PLANT ANIMAL INTERACTIONS

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Pollinator community structure and sources of spatial variation in plant–pollinator interactions in *Clarkia xantiana* ssp. *xantiana*

Abstract The structure of diverse floral visitor assemblages and the nature of spatial variation in plant–pollinator interactions have important consequences for floral evolution and reproductive interactions among pollinator-sharing plant species. In this study, I use surveys of floral visitor communities across the geographic range of *Clarkia xantiana* ssp. *xantiana* (hereafter *C. x. xantiana*) (Onagraceae) to examine the structure of visitor communities, the specificity of the pollination system, and the role of variation in the abiotic vs. biotic environment in contributing to spatial variation in pollinator abundance and community composition. Although the assemblage of bee visitors to *C. x. xantiana* is very diverse (49 species), few were regular visitors and likely to act as pollinators. Seventy-four percent of visitor species accounted for only 11% of total visitor abundance and 69% were collected in three or fewer plant populations (of ten). Of the few reliable visitors, *Clarkia* pollen specialist bees were the most frequent visitors, carried more *Clarkia* pollen compared to generalist foragers, and were less likely to harbor foreign pollen. Overall, the core group of pollinators was obscured by high numbers of incidental visitors that are unlikely to contribute to pollination. In a geographic context, the composition of specialist pollinator assemblages varied considerably along the abiotic gradient spanning the subspecies' range. However, the overall abundance of specialist pollinators in plant populations was not influenced by the broad-scale abiotic gradient but strongly affected by local plant community associations. *C. x. xantiana* populations sympatric with pollinator-sharing congeners were visited twice as often by specialists compared to populations occurring alone. These positive indirect interactions among plant species may promote population persistence and species coexistence by enhancing individual reproductive success.

Keywords Pollination · Facilitation · Positive interactions · Geographic variation · Specialization

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Introduction

The diversity and structure of pollinator communities can have important influences on floral evolution and reproductive interactions among plant species. The great diversity in floral morphology and its utility in plant systematics have supported the idea that specialized pollinator relationships were important in the radiation of angiosperms by allowing for rapid reproductive isolation (Grant 1949; Stebbins 1970). Historical studies have similarly indicated that flowering plant diversification coincided with the appearance of faithful animal pollinators (Crepet 1984; Eriksson and Bremer 1992). However, contemporary investigations of pollination systems suggest that plant–pollinator associations are diffuse because plants are visited by a broad spectrum of animals and likewise, pollinators often use a wide array of plant taxa (Herrera 1996; Waser et al. 1996). Following these ideas, an increasing number of community-level studies has concluded that generalization is the rule and specialization rare (e.g., Olesen and Jordano 2002) while new discoveries of highly specialized pollination systems have been reported from poorly studied regions (e.g., Steiner and Whitehead 1996; Manning and Goldblatt 1997; Momose et al. 1998; Moog et al. 2002; Kato et al. 2003). The variety of findings suggests that pollination systems range across a continuum of generalization

(specialization). However, for plants with diverse visitor assemblages, it is often unclear whether most visitor species play an important role in pollination and therefore influence selection on floral traits or community processes.

Pollination systems are often considered generalized when many pollinators effect reproduction in individual plant populations or when plant populations vary extensively in their associations with pollinators, without related floral evolution. The challenge in systems where visitor assemblages are diverse is to distinguish important pollinators from rare or ineffective visitors. There is increasing interest in measuring levels of generalization in plant–pollinator networks using either data on the species richness of visitor communities or calculations of the fraction of possible interactions between plant and potential pollinator species within a network that are established (i.e., connectance). Most surveys have revealed extensive generalization or connectance (Waser et al. 1996; Olesen and Jordano 2002) but have been unable to distinguish pollinators from visitors. However, substantial variation in pollination effectiveness among animal visitors has been shown in many systems (Primack and Silander 1975; Herrera 1987; Fishbein and Venable 1996; Olsen 1997; Gómez and Zamora 1999; Tepedino et al. 1999; Mayfield et al. 2001) suggesting that the total number of visitors may not always be a good indicator of important mutualistic interactions.

Pollination systems can be examined in the same general framework used to understand community structure and assembly. For example, the distribution of abundance of flower visitors within plant populations and their spatial predictability among populations can reveal which animals regularly use floral resources (component community, Root 1973) versus those that are incidental and less likely to make consecutive visits among conspecific plants and effect pollination. Studies of species diversity in natural communities have suggested that uncommon, immigrant taxa that are unlikely to maintain population growth often account for a large percentage of species in communities (Shmida and Ellner 1984; Bell 2000). Likewise, in pollination systems, incidental visitors may obscure identification of the core pollinator community when they account for a large portion of visitor taxa. At present, data on the structure of whole visitor assemblages and the role of individual visitor species in pollination remain limited for diverse systems, but should reveal which visitors make important contributions to plant reproductive output and most strongly influence selection on floral traits.

