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VIEWPOINT

Ecology and evolution of plant–pollinator interactions

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• *Background* Some of the most exciting advances in pollination biology have resulted from interdisciplinary research combining ecological and evolutionary perspectives. For example, these two approaches have been essential for understanding the functional ecology of floral traits, the dynamics of pollen transport, competition for pollinator services, and patterns of specialization and generalization in plant–pollinator interactions. However, as research in these and other areas has progressed, many pollination biologists have become more specialized in their research interests, focusing their attention on either evolutionary or ecological questions. We believe that the continuing vigour of a synthetic and interdisciplinary field like pollination biology depends on renewed connections between ecological and evolutionary approaches.

• *Scope* In this Viewpoint paper we highlight the application of ecological and evolutionary approaches to two themes in pollination biology: (1) links between pollinator behaviour and plant mating systems, and (2) generalization and specialization in pollination systems. We also describe how mathematical models and synthetic analyses have broadened our understanding of pollination biology, especially in human-modified landscapes. We conclude with several suggestions that we hope will stimulate future research. This Viewpoint also serves as the introduction to this Special Issue on the Ecology and Evolution of Plant–Pollinator Interactions. These papers provide inspiring examples of the synergy between evolutionary and ecological approaches, and offer glimpses of great accomplishments yet to come.

Key words: Floral traits, generalization and specialization, global change, male fitness, mating systems, multiple paternity, plant–pollinator networks, pollen and gene dispersal, pollinator behaviour, pollination syndromes, pollination webs, self-fertilization.

INTRODUCTION

Research on plant–pollinator interactions requires and invites a variety of viewpoints and conceptual approaches, ranging from developmental biology to community ecology, animal behaviour to floral evolution, and genetics to ecosystem studies (Chittka and Thompson, 2001; Harder and Barrett, 2006; Waser and Ollerton, 2006). These diverse approaches reflect the two historic starting points for the discipline. One approach emphasized detailed observation of floral mechanisms and the natural history of the ecological relationships between plants and pollinators, and originated with pioneering work by Sprengel (1793), Müller (1873) and Robertson (1895). The second approach focused on evolutionary processes that might affect and be affected by pollination, beginning with the insightful work of Darwin (1862, 1876, 1877). Both views have greatly expanded and matured since their origins, but remained largely separate until the mid 20th century, when experimental studies of mechanisms were increasingly used to investigate questions about the ecology and evolution of pollination within a strong theoretical framework (e.g. Bateman, 1947). The field flourished in the 1960s and 1970s with this unification of pattern and process (e.g. Baker, 1963; Grant and Grant, 1965; Macior, 1966; Levin and Kerster, 1969*a*, *b*; Levin and Anderson, 1970; Linhart, 1973; Feinsinger, 1978; Waser, 1978; Thomson and Plowright, 1980), a trend that mirrored the development of the fields of ecology and evolution at large (e.g. Connell, 1961; Grant, 1963; Paine, 1966).

During the early 1980s publication of two seminal edited volumes (Jones and Little, 1983; Real, 1983) stimulated a flurry of new research that continues today. From these works emerged several themes of continuing interest in the study of pollination biology, such as the functional ecology of floral traits, the dynamics of pollen transport, competition for pollinator services, niche relationships, and the community ecology of pollination. As research on these questions progressed, many pollination biologists became more specialized in their interests, as noted by several authors (e.g. Harder and Barrett, 1996; Holsinger, 1996). Such specialization in evolutionary and ecological perspectives can result in a separation of evolutionary and ecological approaches. However, the continuing vigour of a synthetic and interdisciplinary field like pollination biology depends on renewed connections between evolutionary and ecological perspectives.

