Effects of alien species on plant-pollinator interactions: how can native plants adapt to changing pollination regimes?

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Abstract
Invasive alien species are of major concern in the management and conservation of habitats and species worldwide. Recent research has highlighted the importance of alien species' integration into plant-pollinator interactions, and its possible consequences for native species. Here we focus on the implications of alien plant and animal invasion for the pollination and reproductive success of native plants. We review the different mechanisms by which native plants might adapt to novel pollination regimes imposed by invading plants and animals, mainly changes in flower morphology and attractiveness, changes in blooming time and location, and shifts to reproductive modes that are independent of animal visitation. These adaptations may allow some native plant species that are negatively affected by invasive species to survive alongside the invaders. However, not all native plant populations and species are equally likely to undergo such adaptation. We outline the main factors that are likely to affect the potential for such adaptive processes across different taxa and ecosystems, and highlight the need to evaluate these factors in future research. Understanding the mechanisms by which native plants adapt to changing pollination regimes and the main characteristics that allow them to do so may provide an important tool for managing and conserving diversity and functionality in pollination networks.

Invasive alien species are a major concern in the management and conservation of habitats and species worldwide (Crooks 2002; Bax *et al.* 2003; Levine *et al.* 2003; Vilà *et al.* 2010). The direct effects of these species may further cascade in the ecosystem and affect inter- and intraspecific ecological interactions. The introduction of alien plants and animals can have severe consequences not only for individual native plant and pollinator species, but also for their ecological interactions through plant-pollinator networks (Morales and Traveset 2009; Dohzono and Yokoyama 2010; Schweiger *et al.* 2010). Integration of alien plant and pollinator species into pollination networks inevitably creates new interactions and may also affect the strength and quality of existing ones. These changes are open niches for novel evolutionary adaptations of both alien and native species (Mooney and Cleland 2001). However, research in this topic is very limited, and has focused mostly on adaptations of alien plant species to pollinator-independent reproduction modes (Barrett *et al.* 2008). We know of no study investigating adaptations of native plant and pollinator species to invaders, and the ecological and possibly evolutionary consequences of these adaptations in the context of plant-pollinator networks. Such adaptations might have far-reaching ecological and evolutionary implications, as has been shown in plant-herbivore and predator-prey interactions (Cox 2004). Here we outline the main effects of species invasions on plant-pollinator interactions, and deduce the main adaptive mechanisms that native plant species can exhibit in response to changes in

their pollination regime. Finally, we explore the characteristics of plant populations that are likely to affect their probability of exhibiting such adaptations and their conservation implications.

Effects of alien plant and animal species on native plant pollination

Several groups of alien organisms have been shown to affect native plant pollination. Most research has focused on alien plants (Morales and Traveset 2009) and flower visitors (Lach 2003; Dohzono and Yokoyama 2010); however, other groups, such as alien herbivores and predators, can also be influential (Traveset and Richardson 2006). In the following we explore the possible effects of different groups of alien organisms on pollination of native plants.

Effects of alien plants

Alien plant species can exert both positive and negative effects on native plant pollination. Especially important in this regard are alien plant species that are highly attractive for pollinators. Such species often display conspicuous advertizements such as large, showy flowers, offer high rewards for their visitors, and/or employ a super-generalist pollination strategy (Morales and Traveset 2009). The attraction of pollinators to these invasive plants can have major effects on native plant species in the invaded community (Bjerknes *et al.* 2007; Morales and Traveset 2009). The frequency of visits to native plants can either decrease, if pollinators visit alien plants instead of natives (pollinator usurpation; Chittka and Schürkens 2001; Brown *et al.* 2002) or increase, if more pollinators are attracted to native plants that grow near highly attractive aliens (pollinator facilitation; Moragues and Traveset 2005; Nielsen *et al.* 2008). In addition, the composition of the pollinator fauna that visits native species can be changed, possibly affecting also the quality of individual visits (Ghazoul 2002; Muñoz and Cavierez 2008). The movement of pollinators between alien and native plants may increase heterospecific pollen deposition on native plant stigmas (Grabas and Laverty 1999; Ghazoul 2002), as well as loss of native plant's pollen (Larson *et al.* 2006; Flanagan *et al.* 2009); both of these processes may impede plant reproduction. These effects can be changed and even reversed when tested across varying plant densities or spatial scales, if different interaction mechanisms (e.g. pollinator usurpation vs. facilitation) operate at different plant densities or geographical distances (Muñoz and Cavieres 2008; Jakobsson *et al.* 2009). When larger spatiotemporal scales are considered, alien plant invasion may change the overall carrying capacity of pollinators in the ecosystem, which can also affect native plant pollination (Bjerknes *et al.* 2007; Tepedino *et al.* 2008; see below).