In a geographic context, the spatial structure of variation in pollinator abundance and community composition can also have important implications for floral evolution. There is now abundant evidence of spatially variable plant–pollinator interactions (e.g., Herrera 1988; Horvitz and Schemske 1990; Eckhart 1992; Cane and Payne 1993; Fenster and Dudash 2001), but the spatial scale of variation and the ecological factors that underlie variation in pollinator communities remain less clear. For example, is pollinator community variation shaped by environmen-tal gradients over which plant populations occur, habitat suitability for pollinators, or local variation in plant community interactions? The first two reasons may suggest that the composition of the pollinator community is determined, in part, by edaphic or climatic factors while the third reason may indicate that landscape features or indirect interactions in plant communities have important influences on patterns of pollinator visitation. Distinguishing sources of variation in plant–pollinator interactions and the spatial scale over which important factors vary can provide insight into the evolutionary consequences of variable interactions between plants and pollinators.

This study focuses on *Clarkia xantiana* ssp. *xantiana* A. Gray (hereafter *C. x. xantiana*), an annual plant endemic to southern California. The subspecies is abundant across a narrow geographic range, spans a strong gradient in abiotic factors, and exhibits local variation in associations with pollinator-sharing congeners across its range, making it an ideal system for disentangling sources of variation in plant–pollinator interactions. In this study, I characterized the bee visitor communities of ten populations of *C. x. xantiana* spanning most of its geographic range (only bees were observed visiting *C. x. xantiana* in this study). Information on the distribution of abundance of all visitors within communities, the spatial predictability of visitors among communities, and the composition of pollen loads were used to assess the structure of pollinator communities and the specificity of the pollination system. Second, I examined spatial variation in plant–pollinator interactions and the ecological correlates of variation in pollinator communities. Analyses of spatial variation were used to distinguish the relative contribution of broad-scale environmental variation vs. local interactions between *C. x. xantiana* and pollinator-sharing congeners in influencing the abundance and diversity of pollinators.

Materials and methods

Study species

C. x. xantiana (Onagraceae) is self-compatible but highly outcrossing (Moore and Lewis 1965; Eckhart and Geber 1999). Flowers consist of a four-petaled rotate corolla (wheel-shaped), two whorls of four stamens which produce large pollen grains connected by viscin threads, and a pistil with the stigma typically exserted well beyond the anthers. The subspecies occurs primarily on steep, sandy slopes in the southern-most portion of the Sierra Nevada (Lewis and Lewis 1955; Eckhart and Geber 1999). Western populations occur primarily in open California grassland or blue oak woodland (*Quercus douglassii*) and at low to mid-elevations while eastern populations occur in more arid, gray pine woodland (*Pinus sabiniana*) at higher elevations where rainfall is less abundant and predictable. Populations are generally discrete, occur patchily throughout the subspecies' range, and frequently coexist with as many as three other outcrossing *Clarkia* taxa: *C. cylindrica* ssp. *clavicarpa*, *C. speciosa* ssp. *polyantha*,

and *C. unguiculata*. *Clarkia* species flower at the end of the spring when most other species have completed flowering, which makes this a tractable system for examining reproductive interactions. *Clarkia x. xantiana* and all associated congeners are visited both by generalist (polylectic) bees and ten pollen specialists (oligolectic bees) representing four bee families (Andrenidae, Apidae, Megachilidae, and Melittidae) (MacSwain et al. 1973). Specialists collect pollen in scopae formed by sparse, weakly branched hairs, which are considered structural adaptations to the large, clumped pollen grains of *Clarkia* (MacSwain et al. 1973). *Clarkia* pollen specialists are solitary and construct nests and forage within or near single *Clarkia* populations or communities of *Clarkia* species (Burdick and Torchio 1959; Stage 1966).

Survey methods

I characterized the bee visitor communities of ten populations along a 28-km geographic transect spanning the west to east distribution of *C. x. xantiana* in the southern Sierra Nevada (see S1, Electronic Supplementary Material, for details of site locations). Five populations were sympatric with pollinator-sharing *Clarkia* species while the other five populations occurred alone. Both mixed and single-species communities were sampled across the geographic transect such that community types were not spatially autocorrelated and differences between community types could not be attributed to longitudinal position (see S1, Electronic Supplementary Material). Populations were a minimum of 2.7 km apart (mean distance to nearest population=4.6 km). I exploited variation in flowering time among populations in order to sample thoroughly across the subspecies' range (populations flower at different times depending upon elevation and the timing of seasonal drought) .