This Special Issue aims to renew the dialogue between subfields within pollination biology (Fig. 1), to draw attention to recent advances in both evolutionary and ecological approaches to the topic, and to highlight important avenues for future research. Here we discuss case studies on two themes in pollination biology at the interface of evolutionary and ecological study: (1) the link between pollinator behaviour and plant mating patterns and (2) generalization and specialization in pollination

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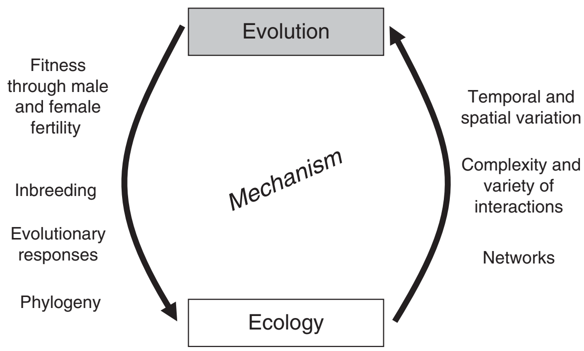

Fig. 1. Conceptual representation of the interplay between ecology and evolution in the study of plant–pollinator interactions. Research in pollination biology provides the opportunity to unite both ecological and evolutionary perspectives through the mechanism of pollination.

systems. We provide a historical perspective on these two themes and discuss how contributions to this Special Issue advance our understanding of the evolutionary and ecological perspectives within each of them. Throughout, we focus on pollination mediated by biotic pollinators; Friedman and Barrett (2009, this issue) provide insight into the evolutionary ecology of wind-pollinated plants. We then highlight how recent progress on mathematical models and synthetic analysis has increased our understanding of pollination biology, especially in human-modified systems. We conclude with some suggestions for future investigations that we hope will further unite research in evolutionary and ecological pollination biology.

CASE STUDY I: LINKING POLLINATOR BEHAVIOUR TO PLANT MATING PATTERNS

Flowering plants cannot directly control gamete receipt or export. Instead, nearly three-quarters of Angiosperms rely on animal vectors to move pollen among flowers (National Research Council, 2007), a form of indirect control mediated through pollinators. The resulting patterns of pollen dispersal often reflect pollinator foraging behaviour, and may not optimize the quality or quantity of matings (Campbell and Dooley, 1992). For example, foraging pollinators typically move short distances between flowers, often visiting neighbouring plants (Bateman, 1947; Levin and Kerster, 1969*a*, *b*) and probing several flowers in sequence on multi-flower displays (Robertson, 1992). These foraging behaviours have important implications for plant mating. Short pollinator flights may limit the extent of pollen-mediated gene dispersal, influencing the genetic structure of populations (Wright, 1931; Turner *et al.*, 1982), neighbourhood size (Wright, 1946; Levin and Kerster, 1968; Crawford, 1984; Levin, 1988), and the frequency of bi-parental inbreeding (Ellstrand *et al.*, 1978; Griffin and Eckert, 2003). In self-compatible species the tendency of pollinators to visit several flowers in sequence on a single plant also increases the opportunity for geitonogamous (among-flower) self-pollination and a resulting increase in the selfing rate (Harder and Barrett, 1995, 1996; Snow *et al.*, 1996; Karron *et al.*, 2009, this issue). In self-incompatible species geitonogamous pollination can reduce seed production if self-pollen clogs stigmas, interferes with outcrossed pollen-tube growth, usurps ovules, or increases fruit abortion, and can reduce siring success through pollen discounting (reviewed in Snow *et al.*, 1996).

Studies combining observations or manipulations of pollinator behaviour with measurement of pollen-mediated gene dispersal can greatly enhance our understanding of the mechanisms responsible for mating patterns (Harder and Barrett, 1996). For example, although both pollinator movements and gene movements tend to occur over short distances, comparisons in the same populations indicate that pollinator flight movements usually underestimate the extent of pollen-mediated gene dispersal (Schaal, 1980; Levin, 1981; Fenster, 1991; Karron *et al.*, 1995*b*). This discrepancy is especially apparent when pollen carry-over is extensive (Broyles and Wyatt, 1991).