It is not yet fully understood why in certain situations, alien animal-pollinated plants facilitate the pollination of natives, whereas in others, pollinators are usurped. Multiple factors are involved in such interactions, and the final outcome will depend on the relative characteristics of the native vs. alien plant species, such as flower density, morphology and attractiveness to pollinators, as well as on the unique pollinator species involved. Theoretically, the larger the niche overlap between alien and native plant species, the higher the chances that pollinators' visits to the native plant will be affected (Goodell 2008). In particular, plants sharing similar floral traits

and pollination syndromes have increased chances of sharing also their pollinator guild and therefore having interspecific pollinator transitions (Schemske 1981; Internicola *et al.* 2007). There is evidence that when alien and native plants share flower shape and/or color, the probable outcome for the native species will be pollinator usurpation rather than facilitation, and ultimately, decreased reproductive success (Morales and Traveset 2009). However, we hypothesize that both pollinator usurpation and facilitation will be more probable when floral advertizement traits are similar, because some pollinators that are attracted to the more showy or rewarding alien, may mistake a nearby growing native plant for the alien, thus facilitating visits to the native (Dafni and Ivri 1981a,b; Johnson *et al.* 2003). The unique outcome under such circumstances will depend on the extent of similarity in visual and/or olfactory signals and in rewards between the two plant species, as well as on the pollinator's sensory and learning capabilities. A possible scenario is one of mixed effects—the alien plant will usurp the more skilled and loyal pollinators, that distinguish between the two plants, but will facilitate visits of other, more naive pollinator species to the native. If the alien plant offers a higher reward than the native, usurpation of pollinators may also increase gradually during the flowering season, as naive newly emerged pollinators will learn over time to discriminate between the two plant species (Dafni 1984).

Effects of alien flower visitors

Like alien plants, alien species of pollinators and flower visitors may also either hamper or facilitate native plant pollination and seed set. The pollination services delivered by alien visitor species may differ markedly from those provided by native visitors, due to behavioral and/or morphological differences (Dafni and Shmida 1996; Lach 2003; Dohzono and Yokoyama 2010). Moreover, alien visitors often usurp native plants of their native visitors, by depletion of rewards (Dafni and Shmida 1996; Hingston and McQuillan 1999), damage to floral tissues (Dohzono *et al.* 2008), or physical deterrence (Gross and McKay 1998; Hansen and Muller 2009). Theoretically, however, it is possible that deterrence by alien visitors will enhance native pollinators' efficiency by forcing native pollinators to move more frequently among flowers, thus increasing their visit frequencies (Lach 2007; see also Greenleaf and Kremen 2006). In addition, deterred pollinators may fly greater distances between consecutive visits, possibly enhancing outcrossing. Both of these processes might benefit plant reproduction. Furthermore, native pollinators that are deterred from visiting native focal plants may switch to foraging on other native plant species, affecting these latter species' reproduction as well (Roubik and Villanueva-Gutiérrez 2009). The effects of alien flower visitors on native plant pollination have been studied mostly in alien species of social bees (reviewed in Vergara 2008 and in Dohzono and Yokoyama 2010) and ants (Lach 2003, 2007, 2008a,b; Roberts and McGlynn 2004; Blancafort and Gómez 2005; Hansen and Müller 2009). However, other groups of alien flower visitors may also be influential, for instance solitary bees (Cane 2003; Pemberton and Liu 2008), birds (Cox 1983; Kelly *et al.* 2006), and wasps (Morales and Aizen 2002). There are many examples of native plant species that suffer reduced pollination services due to the effects of alien visitors (e.g. Dafni and Shmida 1996; do Carmo *et al.* 2004; Hansen and Müller 2009). However, in many other cases, alien visitors have no effect on native plant seed set (e.g. Dupont *et al.* 2004; Lach 2007), and sometimes even positive influences have been documented (Chamberlain and Schlising 2008),

particularly when the native plant was dependent upon a native pollinator species that had gone extinct locally or globally (Traveset and Richardson 2006; Cox 1983; Lord 1991). Hence, empirical work to date does not point to any general trend regarding the impacts of alien flower visitors on native plant species.

