xeric gray pine (*Pinus sabiniana*)

woodland (regions 3 and 4), and a transition zone including gray pine and chaparral (region 5). The frequencies of *C. x. xantiana* populations occurring with no congeners, one congener, or two or more congeners were compared among regions using the Fisher-Freeman-Halton exact test (StatXact; Cytel Software 2003) because many cells had low expected values. Second, I partitioned the contingency table to isolate the main regional differences in association frequencies by comparing the center of the range (regions 1 and 2) to the periphery of the range (regions 3–5).

Flowering phenology

I documented flowering phenology of *C. x. xantiana* and coexisting congeners during the spring and summer of 1999 at 20 sites in three geographic regions (1, 2, 4; Fig. 1). Populations occurred either with zero ($n = 5$), one ($n = 10$), or two ($n = 5$) species of congeners. In each site, the area occupied by all *Clarkia* species was measured and divided into 4 to 6 sections depending upon site area. A 10 × 1 m plot was randomly placed in each section and the number of open flowers of each species was counted every five to six days. I examined patterns of flowering phenology by (1) comparing flowering distributions among *C. x. xantiana*

populations with contrasting community backgrounds and (2) using null-model tests to ask whether whole-community patterns deviate from random expectations.

Flowering phenology of C. x. xantiana.—I described the flowering phenology of each population using the first four moments of the distribution of flowering times (mean, variance, skewness, and kurtosis). Flowering distributions were compared between populations occurring with and without congeners using a two-way ANOVA with community type and geographic region as independent variables and the moments of the flowering distributions as dependent variables. This analysis tests whether interactions with congeners have generated character displacement in *C. x. xantiana*'s flowering phenology. Because *C. x. xantiana* is the last *Clarkia* species to flower in this region, character displacement due to competition is expected to shift mean flowering time later or alter the shape of the flowering distribution to minimize overlap.

Null-model tests of community phenology.—The second analysis tests whether community-level flowering patterns are significantly segregated or aggregated relative to expectations generated using random community assembly rules. I constructed null models following the general approach of Ashton et al. (1988) because it eliminates biases previously identified for null models of flowering phenology (reviewed in Gotelli and Graves 1996). Null-model tests were conducted for each of the three-species communities.

A complete description of random community assembly rules for null models is presented in Appendix A. For each species, I used data from periodic censuses to interpolate daily flower production. The distribution of daily flower production for a given species was then re-scaled so that relative abundance did not influence the degree of species overlap (i.e., area under each flowering curve is identical). In each iteration of the simulation, species within a community were randomly assembled such that the realized length of the simulated flowering season was constrained to equal the observed length; this restriction eliminates a bias toward rejecting the null hypothesis in favor of segregation (Ashton et al. 1988). The community assembly rules were also unbiased with respect to the identity of terminal species and the position of the middle species in the flowering season. Overlap in flowering between pairs of species was calculated as the area of overlap between flowering distributions and ranges from 0 (no overlap) to 1 (complete overlap). Pairwise overlap was used to calculate two community-level measures of overlap, total and maximum overlap, which reflect the combined behavior of all species and allow for the most appropriate tests of character displacement or convergence (Pleasants 1990). Total overlap in the community is the sum of pairwise overlaps. Maximum overlap was taken as the highest overlap value across the three pairwise species combinations. In simulations of three-species communities, maximum overlap is more powerful than total

overlap for detecting aggregation in communities. For both overlap measures, I calculated two-tailed P values; the null hypothesis was rejected when the observed overlap was greater or less than 97.5% of simulated overlap values ($\alpha = 0.05$).

Community- and population-level effects on pollinator availability

I examined the effects of coexisting congeners, population size, and mean population density on pollinator availability in one year (1999) and pollen limitation of reproductive success in three years (1999–2001). I selected populations that varied in the number of congeners coexisting with *C. x. xantiana* (0, 1, or 2), population size, and mean population density; population sampling occurred such that these variables were not confounded with one another and such that the entire spectrum of variation for each factor was represented. In 1999, population attributes were measured for 20 populations; in each year, pollen limitation experiments were conducted in a subset of these sites. Mean population density was calculated as the mean density of *C. x. xantiana* across all 10×1 m plots (see *Methods: Flowering phenology*). I measured the area occupied by each population in order to calculate an estimate of population size (density × area). Quantitative estimates were converted to categorical variables according to natural breaks in the distributions; categories encompass modes in the distribution of population size and density. Population size was divided into small (550–2200 individuals), medium (3100–7500), and large populations (12 000–33 000). The distribution of densities was bimodal and was divided into two groups: low (0.6–2.9 plants/m²) or high (3.3–6.5 plants/m²) density.