Research comparing the movements of different pollinator classes with the resulting patterns of pollen and gene dispersal can highlight an important mechanism for spatial and temporal variation in gene movement (Young, 2002; Adler and Irwin, 2006; J. Brunet and K. Holmquist, University of Wisconsin-Madison, pers. comm.). This integrated approach also holds promise for studies of long-distance pollinator and gene movement (e.g. Ellstrand *et al.*, 1989; Nason *et al.*, 1998; Sork *et al.*, 1999; Kreyer *et al.*, 2004). Surprisingly little is known about how these two long-tailed distributions influence each other. Quantifying landscape-scale movements is also important for understanding the factors influencing genetic differentiation among populations (Slatkin, 1985) and the potential for gene flow in genetically modified crop plants (Hayter and Cresswell, 2006).

Pollinator foraging patterns strongly influence selfing rates within and among populations (Karron *et al.*, 1995*a*, 2004; Harder and Barrett, 1995), and may therefore play an important role in the evolutionary stability of mixed-mating systems, a topic of considerable recent theoretical research (e.g. Goodwillie *et al.*, 2005; Johnston *et al.*, 2009). Several workers have recently shown that selfing rates are influenced by spatial and temporal variation in the composition and abundance of the local pollinating fauna (Brunet and Sweet, 2006; Kameyama and Kudo, 2009, this issue; Whelan *et al.*, 2009, this issue). Selfing rates may even vary on much finer spatial scales, due to the effects of the composition of co-flowering species competing for pollination (Campbell, 1985; Bell *et al.*, 2005; Mitchell *et al.*, 2009, this issue), variation in floral morphology among neighbouring plants (Karron *et al.*, 1997; Medrano *et al.*, 2005), and variation in the order of pollinator probes on individual floral displays (Karron *et al.*, 2009, this issue).

Patterns of pollinator visitation are also thought to influence several other important aspects of mating systems, such as variation in male fertility (Devlin *et al.*, 1992; Conner *et al.*, 1996; Irwin and Brody, 2000), patterns of mate diversity at the whole-plant level (Nason *et al.*, 1998), and patterns of multiple paternity within fruits (Dudash and Ritland, 1991; Campbell, 1998; Karron *et al.*, 2006). These topics have received much less attention than studies of selfing rates, yet they are essential for a meaningful understanding of mating patterns. Indeed, evaluation of fitness through pollen donation is still a rarity in pollination studies (Bernasconi, 2003), even though any study that examines fitness in hermaphroditic plants is only half complete if male function is not measured. Likewise, the existence, magnitude and mechanisms of multiple paternity and mate diversity have important implications for plant evolution (Karron and Marshall, 1990; Bernasconi *et al.*, 2004), but remain poorly understood (Bernasconi, 2003).

CASE STUDY II: GENERALIZATION AND SPECIALIZATION IN POLLINATION SYSTEMS

Plant–pollinator interactions are often viewed as mutualistic, tightly coevolved, relationships. Despite the potential for mutual benefits, these interactions also entail inherent conflicts (e.g. Waser, 1983; Pellmyr and Huth, 1994; Thomson, 2003), which may vary spatially and temporally (Thompson, 1988) and need not involve tight, pairwise coevolution (Schemske, 1983; Herrera, 1993). Recognition of these complexities has provided an important framework for research on pollination biology, and several articles in this Special Issue address these conflicts (Bronstein *et al.*, 2009; Herrera *et al.*, 2009; Irwin, 2009).