I surveyed bee visitors in *C. x. xantiana* populations using standardized collections on 20 days from 16 May to 7 July 2001. Each site was sampled intensively for 2 full days during the peak of flowering and sampling days were separated by 4–5 days (most plants in a single population flower within a 2-week period). I employed a stratified random sampling protocol to account for possible within-site spatial variation in the distribution of bees due to differences among taxa in their preferred nesting or foraging sites. I divided each population into four belts of equal area and placed a 35-m transect through each belt. In addition, I recorded the number of *C. x. xantiana* plants and open flowers in each transect for estimates of density and population size. During eight separate collecting periods (35 min each) in a given day, I repeatedly walked transects and collected all bees via aerial netting that I observed visiting *C. x. xantiana* within 1 m of each side of the transect. Collections were made from 0800 to 1400 hours, the period in which nearly all flower visitation occurs. Each of the four transects was sampled in the morning (0800–1100 hours) and again in the latter part of the day (1100–1400 hours). I only collected bees that were

observed to contact the reproductive organs of *C. x. xantiana*. In populations that coexist with other *Clarkia* species, I collected only from *C. x. xantiana*. Bees were identified to species and categorized as *Clarkia* pollen specialists according to MacSwain et al.'s (1973) monograph on *Clarkia* bees. *Lasioglossum* (*Evylaeus*) *pullilabre*, a putative specialist, is included with specialists because it is constant in its foraging on *Clarkia* and infrequently harbors other species' pollen. I used these data to investigate pollinator community structure for individual plant populations and the spatial predictability of bee species among plant populations (the likelihood of encountering bee species across the landscape) for all bees and for comparisons between specialists and generalists.

Measures of pollination effectiveness and pollinator importance

I investigated the potential pollination effectiveness of bees by quantifying pollen loads. Direct measures were not feasible because of the great diversity of visitors to *C. x. xantiana*, the pronounced spatial variation in bee community composition, and the rarity of encounters with most species. While I recognize the limitations of indirect measures, they provide an initial assessment of variation in the potential for bee species to act as pollinators, especially for plant species with simple flowers where there is not a clear morphological fit between the corolla and the pollinator body (as in *C. x. xantiana*). I examined the potential effectiveness of the ten most abundant bee taxa (four specialists, six generalists) along with three less common specialists (which together comprise >90% of the collection). For each species, I randomly selected 40 individuals to examine pollen loads (or examined all specimens when <40). For each individual, I scored the amount of *Clarkia* pollen and foreign (non-*Clarkia*) pollen on the body and the scopae. Scopal pollen is relevant to pollen transfer in *Clarkia* because pollen clumps in masses on the exterior of the scopal hairs where it is easily transferred to the stigma (personal observation); scopal pollen has been shown to be important for pollination of other plant species (*Oenothera elata*; Barthell and Knops 1997). Because all scopal pollen was incorporated in pollen load scores, my measure may overestimate the quantity of pollen available for pollination.

Pollen load scoring was conducted by first determining whether a bee was carrying a pollen load in its scopa(e) for nest provisioning. For bees without scopal pollen, I estimated whether there were: (1) <20 pollen grains, (2) 20–80 pollen grains, or (3) >80 pollen grains on the body. The number of pollen grains in the scopae was counted directly when pollen grains were few or scored categorically as: (1) half full, or (2) full of pollen grains. Estimates of maximum pollen load were made for each bee species to calibrate for species differences in maximum pollen load. I removed pollen from the scopae of two bees of each species with full scopae and suspended pollen in

500 µl of 3-(4,5-dimethylthiazol-2-yl)- 2,5-diphenyltetrazolium bromide) (Norton 1966). For each individual, two separate 100-µl aliquots were dispensed onto gridded slides and counted using a dissecting microscope. Estimates of maximum scopal load for each bee species were used to replace categorical scores for pollen load size and the sum of body and scopal pollen was taken.

To compare the role of specialists vs. generalists in pollination, I tested for differences in the quantity of *Clarkia* pollen carried. I also tested for differences between specialists and generalists in the probability of harboring foreign pollen. For both analyses, the assumption of equal variance between samples for parametric statistics was violated so I used randomization tests. The level of significance of the difference between means of two independent samples was determined by comparing the observed difference to a null distribution of differences generated by reshuffling data and species associations 1,000 times. To assess the potential contribution of individual bee species to the pollination of *C. x. xantiana*, I calculated pollinator importance as the product of bee abundance and mean pollen load and then relativized values by the highest importance score.

Spatial variation in bee visitor abundance, species richness, and community composition

I examined the relative strength of associations between broad-scale abiotic variation (described by longitude) versus local variation in plant community background (presence/absence of pollinator-sharing congeners) and bee community variation (bee abundance and species richness) using analyses of covariance (ANCOVAs). I conducted analyses separately for all visitors and for *Clarkia* specialists alone. In order to compare bee species richness among sites, I used sample-based rarefaction curves and compared bee species richness at common levels of abundance. Rarefaction was necessary because taxon accumulation curves failed to reach asymptotes (reviewed in Gotelli and Colwell 2001). For each *C. x. xantiana* population, I generated rarefaction curves for all bees and for specialists alone using 300 randomizations in EstimateS (Colwell 1997). In order to compare species richness at the same level of sampling intensity for each site, I re-scaled the curves by plotting accumulated species richness against the accumulated number of individuals.