I examined pollinator availability to *C. x. xantiana* individuals in 17 populations throughout their flowering periods. Populations were censused every five to six days to record the number of bees foraging in permanent plots; all visitors observed in this study were bees. During each day of observation, populations were censused early (08:00–11:30 hours) and late in the day (12:00–15:00 hours); bee visitors to *Clarkia* are uncommon before or after this period. The order in which sites were observed in a given day was rotated across the flowering period. During observations at a site, one person walked along each of the 10×1 m plots and recorded the number of bees foraging on *C. x. xantiana* (the same amount of time was spent censusing each plot); this procedure was repeated three times during each site census. Pollinator availability was expressed as the number of bees observed per plant. Bee species could not be identified by sight and few collections were made to avoid influencing plant reproduction. A detailed analysis of the composition of bee pollinator communities of *C. x. xantiana* and in relation to plant community diversity has been reported elsewhere (Moeller, *in press*). Repeated-measures ANOVA (the

Mixed procedure, SAS Institute 1997) was used to examine the influence of coexisting congeners, population size, mean population density, and geographic region on pollinator availability (square-root transformed). The within-subject factor, census day, was considered a fixed effect as populations were deliberately visited at even intervals over the flowering period. I selected the autoregressive covariance structure with heterogeneous variances for the analysis after comparing plausible models using Akaike's Information Criterion (Littell et al. 1996). The significance of the random effect, population identity, the subject upon which repeated measures were taken, was determined by a likelihood ratio test, with df = 5. Denominator degrees of freedom for tests of fixed effects were estimated using the Satterthwaite approximation.

Community- and population-level effects on pollen limitation of reproduction

I evaluated the magnitude of pollen limitation of reproductive success in a total of 39 replicate populations (20 unique populations) over three years (no. populations = 15, 11, and 13 for 1999, 2000, and 2001, respectively). I compared the reproductive success of plants that received supplemental pollen to those left unmanipulated. Hand-pollinations were conducted at the peak of flowering at each site when *C. x. xantiana* overlapped in flowering with congeners. I selected 50 pairs of plants distributed throughout each population to receive alternate treatments; plants were paired based on vegetative size. One flower on each plant either received supplemental pollen or was marked but not manipulated. I gathered freshly dehisced pollen for hand-pollinations from plants at least 5 m from the recipient and pollinated receptive stigmas. Hand-pollinations occurred at the same time of day as pollinators were active. A preliminary experiment provided no evidence that resources are shunted to flowers receiving supplemental pollen at the cost of open-pollinated flowers (D. A. Moeller, *unpublished data*). In addition, progressive hand-pollination of all flowers on a plant does not curtail subsequent flower production despite elevating fruit and seed set (M. A. Geber, *unpublished data*). Taken together, these data suggest that estimates of pollen limitation are unlikely to be biased by dynamic resource allocation within plants. In each year, pre-dispersal seed herbivory strongly reduced sample sizes in some populations, but herbivore damage was unbiased with respect to pollination treatment (χ^2 = 0.88, df = 2, P = 0.64). I excluded populations from the analysis when one of the treatment groups consisted of <20 individuals. I calculated the magnitude of pollen limitation for each population using treatment means (rather than differences between paired plants) because high rates of herbivory rendered many pairs incomplete. An index of pollen limitation of reproduction was calculated as the difference between the mean seed set of the supplemental-pollen treatment (an

estimate of maximum seed output) and mean seed set of open-pollinated treatment, standardized by the former: pollen limitation index = (supplemental − open)/ supplemental. Using a standardized index eliminates potential variation in reproductive success due to differences in resource availability among sites; the index expresses the percentage reduction in seed set that may be explained only by pollinator or mate availability. This approach is critical for separating pollen limitation from resource limitation.

I examined the effects of coexisting species, population size, and mean population density on pollen limitation (and all two-way interactions) using a mixed-model ANOVA (the Mixed procedure, SAS Institute 1997) with year and geographic region (and their interaction) included as covariates. Multicollinearity among independent variables was low. Population identity was initially included in the model as a random effect, but was dropped because it explained little variance (χ^2 = 0.02, df = 1, P = 0.89). After examining the results of the full fixed-effects model, the community × density interaction was also dropped (P > 0.9). The significance of multiple comparisons of least square means was adjusted using the Tukey-Kramer procedure.