The shifting costs and benefits of plant–pollinator interactions may also play an important role in determining whether plant–pollinator interactions are more ‘generalized’ or ‘specialized’. The contrast between generalized and specialized interactions dates back to Faegri and van der Pijl’s (1971) descriptions of ‘pollination syndromes’, and in less explicit form to Sprengel (1793), Müller (1873), Robertson (1895) and Darwin (1862). If a plant species has many different visitor taxa that provide similar pollination services, and if costs of the interaction are comparable, the net benefits to plants should also be similar and there is little incentive for plants to specialize on attracting a particular group of pollinators. On the other hand, if some floral visitors are more effective in the quantity or quality of pollen transfer (see Muchhala *et al.*, 2009, this issue), selection should favour traits promoting these effective pollinators (Aigner, 2001; Whittall and Hodges, 2007; Brunet, 2009, this issue; Schlumpberger *et al.*, 2009, this issue). Such selection favouring specialization on particular pollinator species or functional groups would provide a useful mechanism for the evolution of ‘pollination syndromes’, and might explain why some plants have traits that appear to restrict the suite of visitors and pollinators.

Two developments in the mid-1990s led to an expansion of research on generalization and specialization. First, an infusion of ideas from community ecology and social science network theory opened new avenues for research on pollination-based food webs and networks (e.g. Memmott, 1999; Olesen *et al.*, 2007; Stang *et al.*, 2009, this issue; Vázquez *et al.*, 2009, this issue). This work has promoted a detailed understanding of the complex web of interactions between plants and pollinators, and provided a necessary counterweight to the understandable (and perhaps even necessary) simplifications of earlier work that emphasized one or a few pollinators of one or a few plant species. These methods have brought to light several new observations that bear on the topic of generalization and specialization. For example, the findings that specialized plant species tend to have generalized pollinators, and specialized pollinators tend to visit generalized plant species (see Vázquez *et al.*, 2009, this issue, and references therein), has forced many to rethink just what is meant by the terms generalization and specialization, and to more consciously recognize the distinction between the viewpoints of plants and pollinators. Furthermore, the nested structure of plant–pollinator networks (meaning that specialists interact with subsets of the interaction partners of generalists; Bascompte and Jordano, 2007; Vázquez *et al.*, 2009, this issue) has important implications for the conservation and stability of pollination interactions. For example, nestedness confers stability in plant–pollinator networks in simulated pollinator extinctions (Memmott *et al.*, 2004). The degree to which these simulations mirror the natural world is not yet known.

Second, researchers began to re-examine the concept of ‘pollination syndromes’ (Waser *et al.*, 1996), and this helped renew interest in how ecological interactions between plants and pollinators affect evolutionary patterns. This vigorous discussion largely revolves around two contradictory observations: (a) plants show remarkable diversity in morphology, scent and reward, and are often recognized as being clustered in phenotype-space around some of the classic ‘syndromes’ (Ollerton, 1996); and (b) flowers are often visited by a wide array of potential pollinators that do not fit the traditional ‘syndromes’. This disconnect between (a) pattern and (b) process has sparked a healthy and wide-ranging discussion about many facets of the pollination-syndrome concept, and about the ecology of species’ interactions and the evolution of adaptations in general (Fenster *et al.*, 2004; Wilson *et al.*, 2004; Armbruster and Muchhala, 2009; Ollerton *et al.*, 2009*a*, *b*, this issue). Many of the papers in this Special Issue contribute to this topic, often using new tools to re-examine these ideas (e.g. Armbruster *et al.*, 2009; Ollerton *et al.*, 2009*a*, *b*). Progress has been most rapid when both ecological and evolutionary approaches are combined, for example by documenting both patterns of diversity and the pollination services provided by different visitor taxa (Castellanos *et al.*, 2003; Wilson *et al.*, 2007), or uncovering the molecular basis of species’ differences and their ecological effects (Schemske and Bradshaw, 1999; Bradshaw and Schemske, 2003).