Based on scores for pollinator importance, I examined spatial variation in the occurrence of the bee species with the highest scores (four *Clarkia* specialists). For each plant population, I calculated the proportion of all specialists represented by: *Hesperapis regularis*, *Lasioglossum pullilabre*, and *Megachile gravita*+*M. pascoensis* (*M. gravita* and *M. pascoensis* were combined in all analyses because females of the two species could not be distinguished). By examining species representation, I factored out the contribution of overall abundance because my objective was to examine variation in community composition. I examined the relative importance of abiotic variation

(longitude) versus local biotic variation (presence/absence of congeners) in influencing individual bee species relative abundance using an ANCOVA. For all analyses of spatial variation, the interaction between longitude and plant community was non-significant ($P \geq 0.3$ for all analyses) and dropped from the models.

Results

The structure of pollinator communities

I observed a total of 1,380 individuals from 49 bee species. Of these, 61% (835) were *Clarkia* specialists. The vast majority of visitors were rare: 74% (36) of the species were represented by fewer than 15 individuals and accounted for only 11% (145) of total visitor abundance. Conversely, only 12% (6) of the species comprised >75% (1,041) of the total abundance (Fig. 1; S2). The mean (median) number of individuals representing each bee species was 28.8 (4). The overall distribution of abundance can be interpreted as a truncated log-normal or log-series distribution where the great majority of species fall into low abundance classes. In addition, species of high abundance (>15 individuals) were more often specialists while those of low abundance (<15 individuals) were more frequently generalists or specialists of other plant taxa (Fisher's exact test: $P=0.011$).

When individual plant populations were considered separately, patterns of abundance were qualitatively similar to the overall distribution and were similar among populations (Fig. 1). In all populations, the most frequent abundance class consisted of species represented by one individual. The most abundant species in nine of ten populations was a pollen specialist and in most cases, multiple specialist species dominated the high abundance classes. These similar patterns indicate that the composite distribution adequately represents the organization of bee visitor communities in individual populations rather than being driven by unusual samples. More importantly, pollinator communities exhibit a similar structure across plant populations where most visitor species are encountered at very low frequency.

The majority of visitor species (34; 69%) were collected in three or fewer populations (Fig. 2a). Only seven species (14%) were collected in eight or more sites. The mean (median) number of sites occupied by bee species was 3.2 (2) of ten. The spatial predictability of *Clarkia* specialists mirrors data on abundance; four specialists were among the most highly predictable and abundant species collected across all populations (Fig. 2a; S2). I used a linear regression to examine the relationship between bee species range size (the maximum distance between occupied sites) and the number of occupied sites to ask whether bee species found in a subset of sites were: (1) restricted in distribution to a portion of *C. x. xantiana*'s range (a linear relationship), or (2) widespread across this region but rarely encountered (a positive saturating relationship). A lack of fit test showed that the relationship deviated
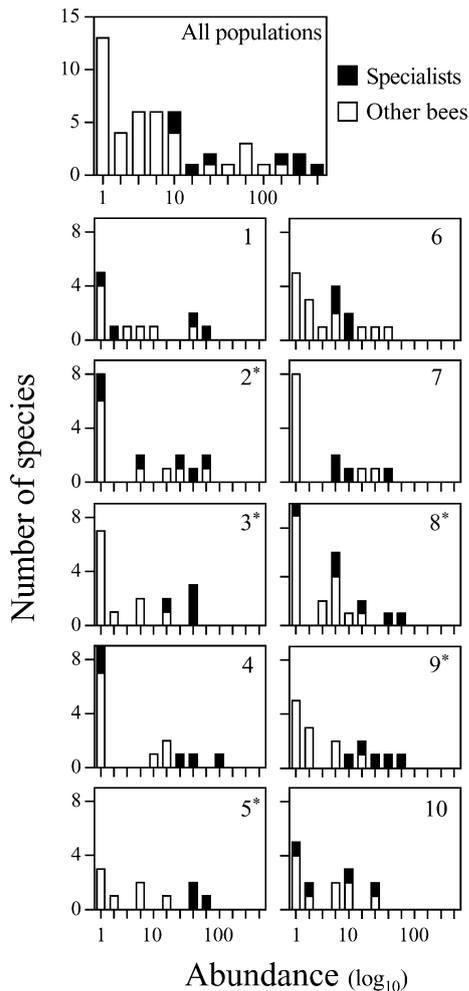
Fig. 1 The distribution of abundance for flower visitors to *Clarkia xantiana* ssp. *xantiana* (hereafter *C. x. xantiana*) (note that abundance is $\log_{10}$ transformed). A composite distribution is presented for data pooled across all populations and separate distributions are shown for each population (see S1, Electronic Supplementary Material). Populations are ordered from west to east across the geographic range and populations occurring with congeners are indicated by *asterisks*

significantly from linearity ($F_{1,8}=25.9$, $P<0.001$) suggesting that bee species collected in few sites were often widespread across *C. x. xantiana*'s range but uncommon (Fig. 2b).