The integration of an alien pollinator into a native plant-pollinator network can result in significant breakage of pollination syndromes. For example, several cases have been documented of honeybees visiting native plants adapted for bird pollination, especially in Australia. In some of these cases, honeybees were the main visitor; some plant species were efficiently pollinated by honeybees, whereas others only poorly or not at all (Paton 2000; Fumero-Cabán and Meléndez-Ackerman 2007).

Indirect effects

Alien species can also influence native plant pollination indirectly, by affecting native pollinator populations through diverse ecological interactions and mechanisms, including competition, predation, herbivory, parasitism, and habitat modification. Highly attractive alien plants can increase native pollinators' carrying capacities by providing increased forage resources (Bjerknes *et al.* 2007; Tepedino *et al.* 2008). Some alien plants can also provide feeding substrates for herbivorous pollinator larvae such as butterfly caterpillars (Graves and Shapiro 2003), or nesting substrates for bees (Hurd 1978). An opposite effect may be induced by unattractive invading plant species that spread vigorously and create dense monospecific stands, thereby outcompeting native flowering plants that provide forage resources, and transforming nesting habitats such as bare ground (Johnson 2008; Moroń *et al.* 2009). Alien animal species can also affect pollinator abundance and diversity. For instance, alien flower visitor species may compete with native pollinators for forage resources (Thomson 2004; Paini and Roberts 2005) or nesting substrates (Inoue *et al.* 2008); alien predators may prey heavily on pollinators, and even cause their extinction (Fritts and Rodda 1998; Abe *et al.* 2010); and alien herbivores may consume important forage plants or trample them (Traveset and Richardson 2006). However, secondary species interactions may also induce positive effects, e.g. an alien predator that preys on a native herbivore. Alien species of parasites and pathogens, often introduced with alien animal species, can also have disastrous consequences for native pollinator faunas (Cox and Elmqvist 2000). Generally speaking, the effects of alien species on native pollinator populations are still poorly understood and need to be further explored.

Table 5.1 summarizes the different impacts exerted by each group of alien organisms on native plant pollination and seed set. As can be seen, alien species from diverse functional groups can impose drastic positive or negative effects; there seems to be a greater focus on the negative aspects in the literature, although this may represent a methodological bias. From a conservational point of view, negative effects seem to be the most important, given the frequent evidence of species decline and extinction due to alien species invasions (Coblentz 1990; Mooney and Cleland 2001). Therefore, in the following sections, we will focus mainly on the negative effects of alien species on native plant pollination and reproduction, and the potential of evolutionary adaptations to overcome them.

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Possible adaptive mechanisms of native plants in response to alien plant and pollinator invasions

Native plant species experiencing changes in pollination and/or reproductive success due to the processes described above, may adapt to their altered environments in several, not necessarily mutually exclusive ways (Bjerknes *et al.* 2007; Harder and Aizen 2010). These can be broadly classified into two categories: 1. alteration of flower traits and/or blooming characteristics to attract the highest number of efficient pollinators, and 2. development of reproductive modes that are not animal-mediated, or increased reliance on such mechanisms that already exist. Next we explore each of these adaptive paths and their evolutionary consequences.

Optimization of biotic pollination

Flower morphology. Major changes in the composition of pollinator species visiting a plant species can induce morphological changes in flowers that will allow a better fit to the behavioral and/or morphological characteristics of the new visitors, especially to those species that are the most common and/or efficient pollinators (Bernardello *et al.* 2001; Johnson 2006). For example, a shift to pollinators with larger bodies and shorter tongues will select for wider and shorter corollas, respectively, and vice versa (e.g. Dohzono *et al.* 2008; but see Harder and Aizen 2010). The more generalist and attractive the plant, the higher the chances that spatiotemporal changes in the relative abundances of different pollinator species will eliminate any adaptive effect that a particular pollinator exerts on the flowers (Johnson and Steiner 2000; Gomez and Zamora 2006). If, however, a plant is pollinated exclusively by a single species or a narrow suit of closely related species in its invaded environment, these pollinators will select for flower morphologies that fit them best, potentially initiating a process of specialization. Conversely, if the plant's main pollinator becomes rare, and other visitors are also uncommon or inefficient, a process of generalization will initiate (Harder and Aizen 2010).