Local conspecific density and pollination

I examined the relationship between pollen deposition and the local density of conspecific flowers in 11 populations in 1999. In each population, I sampled 32 plants at 3-m intervals along transects bisecting the population. At each sampling location, I selected the nearest large plant (>0.5 m to control for plant size) with a flower that had been receptive for at least two days (to control for the time available for pollination to occur). The minimum duration of stigma receptivity could be easily discerned because stigma lobes open gradually and are not recurved until at least the second day after the stigma opens. The stigma was harvested from each flower and stored in a glassine envelope to dry. Local flower density was measured by counting all open *C. x. xantiana* flowers in a 1-m² circle centered on the target plant. Because *Clarkia* pollen could not be identified to species, I sampled from populations without congeners or I sampled after congeners had flowered to avoid the possibility of heterospecific pollen on stigmas. Stigmas were stained with aniline blue and ethidium bromide (0.1% aniline blue and 0.01% ethidium bromide in 0.03 mol/L K_3PO_4) for 16–24 h and squashed on slides with glycerine. I used a compound microscope with an epi-fluorescence attachment (Olympus Optical Company, Tokyo, Japan) to count the number of *C. x. xantiana* pollen grains on each stigma. The relationship between pollen deposition and local flower density was examined across all populations and within each population using linear regressions. Pollen deposition was square-root transformed

and density was $\log_e$-transformed to improve the homoscedasticity and normality of the residuals.

RESULTS

Patterns of spatial coexistence

Overall, 48% of *C. x. xantiana* populations coexisted with congeners (41 of 85), but the frequency of coexistence varied among regions (Fisher-Freeman-Halton exact test, $P = 0.013$). In the center of its range (regions 1 and 2), 65% (34 of 52) of *C. x. xantiana* populations coexisted with congeners; at the periphery of its range (regions 3–5), only 24% (8 of 33) of populations coexisted with congeners (Fisher-Freeman-Halton exact test, $P < 0.001$). In particular, *C. x. xantiana* rarely occurred with congeners at the arid eastern margin (region 3) and the high-elevation northern margin (region 5) of the range (Fig. 1). The identity of coexisting *Clarkia* species also varied among regions. *Clarkia cylindrica* and *Clarkia unguiculata* were the most common associates (25 and 24 populations, respectively); *Clarkia speciosa* coexisted with *C. x. xantiana* less frequently (13 populations). Both *C. unguiculata* and *C. speciosa* are widespread in the southern Sierra Nevada (regions 1–4 for both), but *C. speciosa* is less frequent across the landscape. By contrast, *C. cylindrica* is only found in the southwestern section of the range (Fig. 1, regions 1 and 2), but is highly abundant and frequently associated with both *C. x. xantiana* and *C. unguiculata*.

Organization of flowering phenology

Based on comparisons of populations occurring with and without congeners, there was no clear evidence of character displacement in the flowering distribution of *C. x. xantiana* due to interactions with congeners. Neither mean flowering time, nor the shape of the flowering distribution differed significantly between populations with or without other *Clarkia* species (mean, $F = 1.06$, $P = 0.37$; variance, $F = 0.32$, $P = 0.73$; skewness, $F = 0.61$, $P = 0.55$; kurtosis, $F = 0.08$, $P = 0.92$; df = 2, 15). Geographic region most strongly influenced mean flowering time ($F = 4.78$, $P = 0.02$, df = 2, 15) and the skewness of the flowering distribution ($F = 12.93$, $P < 0.001$, df = 2, 15); region had no significant effect on other attributes of flowering distributions (variance, $F = 1.30$, $P = 0.30$; kurtosis, $F = 0.86$, $P = 0.44$; df = 2, 15). Mean flowering time was approximately one week later in the upper foothills (region 2) compared to the other regions where seasonal drought occurs earlier (regions 1 and 4). Populations near the eastern range margin had skewed-right distributions, which increased aggregation with congeners in flowering time.

Analyses comparing observed overlap among coexisting *Clarkia* species with null distributions of species overlap indicated that communities ranged broadly in organization. While the null hypothesis of random pattern could not be rejected for any community, two sites exhibited strong segregation in flowering phenology based on total overlap (sites 2 and 11), two sites were random in pattern based on both overlap measures (sites 6 and 10), and one site was highly aggregated based on maximum overlap (site 16; Fig. 2). In the segregated and random communities, *C. x. xantiana* co-occurred with *C. cylindrica* and *C. unguiculata*, whereas in the aggregated community, it co-occurred with *C. unguiculata* and *C. speciosa* (the presence of the latter resulted in high overlap).

In two-species communities, I also observed considerable variation in percent overlap between *C. x. xantiana* and congeners (*C. cylindrica*, overlap range = 0.07–0.39; *C. unguiculata*, overlap range = 0.03–0.82; *C. speciosa*, overlap range = 0.44–0.92; Appendix B). Although overlap with *C. speciosa* was generally high, overlap with other congeners varied among regions. For example, overlap with *C. cylindrica* and *C. unguiculata* was relatively low in the center of the range and moderate to high in both the extreme western and eastern regions (Appendix B). In general, *Clarkia* species exhibited substantial overlap in flowering periods. However, flowering modes and distributions rarely coincided resulting in protracted flowering seasons, thereby extending the period over which floral resources were available to pollinators.

