CHAPTER 6

Pollinator responses to plant communities and implications for reproductive character evolution

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Outline

Reproduction by most plant species occurs in a community of other flowering species and a diverse fauna of potential pollinators. This community context shapes both pollinator behaviour and ecology and the outcome and evolution of plant reproduction. We consider the effects of communities of pollinator-sharing plant species on three pollinator responses, behaviour (functional response, preference and constancy), demography (numerical and aggregative responses), and community structure (diversity and relative abundance of pollinator taxa). Pollinator responses may differ between multi-species plant communities and single-species populations and these differences can alter patterns of selection on, and evolution of, plant reproductive traits. Plant-pollinator studies that ignore community context can therefore misrepresent the causes of selection on reproductive traits. Pollinator responses to plant communities also influence the extent of heterospecific pollen transfer, a form of interference competition, and affect whether plant species compete (exploitatively) or facilitate each other for pollinator visits. We describe how interference competition, exploitative competition, and facilitation can have opposing selective effects on important reproductive characters, such as floral attractive features, flowering time, and mating-system traits. As an example of the implications of community interactions, we review our work on *Clarkia*, a genus of annual plants that shows facilitative interactions among pollinator-sharing congeners. This facilitation affects pollinator availability and reproductive success, and appears to shape patterns of selection on key floral traits (herkogamy and protandry) affecting plant mating systems (outcrossing versus selfing). Last, we explore potential broad-scale consequences of community interactions for the biogeography of floral variation using data on regional species richness and mating systems of *Clarkia* taxa.

6.1 Introduction

Plants rarely grow solely with conspecifics (single-species population), but instead co-occur and flower with other plant species in a community. Furthermore, studies of community patterns of plant-pollinator interactions clearly show that plant species are typically visited by multiple species of potential pollinators and that most flower visitors visit multiple plant species (Waser and Ollerton 2006). Thus, co-flowering plant species often share flower visitors, and most pollinators are embedded in a community of visitors with whom they share floral resources. In 1983, Rathcke and Waser published seminal papers on the nature of plant species interactions for pollinator services in communities. Surprisingly, their broad-ranging treatment of the subject appears not to have stimulated much empirical study of the community context of plant-pollinator interactions. Studies of plants and their pollinators often emphasize interactions between a pair of plant-pollinator species or at most between one plant and a few of its pollinators. This approach is particularly common for evolutionary studies of pollinators as agents of selection on floral, inflorescence and whole-plant reproductive traits (Fenster *et al.* 2004). Although the individual plant species considered in each such study is embedded in a plant community, the effects of other plant species on the ecology and evolution of the target plant are often ignored (but see Armbruster 1985; Fishman and Wyatt 1999; Caruso 2000; Hansen *et al*. 2000).

In this chapter, we ask how the presence of pollinator-sharing plants alters interactions between plants and pollinators relative to interactions in single-species plant populations. Altered interactions result from changes in pollinator ''responses'' to multiple versus single species. We ask how differences in response can lead in turn to different trajectories of reproductive-character evolution between the two ecological settings. We argue that pollinator-mediated selection in communities cannot always be predicted from studies in single-species populations.

Our discussion begins by considering the properties of plant communities that affect interactions with pollinators and that differ from single-species populations (e.g., interspecific variation in the quantity, quality, and type of reward: Fig. 6.1, Box A, Section 6.2). Next we discuss the direct effects of these plant-community attributes on three pollinator responses: pollinator behaviour, demography, and community structure (i.e., identity, diversity, and relative abundance of pollinator species: Fig. 6.1, Box B, solid arrow (1); Section 6.3). We follow with a discussion of the direct effects of these responses on patterns of selection on plant reproductive traits (Fig. 6.1, Box C, solid arrow (2); Section 6.4). The sum of these ''direct'' effects causes an indirect effect of plant communities on reproductive character evolution (Fig. 6.1, broken

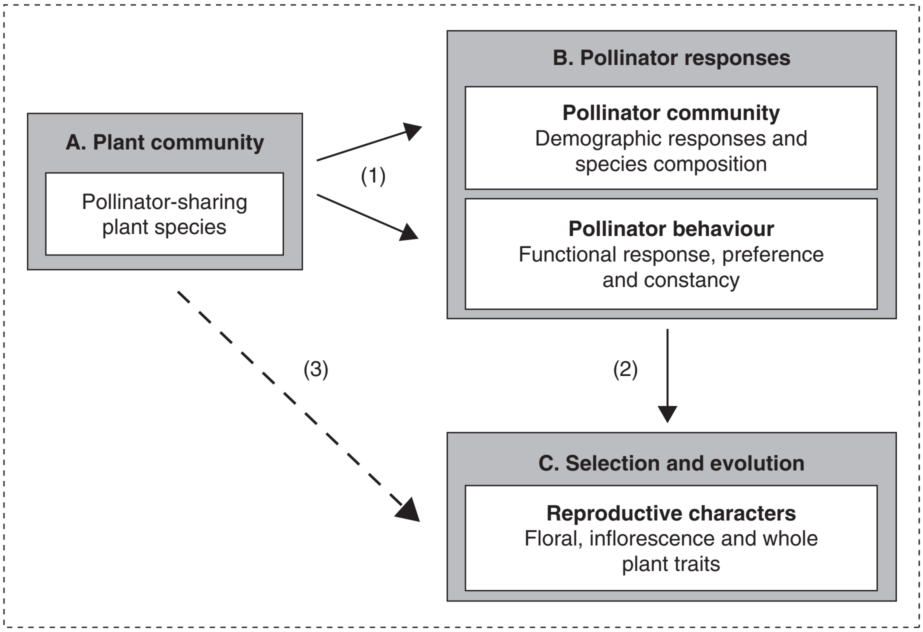

Figure 6.1 Framework for the evolution of plant reproductive traits as mediated by pollinator responses to a community of pollinator-sharing plants. The plant community affects pollinator community structure and foraging behavior (solid arrows, (1)). In turn, these responses influence patterns of selection and evolution in plant reproductive characters (solid arrow, (2)). The combined effect of (1) and (2) produces an indirect effect of plant communities on reproductive character evolution in member species (broken arrow, (3)).

arrow (3)). We then describe an example of the indirect effect of plant communities on selection on mating systems from our work on *Clarkia xantiana*, a plant species that co-occurs with congeners and shares with them a suite of specialist solitary-bee visitors (Section 6.5).

Before proceeding, we define the meaning of several terms that are used throughout the chapter. We refer to pollinators and flower visitors interchangeably, although we realize that not all flower visitors pollinate. In addition, by plant community we refer to a subset of species that share a common set of flower visitors. Among the shared visitors, consideration can generally be restricted to the plants' most abundant and/or effective pollinators. Descriptions of plant-pollinator networks in communities have sometimes identified ''nested'' subsets of plants and pollinators that interact strongly (Dicks *et al.* 2002; Bascompte *et al.* 2003). We focus on these subsets as they are good places to start in studies of plant-community effects on reproductive character evolution. Finally, we emphasize the role of pollinator responses to communities for *in situ* evolution of plant reproductive characters and the consequent distribution of adaptive character states among species. However, similar patterns of reproductive character distribution can arise by ecological sorting among a regional pool of species, where a subset of species co-exist because they already possess the reproductive attributes favoured by pollinator-mediated selection (see Armbruster *et al.* 1994).