Quantity and composition of pollen loads

The analysis of pollen loads showed that *Clarkia* specialists carried over 4 times more pollen than generalists (mean±SE; specialists, 335±73 pollen grains/bee; generalists, 81±29; $P=0.01$; Fig. 3b; S2). The variance in pollen load was low within and among generalist species because very few individuals actively collected pollen from *C. x. xantiana* and either very little was obtained through casual contact or pollen was frequently groomed from the body. Variance was higher in specialists because most female specialists were collected while foraging for
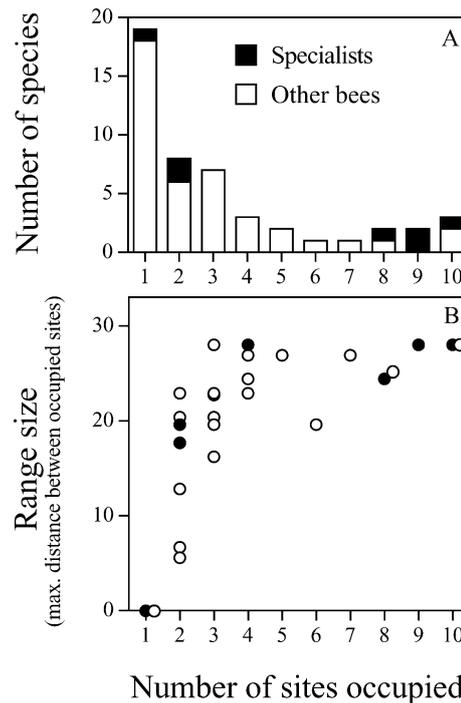

Fig. 2 **a** The spatial predictability of flower visitors to *C. x. xantiana*, shown as a frequency distribution of the number of sites occupied. **b** The geographic range of bee species (only in the southern Sierra Nevada) in relation to the frequency with which they were encountered among plant populations

pollen while male specialists were collected while foraging for nectar or using flowers as mating sites and therefore were less likely to harbor pollen. When overall abundance and the likelihood of carrying pollen were jointly taken into account, four pollen specialists had the highest potential to be important pollinators: *H. regularis*, *L. pullilabre*, and *M. gravita*+*M. pascoensis* (Fig. 3c).

The probability of carrying foreign pollen was 5 times higher for generalists (mean±SE; specialists, 0.04±0.02; generalists, 0.2±0.05; $P=0.006$; see S2). Notably, *Bombus vosnesenskii* and *Hoplitis albifrons*, both moderately abundant visitors, harbored foreign pollen 39% and 33% of the time, respectively. Only three of the 193 specialists examined (1.6%) carried foreign pollen.

Spatial structure and ecological correlates of variation in pollinator assemblages

Bee visitor abundance was influenced by both broad-scale abiotic variation across the subspecies' range as well as local variation in plant community associations among *C. x. xantiana* populations. At the geographic scale, the abundance of bee visitors to *C. x. xantiana* declined from west to east across the region. At the population scale, visitor abundance was significantly greater for populations coexisting with congeners after factoring out variation in the abiotic environment (Fig. 4, Table 1). *C. x. xantiana* populations with contrasting community backgrounds did not differ in population size, plant density, or flower

Fig. 3 **a** Overall bee abundance (number of bees), **b** mean pollen load+1 SE (number of pollen grains per bee), and **c** the product of abundance and pollen load (relativized by the highest score) for each of 13 bee taxa. The latter two are indirect measures of pollination effectiveness and pollinator importance, respectively
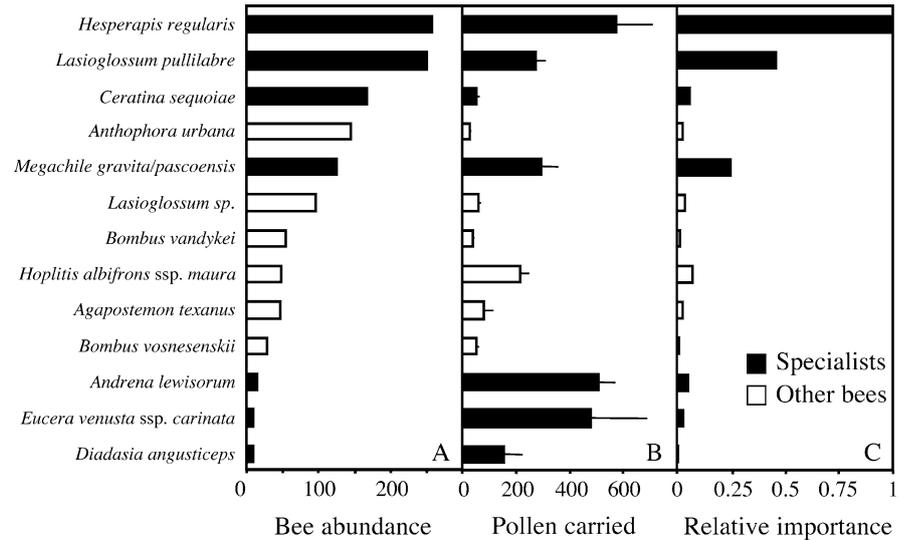
density (population size, t=1.2, P=0.25; plant density, t=0.4, P=0.72; flower density, t=0.47, P=0.65) and population attributes explained little or no variation in bee abundance (population size, R^2=0.09, P=0.41; plant density, R^2=0.00, P=0.97; flower density, R^2=0.00, P=0.90). Therefore, population attributes do not confound community effects on bee visitation to *C. x. xantiana*. The difference in bee communities between plant community types was primarily due to a higher abundance of specialists in populations with congeners rather than to a greater diversity of specialists (Fig. 4, Table 1). Specialist community composition was very similar for populations with contrasting plant community backgrounds (Table 2).