THEORIES, MODELS AND SYNTHESES IN POLLINATION SYSTEMS

As the field of pollination ecology has grown and expanded, integration of theory, modelling and synthesis with field observations and experiments (Kareiva, 1989; Pickett *et al.*, 1994; Werner, 1998) has provided opportunities to generalize and move beyond system-specific studies. Research in pollination biology has been at the forefront of theory-testing and model-building. In evolutionary biology, pollination systems have provided some of the best tests of theories of evolution by natural selection and the adaptive nature of floral traits (Levin, 1985; Nilsson, 1988; Hodges, 1995; Campbell *et al.*, 1996; Galen, 1996; Schemske and Bradshaw, 1999; Campbell, 2009, this issue; Conner *et al.*, 2009, this issue, and references therein). In ecology and animal behaviour, pollinators have been used as models in tests of optimal foraging theory (e.g. Pyke, 1984). Foraging models and simulations of pollinator flight movements are now being extended to understand the consequences for pollen movement, gene flow and patterns of mating (Cresswell, 2005; Ohashi and Thomson, 2009, this issue).

Models and syntheses are also being employed to study pollination biology in human-dominated systems, which are the fastest growing habitats worldwide (Turner *et al.*, 1990; Vitousek, 1994; McKinney, 2002). Plants and their pollination systems are embedded in these human-modified landscapes (e.g. McFrederick and LeBuhn, 2006; Cheptou and Avendaño, 2006; Winfree *et al.*, 2007) and pollination, especially in agricultural landscapes, confers billions of dollars annually as an ecosystem service (Losey and Vaughan, 2006). Models are being developed to predict the relative abundance of pollinators in agricultural habitats based on landscape-level field parameters, such as pollinator nesting resources, floral resources and pollinator foraging distances (Lonsdorf *et al.*, 2009, this issue). Models and syntheses are also being used to predict the consequences of loss of pollinators on crop yield (Aizen *et al.*, 2009, this issue). These models have become essential for developing land-use management practices and policies that promote pollinator conservation and pollination services. Moreover, both comparative studies and quantitative syntheses are proving integral in the study of pollination in disturbed landscapes. Pollination of invasive versus native congeners is only beginning to be examined (e.g. Brown *et al.*, 2002; Kandori *et al.*, 2009; Mitchell *et al.*, 2009, this issue; T. Knight, Washington University St. Louis, pers. comm.), and quantitative syntheses are starting to provide an enhanced understanding of levels of pollen and pollinator limitation (Ashman *et al.*, 2004; Hegland *et al.*, 2009). The next step is to link the ecology of human-modified systems to the evolution of plant–pollinator interactions, potentially through changes in patterns of natural selection.

FIG. 2. One important question to be addressed in the coming decade is how the genetic composition of pollen on a pollinator's body compares to the genetic composition of pollen deposited on the next conspecific stigma probed by that pollinator. In this figure two very different floral visitors (*Bombus vagans* and a Halictid bee) are shown visiting *Dalea purpurea* (Fabaceae). These visitors handle flowers differently, carry pollen on different parts of the body, have different foraging movement patterns, groom differently, contact different floral parts, carry different amounts of pollen, and probably cause very different patterns of pollen carry-over. Each of these differences might affect the genetic composition of pollen carried on the body and deposited on stigmas. Image by J. Karron.

AVENUES FOR FUTURE RESEARCH

Many challenges remain in linking the evolution and ecology of plant–pollinator interactions. In this section we identify some of the areas that would benefit from additional dialogue and research, and highlight some important unanswered questions. While this is by no means an exhaustive list, we hope these questions – as well as those identified in the preceding sections – will inspire future research.

What factors influence male reproductive success in plant populations?

Equipped with powerful molecular genetic tools and new analytical methods for paternity assignment, pollination biologists have begun to tackle important questions concerning the causes and consequences of variation in paternal success (Conner *et al.*, 1996; Cruzan, 1998; Barrett, 2003; Bernasconi, 2003; Burczyk *et al.*, 2006). This aspect of plant–pollinator interactions can be technically challenging to study, but is critically needed because it both addresses an essential component of fitness and highlights the mechanisms of pollen transfer. Despite well-developed theory concerning the dynamics of pollen transport (Harder and Barrett, 1996; Harder and Wilson, 1998), there are no studies documenting the genetic composition of pollen on a pollinator's body (Fig. 2). However, such investigations are now possible through direct microsatellite genotyping of individual pollen grains (Matsuki *et al.*, 2008). Genetic analysis of pollen sampled from different locations on a pollinator will help refine models of pollen dispersal (Harder and Barrett, 1996; Harder and Wilson, 1998), since researchers will be able to explore whether sites exposed to pollinator grooming differ in pollen donor composition from 'safe' sites not exposed to grooming (Harder and Wilson, 1998). Reseachers will also be able to test whether layers of pollen on a pollinator's body differ in pollen-donor composition (Harder and Wilson, 1998).

