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REVIEW

New frontiers in competition for pollination

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• *Background* Co-flowering plant species frequently share pollinators. Pollinator sharing is often detrimental to one or more of these species, leading to competition for pollination. Perhaps because it offers an intriguing juxtaposition of ecological opposites – mutualism and competition – within one relatively tractable system, competition for pollination has captured the interest of ecologists for over a century.
• *Scope* Our intent is to contemplate exciting areas for further work on competition for pollination, rather than to exhaustively review past studies. After a brief historical summary, we present a conceptual framework that incorporates many aspects of competition for pollination, involving both the quantity and quality of pollination services, and both female and male sex functions of flowers. Using this framework, we contemplate a relatively subtle mechanism of competition involving pollen loss, and consider how competition might affect plant mating systems, overall reproductive success and multi-species interactions. We next consider how competition for pollination might be altered by several emerging consequences of a changing planet, including the spread of alien species, climate change and pollinator declines. Most of these topics represent new frontiers whose exploration has just begun.
• *Conclusions* Competition for pollination has served as a model for the integration of ecological and evolutionary perspectives in the study of species interactions. Its study has elucidated both obvious and more subtle mechanisms, and has documented a range of outcomes. However, the potential for this interaction to inform our understanding of both pure and applied aspects of pollination biology has only begun to be realized.

Key words: Alien plants, climate change, competition for pollination, facilitation, mating system, mechanism, *Lythrum*, *Mimulus*, pollinator visitation, sexual function, invasive species, pollen loss.

INTRODUCTION

Pollination is a classic ecological mutualism in which plants provide floral visitors with rewards such as nectar, and pollinating animals in turn facilitate plant reproduction by dispersing pollen to conspecific plants. Yet this well-recognized mutualism may be substantially altered if co-flowering species compete for the services of shared pollinators. This intriguing counterpoint of mutualistic and competitive interactions may be one reason for a recurring interest among pollination biologists in aspects of competition for pollination (e.g. Robertson, 1895; Waser, 1978*a*, *b*, Brown *et al.*, 2002).

Competition for pollination exemplifies the richness of questions and approaches inherent in pollination biology. Its study touches on a range of disciplines, from animal behaviour to plant morphology, and brings to the fore the diverse ecological and evolutionary perspectives that dominate modern pollination biology. The interaction casts into sharp relief the inherent conflict of interest between plants and pollinators, which must be appreciated to understand this and other mutualisms (Bronstein, 2001). Because competition for pollination, unlike other forms of competition among sessile organisms, acts at a distance that varies with and derives from the animals' perspective, it raises fascinating issues of scale and spatial or landscape context. Furthermore, unlike vegetative competition between plants, competition for pollination directly involves reproductive success.

Competition for pollination also serves as a model for theoretical and experimental dissection of mechanisms. Recognition that competition may occur, not only through reduced visitation of flowers by pollinators, but also through changes in the amount and quality of pollen dispersed, has opened new perspectives on the interaction. Indeed, some of the subtle mechanisms of competition for pollination do not easily fit within common definitions of competition that stress a limited supply of essential resources (e.g. Keddy, 1989), thus forcing us to expand our thinking about competition more generally. Because of the importance of pollination as an ecosystem service (Nabhan and Buchmann, 1997; Aizen *et al.*, 2009; Lonsdorf *et al.*, 2009), competition for pollination has recently resurfaced as a topic of interest in new contexts related to a changing planet.

For these and other reasons, we feel a review is in order. But in truth this is not a typical review. Although we briefly consider past work, our aim is to muse about future research direction. Rather than compile and analyse all past studies, we wish to combine our various perspectives on competition for pollination so as to identify frontiers where further research will be most exciting and profitable. Following a brief historical sketch, we present a heuristic model that delves in more detail into competition for pollination through the two types

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of mechanism already noted: changes in pollinator visitation and in pollen import and export. This conceptual model clarifies, we hope, how different mechanisms influence fitness by different pathways, some of which are subtle and many of which are ripe for investigation. We next turn to several aspects of competition for pollination on a changing planet that, to our minds, invite exploration. Our overall intent is to stimulate thinking and research.

SETTING THE STAGE: A BRIEF HISTORY

Competition via shared pollinators appears to have been recognized first by the American entomologist Charles Robertson. In formulating a Darwinian view of flowering phenology, Robertson (1895, pp. 100–101) reasoned that evolution could produce similar species that flower together at the same time, thus placing 'nearly related forms in competition . . . for the aid of the same pollinating agency'. Such competition, if sufficiently severe, might make it 'advantageous . . . for some of the forms to avoid competition . . . [by modifying] their floral characters so as to attract a different set of visitors, or [by separating] their times of blooming so they may not have to compete with a great many similar flowers for the attention of the same kinds of insects'. In this remarkably modern idea Robertson predicts an evolutionary outcome (which he calls 'avoidance of competition' and we might call resource partitioning), but is not explicit as to *mechanism*. Surely Robertson was thinking of competitors drawing away visitors, and thus of a mechanism involving a reduced number of visits (Fig. 1, top left) – an interpretation consistent with his reference (which persists in much modern literature) to 'competition for pollinators'. At the same time, we are intrigued that Robertson (1895, p. 103) discussed wind-pollinated plants, suggesting that he was on the verge of recognizing mechanisms that do not derive from the behaviour of pollinating animals.