6.2 Properties of plants and communities

Plant communities differ from single-species populations for the simple reason that species vary in relative abundance and in floral, inflorescence, and whole-plant traits that influence the quantity (e.g., nectar volume), quality (e.g., nectar chemistry), and type (e.g., nectar, resin, oil) of rewards per flower or per plant. If species offer rewards of the same quality and type, a pollinator can readily use one species' rewards in the place of another's, (i.e., species provide substitutable resources: Tilman 1982). More often, however, rewards will not be fully substitutable across species. A pollinator may then avoid species that offer rewards of the wrong type (e.g., nectarless flowers for butterflies) or of low quality, especially if the species is rare. On the other hand, a pollinator may visit multiple species that provide non-substitutable, but essential or complementary rewards.

Species differ in traits that affect a pollinator's search time (e.g., flower colour, scent, number) and handling time (e.g., flower and inflorescence shape, flower scent, nectar guides), which determine a pollinator's rate of resource extraction or *proficiency* on a plant. The quantity, quality, and type of reward, along with a pollinator's proficiency, all influence the *profitability* of flowers and plants to a pollinator. Finally, interspecific variation in profitability per plant, combined with variation in species' relative abundances, determines the potential *resource value* of different species and the combined resource value of the entire community to a pollinator.

Species also differ in the seasonal and diurnal schedule of flowering, and these differences affect resource availability over time. In the presence of a single plant species, a pollinator's foraging may be limited by its flowering duration during the day or season. In contrast, interspecific segregation of flowering time in a community can extend the period of resource availability (Chapter 8). For example, co-flowering African acacias release pollen at different times of the day and pollinators make coordinated transitions from one species to another as their pollen becomes available (Stone *et al*. 1998).

Interspecific variation in flower morphology, the location of rewards, and the placement of sexual organs affect where on a pollinator's body pollen is picked up and how it is deposited on stigmas. The placement and timing of maturation of sexual organs within flowers, as well as in the sexual phase of flowers within and among inflorescences, also influence the likelihood of pollen transfer within or between flowers of the same plant and between plants of the same or different species. For example, in self-compatible plants, outcrossing from pollen transfer between conspecifics is facilitated by separation in the placement (herkogamy) and the timing of maturation (dichogamy) of sexual organs.

These floral, inflorescence, and whole-plant attributes also vary among individuals of a species, but intraspecific variation is smaller than interspecific variation. Nevertheless, this intraspecific variation supplies the ''raw material'' for pollinator-mediated selection and evolution. This chapter focuses on how pollinator responses to variation in abundance and traits *among* species in communities shape patterns of selection on these same traits *within* a species.

6.3 Plant-community effects on pollinator responses

Pollinator responses to interspecific variation in plant attributes are manifold. We focus on three responses—behavioural responses, demographic responses, and pollinator-community composition (pollinator species identity, abundance, and diversity)—and consider differences in responses to communities and to single-species populations. Note that although we contrast plant communities with single-species populations, these two ecological contexts represent extremes of a continuum; similar comparisons apply to species-rich versus species-poor communities.

6.3.1 Pollinator behavioural responses

Once a pollinator begins foraging in a community, three behavioural responses affect the reproductive success of a community member: the pollinator's functional response (i.e., the relation of consumption rate to resource density: Holling 1959), its preference for one or more species, and its fidelity (constancy) to a species while foraging.

Functional responses have been described in relation to the density of a single resource or of multiple resources. In general, a pollinator's consumption rate increases with the density of suitable flowers, as search time declines. At high floral density, the foraging rate reaches an asymptote because a pollinator's consumption becomes limited by handling time on flowers or it becomes satiated. Functional responses can increase linearly (type I response), in a saturating manner (type II), or in a sigmoidal fashion (type III) to the asymptote, with the latter two responses being more common (Holling 1959). Type II responses are typical of oligolectic consumers that use only a few plant species, whereas type III responses are typical of generalist consumers that switch between food hosts (Schenk and Bacher 2002). Type III functional responses also characterize consumers that move shorter distances in high-density patches (area-restricted foraging; Murdoch 1969; Keasar *et al*. 1996) or learn to find and handle hosts better once resources are encountered. In Section 6.4.2, we consider how a pollinator's functional response to the presence of multiple species may differ from its response to single species.

Pollinator preference and flower constancy are uniquely applicable to plant communities and irrelevant in single-species population. Preference occurs when a pollinator visits one species more frequently than expected based on its resource density and is probably shaped by interspecific variation in the resource value of a species to a pollinator. Preference clearly influences the relative visitation rate to flowers of different species. Constancy is a measure of the degree to which a pollinator restricts its visits to one plant species during a foraging bout (or several foraging bouts). The limited ability of pollinators to remember floral characters of more than one species at a time is thought to be a major contributing factor to constancy (Chittka *et al*. 1999). Constancy can also be economically beneficial when pollinators bypass species with lower rewards for ones with higher rewards (Gegear and Thomson 2004). Constant pollinators fly more frequently between plants of the same species and thus are better at transferring conspecific pollen than inconstant ones. Preference and constancy have been discussed extensively elsewhere (Waser 1986; Chittka *et al*. 1999; Chittka and Thomson 2001) and are largely beyond the scope of this chapter.

6.3.2 Pollinator demographic responses

Interspecific variation in reward quantity, quality, and type can affect the size of pollinator populations through numerical or aggregative responses. Numerical responses are changes in the per capita reproductive rate of consumers (e.g., pollinators) associated with resource availability (Holling 1965). Aggregative responses, on the other hand, involve the redistribution (i.e., movement) of consumers among patches (e.g., communities) of varying resource density (Murdoch 1977, Bosch and Waser 1999). As with functional responses, the form of numerical and aggregative responses can be of type I, II or III.

Surveys of pollinator populations indicate that pollinator abundance can track the availability of floral resources. For example, during a long-term study of euglossine bees in tropical forests, the abundance of all bees varied 4-fold and the abundance of individual species varied up to 14-fold among years (Roubik 2001). These dramatic fluctuations in population size were largely explained by the effect of climatic variation on flower production.

Whether pollinator abundance results from a numerical or aggregative response may be difficult to determine in any given situation, and indeed both responses may operate simultaneously. Perhaps, the most convincing evidence of a numerical response comes from changes in pollinator abundance between years of differing flower abundance in pollinator species that nest at or near foraging sites (Strickler *et al*. 1996; Gathmann and Tscharntke 2002) or return to the same foraging site year after year. For example, Minckley *et al.* (1994) found that the reproductive success of a specialist solitary bee increased three-fold during a year of abundant flowering in their sunflower host compared to years of limited flowering. The elevated reproductive success caused a three-fold increase in bee abundance the year after copious flowering. Potts *et al*. (2003) also found that variation in bee abundance among communities in Israel correlated positively with nectar abundance, though the relation was weak. Furthermore, variation in bee abundance during one year depended more strongly on floral abundance during the previous year than during the same year, suggesting a numerical response.