Some of the most informative studies will combine detailed genetic analyses with rigorous field experimentation (Barrett, 2003). For example, experiments comparing sire profiles and effective mate number for flowers receiving a single pollinator probe and flowers receiving multiple pollinator probes can provide important insights into the mechanisms of multiple paternity and the opportunity for competition among pollen grains (Karron *et al.*, 2006). Recent theoretical work suggests that variation in the number of effective mates in a fruit may also reflect patterns of pollen carry-over (Mitchell *et al.*, unpubl. res.), which often differ markedly for grooming pollinators, such as bumble-bees, vs. non-grooming pollinators, such as hummingbirds (Waser, 1988; Castellanos *et al.*, 2003). Direct genetic tests comparing the effects of different pollinator classes on progeny genetic composition are rare, especially within populations (Brunet and Sweet, 2006), and have not yet quantified effects of pollinator class on the diversity of mates siring progeny within fruits.

Experimental studies will also enhance our understanding of the effects of floral design and display on patterns of male fertility (Campbell, 1998; Elle and Meagher, 2000; Barrett, 2003). How do floral traits influence male fitness and functional gender? Are male and female reproductive success positively correlated or is there a trade-off between these fitness components (Conner *et al.*, 1996; Ashman and Morgan, 2004; Hodgins and Barrett, 2008)? Few paternity studies have explored the role of ecological context, such as the effects of habitat fragmentation (Trapnell and Hamrick, 2006) or the role of competitors for pollination (Mitchell *et al.*, 2009, this issue), and we believe such studies will further advance our understanding of the complex factors influencing mating patterns in flowering plant populations. Finally, while studies on multispecies' interactions involving plants, pollinators and antagonists (such as herbivores and nectar robbers) often provide the caveat that male function should be measured, surprisingly few experimental studies have done so (but see Irwin and Brody, 2000; Paige *et al.*, 2001). Most studies (including many of our own) either don't measure male reproductive success, or still rely on indirect estimates such as flower production, pollen removal or pollen (fluorescent dye) donation; these estimates of male plant function may or may not be tightly correlated with realized seeds sired (Campbell, 1991). Although there is also a strong need for more studies on selection through female reproductive success, incorporating estimates of male reproductive success into studies of multispecies' plant–pollinator and plant–herbivore interactions still represents a relatively unexplored frontier. Study of selection through both female and male reproductive success, perhaps using path analysis to separate direct and indirect effects, should yield novel insights into how pollinators and herbivores affect whole-plant fitness.

How does spatial and temporal variation affect webs of plant–pollinator interactions?