Almost three decades later, Clements and Long (1923, p. 10) echoed Robertson, reasoning that 'competition is regarded as natural when plants of two or more species grow so close or intermingled that their flowers compete for the same group of visitors'. To extend his studies on vegetative competition among plants into the realm of reproductive competition, Frederic Clements undertook experimental studies of the phenotypic traits of flowers that induce insect visits. However, his monograph with Francis Long drew no conclusions as to the commonness of competition for pollination, and did not look beyond the most obvious mechanism involving number of pollinator visits.

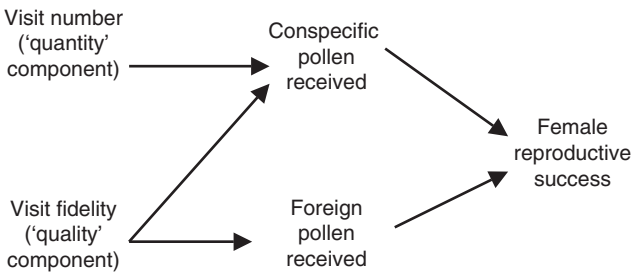

FIG. 1. A starting framework for mechanisms of competition for pollination. Most early authors and many current ones focus on a reduction in number of visits to flowers in the presence of putative competitors. However, changes in visit 'quality' are also possible. In this conceptual model 'quality' refers to the degree to which pollinators restrict their visits to a focal plant species (see Thomson, 1978, 1981; Waser, 1983*b*), whereas Waser (1983*b*) and Waser and Price (1983) used the term to refer to genetic quality of conspecific pollen (one example being the degree of genetic similarity of pollen and pistil; an aspect also treated in this paper), and Herrera (1987) used it simply to refer to the per-visit deposition of conspecific pollen.

Relatively little was added to this picture for several more decades. Various authors advanced 'plausibility arguments' about the reality of competition, based on observations of multiple plant species with morphological similarity and phenological overlap, and the expectation that they should compete because of a surplus of flowers relative to pollinators (e.g. Free, 1968; Hocking, 1968; Mosquin, 1971; Schemske *et al.*, 1978; see also Zimmerman, 1980). Others put forward observations of apparent displacement of phenologies as evidence for resource partitioning as a response to competition (e.g. Macior, 1971; Reader, 1975; Heinrich, 1975; Lack, 1976; Stiles, 1977; Whalen, 1978). But direct evidence of competition, especially experimental demonstration of fitness cost to species in the presence of putative competitors, remained a rarity, as did consideration of mechanisms beyond those involving pollinator visitation (for a review, see Waser, 1983*a*).

Early signs of an expanded conceptual focus can be found. In mixed plantings of two species of *Clarkia*, Lewis (1961) clearly saw the possibility of fitness cost to one species (in the form of loss of ovules due to the formation of sterile hybrids) resulting from the receipt of pollen from other species. This is an aspect of competition derived from the movement of pollinators between the two species, rather than from their relative scarcity, i.e. involving a 'quality' rather than 'quantity' component of pollination (Fig. 1). Levin and Kerster (1967) and Levin (1969), reported similar findings in experimental plantings of *Phlox*, and speculated on phenotypic divergence of species as an evolutionary consequence. Levin and Anderson (1970) and Straw (1972) also provided theoretical models for the ecological dynamics of competition for pollination.

From such work emerged a realization that different mechanisms of competition must be distinguished. In discussing ecological, genetic and evolutionary consequences of hummingbird pollination, Feinsinger (1978) contrasted competition based on visit number with competition based on purity of pollen loads, and echoed the conclusion of Levin and Anderson (1970) that in two-species mixtures 'mixed pollen loads reduce the effective pollination of the rare species'. Waser (1978*b*, 1983*a*) similarly distinguished 'competition through pollinator preference' from 'competition through interspecific pollen transfer'. The latter mechanism includes loss of pollen deposited on foreign flowers, loss of receptive stigma surface, and loss of pollen and ovules in the formation of hybrids of low or zero fitness, all mechanisms involving visit fidelity (Fig. 1, bottom left) rather than visit number (see also Rathcke, 1983).

These advances foreshadowed further empirical progress. The cleanest way to determine whether competition occurs is to add individuals of one species to populations of other species, thus avoiding the confounding of intraspecific and

interspecific effects that occurs when overall plant density is held constant as species composition of a mixture is varied (see Connolly, 1988; Keddy, 1989). Experimental addition of putative competitors for pollination soon demonstrated for several systems that the interaction exists and that it can involve interspecific pollen transfer (e.g. Waser, 1978*a*; Kephart, 1983; Campbell and Motten, 1985; Galen and Gregory, 1989; Jennersten and Kwak, 1991). The more exact mechanistic effects of interspecific pollen transfer were elucidated in a number of cases (Thomson *et al.*, 1981; Waser and Fugate, 1986; Feinsinger *et al.*, 1988; Feinsinger and Tiebout, 1991; Murphy, 1992; Murcia and Feinsinger, 1996; see the recent review by Morales and Traveset, 2008). A finding of competition was far from universal, however: a number of studies detected no effect of plant species on each others' reproductive success (e.g. Mitchell, 1987; Rathcke, 1988; Armbruster and McGuire, 1991; McGuire and Armbruster, 1991; see also the review by Feinsinger, 1987).