Species richness did not vary geographically or with local biotic conditions when considering all bee species or specialist species alone (Table 1). Species accumulation curves for whole bee communities failed to approach asymptotes (Fig. 5a) while the majority of accumulation curves for specialists saturated (Fig. 5b) suggesting that while specialist species richness was fully characterized, further sampling would result in greater total species richness. These additional species are unlikely to be
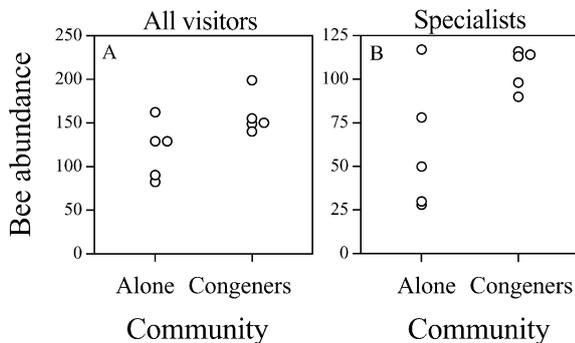
Table 1 Analysis of covariance for the effect of the local plant community (presence or absence of co-flowering congeners) versus geographic position on bee availability and bee species richness in *Clarkia xantiana* ssp. *xantiana* populations. Analyses were performed for both the abundance and species richness of all bees vs. specialists only. Measures of species richness were rarefied (see Materials and methods). For community-level effects, factor levels are shown in Figs. 4, 5. Numerator df=1, denominator df=7

Source	Abundance				Species richness			
	All visitors		Specialists		All visitors		Specialists	
	F	P	F	P	F	P	F	P
Community	6.70	0.04	6.79	0.04	0.41	0.54	2.02	0.20
Longitude	5.88	0.05	1.98	0.20	0.35	0.57	0.49	0.51

important for pollination, however, because of their rarity and unpredictability.

The composition of communities of specialist pollinators was variable among populations of *C. x. xantiana* and geographically structured. Longitudinal position had a much stronger effect on specialist community composition compared to local plant community variation. Specifically, *H. regularis* and *L. pullilabre* declined while *M. gravita* +*M. pascoensis* increased in relative abundance from west to east across the subspecies' range (Fig. 6).

Discussion

The structure of pollinator communities

Surveys of plant–pollinator associations have investigated the degree to which pollination systems are generalized vs. specialized by cataloging the number of visitor species to a suite of plant species (Waser et al. 1996) or by documenting the number of animal orders represented by visitors to each plant species in a community (Herrera 1996). In other applications, visitor lists have been used to examine the connectance of plant and pollinator communities (Jordano 1987; Olesen and Jordano 2002). These

Fig. 4 A comparison of bee abundance between *C. x. xantiana* populations occurring alone versus coexisting with congeners for **a** all bees and **b** *Clarkia* pollen specialists. Each *data point* represents a *C. x. xantiana* population. Results of statistical tests including longitude as a covariate are shown in Table 1

Table 2 ANCOVA for the effect of the local plant community (presence or absence of pollinator sharing congeners) versus geographic position on the relative abundance of the primary specialist pollinators. Numerator $df=1$, denominator $df=7$, the nature of the relationships are displayed in Fig. 6

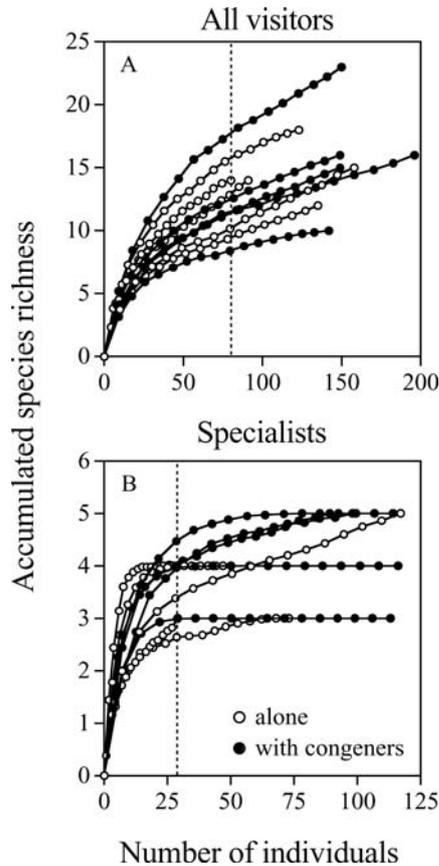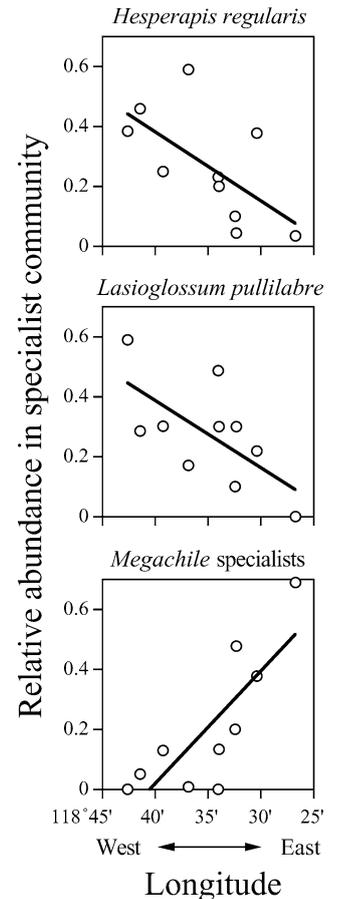| Source	Hesperapis regularis		Lasioglossum pullilabre		Megachile pascoensis+M. gravita	
	F	P	F	P	F	P
Community	0.01	0.91	0.53	0.49	0.14	0.72
Longitude	4.52	0.07	5.20	0.05	12.90	0.01