Aggregative responses should be most characteristic of long-distance foragers that can assess patch variation in resource pools. Studies of single plant species indicate that pollinators often select high-density or large patches of plants over low-density or small patches (e.g., Kunin 1997; Grindeland *et al*. 2005) and there is no reason to believe that pollinators cannot assess site variation in the combined resource value of multiple plant species. For example, social pollinators, such as the generalist honey bee (*Apis mellifera*), survey floral resources over broad areas (>10 km) and often focus their foraging on a small subset of highly profitable patches (Visscher and Seeley 1982; Beekman and Ratnieks 2000). Furthermore, Steffan-Dewenter *et al*. (2002) found that honey bees responded to variation in resource patchiness in a fragmented landscape (percentage of semi-natural habitat) only at large spatial scales (up to a 3000 m radius) whereas solitary bees responded only at small spatial scales (<750 m radius). Social animals that share information are particularly likely to exhibit aggregative responses, because few individuals incur the search cost of scouting for high-quality resource patches that all solitary foragers would sustain. Nevertheless, solitary foragers, such as trap-lining hummingbirds and some euglossine bees that travel long distances in search of resources, may also exhibit aggregative responses (Thomson *et al.* 1987).

The population size of a pollinator can be larger or smaller in communities than in single-species population, depending on whether the resource value is higher or lower in the former than in the latter. If floral rewards are not substitutable across species and some are non-essential or unprofitable, the combined resource value and hence pollinator population size may be lower in a plant community than in a population consisting entirely of a plant species with essential and/or profitable rewards. However, we argue that a community often offers more predictable resources than single-species populations. First, many pollinators are generalists and even specialist pollinators typically consume resources from several, usually closely-related species. Thus, multiple plant species may typically provide partially substitutable or complementary resources to pollinators and therefore offer a combined resource value that exceeds that of a single species. For example, Williams and Tepedino (2003) found that, despite added travel costs, the solitary bee, *Osmia lignaria*, regularly foraged on two plant species, even when one species grew further from nests or was rarer than the other, apparently because one species was more profitable as a source of pollen and the other as a source of nectar. Second, as noted above, interspecific displacement in diurnal and seasonal flowering extends the period of resource availability, which can then support a larger population of a pollinator that forages throughout the day or the season (Waser and Real 1979; Rathcke and Lacey 1985*)*. For example, six mass-flowering dipterocarps share thrips pollinators, which persist at very low abundance between mass-flowering events and then build up rapidly in number as successive species flower (Ashton *et al*. 1988).

Last, plant species generally differ in the environmental conditions best suited for growth and reproduction (e.g., soil moisture, shade, nutrients)—conditions that vary both spatially and temporally within sites. Communities may therefore support higher plant densities and more rewards than single-species populations, because spatial environmental variation within sites allows for greater plant occupancy. Floral rewards may also be more predictable in communities if optimal environmental conditions for one species are followed during the next year by optimal conditions for another species (Chesson and Huntley 1989). High resource predictability should dampen fluctuations in pollinator population size among years.

6.3.3 Pollinator-community structure

Many plant species are visited by a diversity of pollinators, whether or not they grow alone or as members of a community. However, the assemblages of pollinators visiting different species are not identical. Therefore, communities probably present more abundant and diverse pollinator faunas than single-species populations, exposing plant species to altered patterns of visitation in the two settings. Indeed, Potts *et al*. (2003, 2004) found that bee species richness correlated strongly with floral species richness among communities and also varied with nectar resource diversity, an index of the diversity of nectar quantity and sugar concentration among plant species.

In concluding this review of pollinator responses, we emphasize that community effects on pollinator behaviour, demography, and community structure occur at multiple spatial and temporal scales. Behavioural and numerical responses are sensitive to the resource value of species of one community, aggregative responses vary with differences in resource value among communities, and pollinator communities reflect resource distribution within and among plant communities. From a temporal perspective, community context influences pollinator behaviour only on species that flower simultaneously, whereas community context can influence demography and pollinator-community structure even when species flower sequentially. In the case of sequential flowering, the effects of pollinator demographic responses and community structure on plant reproduction may differ between early- and late-flowering species.

6.4 Consequences of pollinator responses for selection on plant reproductive traits

A plant's reproductive success depends primarily on the quantity and quality of seeds it produces and sires. These fitness components are, at least partially, a function of pollen receipt and export and the latter, in turn, are determined by floral visitation rate and the effectiveness of pollinators at transferring pollen between compatible mates (Stebbins 1970; Herrera 1987; Chapters 2, 4, and 5). Floral visitation rate depends on pollinator abundance (demographic responses), consumption rate (functional response), and, in communities, the partitioning of pollinator visits among species (preference). The per-visit effectiveness of pollen transfer depends partially on pollinator constancy during a foraging bout, although preference increases pollinator fidelity to a preferred species.

The presence of multiple plant species can affect pollinator-mediated interspecific interactions in three ways. First, plants are subject to the exchange of heterospecific pollen, which can be viewed as a form of interference competition. The export of an individual's pollen to another species is always detrimental, because pollen is lost to incompatible mates (Waser 1978; Campbell and Motten 1985; Murcia and Feinsinger 1996). The receipt of heterospecific pollen can also interfere with fertilization by conspecific pollen (e.g., Waser 1978; Bell *et al*. 2005) or result in inferior hybrids (Chapter 18).

In addition, plant species may interact competitively or facilitatively for pollinator visits (Rathcke 1983). Facilitation has traditionally received less emphasis than competitive interactions, but has nevertheless been documented in a few instances (Thomson 1981; Johnson *et al*. 2003; Moeller 2004). Competition for pollinator visits is a form of exploitative competition for a shared resource (Waser 1983). For the purposes of this discussion, we define facilitation as the enhancement of visitation rate in the presence of multiple species (i.e., the opposite of exploitative competition). Our definition of facilitation differs from that of other researchers. For example, Rathcke defined facilitation as the net effect of beneficial increases in visitation rate and detrimental interspecific pollen exchange. We separate the effects of heterospecific pollen exchange from facilitation for pollinator visits, because they can have different selective consequences for plant reproductive traits. In a model of interspecific interactions that included enhanced visitation, heterospecific pollen transfer, and interspecific competition for seedling establishment, Feldman *et al*. (2004) defined facilitation as the demographic rescue from extinction of a rare species by a more common one when the latter boosts the former's population growth rate. We have elected to exclude competition for non-pollinator resources to distinguish it from pollinator-mediated selection.