Indeed, we must briefly consider the opposite possibility of facilitation rather than competition. If pollinators view flowers of several species as equivalent in a sensory, cognitive, and ultimately behavioural sense, adding more flowers of another species should increase the total number of pollinators attracted to the community. Facilitation is suggested if this also increases the *per-capita* visitation to one or more species [Feldman *et al.* (2004) showed formally that a sigmoidal increase is necessary], although facilitation in visitation still might be accompanied by reduced visit quality (Fig. 1, bottom left), and so in itself does not demonstrate overall reproductive facilitation. The possibility of facilitation was raised by Macior (1971) and Watt *et al.* (1974), and Straw (1972) and Bobisud and Neuhaus (1975) included it in theoretical models of plants interacting via shared pollinators. Waser and Real (1979) presented evidence for 'effective mutualism' between early-flowering and later-flowering species, wherein the first-flowering species supports the pollinators of the next to flower (although in periods of flowering overlap these species might also compete for pollination). Soon thereafter, Thomson (1981) offered an elegant analysis of the spatial domain, explicitly considering how insect behaviour affects and is affected by plants. In the process he provided the first clear empirical demonstration of enhanced per-flower visitation with increasing density in natural plant mixtures. Simultaneously, Schemske (1981) argued that striking floral convergence in two neotropical gingers represents an adaptation derived from facilitation, although he did not present information on pollinator visitation. Rathcke (1983) reviewed the early literature on both facilitation and competition, and extended Thomson's line of thought (Thomson, 1981) to propose that increasing plant density could cause a shift from facilitation to competition.

AN UPDATED CONCEPTUAL FRAMEWORK

The view of competition summarized above has developed in our minds into a more complete picture (Fig. 2). This is indeed a picture, although (as with Fig. 1) we present it as a path diagram. Our goal here is to focus thinking on the issue, emphasizing the mechanistic causes and consequences of pollinator sharing.

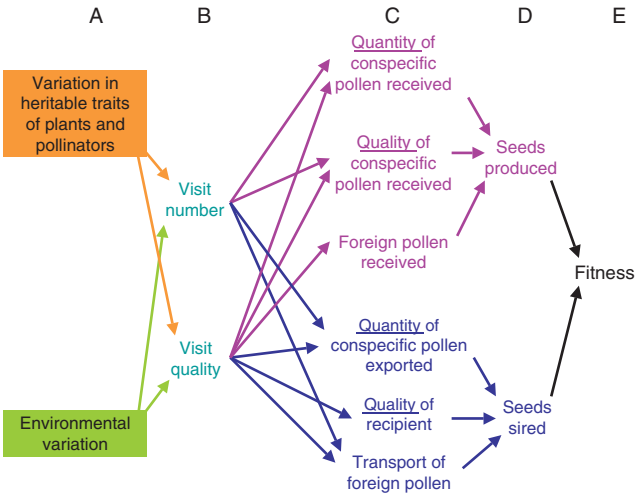

FIG. 2. A more complete conceptual framework for mechanisms of competition for pollination, including effects of the number of visits (their 'quantity') and aspects of their 'quality'. Visit quality in turn might affect the amount of pollen received from conspecifics and competitors, as well as qualities of that pollen. To the left are drivers that determine how the system behaves in space (roughly, ecology) and time (both ecology and evolution). In equating ecology with environmental variability, both the abiotic and the biotic environments are included. The lower portion of the diagram (in blue) indicates pollination success through male sexual function. The upper (pink) indicates female function.

Our expansion of Fig. 1 suggests that the extent to which plant species affect one another's pollination is influenced by the *ecological* context (Fig. 2A, bottom), including pollinator abundance and the number and proximity of conspecific and foreign plants. This context is extrinsic to the focal species being considered, so it is labelled 'environmental variation' to stress its variation in time and space, in itself a critical thing to study. Furthermore, the interactions among plant species are influenced by the *evolutionary* context. This is labelled as 'variation in heritable traits of plants and pollinators' (Fig. 2A, top), again to acknowledge that such variation underlies phenotypic variation intrinsic to the participants such as variation in the behaviour and morphology of pollinating animals and the flowers they visit. Both central tendency and variation in the phenotype evolve via natural selection, in part imposed by the interplay of mutualism and competition, and they represent a legacy from prior generations of the plant–pollinator interaction.

As in Fig. 1, two important general components of pollination are the numbers of flower visits a plant receives, and their quality (Fig. 2B). 'Visit quality' reflects the amount and genetic attributes of the pollen delivered to flowers by animal pollinators. The limits of language are apparent here, because (as hinted by Robertson, 1895) even wind-pollinated plants of one or more species might compete by altering the quantity of pollen received and its genetic properties, including the identities of its conspecific sources and the degree to which it is mixed with 'foreign' pollen, i.e. that of other species (Waser, 1983*a*). Competition for pollination among wind-pollinated species is largely unstudied (but see Niklas and U, 1982; Culley *et al.*, 2002), and should certainly not remain so, but the remainder of our comments return to animal-pollinated species.

Quantity and quality of visits are partly but not completely independent; both respond to certain aspects of pollinator behaviour, such as flower constancy (e.g. Chittka *et al.*, 1999), the time spent probing flowers (e.g. Cresswell and Galen, 1991), foraging posture (e.g. Sigrist and Sazima, 2004), and the extent of grooming (e.g. Harder and Wilson, 1998). Our conceptual framework makes more explicit the mechanisms by which competitors might affect reproduction through changes in visit number and quality. It incorporates the idea that the number and quality of visits can affect the amounts of both conspecific and foreign pollen transferred (Fig. 2C). Additionally, visit quality has the potential to influence the fitness value of that pollen (e.g. degree of kinship of conspecific pollen to the pistil on which it arrives, intrinsic genetic quality of specific donors, diversity of donors, and the effects of foreign pollen on the transport and germination of conspecific pollen). Finally, the framework reminds us that every member of a sexual species has a father and a mother, so that sharing pollinators might affect not only success in receiving pollen, but also success in exporting it to other plants (Fig. 2D, blue portions).