Community- and population-level effects on reproduction

In 106 censuses of 17 *C. xantiana* populations throughout their flowering periods, I observed 563 bees foraging on *C. x. xantiana*. The number of bees per plant was positively associated with the presence of coexisting *Clarkia* species (Fig. 3a, Table 1). Bee pollinator availability was nearly two times greater in populations with congeners vs. those occurring alone. Population attributes (population size, mean population density) and geographic region did not significantly influence population variation in pollinator availability in this study.

The analysis of pollen limitation of reproduction was based on 79 324 seeds from 2464 plants (one fruit/plant) in 39 populations. Pollen limitation varied among populations from a 40.3% reduction in seed set to no detectable reduction in seed production in open pollinated plants relative to plants with supplemental pollen. The ANOVA revealed that the plant community and population size most strongly influenced the magnitude of pollen limitation. Notably, coexisting *Clarkia* species had facilitative to neutral effects on reproduction in *C. x. xantiana*. Populations with two congeners showed very little pollen limitation, when accounting for other variables, whereas seed production of open-pollinated flowers was reduced by 17–18% at sites where *C. x. xantiana* grew alone or with a single congener (Fig. 3d).
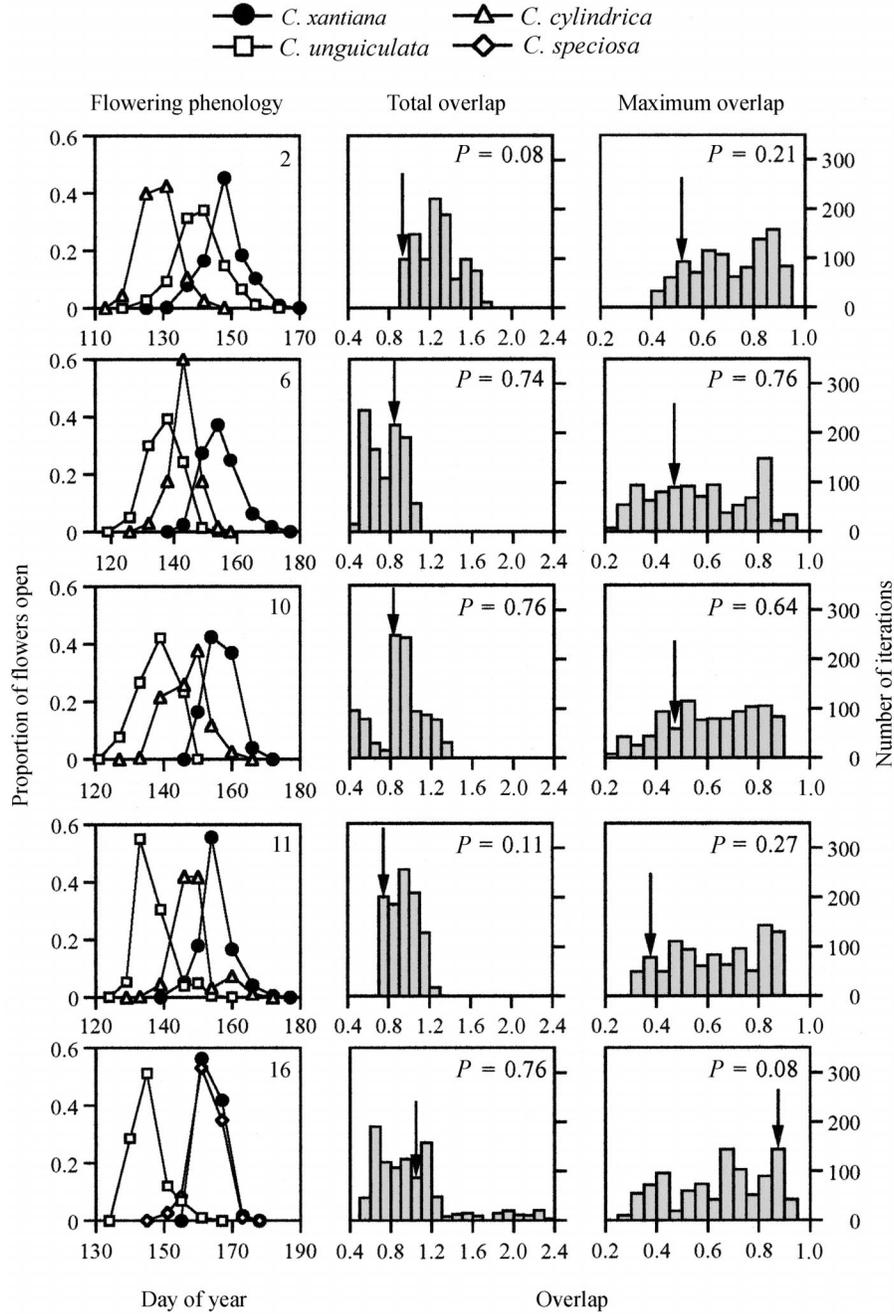
FIG. 2. Flowering phenology and null-model tests of flowering schedules for five *Clarkia* communities which include *C. x. xantiana*. The left column of graphs shows scaled flowering distributions for each of three species (*x*-axes are not equivalent). The middle and right column of graphs show the null distributions generated for random communities using total overlap and maximum overlap as measures of community organization. Arrows indicate the observed overlap for each community, and significance is indicated by two-tailed *P* values. The geographic position of each community is shown in Fig. 1.