Interspecific pollen transfer can occur simultaneously with either competition or facilitation for pollinator visits. The net effects of these interspecific interactions on reproductive success can obviously reduce or increase population growth rates of community members. However, even when growth rates remain the same, selection within species in response to interactions can occur if variation in reproductive success is linked to variation in phenotypes that influence the interaction.

Finally, we note that the net effect of interactions need not be reciprocal among species. For example, one species may suffer from the presence of others, but the latter may experience either no effect or benefit from the presence of the first (Ratchke 1983). Non-reciprocal effects may be common when species differ in relative density or rank order of pollinator preference.

6.4.1 Heterospecific pollen transfer

Selection to minimize heterospecific pollen transfer will always favour traits that promote pollinator constancy and may also favour interspecific divergence in the timing of pollen release during the day (Armbruster 1985; Stone *et al*. 1998), as both changes minimize temporal overlap in visits by the same pollinator and the chance that a pollinator carries a mixed pollen load. Selection may also favour species to forgo pollinator-dependent outcrossing to diminish the detrimental effects of heterospecific pollen. For example, self-pollination has evolved in *Arenaria uniflora* where it co-occurs with *Arenaria glabra*. This evolution probably reflects selection against interference from *A. glabra* pollen, because pollen receipt from *A. glabra* results in non-viable seed and reduces overall seed set (Fishman and Wyatt 1999).

Selection should also favour divergence among species in floral characters that affect where a pollinator contacts anthers and stigma. These traits include the position of sexual organs and features, such as flower shape and nectar guides, that manipulate how pollinators handle flowers (Grant 1950; Waser 1983).

In short, the detrimental effects of heterospecific pollen transfer favour interspecific differentiation in the spatial and temporal mechanics of pollen transfer, at the same time that selection favours convergence in these same traits among individuals within a species.

6.4.2 Pollinator visitation rate

A pollinator's functional and demographic responses to community resource density may or may not translate into higher visitation rates per flower to a member species relative to that which it experiences in isolation (Bosch and Waser 1999). A simple graphical model illustrates this point and

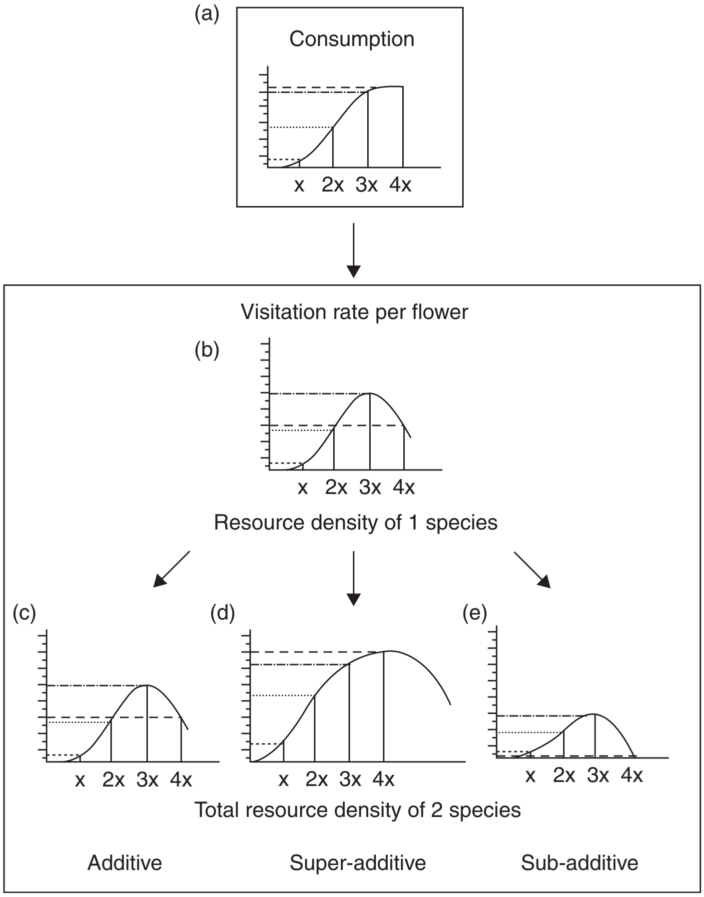

Figure 6.2 Relations between the pollinator functional response and per-flower visitation rate in a single-species population and the per-flower visitation rates of co-flowering species in a community. (a) Functional response and (b) visitation rate per flower by a pollinator to resource density in a single-species plant population. The visitation rate per flower is positively density dependent at low resource levels and negatively density dependent at high resource levels. In a two-species community, the visitation rate per-flower to both species can be (c) an additive, (d) super-additive, or (e) sub-additive function of the visitation to each species alone.

shows the kind of data that would elucidate response differences between communities and single-species populations. Consider, for example, a pollinator's functional response to the resource density of a single species growing alone (Fig. 6.2a). The translation of this response into visitation rate per flower is shown in Fig. 6.2b. The visitation rate first increases (i.e., is positively density-dependent at low resource density), but then decreases as the functional response saturates (i.e., negatively density dependent at high resource density). This transition from positive to negative density dependence is expected regardless of the shape of the functional response. Now consider a community of both species. If the functional responses and visitation rate per flower for both species in isolation are identical, then visitation rate on both species combined may remain the same (Fig. 6.2c; additive model). This result could arise if the two species provide perfectly substitutable rewards and pollinators do not discriminate against either species. In this case, the visitation rate per flower on both species at density x (total density $2x$) will be higher than the rate in isolated populations of either species at density x, but the same as the visitation rate in isolated populations of either species at density $2x$. If the two species have resource densities of x and $3x$, respectively, in a community, visitation rate to the rare species (x) is higher in the presence of the common one, but the latter now suffers from the presence of the first. Still, each species would do equally well in isolated populations at resource densities of $4x$.

The visitation rate per flower in two-species communities need not combine additively. It might be super-additive (Fig. 6.2d), if, for example, the two species provide complementary resources that are required by a pollinator. Alternatively, the visitation rate could be sub-additive, relative to the rate on each species alone (Fig. 6.2e), if a pollinator must adopt a different search image or handling method on each species and is therefore less efficient at obtaining resources from both. In the super-additive case, the rare (density x) and common ($3x$) species both benefit in the presence of the other (facilitation; *i.e.*, visitation rate at the combined density, $4x$, is higher than at the density of each species alone, x and $3x$). In the sub-additive case, both species suffer in the presence of the other (competition).

The same logic can be applied if the functional responses and per-flower visitation rates in isolation differ between the two species (e.g., one species produces lower-quality rewards). In this case, the more profitable species is likely to suffer in the presence of the other. In contrast, the less profitable one may benefit from the first, unless a pollinator can discriminate between the two species and prefers the profitable species. In the latter case, the cost to the profitable species from the presence of the less profitable one will diminish or disappear, as will the benefit to the less profitable species.

The graphical model can also be applied to numerical and aggregative responses to co-flowering plants. Because functional and demographic responses can operate simultaneously, their net effect on visitation rate per flower may differ from each response taken alone. For example, if a demographic response to the combined resource value of a community is very strong, the number of pollinators in a patch will also be high and the resource density required to satiate an individual pollinator will be higher than if fewer pollinators were present. In other words, pollinators compete for plant resources. In turn, the visitation rate per flower will peak at a higher resource density (super-additive) and both species may be facilitated by the presence of the other.