This framework is a *generalization*; each case to which it is applied will require some tailoring to fit specific circumstances. Occasionally it might be possible and profitable to develop and fit a formal path analysis to a tailored version of the general framework, i.e. to treat it as a formal model. However, our own intent with the framework is to present a *heuristic*; a less-formal model intended to guide understanding. It may often serve well as a checklist of major topics to consider in studying any specific facet of competition for pollination. We hope, too, that it will stimulate fresh thinking. Indeed, generating this framework has stimulated us to consider new views on mechanisms of competition involving pollen loss, on the role of community context on competition, and on the effect of competition on plant mating systems and different components of plant fitness. We turn next to these topics.

The importance and magnitude of pollen loss in competition for pollination

A relatively subtle mechanism of competition for pollination involves the loss of pollen on stigmas or other flower parts of a competitor (Morales and Traveset, 2008; Fig. 2C). This may be an important mechanism because of the intrinsic inefficiency of pollination itself. In most animal-pollinated species, even in the absence of competitors, $<1\,\%$ of pollen is exported to conspecifics (Harder and Thomson, 1989; Holsinger and Thomson, 1994; Johnson *et al.*, 2005). This low efficiency follows from factors at several levels (Inouye *et al.*, 1994), including limited pollen pick-up by pollinators (Sahli and Conner, 2007), passive loss during transport (Thomson, 2003), removal of pollen from the pollinator's body by active grooming or preening (Harder, 1990), moving of the pollen to corbiculae or scopae of bees (Thorp, 2000) and pollen deposition on flowers of the same plant (a form of pollen discounting; Rademaker *et al.*, 1997). Even this partial list suggests that pollen might have little prospect of reaching stigmas of other conspecifics, but when we add in competition for pollination the opportunities for loss multiply. Interspecific movements of pollinators may amplify the factors just listed, and can add new possibilities, some of which are noted below. In our conceptual framework (Fig. 2), pollen loss is represented by a reduction in visit quality through reduced pollen receipt or export. A number of questions beg for further attention.

What circumstances encourage pollen loss? Pollen-harvesting visitors such as bees are more likely to cause pollen loss than are non-harvesters or pollinators that groom or preen relatively infrequently (such as hummingbirds; e.g. Schemske, 1975). Likewise, a floral competitor that produces abundant pollen, or that contacts a similar area of the pollinator's body with reproductive parts, might foster more pollen loss (Waser, 1983*a*; Murcia and Feinsinger, 1996; Fig. 2A). All of these factors are also likely to reduce the proportion of pollen carried over to successively visited flowers, and therefore reduce the genetic diversity of pollen deposited on each conspecific stigma (one aspect of quality). It is also possible that the extent of pollinator grooming changes with the presence of a competitor. Investigating these possibilities by determining pollen fate and carry-over patterns (e.g. Thomson, 1986; Morris *et al.*, 1994, 1995; Fenster *et al.*, 1996; Matsumara and Washitani, 2002) would be especially rewarding for plants with a variety of shared pollinators (e.g. birds, bats, insects).

Does pollen loss occur because of co-transport? We use the term 'co-transport' to indicate that pollen of several species is carried by a pollinator (Fig. 2). Limited space on the pollinator's body might restrict the load that can be carried, so that adding pollen of one species reduces the amount of pollen of another species. Likewise, pollen from conspecifics might be buried under pollen from a competitor (e.g. Lertzman, 1981). Such co-transport losses would affect receipt and export not only of conspecific but also of foreign pollen. Although there is an extensive literature on character displacement of floral parts that affect the site of pollen deposition on visitors (e.g. Waser, 1983*a*; Armbruster *et al.*, 1994; Caruso 2000; Muchhala and Potts, 2007), direct exploration of such costs of co-transport seems to be rare [although Waser and Price (1984, p. 266) reported results suggesting no overall cost for one hummingbird-pollinated system].

How does the number of consecutively probed competitor flowers affect pollen loss? Although there is evidence that interspecific movements reduce pollen receipt (e.g. Campbell, 1985; Campbell and Motten, 1985; Feinsinger *et al.*, 1988), little is known about how the *number* of competitor flowers visited affects pollen receipt, and even less about pollen export (but see Murcia and Feinsinger, 1996). Visiting more competitor flowers should generally reduce the amount of pollen of the focal species which is carried, especially when the competitor's floral parts brush pollen off the visitor. But even when pollen is segregated on the pollinator's body, if foragers departing a focal species continue grooming while visiting a competitor the amount of pollen available to deposit on subsequent focal species flowers will decline rapidly, reducing pollen transport (Flanagan *et al.*, 2009).