Pollen limitation declined with increasing population size, but there was not a significant relationship between population size and pollinator availability (Fig. 3b, e; Tables 1 and 2). This suggests that Allee effects limit reproductive success in small populations because of low mate availability. In addition, there were non-

additive effects of mean population density and population size on the degree of pollen limitation. Small and medium populations exhibited positive density dependence, whereas there was little evidence of density dependence in large populations (Fig. 4, Table 2). I found no direct support for the hypothesis that facili-
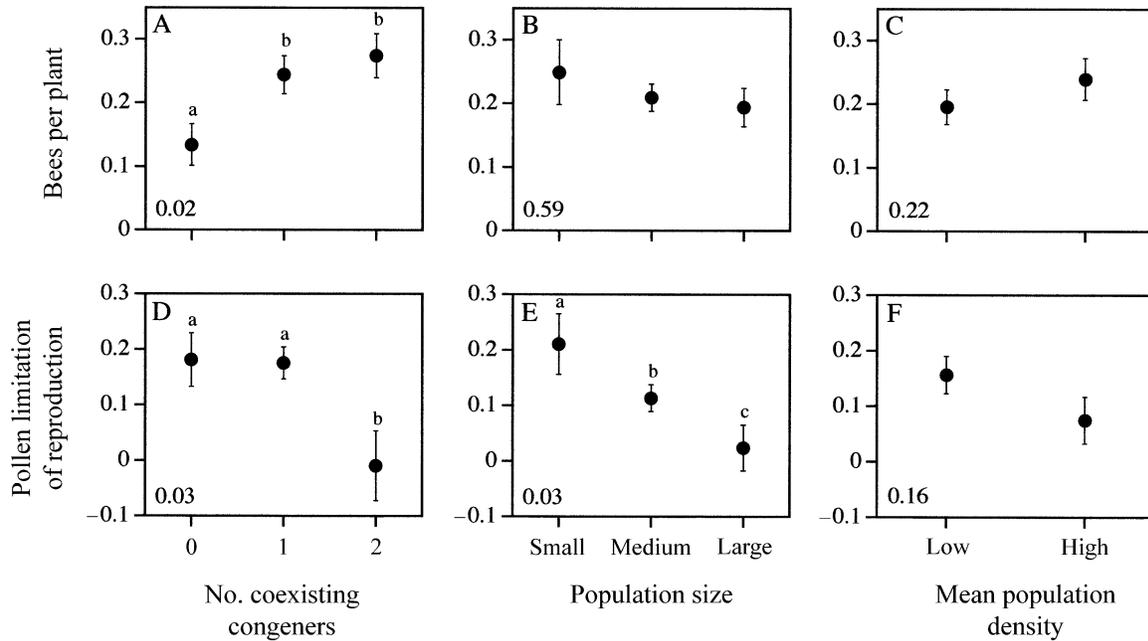
FIG. 3. Least-square means (±1 SE) for pollinator availability (no. bees per plant per site census) and pollen limitation of reproduction in relation to community diversity, population size, and mean population density. For significant overall effects (*P* values are shown in the lower left corner of each panel), different lowercase letters indicate significant differences between factor levels using the Tukey-Kramer test. Pollen limitation is expressed as the percentage reduction in seed set for open-pollinated flowers relative to hand-pollinated controls.

tation by congeners was most pronounced for small populations (community × population size interaction term was not significant); however, this test suffered from low power due to small sample sizes.

There was some evidence of regional variation in the magnitude of pollen limitation (Table 2), but the nature of regional effects varied markedly among years suggesting that year-to-year climatic variation across the species' range is likely to account for these results. Finally, I also performed analyses excluding populations from region 4, where congeners were somewhat less common, to determine if this region had a strong influence on the results. The results were qualitatively the same, suggesting that region 4 did not unduly influence the analysis.

Local density effects on pollen deposition

Pollen deposition was positively related to local conspecific flower density when data were pooled across all populations (Table 3). For individual populations, the relationship was significant or marginally significant in 6 of 11 populations. The relationship was positive but nonsignificant in the remaining five popula-

TABLE 1. Repeated-measures mixed-model ANOVA for effects on pollinator availability (bees observed per plant) in 1999.