Functional and demographic responses differ in an important way. As noted previously, the functional response is sensitive to only the combined resources of co-flowering species, whereas demographic responses can extend across sequentially flowering species, and, in the case of numerical responses, across years. Because demographic responses extend through time, the shape of the visitation function for a species should not differ between isolated populations and communities, except that, in communities, increases in pollinator abundance earlier during the season will elevate the visitation rate for a late-flowering species at low density (larger y-intercept, Fig. 6.2). Thus, facilitation should occur most often in species that succeed others in flowering (Waser and Real 1979), whereas early-season species should experience benefits only if pollinators or their offspring stay or return to the same site between years.

Although pollinator responses to resource density of single species have been demonstrated often, very little is known about the actual shape of the responses and even less is known about pollinator responses to the combined resources of multi-species communities. Only comparative studies of a focal species at varying density, both in isolation and in combination with other species, can provide the relevant data. If species compete for pollinator visits (e.g., sub-additive response), selection may result in an ‘‘arms race’’, whereby each species evolves to become more profitable and preferred by a pollinator. Selection could also favour interspecific divergence in flowering time to minimize direct competition for pollinator visits. When species interact facilitatively, functional and demographic responses can also generate varying forms of selection. For species that flower simultaneously, strong pollinator responses may result in selection for convergence in attractive characters (Brown and Kodric-Brown 1979; Johnson *et al.* 2003a; Chapter 8). On the other hand, for sequentially flowering species demographic responses need not generate selection for either convergence or divergence in reproductive traits.

Patterns of selection are likely to differ between co-flowering species when the effects of competition or facilitation are asymmetric. For example, when species' rewards are substitutable and pollinators do not discriminate between them, a rare species can experience facilitation from the strong functional response engendered by a common species (Feldman *et al*. 2004; see Fig. 6.2c). Selection may then favour convergence in floral characters and flowering phenology by the rare species on the common one. When species differ in profitability, less rewarding species may be selected to avoid direct competition with profitable ones through shifts in seasonal phenology, to mimic the outward appearance of profitable species (Gumbert *et al.* 2001; Johnson *et al.* 2003a), or selection may favour floral mechanisms that enhance self-pollination such that less rewarding species forgo entirely their reliance on pollinators (Lloyd 1965, 1992; Chapter 10). Mimicry can cause pollinators to mistake less rewarding species for rewarding ones. For example, rewardless species receive more visits when growing near rewarding species that they resemble in flower colour (Johnson *et al.* 2003b). Asymmetry in benefit between rewardless and rewarding plant species is very much like the asymmetry experienced by palatable versus unpalatable prey that are attacked by the same predators. Both interactions select for mimicry of the beneficiary on the benefactor (Johnson 1994), and the benefit to the ''mimic'' is expected to diminish as its abundance relative to the ''model'' increases.

6.4.3 Pollinator-community composition

If pollinator assemblages differ between plant communities and single-species populations, a plant species may encounter a new flower visitor in the presence of other plant hosts (Ginsberg 1983). For example, in agricultural landscapes, pollinators attracted to native plants are likely to spread to neighbouring crops and vice versa (Kremen *et al*. 2002; Ricketts *et al*. 2004; see also Memmott and Waser 2002; Chapter 9). Similarly, in polyculture systems, pollinators attracted to one crop can visit interplanted crops (Jones and Gillett 2005).

Just as different pathogen and herbivore species are deterred by, and act as selective agents for, different plant defences, different pollinators can favour different trait optima in attractive characters and rewards (Galen *et al.* 1987; Campbell *et al.* 1997). Thus, intra- and interspecific variation in floral phenotype can correlate with changes in the dominant pollinator at small and large spatial scales (e.g., Galen 1989; Schemske and Bradshaw 1999). However, the role of spatial variation in plant (and pollinator) community structure in the evolution of plant reproductive characters is largely unknown (Chapter 15).

Higher pollinator diversity may also expose plant species to more variable selection in communities than in single-species populations. Highly variable selection generally slows adaptation to specific biotic or abiotic factors and favours a generalized phenotype (Levins 1968). On the other hand, greater pollinator diversity might expose large inequalities in the effectiveness of different pollinator species and so strengthen selection for adaptations that increase preferential visitation by the best pollinators and exclude the worst pollinators (but see Aigner 2004). For example, does a plant species pollinated most effectively by long-tongued pollinators evolve greater barriers to short-tongued pollinators (e.g., longer or thicker corollas) when it co-flowers with species that attract short-tongued pollinators?

6.5. Community context and mating-system evolution in *Clarkia*

Studies of the ecological consequences of pollinator sharing have focused mainly on the negative effects of competition for pollinator visits and interspecific pollen transfer. In contrast, only a few studies have investigated the ecological and evolutionary consequences of positive interactions. In this section, we relay results from our own research on positive interactions for pollination between the annual plant, *C. xantiana*, and its congeners. First, we address the effects of pollinator sharing by *Clarkia* species on visitation rate and pollen limitation in *C. xantiana* and assess the possible influences of pollinator demography, behaviour, and community structure on its reproductive success. We then describe experimental studies on the evolutionary consequences of pollinator responses to *Clarkia* communities for mating-system evolution in *C. xantiana*. Although our work is certainly incomplete, we use it to illustrate a research approach that merges ecological and evolutionary perspectives on floral biology in plant communities. We end with a discussion on intriguing biogeographic patterns of mating-system distribution that suggest facilitation throughout the genus.

6.5.1 Study system

Clarkia comprises 44 annual species endemic to western North America and reaches its highest diversity in California (Lewis and Lewis 1955). Three attributes of the genus make it especially suitable for community-level studies of pollination. First, there is considerable sympatry among taxa and co-existence is common over small spatial scales (Lewis and Lewis 1995). Second, virtually all *Clarkia* are bee pollinated, and, in most species, the most common visitors are a small set of specialized solitary bees (MacSwain *et al.* 1973). Thus, the limited size of the plant-pollinator network makes the system tractable for observational and manipulative studies. Finally, most *Clarkia* exhibit a great deal of intraspecific variation in floral traits, which makes them ideal for microevolutionary studies. Our work has concentrated on a focal species, *C. xantiana*, which includes a predominantly outcrossing subspecies (ssp. *xantiana*) and a parapatric, predominantly selfing subspecies (ssp. *parviflora*) (Eckhart and Geber 1999).

6.5.2 Pollinator responses to *Clarkia* communities

Across most of the range of the outcrossing subspecies, 60% of *C. xantiana* populations co-occur with congeners (*Clarkia cylindrica, Clarkia unguiculata, Clarkia speciosa*). Congeners overlap in flowering time, but flowering modes tend to be staggered, with *C. xantiana* being the last to flower (Moeller 2004). The flight period of generalist and specialist bees extends through the flowering of several *Clarkia* species, so that pollinators can benefit from the prolonged period of resource availability in multi-species communities (MacSwain *et al.* 1973).