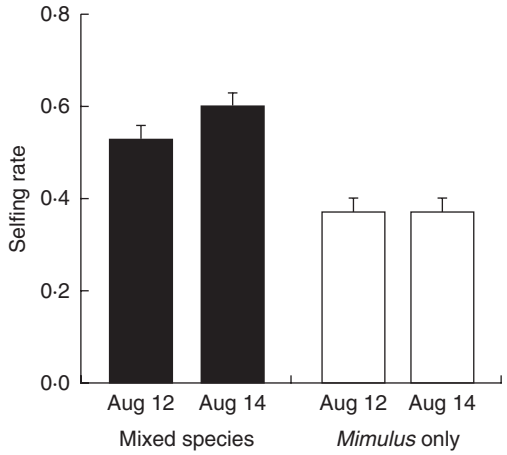

FIG. 3. Effect of the presence of *Lobelia siphilitica* on selfing rate for *Mimulus ringens*. Selfing in *Mimulus* increased significantly when the competitor was present, and this pattern was consistent among days.

Effects of pollinator sharing on plant mating systems

Plant mating systems vary widely within and among populations (Barrett, 2003), and competition for pollination might contribute to this variation (Campbell, 1985). This possibility arises because frequent pollinator movements between co-occurring species may lead to substantial pollen loss and reduced outcross pollen deposition (Fig. 2C). Assuming that the amount of self-pollen arriving on flowers remains unchanged, the proportion of offspring resulting from selfing should increase. Bell *et al.* (2005) found strong support for this hypothesis in a study of *Mimulus ringens*, using experimental arrays of plants with and without a co-flowering competitor, *Lobelia siphilitica* (Fig. 3). To our knowledge, no other studies have directly explored the effects of competition for pollination on selfing rates (but, for a related study, see Fishman and Wyatt, 1999). Additional work is needed to evaluate the generality of these effects in other taxa, and to address additional questions, as follows.

How does competition for pollination affect selfing? Competition for pollination may potentially influence two components of self-fertilization: the amount of selfing within flowers and, if there are multiple flowers, the amount of selfing among flowers on a display (geitonogamous selfing). Relative changes in these two components may depend on the ways competitors influence patterns of pollinator behaviour, and this might affect the overall selfing rate. For example, if the proportion of geitonogamous moves declines in the presence of an attractive competitor, then the decrease in geitonogamous selfing may partially offset any increase in intrafloral selfing due to pollen loss. Through a simple modification of the checkerboard experimental design used by Bell *et al.* (2005) it would be possible to tease apart the relative contributions of competition for pollination to these two forms of selfing. A researcher could manipulate floral displays of the focal species so that half of the displays have a single open flower, and the other half have some set number greater than one.

Do competition-mediated changes in the selfing rate have important effects on plant reproductive success? Increases in the selfing rate are less important if inbreeding depression is weak, since the fitness reduction due to increased selfing is equal to the increase in selfing rate multiplied by the magnitude of inbreeding depression under selfing (Fig. 2C – 'pollen quality', and 2E – 'fitness'). For example, competition for pollination with *Lobelia siphilitica* increased selfing in *Mimulus ringens* by 20 %, and reduced *Mimulus* seed set 37 % (Bell *et al.*, 2005). Since inbreeding depression in *Mimulus ringens* is fairly weak (21 %), the reduction in seed quality in this case had much less of an effect on reproductive success than did the reduction in offspring number. Note that greenhouse measures of inbreeding depression often underestimate field values (Dudash, 1990); if inbreeding depression is higher in the field, the mating system effect would become increasingly important. More work on mating system effects in species or populations varying in selfing rate and inbreeding depression would be informative.

How does competition for pollination influence other aspects of the mating system, such as the diversity of mates? The number and relative abundance of mates contributing to a seed crop can affect reproductive performance, including seed production, fruit maturation, and the vigour of resulting offspring (Karron and Marshall, 1990; Paschke *et al.*, 2002). Competition for pollination may lower mate diversity by reducing the amount of pollen delivered to stigmas, and the distance it moves (Fig. 2C). For example, the diversity of pollen donors siring seeds is strongly influenced by patterns of pollen carry-over (Campbell, 1998; R. J. Mitchell *et al.*, unpubl. res.), and pollen loss due to competitors should reduce the extent of carry-over (Fig. 4). Thus, competition for pollination should reduce both mate diversity and gene dispersal distance (Campbell, 1985). The effects of competition for pollination on mate diversity are likely to be most pronounced in species with limited carry-over, such as those pollinated by bees, or other visitors that groom intensively. Studies that examine how mate diversity and pollen carry-over are affected by competition for pollination would provide important insights.

Multi-species interactions and the effect of community context

Ecological communities are often characterized by their considerable diversity of species and of interspecific interactions, but few studies investigate how this element of the ecological context (Fig. 2A) relates to competition for pollination. There is an especially strong need for manipulative experiments in this area. To date, most experimental studies of competition for pollination (including our own) have focused on pair-wise interactions (there are exceptions; e.g. Feinsinger, 1978; Rathcke, 1988). Assessment of more realistic and diverse community contexts would be valuable (Strauss and Irwin, 2004; Geber and Moeller, 2006; Sargent and Ackerly, 2008), and this suggests several pertinent questions.