Floral mimicry. Selection can favor floral advertizing cues that mimic those of a highly attractive invasive plant growing nearby, so that some visitors will move between the two species indiscriminately, leading to pollinator facilitation (Mullerian mimicry, Dafni 1984) (Dafni and Ivri 1981a,b; Johnson *et al.* 2003). The extent of the similarity in advertizement depends on relative flower sizes, colors, shapes and scents. This mechanism may be problematic, however, if the frequent movement of visitors between species negatively affects the native plant due to heterospecific pollen deposition or major losses of conspecific pollen. The problem of interspecific pollen transfer may be reduced by a shift in the sexual organs' point of contact with the pollinator in the native plant, such that different areas on the pollinator's body come into contact with different plant species' sexual organs (Caruso 2000).

Flower attractiveness. Changes in the quantity or quality of pollinator visits can affect the attractiveness of flowers. Plants often respond to decreased/increased pollination services by respectively increasing/decreasing various parameters of reward and/or advertizement (Ashman and Morgan 2004). Such parameters include: nectar sugar content, nectar volume, corolla size, scent, flower longevity, and blooming synchronization. Different pollinator species are attracted by different floral

cues and rewards, and thus changes in the visiting fauna can also induce changes in flower attractiveness. Blooming synchronization among flowers on different plants and/or on an individual plant, can also be modified as a means of minimizing negative effects of interspecific pollen transfer by disloyal visitors on the one hand, and excess geitonogamy (i.e. the transfer of pollen among flowers of the same individual plant) by more constant visitors on the other (Harder and Aizen 2010). Plants that receive increased pollination services and can invest more resources in reproduction, can further increase their fitness by producing more flowers per plant.

Adaptations to illegitimate visitors. A high incidence of pollen or nectar robbing by alien visitor species may select for morphologies that better conceal these rewards, and that allow access only to legitimate pollinators, or (in the case of pollen robbery) for no visitors whatsoever. For example, small bees that rob nectar from a large flower may select for concealment of the nectar deeper inside the corolla; corolla piercing by alien bumblebees might be prevented by selecting for a thicker and/or longer calyx (Maloof and Inouye 2000); nectar robbing by ants may select for hairy stems (Howarth 1985). If, however, robbing cannot be prevented, plants may adapt by producing more rewards, to compensate for the amount robbed (Maloof and Inouye 2000).

Spatiotemporal adaptations. Plants adapt to changes in pollination regimes also by shifting their spatiotemporal flowering niches (Waser 1978; Ghazoul 2002). In the case of usurpation of pollinators by alien plant species, competitive exclusion can trigger adaptation to a new habitat, by favoring plants or populations that grow relatively far from the invader (Waser 1978). Similarly, a shift in the blooming period will reduce temporal overlap with the alien (Waser 1978; Ghazoul 2002). Facilitation will favor opposite trends. These trends can also operate on smaller scales, for instance height of flowers on plants, and daily timing of flower opening and closing. However, some alien plant species (Ghazoul 2002), and most alien species of ants and social bees (Vergara 2008), have relatively wide and flexible spatial and/or temporal niches, and it is therefore less likely that a shift in blooming time or location will help minimize any negative effects they may have. Different pollinators can also prefer flowers located on different parts of plants (e.g. inner vs. outer branches, lower vs. upper branches), and thus a change in the pollinator fauna can induce a change in the position of blossoms. Furthermore, if different species of pollinators consistently visit the same different parts of the plant, the flowers in each part can develop somewhat different morphologies or offer different amounts of rewards (Colwell *et al.* 1974; Willmer and Corbet 1981; Maloof and Inouye 2000).

Reproductive modes which are not animal-mediated

Three major reproductive modes that are independent of animal visitation are known in terrestrial plants: autonomous self-pollination, wind pollination, and asexual reproduction. Each of these modes can be utilized as either a complementary strategy to biotic pollination, providing reproductive assurance, or a sole, obligate strategy. Species that rely on two or more reproductive strategies may shift between them according to their environmental conditions and developmental stages. Thus, for a given species, the relative importance of each reproductive mode may change among different populations, individuals, flowers, and seasons, and even during the lifetime

of a single flower. The facultative reliance on these reproductive modes as reproductive assurance mechanisms may enable some highly pollinator-specialist plant species to persist for prolonged periods with little or no biotic pollination (Bond 1994).