Comparative studies and experimental manipulations of community composition during three years have shown that *C. xantiana* receives more frequent pollinator visits and suffers less pollen limitation of seed set in the presence of congeners than in their absence (Fig. 6.3; Moeller 2004, 2005; Moeller and Geber 2005). The difference in pollinator availability stems principally from a greater abundance of specialists, rather than a change in bee species richness, in communities (Moeller 2005). In turn, higher pollinator abundance enhances pollen receipt, as hand-pollination experiments conducted during three years indicate less pollen limitation of seed production in *C. xantiana* in the presence versus the absence of congeners (Fig. 6.3; Moeller 2004).

Numerical and/or aggregative pollinator responses to *Clarkia* communities are likely to be the causes of higher visitation rates and seed production in *C. xantiana* populations coexisting with

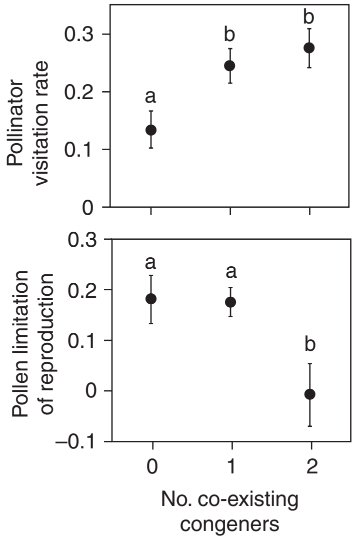

Figure 6.3 The effect of co-existing *Clarkia* congeners on pollinator availability (number of bee visits per plant per site census) and pollen limitation of reproduction in *Clarkia xantiana*. Pollen limitation was measured as the difference in seed set between open-pollinated flowers with or without supplemental hand-pollination, standardized by the seed set of flowers with supplemental pollen. Low values indicate little pollen limitation. Plots show least-square means (± SE) from an ANOVA that accounted for the effects of plant population size and population density. Different lower-case letters indicate a significant difference between factor levels based on the Tukey-Kramer test (from Moeller 2004).

congeners. Numerical responses may be important because the specialist bees nest within *Clarkia* communities and tend to forage locally (e.g., Burdick and Torchio 1959). Consequently, the resource value of the entire community probably affects the per capita reproductive rate of bees. Pollinator abundance may also be influenced by aggregative responses over hundreds of metres to a few kilometres, a scale which typically encompasses multiple, distinct *Clarkia* communities. Finally, the possibility that stronger functional responses contribute to higher visitation rates to *C. xantiana* in diverse communities cannot be excluded. However, the staggered flowering periods of *Clarkia* species should limit the strength of these responses.

Higher visitation rates do not appear to reflect a preference by bees for *C. xantiana*. The two most common visitors, *Lasioglossum pullilabre* and *Hesperapis regularis*, visited *C. xantiana* 26 and 16% less often than expected given its frequency (51%) in mixed patches with *C. speciosa* (L. Evanhoe and M.A. Geber unpublished data). Undervisitation of *C. xantiana* may be balanced by relatively low interspecific pollen transfer for two reasons. First, the staggered flowering of *Clarkia* species should, by itself, minimize heterospecific pollen transfer during the late portion of *C. xantiana*'s flowering. Second, even when species overlap in flowering time and grow in mixed patches, a large percentage (83%) of foraging transitions between plants by specialist bees were between conspecifics.

Pollen limitation of seed set also tends to be lower in large *C. xantiana* populations, particularly those of high density, suggesting strong Allee effects where plants are scarce (Moeller 2004). Based on these and the previous results, we predicted that facilitative effects of congeners mitigate Allee effects and reduce extinction risk in small populations. A survey of 85 populations showed that small populations of *C. xantiana* occur more often with congeners whereas populations isolated from congeners tend to be large (Moeller 2004).

6.5.3 Consequences of community context for selection on the mating system

Mating-system variation among *C. xantiana* populations correlates geographically with variation in population size and *Clarkia* species diversity: selfing populations (ssp. *parviflora*) tend to be smaller, of lower density, and occur largely outside the range of other outcrossing *Clarkia* species (Moeller and Geber 2005). We tested for the effects of population size and plant-community context on patterns of selection on two mating-system traits: herkogamy and protandry. We introduced large and small experimental populations of *C. xantiana* into sites where congeners were present or absent. Experimental populations consisted of plants derived from crosses within and between the two subspecies and exhibited a wide range of floral phenotypes. We found that selection strongly favoured traits that promote self-pollination (reduced herkogamy and protandry) in small, but not large, populations (Moeller and Geber 2005). In small populations, mating-system traits experienced weaker selection when congeners were present (Fig. 6.4a). The strength of selection on herkogamy depended largely on pollinator availability, which was influenced by community context (Fig. 6.4b; Moeller and Geber 2005).

These results are consistent with the hypothesis that reproductive assurance is an important factor shaping mating-system evolution in this system. This causal mechanism for the evolution of selfing is further supported by geographic variation in pollinator abundance and floral traits in *C. xantiana* (see Chapter 10). Pollinator abundance (on a per flower basis) is 4.4 times higher in ssp. *xantiana* than in ssp. *parviflora* populations and specialist solitary bees are absent from the exclusive range of ssp. *parviflora* (Fausto *et al*. 2001; Moeller 2006). Furthermore, common-garden studies of subspecies *xantiana* show that genetic differences among populations in herkogamy are correlated with pollinator abundance, particularly of specialists, and with the composition of pollinator communities (Fig. 6.4c; Moeller 2006).

6.5.4 Biogeographic patterns of mating-system variation and plant-community diversity

Patterns of reproductive character variation across a species' range may extend to larger biogeographic patterns, depending on whether the nature of interactions between a set of pollinator-sharing