Fig. 5 Sample-based rarefaction curves generated separately for each population for **a** all bees or **b** *Clarkia* pollen specialists. Accumulated species richness is plotted against the number of individuals to allow for comparisons of species richness. The *vertical dotted lines* show the greatest abundance value common to all sites at which species richness was taken

Fig. 6 Variation in specialist community composition among *C. x. xantiana* populations and in relation to longitude for the most abundant specialists: *H. regularis*, *L. pullilabre*, or *M. gravita*+*M. pascoensis*. The *x*-axis displays longitudinal coordinates for the west to east axis from 118°45′W to 118°25′W. The *y*-axis shows the proportion of all specialists in a given bee community represented by each specialist taxon

studies have revealed that most plant taxa are visited by a diverse array of animals suggesting that pollination systems may be frequently generalized, a finding that challenges traditional views of specialization in plant–pollinator interactions [e.g., pollination syndromes (Faegri and van der Pijl 1979); coevolutionary interactions (Gilbert 1975)]. In some systems, there appears to be a correspondence between the most important pollinators and predictions based on floral traits that identify pollination syndromes (Fenster and Dudash 2001; Kay and Schemske 2003) while in others the relationship is less clear (Fishbein and Venable 1996; Mayfield et al. 2001).

In *Clarkia x.* ssp. *xantiana*, all visitors were bees and whole assemblages of bees were dominated by rare, incidental visitors that are unlikely to contribute to pollination (Figs. 1, 2a). Species accumulation curves for whole visitor assemblages did not saturate even when sample sizes were large (Fig. 5a) suggesting that continued sampling would result in the addition of new species to low abundance classes, further obscuring identification of the core pollinators from visitor lists. Several pollen specialist species dominated both the high abundance classes and comprised the majority of the highly predictable visitors (Figs. 1, 2a). Minckley et al. (1999) similarly found that pollen specialists of *Larrea tridentata* were more abundant and encountered at more sites than generalist bee species. The close correspondence between abundance and spatial predictability suggests that there are few core visitor taxa to *C. x. xantiana* despite a great diversity of visitors overall. The structure of visitor communities in this study exhibits parallels with many other natural communities [e.g., estuarine fish communities (Magurran and Henderson 2003)]. Specifically, the

phenomenon of an excess of rare species in communities appears to be caused by large numbers of "occasional" species that typically have little or no affiliation with a habitat (or resource in this study) but account for a high proportion of species encountered in comprehensive community surveys.

The same specialists forming the core visitor group were consistently found collecting and harboring pollen whereas most generalist foragers carried little pollen (Fig. 3b) suggesting that the former are more likely to be effective pollinators. Preliminary studies using direct measurements of pollination effectiveness mirror this study in showing that the most common specialist, *H. regularis*, is the most important pollinator based on its high visitation rates and ability to transfer pollen; some generalist foragers (*Bombus* sp.) also effect pollination but visitation rates are low (G. M. Hart and V. M. Eckhart, unpublished data). The discrepancy between specialists and generalists in pollen loads primarily reflects differences in resource acquisition. Generalists principally foraged for nectar from *Clarkia* and used other plant species as sources of pollen. Two aspects of *Clarkia* pollen morphology and dissemination are likely to discourage generalists from visiting flowers to collect pollen and may minimize inadvertent pollen removal. First, *Clarkia* pollen is very large and clumped via viscin threads; *Clarkia* specialists have structural and behavioral adaptations that facilitate pollen uptake (MacSwain et al. 1973). Second, pollen is gradually shed from anthers over several days, which can result in a small standing crop of pollen, especially when pollen foraging specialists are very abundant (MacSwain et al. 1973; personal observation). It is possible that some generalist foragers (e.g., *Bombus* sp.) play a more important role in pollination when specialists are uncommon.