Source	df	F or χ^2	P
Fixed			
Region	2, 8.0	1.9	0.211
Community	2, 8.0	7.32	**0.016**
Population size	2, 7.6	0.56	0.594
Population density	1, 8.6	1.75	0.219
Day	3, 21.9	1.19	0.336
Random			
Population identity	5	8.70	0.122

Notes: Denominator degrees of freedom for fixed effects were estimated using the Satterthwaite approximation. The significance of the random effect, population identity, was tested using a likelihood-ratio test. The significant effect is shown in boldface.
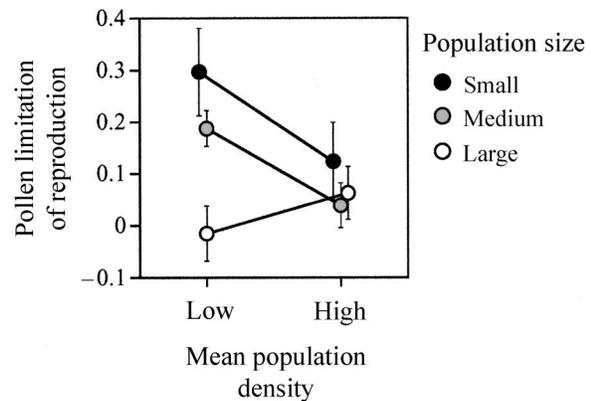

FIG. 4. Least-square means (±1 SE) for pollen limitation of reproduction showing the nonadditive effects of population size and mean population density (see Table 2).

TABLE 2. ANOVA for community- and population-level effects on pollen limitation of seed set.

Source	df†	F	P
Year	2	1.43	0.26
Region	2	4.73	**0.02**
Year × region	4	4.51	**0.01**
Community	2	4.19	**0.03**
Population size	2	4.14	**0.03**
Population density	1	2.14	0.16
Size × density	2	3.81	**0.04**
Community × size	4	0.96	0.45

Notes: The random effect, population identity, and the community × population density interaction were highly nonsignificant ($P \geq 0.9$ for both) and were dropped from the analysis. Significant effects are shown in boldface. See Fig. 3 for comparison of factor levels.

† Denominator df = 19.

tions, apparently because within-site variation in local density was low (regression of slope as a function of density range; $b = 0.063$, $R^2 = 0.64$, $P = 0.003$). Among populations, mean pollen deposition was more closely related to population size than mean population density (two-way ANOVA: population size, $F = 8.13$, $P = 0.02$; mean population density, $F = 1.23$, $P = 0.30$; $n = 10$, one outlier dropped).

DISCUSSION

Pollinator sharing and plant community structure

The prevalence of synchronized flowering and pollinator sharing in temperate plant communities has motivated ecologists to examine how reproductive interactions affect community structure. One idea is that fine-scale adjustments in flowering periods within the flowering season allow coexisting species to partition shared pollinators and reduce both interference and exploitation competition. Indeed, negative reproductive interactions can cause reductions in seed set for at least one plant species (e.g., Campbell 1985, Caruso 2000) and can result in character displacement in breeding system (Fishman and Wyatt 1999), pollen placement

mechanism (Armbruster et al. 1994), or pollen presentation schedules (Stone et al. 1998). However, many reports failed to find evidence of competitive effects on community structure (e.g., Schemske 1981, Motten 1986, Rathcke 1988) and explanations are often elusive. Results from this study provide support for the hypothesis that pollinator-sharing congeners enhance reproductive success in *C. x. xantiana* by jointly supporting populations of shared pollinators. Data on pollinator abundance in 1999 (reported here) mirror a more detailed companion study of bee pollinator communities conducted in 2001, which showed that bee visitation, particularly by specialists, was positively affected by the presence of congeners (Moeller, *in press*). These community-level effects on reproductive success were accompanied by positive density-dependent interactions among conspecifics. Although inter- and intraspecific interactions via pollinators are typically investigated independently, results on *C. x. xantiana* exhibit the complementary, but distinct positive influences of conspecifics and heterospecifics on individual reproductive success; interspecific effects appear to have occurred through pollinator availability, while intraspecific effects were mediated largely by mate availability.

The comparative approach taken in this study provided a means for simultaneously examining the importance of multiple factors that operate at large spatial scales and are challenging to manipulate. At the same time, exploiting natural population and community variation limits one's ability to establish the causes of population variation in plant–pollinator interactions (e.g., it is possible that plant community variation is correlated with other factors that influence pollinator abundance). Ideally, experimental plant species removal from (or addition to) natural communities would provide the best tests of hypotheses on the nature of reproductive interactions among plant species. In *Clarkia*, manipulating whole populations may not be

TABLE 3. Linear regressions of pollen deposition on local flower density for all populations combined as well as within individual populations (b is the regression coefficient; $n = 32$ for each population).