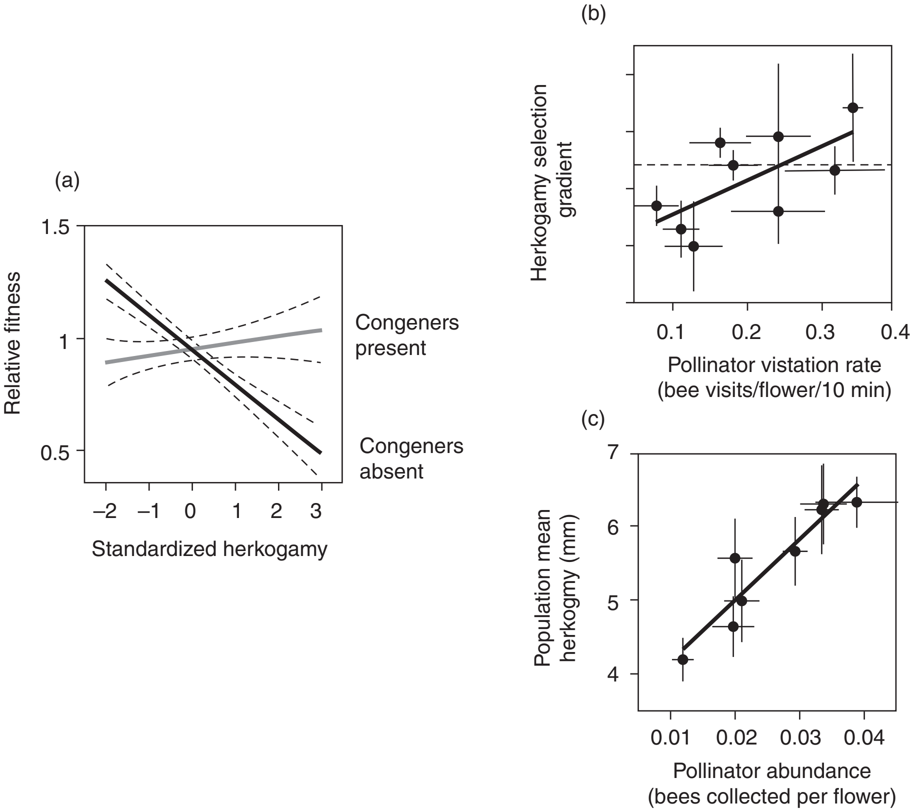

Figure 6.4 Evolutionary consequences of community context for herkogamy (anther-stigma separation). (a) Directional selection gradients (± SE) for herkogamy in small experimental populations introduced into communities where *Clarkia* congeners (*C. cylindrica* and *C. unguiculata*) were present or absent (from Moeller and Geber 2005). (b) The strength of selection on herkogamy among experimental populations varies significantly with bee pollinator visitation rates (from Moeller and Geber 2005). (c) Genetic differences in herkogamy among populations of subspecies *xantiana* correlate significantly with mean pollinator abundance (Moeller, 2006).

plant species is largely consistent across geographic regions. For example, if facilitative interactions are pervasive in *Clarkia*, outcrossing taxa (species or subspecies) should be most common in regions of high species diversity, and vice versa for self-pollinating taxa. To test this hypothesis we classified the mating system of *Clarkia* taxa based on petal size and herkogamy. Although taxa are neither exclusively outcrossing nor selfing (all taxa are self-compatible), there is a strong bimodal distribution in petal size that correlates with herkogamy (Fig. 6.5A), and this bimodality is consistent with the view that taxa are modally outcrossing or selfing (Wyatt 1988). We then used data on the geographic distribution of *Clarkia* taxa in each of 30 floristic provinces in the western United States: 24 provinces in California and 6 neighbouring provinces in the Pacific Northwest and Baja California, Mexico (Plate 1; Lewis and Lewis 1955; Hickman 1993) to examine the relation between mating-system frequency and species diversity. The geographic data do not indicate whether *Clarkia* species co-exist on a local scale, but co-occurrence is common in the genus (Lewis and Lewis 1955). As predicted, the frequency of selfing taxa is lowest in the centre of the genus' range where species diversity is highest (e.g., Sierra Nevada foothills, Outer Coast Range), and highest at the periphery of the range where diversity is lowest (e.g., Great Basin, Pacific Northwest, Baja California) (Plate 1).

The number of selfing taxa varies linearly with the number of outcrossing taxa across biogeographic provinces, with a slope significantly <1 (Fig. 6.5B). Thus, selfing taxa are overrepresented in regions

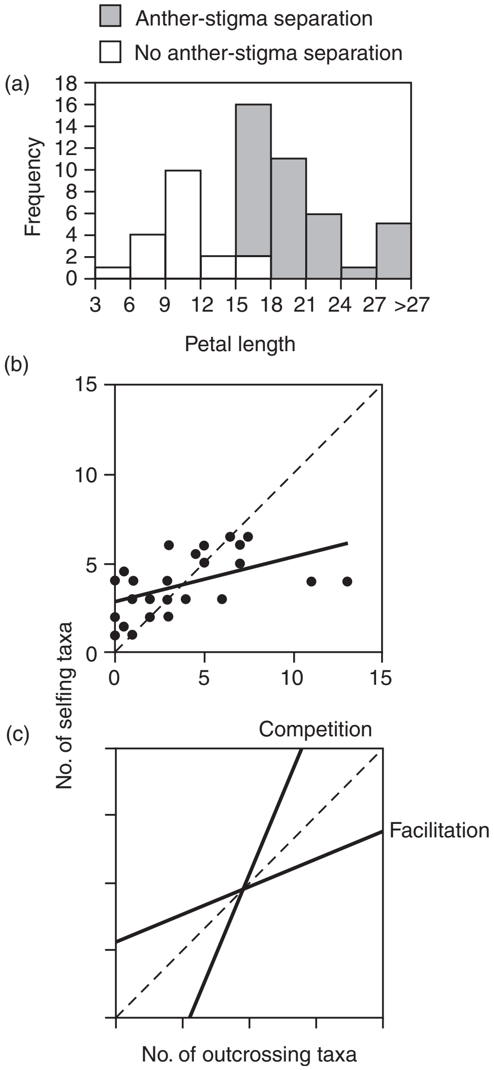

Figure 6.5 Biogeographic consequences of interactions among pollinator-sharing *Clarkia* species. (a) Petal size and herkogamy vary bimodally among *Clarkia* taxa, with taxa at the lower end of the distribution being primarily selfing and those at the upper end primarily outcrossing. (b) The relation between the number of selfing and outcrossing *Clarkia* taxa in 30 floristic provinces of the western United States (middle panel; see Plate 1 for all provinces, except a portion of the Rocky Mountains). *Clarkia* species or subspecies that contain both outcrossing and selfing forms, were assigned a value of 0.5 for each form. The slope is significantly less than one ($y = 0.25x + 2.84$; 95% confidence interval for slope: $0.08 - 0.42$). (c) Expected consequences of competition and facilitation for biogeographic patterns of mating-system distribution. If competition among *Clarkia* species predominates across communities, selfing taxa should be overrepresented in regions with high *Clarkia* diversity (slope > 1), whereas the reverse should hold if species interact facilitatively (slope < 1). A mixture of competition and facilitation across communities would result in a slope near 1.

where outcrossing taxa are uncommon and vice versa. If instead co-occurring *Clarkia* species compete consistently for pollination, the slope of the relation should exceed 1 (Fig. 6.5c). If interactions vary from competitive to facilitative, the relation would not differ significantly from the 1:1 line. Although only correlative, the biogeographic pattern of mating-system distribution in *Clarkia* suggests that community context may have important and wide-ranging effects on patterns of floral diversity. The predictions arising from this exercise may be profitably extended to other taxonomic groups for which co-existence and pollinator sharing are common.