Are competitive effects in assemblages of species predictable from pairwise interactions? Few studies have explored the dynamics of competition for pollination between more than two plant

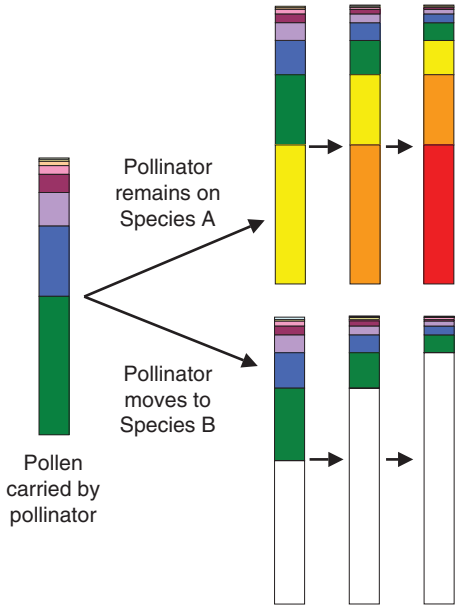

FIG. 4. Potential effects of interspecific pollinator movements on pollen loss and mate diversity. The bar graph on the far left indicates the profile of pollen carried by a pollinator that has been visiting many individuals of Species A (each colour signifies a different donor's pollen). The upper row of pollen profiles indicates the diversity of pollen carried if the pollinator continues visiting Species A (each bar indicates the pollen profile after a successively visited flower). The colours yellow, orange and red correspond to pollen from the next three flowers in the visitation sequence. The lower row of profiles is for a pollinator that moves instead to Species B. As the pollinator visits more flowers of Species B the amount and diversity of Species A pollen should decline.

species. One way to begin investigating multi-species competition would be to plant gardens with different combinations of one, two and three species at a time (e.g. Ghazoul, 2006). Measuring the effect of each species combination on pollinator visitation and reproductive success for a focal species (Fig. 2) would shed light on how the diversity of competitors influences the magnitude of competition for pollination, and its mechanisms. Such experiments might reveal additive effects, in which the result of multispecies competition on reproductive success is a linear combination of the pairwise effects, or instead non-additive or intransitive effects, in which competitive abilities form no consistent hierarchy (Petraitis, 1979). Non-additive effects could strengthen or weaken competition, or perhaps even lead to facilitation. Note that when multiple floral competitors are present, several different mechanisms of competition could occur simultaneously, which might contribute to non-additive and potentially unpredictable outcomes. One non-additive outcome of special interest would be domination of pollination by a plant species that is especially attractive to pollinators (a 'cornucopian species' *sensu* Mosquin, 1971; see also Whitney, 1984; Laverty, 1992), which then greatly reduces success of many or all other species, regardless of their identities. In North America, *Lythrum salicaria* may be an example of such a dominant competitor (Brown *et al.*, 2002; R. J. Flanagan, unpubl. res.).

A limitation to experimental study of large communities is that measuring the response of several species in all combinations geometrically increases the number of sampling units required, making such studies unwieldy even for three or four species (see, for example, Naeem and Wright, 2003). One approach has been to choose one or a few focal species within a larger assemblage and concentrate on these while manipulating aspects of their competitive environment (e.g. Keddy *et al.*, 1994; Bell *et al.*, 2005; Larson *et al.*, 2006; Lopezaraiza-Mikel *et al.*, 2007). This limits the inferences one can draw about multi-species competition for pollination, but may be the only feasible way to proceed in any but the most species-poor communities. Another approach that should not be dismissed is to augment experiments with observational studies of communities of plants that share pollinators (e.g. Feinsinger, 1978; Stone *et al.*, 1998; Larson *et al.*, 2006).

What insights can be gained from a pollination network approach? A distinctly different method for studying multi-species systems is presented by recent work on pollination networks (e.g. Memmott, 1999; Bascompte *et al.*, 2003; Aizen *et al.*, 2008; Stang *et al.*, 2009; Vázquez *et al.*, 2009). Pollination network studies use a form of food-web analysis to investigate the community structure of connections between plants and floral visitors (Fig. 2A). Such studies did not explicitly consider competition for pollination until the pioneering work of Lopezaraiza-Mikel *et al.* (2007). These authors removed flowers of the invasive *Impatiens glandulifera* from some field plots, leaving other plots as controls, and compared pollination networks. Removal substantially affected network structure, with invaded plots having greater pollinator species richness, more total visitors, and more foreign pollen transferred.

What is the scale at which plants affect one another's pollination? Competitive effects involving interspecific pollinator movements surely will be influenced by the scale of individual pollinator foraging ranges, which vary dramatically both within and among species (Steffan-Dewenter *et al.*, 2001; Knight *et al.*, 2005; Greenleaf *et al.*, 2007). For widely foraging pollinators this may mean that plants well-separated from one another still interact through pollinator sharing (as can be true for species separated temporally in their flowering; Waser and Real, 1979). But the factors that determine a pollinator's landscape-scale foraging decisions are not well known, and results might be contingent on idiosyncrasies of each local situation (although see Westphal *et al.*, 2003, 2006; Ricketts *et al.*, 2008). For these reasons, the number and identity of competitors is virtually certain to vary depending on behavioural abilities and propensities, and on ecological context (Fig. 2A). There is a rich, challenging and rewarding field open here for experimental manipulation of plant spacing and context, and comparison of the responses of different pollinator taxa (e.g. small vs. large bees; see Steffan-Dewenter *et al.*, 2001; Kinyo, 2005).