Our understanding of pollinator community structure remains incomplete because studies aimed at dissecting visitor communities have either focused on mechanism (e.g., pollen transfer efficiency for few pollinator species) or broad-scale patterns in whole pollinator assemblages. In some plant species, it appears that a small percentage of visitors make important contributions to seed production. For example, Fishbein and Venable (1996) observed animals from seven orders and 80 species visiting one population of *Asclepias tuberosa*, but only *B. sonorus* and *Apis mellifera* were major pollinators (only *B. sonorous* is native to the US). In addition, most interactions between plant and pollinator in diverse systems are uncommon while very few are frequent (e.g., Memmott 1999; this study). These results have implications for conclusions about generalization in pollination systems and for community analyses of plant–pollinator networks. In particular, failing to incorporate the strength of interactions between plant and pollinator (e.g., frequency of encounter, pollen transfer per visit) into food web analyses may inflate measures of connectance, especially in regions with high insect diversity. Additional community-level surveys including both detailed taxonomic work and estimates of interaction strength are needed to better understand the nature of plant–pollinator networks; the challenge will be to obtain information on pollen removal and transfer when visitor assemblages are highly diverse.

Geographic variation in pollinator communities

One goal of the present study was to extend previous work on spatial variation in plant–pollinator interactions by distinguishing among ecological factors that underlie differences among plant populations in pollinator associations. Variation in visitor abundance among *C. x. xantiana* populations was associated with both geographic variation in the abiotic environment and local variation in plant community background. At a geographic scale, the specialist bee community varied in composition along the west-east abiotic gradient but abundance was similar among populations (Fig. 6, Table 2); the decline in overall bee abundance with longitude was caused by variation in the prevalence of generalist foragers (Table 1). Although it is not yet clear whether *Clarkia* specialists differ in their preferences of floral traits or differ in effectiveness in relation to floral form, community composition varies over a scale where gene flow is likely to be limited and therefore population differentiation in floral traits is possible. Pollinators belonging to a single guild are often considered to exert similar selective pressures; however, it is intriguing that *C. x. xantiana* exhibits genetic variation in floral traits (e.g., petal color, anther-stigma distance) in parallel with bee community variation (Moeller, unpublished data). Future work will need to distinguish selection by individual pollinator species from the influence of abiotic factors on the evolution of floral traits.

Geographic variation in pollinator communities has been shown to correspond with population differentiation in floral traits in several species (Miller 1981; Robertson and Wyatt 1990; Galen 1996; Johnson 1997). These examples of pollination ecotypes provide indirect support for the notion that selection by particular pollinator species is important in the evolution of floral form. Similarly, mechanistic approaches have provided more detail in showing that simple genetic changes can have dramatic effects on patterns of pollinator visitation (Schemske and Bradshaw 1999). Therefore, it appears that in some systems, the interactions between plants and the core pollinator group are strong enough to effect floral evolution despite diverse or variable visitor assemblages. For *C. xantiana*, patterns of population differentiation in breeding system provide insight into the importance of pollen specialists in pollination. *C. xantiana* also includes a highly selfing subspecies, *C. x. parviflora*, which occurs almost exclusively outside the range of pollen specialists but in areas where other bee species are of considerable abundance and diversity (Fausto et al. 2001; Moeller 2003). Moreover, when outcrossing genotypes are transplanted into the range of selfing populations, reproduction is strongly pollen limited (M. A. Geber and V. M. Eckhart, unpublished data). Similar patterns have been observed between the distribution of specialist bees and outcrossing

vs. selfing taxa in other plant genera (Barrett et al. 1989; Thorp and Leong 1996).

Facilitative interactions and local variation in pollinator communities

Over a small spatial scale, there was considerable variation in the abundance of bee visitors to *C. x. xantiana* populations. Bee visitation to *C. x. xantiana*, particularly by specialists, was higher when populations coexisted with pollinator-sharing congeners (Fig. 4a, b). These facilitative effects on bee visitation could not be explained by a higher density or abundance of *C. x. xantiana* flowers in populations coexisting with congeners. Because *Clarkia* bees, and solitary bees in general, exhibit localized foraging patterns in the vicinity of nesting sites (Burdick and Torchio 1959; Stage 1966; Gathmann and Tscharntke 2002), these results suggest that coexisting congeners may jointly maintain populations of specialists by providing more floral resources within years and a more consistent supply of resources across years. In the context of a human-altered landscape, Steffan-Dewenter et al. (2002) similarly found that solitary bee foraging patterns are strongly influenced by local factors while bumble bees and honey bees respond mainly to factors at very large scales. A companion study on *C. x. xantiana* has shown that the positive effects of congeners on specialist bee visitation also result in reduced pollen limitation of reproduction (Moeller, in press). While direct positive interactions among plant species are now well known (e.g., Callaway et al. 2002), evidence of indirect positive interactions is accumulating for situations where plant species interact via enemies (Hay 1986; Hamback et al. 2000) and mutualists (Johnson et al. 2003; Moeller in press). Studies of interactions among pollinator-sharing plant species in a landscape context, rather than only within communities, are likely to be most profitable for understanding the mechanisms of facilitation.

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