6.6 Conclusions and future directions

Understanding of the community context of pollination and floral evolution is in its infancy. Ecological studies of pollinator-mediated plant interactions most often focus on pollinator behaviour (e.g., preferences, flower constancy) at small spatial scales, through experimental manipulation of the abundance and dispersion of a target species. In contrast, functional and demographic responses have received little attention. Functional responses can also be evaluated through manipulations within communities, but will most likely require experimental or observational comparisons among communities. Demographic responses will continue to be overlooked unless the spatial and temporal scales of study are expanded.

Published work on pollinator-sharing plant species suggests that interactions among plant species are more often competitive (exploitative or interference) or neutral than facilitative. Whether this apparent bias in results is truly representative of the real world or is due to an absence of data is unclear. For example, co-flowering plant species may exhibit evidence of interference competition at a local scale (over metres) but floral visitation may be considerably higher in the presence of pollinator-sharing species, so that reproductive success is still greater in communities than in single-species populations.

Ecological studies on interactions among pollinator-sharing species far outnumber evolutionary studies on the selective consequences of these interactions. Even though most studies of natural selection on reproductive characters are, in fact, conducted in plant communities, the role of co-occurring species in shaping patterns of selection in a focal species is not isolated from other selective causes. The few evolutionary studies on the community context of pollination have revealed fascinating results. There is evidence of both competitive and facilitative interactions among pollinator-sharing taxa and these interactions appear to affect selection on traits involved in pollinator attraction and the functional fit between pollinator and flower (Armbruster 1985; Caruso 2000; Hansen *et al*. 2000) and traits that influence the mating system (Fishman and Wyatt 1999; Moeller and Geber 2005).

Evolutionary studies of the community context of pollinator-mediated selection will be most useful when combined with ecological studies of the mechanisms underlying positive or negative interspecific interactions. For example, negative interactions among pollinator-sharing species can be caused by exploitative competition for pollinator visits or interference competition via heterospecific pollen transfer. These two mechanisms cause selection on different traits (e.g., traits affecting pollinator preferences versus constancy), which can be tested only through evolutionary studies. Systems in which plant-community context varies geographically among populations of a focal plant species provide a particularly useful arena for evolutionary studies, because they allow for the combination of process-oriented studies of pollination and natural selection with pattern-oriented studies of population differentiation and character evolution.

Regardless of general patterns, it is important to recognize that the nature of reproductive interactions between species may vary over time. The long-term studies that are necessary to evaluate variability in the nature of pollinator-mediated interactions and in patterns of selection on reproductive traits, as a function of community context, have never been conducted.

In addition to their relevance to understanding plant reproductive ecology and floral evolution, the effects of community context on pollinators have important implications for conservation biology. Food-web analyses have indicated strong linkages among plant and pollinator species, but the implications of these results for the stability of plant-pollinator networks remain less clear (Chapter 9). Long-term monitoring of pollinator populations in natural or manipulated communities can provide important information on whether pollinator populations are in decline and on the importance of multi-species communities to the maintenance of pollinator populations and species diversity (Kearns *et al*. 1998; Chapter 15).

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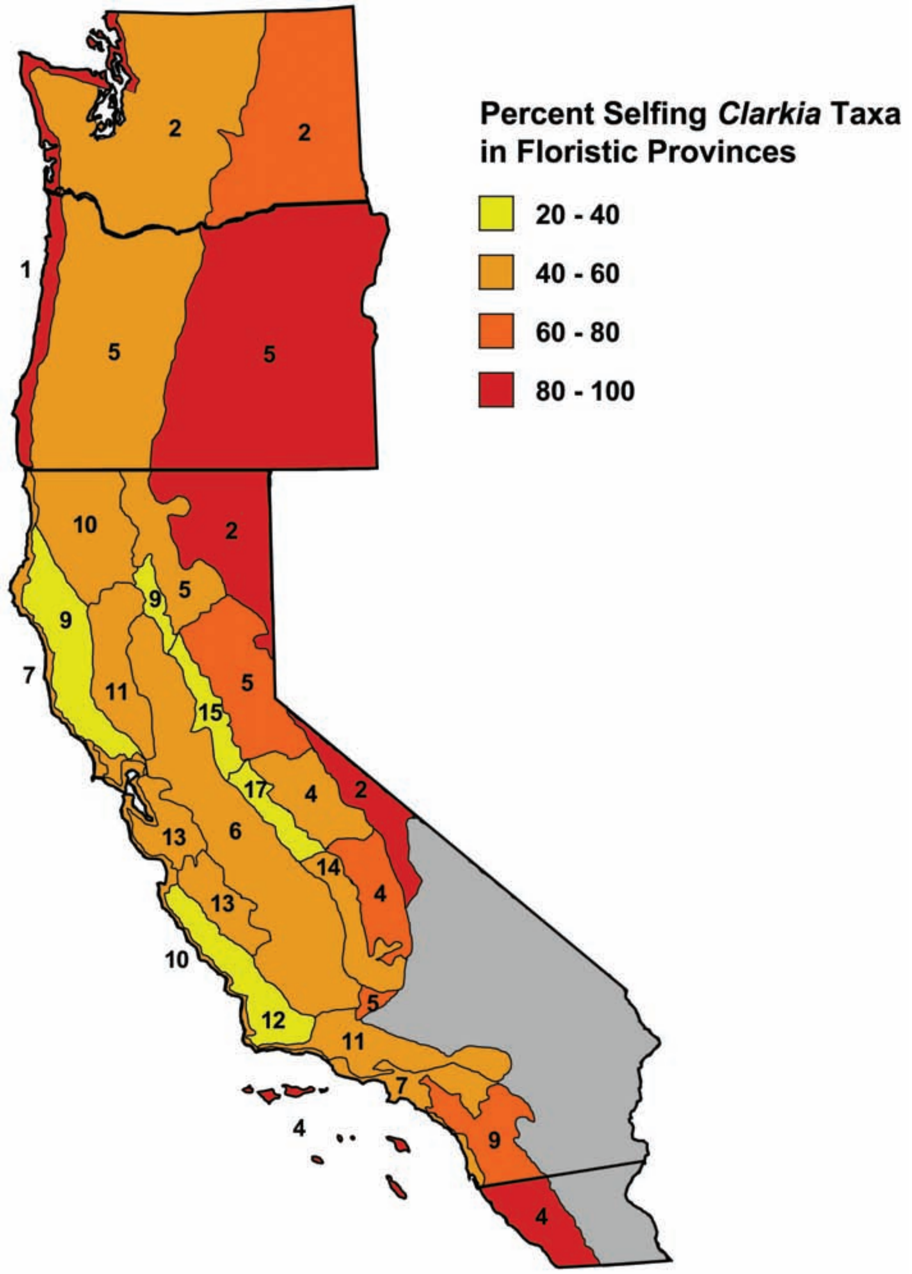

Plate 1 Biogeography of floral traits and mating-system frequency in *Clarkia* (see Chapter 6). The percentage of selfing taxa is shown for floristic provinces of the western United States of America and northern Mexico. Virtually all *Clarkia* taxa occur within this geographical region. The number shown in each floristic province indicates the total number of species (both outcrossing and selfing) in that province.