Population	b	R^2	P
All populations	1.34	0.13	**<0.001**
China Gardens	0.78	0.04	0.315
Mill Creek Trail	1.82	0.23	**0.005**
Old Kern Canyon Road (27.97)	1.32	0.23	**0.006**
Old Kern Canyon Road (28.62)	0.35	0.01	0.622
Old Kern Canyon Road (29.69)	1.76	0.20	**0.011**
Miracle Hot Springs	1.22	0.12	**0.058**
Hobo Campground	0.81	0.05	0.233
Borel Road	1.42	0.08	0.127
Black Gulch	1.85	0.31	**0.001**
Sandy Flat	1.78	0.30	**0.001**
Green Rock	2.42	0.36	**<0.001**

Notes: For all regressions, pollen deposition was square-root transformed, and flower density was $\log_e$-transformed (no. flowers/m^2 + 1) to improve the normality and homoscedasticity of the residuals. Significant and marginally significant relationships are shown in boldface.

TABLE 4. An outline of the proposed mechanisms of facilitation via shared pollinators and their relation to the organization of flowering in plant communities.

Mechanisms of facilitation	Flowering phenology	Mechanisms to avoid competition	Hypothesized conditions promoting facilitative interactions
Joint attraction of pollinators (aggregative response)	aggregated	pollinator foraging constancy spatial aggregation of conspecifics interspecific divergence in pollen-placement mechanisms	patch selection by highly mobile pollinators floral mimicry rewardless plant species co-occurring with rewarding, ''magnet'' species
Joint maintenance of pollinators (numerical response per se)	aggregated segregated	same as above N/A	pollinators resident within plant communities seasonal extent of pollinator activity spans flowering of multiple plant species temporal variation in the abundance or performance of individual plant species specialized pollination system

Notes: For aggregated flowering schedules, I describe mechanisms that may reduce counteracting negative effects of interspecific pollen transfer. For both mechanisms of facilitation, I indicate possible conditions promoting net positive plant–plant interactions via shared pollinators.

feasible given the very large population sizes characteristic of most species. Moreover, because facilitation is most likely to occur via population responses of bees to community diversity, the effects of plant species removal (addition) on resident solitary bee populations will require long time periods to observe. The abundance of *Clarkia* bees in a given year tends to reflect historical plant abundance and solitary bees may remain dormant through unfavorable years (Linsley 1958); both of these factors will act to prolong the period of time over which bee populations exhibit responses to experimental manipulations.

Mechanisms of facilitation

Facilitative interactions between plant species via pollinators are likely to occur through two mechanisms, which parallel numerical population responses of predators to prey (Murdoch 1977). First, plants may exhibit positive interactions when coexisting plant species collectively attract shared pollinators (aggregative response to overall plant abundance). This mechanism may occur through the differential attraction of highly mobile pollinators that forage over large areas (e.g., hummingbirds, many social bees) and is only possible if plant species flower synchronously (Table 4). Although aggregative responses can occur due to spatial variation in the abundance of a single species, niche differentiation among pollinator-sharing plant species along resource axes (e.g., when plant species occupy different microsites within a habitat) may promote a greater local abundance of flowers. There is evidence that plant species without pollinator rewards benefit from close proximity to rewarding species (Laverty 1992, Johnson et al. 2003); however, I am not aware of evidence that collective pollinator attraction positively influences the reproductive success of a plant species.

Facilitation may also occur when coexisting species jointly maintain populations of resident pollinators (nu-merical response per se: Holling 1959). For example, when flowering periods are segregated, facilitation may occur because floral resources are available to individual pollinators or cohorts of pollinators over an extended period of time, thereby enhancing pollinator population growth or size (Waser and Real 1979). When the abundance of individual plant species fluctuates temporally, the presence of alternative host plant species may buffer pollinator population dynamics by providing a more consistent supply of floral resources through time. Although this mechanism may occur regardless of the organization of flowering periods in the community, it is clear that flowering schedules can affect potential counteracting negative effects such as interspecific pollen transfer. Because plant species-specific responses to the environment (e.g., flowering time, temporal variation in relative performance) increase the duration of floral resource availability within years or the reliability of floral resources across years, species identity is likely to be important in this mechanism of facilitation.

In *Clarkia*, the prevalence of some staggering of flowering periods (Fig. 2, Appendix B) and the biology of its specialist pollinators suggests that the joint maintenance of pollinators is a more likely mechanism of facilitation than the joint attraction of highly mobile pollinators. The most important specialist pollinators of *C. x. xantiana* are known to collect pollen from and remain active across the flowering period of multiple *Clarkia* species (Stage 1966, MacSwain et al. 1973) and nest in or adjacent to *Clarkia* communities (Burdick and Torchio 1959, Stage 1966). These characteristics of the system suggest that plant and pollinator population dynamics may be linked. If areas with greater *Clarkia* species diversity provide more resources over the course of a season and more predictable resources for bees across years, these communities should sustain greater numbers of pollinators per plant. Recent work has shown that solitary bees tend to forage

short distances from nesting sites (unlike many social bees) and that foraging trip duration may be reduced when plant species richness is high (Gathmann and Tscharntke 2002). Therefore, the population dynamics and spatial distribution of solitary bee populations is likely to be influenced by the abundance and diversity of local plant hosts, which is consistent with data presented in this study.