Like classic food webs, pollination webs can be imposingly complex. To understand how such webs are affected by internal and external drivers, we must account for changing ecological contexts at a variety of spatial and temporal scales (Alarcón *et al.*, 2008; Petanidou *et al.*, 2008). Whether such effects are non-linear, stochastic or consistent, and whether different pollinators or plants are substitutable, additive or non-additive in effect is not known, but such insights are essential for further empirical and theoretical progress. Moreover, the webs produced to date either treat species' interactions as binary (present/absent) or represent the magnitude of their interaction as a function of visitation rate or pollen transport (e.g. Memmott, 1999; Olesen and Jordano, 2002; Lopezaraiza-Mikel *et al.*, 2007). These networks have provided great insight into the complexity, community structure and evolutionary ecology of species' interactions (e.g. Bascompte *et al.*, 2006; Petanidou *et al.*, 2008; Vázquez *et al.*, 2009, this issue); however, no pollination webs have been produced that estimate the magnitude of the interactions (i.e. no studies measure interaction strength; Paine, 1992), in part because the experimental manipulations required to make such estimates would be intractable in a full web. In food-web studies there is recognition that networks of species' interactions may not predict the dynamics of these systems (Paine, 1988). There is similar recognition of this limitation in pollination networks, although there is some suggestion that rates of visitation may be sufficient as estimates of the strength of interactions (Vázquez *et al.*, 2005). Nonetheless, developing experimental methods to estimate the strength of interactions in pollination webs from both the plants' and the pollinators' perspective is critical for understanding the dynamics of native plant–pollinator communities and the response of these communities to environmental perturbations. These experimental manipulations would be most tractable if developed for a subset of species in the plant–pollinator webs; such an approach focusing on experiments in subsets of interactors has provided valuable insight into food webs (Paine, 1992).

What are the ecological and evolutionary consequences of global environmental change for plant–pollinator interactions?

There is growing recognition that plant–pollinator interactions can be drastically influenced by anthropogenic changes to ecosystems. Climate change, habitat fragmentation, agricultural intensification, urbanization, pollution, pesticides and species' invasions all have the potential to affect plant–pollinator interactions directly and indirectly (Aizen and Feinsinger, 1994; Kearns *et al.*, 1998; Kremen *et al.*, 2002; Memmott *et al.*, 2007; Winfree *et al.*, 2007; Hegland *et al.*, 2009). While research has documented responses of plants, pollinators and interactions to these anthropogenic changes, most studies have been observational in nature, and few experimental studies tease apart the mechanisms and pathways of interactions.

In order to make predictions about when and how anthropogenic change alters plant–pollinator interactions we need to elucidate underlying mechanisms, especially those most directly linked to the disturbance. The most extensive work detailing both pattern and mechanism comes from research addressing the effects of invasive plants on native plant–pollinator interactions and on native plant reproductive success (Chittka and Schurkens, 2001; Brown *et al.*, 2002; Traveset and Richardson, 2006; Bjerknes *et al.*, 2007; Flanagan *et al.*, 2009). Despite recent advances on this topic, there are still no studies that address the degree to which invasive plants affect native pollinator populations (Traveset and Richardson, 2006; Tepedino *et al.*, 2008) nor whether changes in plant–pollinator interactions due to species' invasion affect patterns of natural selection on native species. Studies of natural selection on traits of native species could be coupled with experimental manipulation of the presence or abundance of invasive species to provide new insights on selection through pollination, and the influence of invasive species. Likewise, hand-pollination experiments that isolate the effects of invasive plants on native-plant pollination and reproduction are also still lacking. In particular, if studies find differences in native plant-pollinator visitation and seed production in the presence vs. absence of an invasive plant, hand-pollination experiments are needed to ensure that differences in seed production are actually being driven by differences in pollination and not some unmeasured mechanism (such as competition for light or nutrient resources). Studies that manipulate both invader presence and hand-pollination (pollen supplemented or control) in a factorial design would provide the greatest ecological insight. If differences in seed production were driven by differences in pollination, these studies would find a statistical interaction between invasion and hand-pollination. Similar successes and shortfalls are also apparent in research on the impacts of agricultural intensification on crop and wild plant–pollinator interactions (Kremen *et al.*, 2002).

Ecology and evolutionary biology form the foundation of pollination biology, and some of the most exciting advances in this discipline have resulted from research combining these two perspectives. This Special Issue provides inspiring examples of the advances that result from these combined perspectives, and offers glimpses of great accomplishments yet to come. Here we have tried to highlight some of the strengths of this field, and a sample of new and important questions that are emerging. These research areas provide important avenues for potentially transformative advances in understanding the interactions between plants and pollinators.

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