Effects of pollinator sharing on overall reproductive success and fitness

Hermaphroditic plants achieve reproductive success by both mothering and fathering seeds (Fig. 2D). Patterns of selection through maternal and paternal success often (although not always) differ, making measurement of both sexual functions highly desirable for any evolutionary investigation (Ashman

and Morgan, 2004). The effects of pollinator sharing on siring success are likely to resemble those on maternal function in many ways (Fig. 2), such as reduced export of pollen to conspecifics following from grooming-induced pollen loss. However, male function effects do involve some new possibilities. For example, co-transport losses (caused by limited space on the pollinator's body) are likely to have much stronger impacts on pollen export than on import. Also, pollen deposited on foreign stigmas or otherwise lost during visits to a competitor species may reduce the pollen available to sire seeds on conspecifics, discounting the value of that pollen. Very little is known about these or other possible effects of pollinator sharing on pollen export and siring success. One hint is provided by Flanagan *et al.* (2009), who found that pollinator movements between species significantly reduced conspecific pollen deposition. These losses seemed to primarily occur during transport of pollen (e.g. passively during flight or as a result of pollinator grooming) rather than during contact with structures of the competitor plant. Another detailed study (Murcia and Feinsinger, 1996) identified pollen loss to petals of the competitor as the cause of declines in pollen deposition. Distances of pollen export can also be influenced by competitors (Campbell, 1985).

Admittedly, it is much more demanding to measure pollen export and siring success than to assess comparable female measures (Snow and Lewis, 1993). Furthermore, pollination and reproduction are only *components* of fitness, and subsequent events such as dispersal and germination of seeds, emergence of seedlings, and growth of seedlings to sexual maturity may enhance or reduce effects at the pollination stage (e.g. Price *et al.*, 2008; see also Feldman *et al.*, 2004). The prospect of not only measuring seed production and siring success (Fig. 2D), but also performance through the vegetative part of the life cycle (Fig. 2E) is truly intimidating, and we are not aware of any pollination study that has yet achieved this, in any context. We have no desire to set an unachievable standard, but we do advocate further thought on how conclusions about competition for pollination might be altered by including male function and later parts of the life cycle. For some questions, luckily, a partial accounting of fitness may suffice. For example, a study of plant population dynamics in the presence of competitors might reasonably focus on seed production and ignore male sexual function, although some assessment of success in the seedling generation would seem necessary.

COMPETITION FOR POLLINATION ON A CHANGING PLANET

Anthropogenic change dominates current thinking in ecology. After a period of relative quiescence, studies of competition for pollination are appearing that focus on aspects of anthropogenic change. The apparent speed and severity of this change place an additional premium on diversity and originality of approaches.

Competition between native and alien plants

Over the last few centuries humans have transported invasive alien plant species across the globe. Most considerations of invasive plant species focus primarily on their direct vegetative effects on natives, but many of these plants rely on animal pollinators that they may share with natives. A growing body of work demonstrates that invasive aliens may also affect pollination of native species (e.g. Chittka and Schürkens, 2001; Brown *et al.*, 2002; Moragues and Traveset, 2005; reviewed by Bjerknes *et al.*, 2007; Bartomeus *et al.*, 2008*a*, *b*; Munoz and Cavieres, 2008; Aizen *et al.*, 2008). Studies examining the effects of human-introduced plants on native pollination systems represent a promising and important area for expanded research, and the following emphases occur to us.

Are the effects of invasive species context-dependent? Although a growing body of work is accumulating, the effects of invasive plant species on native pollination systems are largely unknown. Evidence to date suggests that the effect of invasives on natives ranges from negative to neutral to positive (Moragues and Traveset, 2005; Totland *et al.*, 2006; Bjerknes *et al.*, 2007; Lopezaraiza-Mikel *et al.*, 2007; Munoz and Cavieres, 2008; Bartomeus *et al.*, 2008*b*). This range of response may reflect differing ecological and evolutionary contexts (Fig. 2A). These contexts vary widely among systems, and it is important to determine which ones are most likely to foster which responses (see Bjerknes *et al.*, 2007). For example, whether invasives compete with or facilitate natives may depend on the relative abundance or density of the invasive species (Bjerknes *et al.*, 2007; Munoz and Cavieres, 2008), on the abundance or morphology of other co-flowering species, and on the regional abundance of pollinators. It would be valuable to determine the role of competition for pollination (if any) in slowing or facilitating invasions, and whether the likely impact of an invader on pollination services can be forecast from floral morphology or the identity and behaviour of its pollinators, both within its ancestral and introduced ranges.

What are the effects of native plants on pollination of crops, and vice versa? Although not traditionally considered invasive species, insect-pollinated crops are often aliens, and may have some of the same effects as invasives on natives with which they share pollinators. Substantial gene flow can occur from genetically modified crops to weedy relatives (Snow and Palma, 1997; Ellstrand *et al.*, 1999), suggesting the possibility of competition through foreign pollen receipt (Fig. 2C). However, the interaction of crops and wild species has seldom been viewed through the lens of competition (but see Free, 1970). Instead, current work has taken the equally interesting, but opposite viewpoint of investigating how pollination of crops is facilitated by native plant species. These studies have demonstrated that pollinators from nearby wild areas often visit and effectively pollinate crops, providing an important and valuable ecosystem service (Kremen *et al.*, 2002; Ricketts *et al.*, 2004; Winfree *et al.*, 2007). Yet, viewed as a competitive interaction, it is apparent that this subsidy may come at a cost to native plants (Fig. 2), just as natives can suffer from sharing pollinators with invasive species. On a longer time scale, crops (and invasives) may, however, support expansion of pollinator populations. This might provide a long-term benefit through greater pollinator service overall (Waser and Real, 1979; Traveset and Richardson, 2006; Tepedino *et al.*, 2008), without removing the possibility

of competition through interspecific pollen transfer. These and other conflicting effects probably depend on ecological context and scale, so untangling them will be a challenge. This challenge is exacerbated by agricultural use of large and mobile colonies of cultivated generalist pollinators such as honey bees, which may link plant species that would otherwise not share pollinators, and whose abundance may not match local floral resources. Invasive generalist pollinators may also complicate the situation.