Allee effects

Pollen limitation in *C. x. xantiana* was more pronounced in small populations than large (Fig. 3e), but this difference was unrelated to bee abundance (Fig. 3b), suggesting that low mate availability is likely responsible for pollen limitation. Evidence of Allee effects in plant populations has been found mainly when population size drops below 100 individuals (Sih and Baltus 1987, Lamont et al. 1993, Groom 1998, Hendrix and Kyhl 2000, Hackney and McGraw 2001). Population size effects have been attributed to both pollen quantity (Widén 1993, Groom 1998) and pollen quality (loss of S-alleles, Lamont et al. 1993, Byers 1995; inbreeding depression, Heschel and Paige 1995). In *C. x. xantiana*, reduced reproductive success in small populations is most likely explained by insufficient levels of pollen transfer. Because the smallest population of *C. x. xantiana* in the study contained 550 individuals, inbreeding depression is unlikely to explain reduced seed set. Resource limitation in small populations also cannot account for the results because the pollen limitation index eliminated site quality as a source of variation. It is surprising that Allee effects were detected in *C. x. xantiana* despite reasonably large population sizes. It is possible that census population sizes are poor predictors of mate availability because of individual variation in flowering time, skewed sex ratios (due to protandry), or because small plants producing few flowers are discriminated against by pollinators.

The finding that population size effects were only evident in populations of low density is of particular interest because it suggests that both the size of the pool of potential mates and their spatial distribution contribute to the likelihood that mates encounter one another (Fig. 4). Patterns of pollen deposition within and among populations further illustrate this phenomenon. Pollen deposition to individual flowers increased with the density of conspecific neighbors (Table 3), but mean pollen deposition for plant populations was more closely related to population size than mean plant density. Although evidence of density dependence in pollination is hardly unusual (e.g., Kunin 1997), these results suggest that the importance of processes occurring over small spatial scales may be modified by the distribution and abundance of individuals at broader spatial scales, especially when plants interact via animals or pathogens.

Consequences of positive interactions

If small populations suffer from low reproductive success and coexisting congeners facilitate reproduction in *C. x. xantiana*, then small populations could be expected to enjoy a greater advantage from sharing pollinators with congeners than large populations. Although I did not find direct evidence of an interaction between community diversity and population size effects on pollen limitation, the population survey revealed strong associations between these factors. Seventy-six percent of small populations coexisted with one or more congener, while 82% of populations isolated from congeners were large ($\chi^2 = 10.2$, df = 4, $P = 0.037$), suggesting that small populations are more likely to persist in diverse communities and, likewise, that isolated populations are more likely to persist when large. Combined with data on pollen limitation, these patterns suggest important consequences of positive reproductive interactions for the long-term population dynamics and spatial distribution of *C. x. xantiana*.

The results of the present study, along with ongoing research on breeding system variation in *C. xantiana*, also suggest potential evolutionary consequences of facilitative interactions. In the western portion of the species' range, *C. x. xantiana* is frequent across the landscape, tends to occur in large, dense populations, and is regularly associated with congeners. In the eastern section of the range, *C. x. xantiana* is replaced by highly selfing populations of *C. xantiana* ssp. *parviflora* (Eckhart and Geber 1999), which tend to be small, infrequent across the landscape, and do not coexist with congeners. Interestingly, pollinator visitation declines from west to east across the species' range and specialist bee pollinators occur up to but not beyond the eastern limits of the range of outcrossing populations (Fausto et al. 2001, Moeller 2003). Transplant experiments have confirmed that plants from outcrossing populations exhibit low reproductive success when moved into the range of selfing populations, and therefore that selfing provides reproductive assurance (M. A. Geber and V. M. Eckhart, *unpublished data*). Taken together, these results suggest possible links between *Clarkia* species diversity, the joint maintenance of specialist pollinator populations, and the maintenance of outcrossing in *C. x. xantiana*.

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APPENDIX A

Additional details on community assembly rules and measures of species overlap for null-model tests of community flowering phenology are available in ESA's Electronic Data Archive: *Ecological Archives* E085-114-A1.

APPENDIX B

A table showing pairwise overlap in flowering time between 15 populations of *C. x. xantiana* and coexisting congeners that share pollinators is available in ESA's Electronic Data Archive: *Ecological Archives* E085-114-A2.