Does competition for pollination between invasive and native species alter selection on plant traits? Invasives that share pollinators with natives may generate new patterns of natural selection and gene flow with important evolutionary consequences (Fig. 2A). For example, competition might foster character displacement (e.g. Waser, 1978*a*, 1983*a*; Caruso 2000; Armbruster and Muchhala, 2009) or convergence (e.g. Waser and Real, 1979; Schemske, 1981). Most invasions are relatively recent, and can even be dated, so it may be feasible to document evolutionary changes in real time (see Mooney and Cleland, 2001), along with evaluation of the mechanistic basis of selection (e.g. Campbell *et al.*, 1991). For native species with invasive relatives, hybridization may occur (Barbour *et al.*, 2003; Morrison and Mauck, 2007; Johnson and Galloway, 2008). This raises several possibilities, ranging from genetic swamping of natives to introgression of native genes into the genome of the invasive species, which might facilitate expanded invasion.

Climate change, pollinator declines, and competition

Anthropogenic changes in climate are strengthening, and are likely to influence the occurrence and magnitude of competition for pollination by altering ecological context. These influences are virtually certain to be difficult to predict. Climate change should directly and indirectly affect the abundance, geographic range, vigour, phenology and behaviour of both plants and pollinators, all of which can influence interactions among plant species mediated through shared pollinators (Fig. 2; Hegland *et al.*, 2009).

Climate change may most immediately affect plants by altering their resource status – directly through increases in availability of carbon (via increased atmospheric CO_2), or indirectly by increases in nutrients such as nitrogen and phosphorus (mobilized via, for example, increased warm-season precipitation). No work has yet directly investigated how climate change might affect competition for pollination, and other effects on flowering communities are just beginning to be explored (e.g. Price and Waser, 1998, 2000). Immediate plastic responses of plant traits related to pollination are known in some cases, but vary across species. Examples include increased, decreased or unchanged rates of nectar production (Osborne *et al.*, 1997; Rusterholz and Erhardt, 1998); increases in numbers of flowers produced by some but not all species (Osborne *et al.*, 1997), and other changes that might differentially alter attractiveness to pollinators (Wookey *et al.*, 1993). How such responses would affect any element of competition for pollination in a wild community (and with independent responses of different species of plants and pollinators to climate change) requires additional investigation.

Declines in pollinator populations have been reported around the globe (e.g. Buchmann and Nabhan, 1996; Biesmeijer *et al.*, 2006; Colla and Packer, 2008; Goulson *et al.*, 2008), and may in part be the result of climate change (Allen-Wardell, 1998; Committee on the Status of Pollinators in North America, 2007; Fig. 2A). In turn, declines in plant populations may be linked to those of pollinators (Biesmeijer *et al.*, 2006). With such interdependent population dynamics, forecasting the outcome is uncertain – the future may bring a shortage of pollinators relative to plants at some times and places, and a shortage of plants relative to pollinators in others. When there is a shortage of pollinators, forms of competition for pollination derived from changes in visit number should increase (Fig. 2B; see Vamosi *et al.*, 2006). In this situation, pollinators would face a world of relatively under-visited flowers (consequently rich in nectar and pollen), and might therefore reduce their visitation to less-rewarding species or avoid these entirely. Either option would reduce success through both female and male sex functions for the undervisited species. Conversely, if there is a shortage of flowers relative to pollinators, pollinators might broaden their diets, and therefore increase competition through mechanisms derived from a change in visit quality (Fig. 2). Pollinators facing a world depleted of flowers should be less choosy and deposit more foreign pollen. Over the longer term, as declines in populations of plants and animals lead to local extinctions (Biesmeijer *et al.*, 2006, Colla and Packer, 2008; Goulson *et al.*, 2008), and as novel communities of mutualists and antagonists are assembled (e.g. Pitelka *et al.*, 1997; Memmott *et al.*, 2004), competition for pollination is likely to change in unpredictable ways, but could well intensify. Evolutionary responses are also likely (Fig. 2A).

Finally, it seems almost certain that climate change will affect the ecological context by altering the phenological synchrony of interacting species. After all, different species of plants and pollinators respond to different environmental cues in individually differing ways (e.g. Inouye *et al.*, 2000, Lyon *et al.*, 2008). Changes in phenology will alter not only the extent to which different plant species overlap in flowering time, but also their synchrony with different pollinator species (Memmott *et al.*, 2007). Experimental studies of such effects are exceptionally challenging because of the difficulty of manipulating plants on a scale that also will affect mobile pollinators.

CONCLUSIONS

We have attempted here to add our own ideas to a conceptual framework of competition for pollination that has developed over many generations of biologists, and to organize our thoughts on exciting future research avenues in part around this framework. We make no claim to encyclopedic coverage of previous work or future possibilities. We personally find competition for pollination an exciting and intriguing interaction, and our interest has grown rather than diminished with time. We hope that readers will be stimulated by the ideas we have collected, and we especially look forward to completely fresh thinking that goes beyond this work.

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