Autonomous self-pollination. Plants that experience a reduction in quantity and/or efficiency of visits, leading to pollen limitation, often compensate by increasing their rates of autonomous self-pollination (Fishman and Wyatt 1999; Barrett *et al.* 2009; Eckert *et al.* 2009). Adaptation for increased rates of autonomous selfing usually involves a relaxation of spatiotemporal and genetic mechanisms designed to minimize selfing, i.e. dichogamy, herkogamy and self-incompatibility. Thus, the distance between anthers and stigmas is often reduced, the overlap in functional male and female periods is increased, and self-incompatibility is broken (Harder and Aizen 2010). By analogy, dioecious species become andro/gynodioecious, and heterostylous species become monostylous (Barrett *et al.* 2009). There is, however, a genetic limitation to successful autonomous selfing. Increased reliance on selfing may have severe consequences on population dynamics if the population has high levels of inbreeding depression, as most of the selfed progeny will not reach maturity. Autonomous selfing may operate at different stages of the flower's life span. Very low visit frequencies, or a major negative effect of pollen robbing or heterospecific pollen deposition, are expected to select for prior selfing. This often occurs already in the unopened bud (cleistogamy), before any visitors have contacted the flower. On the other hand, high spatiotemporal variation in pollinator activity is more likely to select for competing or delayed selfing, a compromise which maintains reproductive assurance without completely losing the advantages of outcrossing (Eckert *et al.* 2009).

Asexual reproduction. Asexual modes of reproduction, such as vegetative growth and apomixis (asexual seed production), can also compensate for reduced pollination services, although they rarely appear as a sole reproductive strategy (Eckert 2002; Bicknell and Koltunow 2004). Resources freed up by reduced flower production could potentially allow increased asexual reproduction (Fischer and Van Kleunen 2002; Eckert 2002). The evolution of clonal plants from non-clonal ancestors has appeared frequently among the angiosperms; however, the adaptive evolution of vegetative reproduction has been poorly studied (Fischer and Van Kleunen 2002). Apomixis is not as common as vegetative reproduction or autonomous selfing, probably because it requires two or three mutations, each of which is disadvantageous when appearing in isolation (Marshall and Brown 1981). Hence, apomictic mutants are rare in plant populations, and are often polyploids derived from hybridization between reproductively incompatible progenitors, such as interspecific hybrids. However, once such a mutant is formed, it has an automatic selection advantage, and thus spreads rapidly (Holsinger 2000).

Wind pollination. An alternative pollination mode that is independent of animal visitors yet does achieve significant levels of outcrossing is wind pollination. Wind pollination seems to be especially common in plants inhabiting oceanic islands, which seems to be related to the limited pollinator faunas in these ecosystems (Harder and Aizen 2010). Efficient wind pollination is dependent upon several factors, including exposed stigmas and anthers, relatively open habitats or deciduous vegetation, and relatively high conspecific densities (Culley *et al.* 2002; Friedman and Barrett 2009).

Shifts to wind pollination are more likely to evolve in plants with floral morphologies that favor pollen dispersal and capture by wind, such as small flowers, exerted stamens, and short or absent corollas. Such species usually have inconspicuous floral advertizements and attract generalist pollinators (Friedman and Barrett 2009). Plants that receive reduced biotic pollination services due to effects such as pollinator usurpation by alien plants or illegitimate flower visitors, or pollinator predation by alien animals, can compensate for reduced visits by gradually shifting their pollination strategy to wind pollination. However, wind pollination may not be an effective strategy if pollen is robbed by alien flower visitors such as honeybees, which can efficiently locate pollen sources even in the absence of floral advertizing structures, as is common in wind-pollinated plants. There is evidence that wind-pollinated species can be more resistant than animal-pollinated species to negative processes associated with species invasions such as habitat fragmentation; this could be related to increased levels of long-distance pollen dispersal in wind-pollinated species (Friedman and Barrett 2009).

Which species and populations of native plants are most likely to undergo adaptation, and in what direction?

Although plants have numerous different strategies to adapt to changing pollination regimes, not all plant populations are equally likely to undergo adaptive selection in response to species invasion. Several conditions have to be met to allow adaptation. Moreover, the unique adaptive path taken may change among different species and possibly even among different populations of the same species, depending on several environmental, demographic, genetic and phylogenetic factors. In the following, we discuss the conditions that allow for adaptive selection to occur and the factors that determine its direction.

Conditions required for adaptive selection

Plant life cycle. For adaptation to occur, pollination and/or seed production must be a major limiting factor in the plant's life cycle. In many cases, even a significant change in seed set has no effect on overall plant fitness (Ashman *et al.* 2004; Gomez and Zamora 2006). The life strategies of many flowering plants are characterized by the production of a vast amount of offspring per individual, the majority of which do not survive to maturity. The processes governing seed, seedling and juvenile plant mortalities often surpass any effect the amount of seed sired might have on plant fitness, with any modest change in the pollination regime proving completely irrelevant for the demographics of the population (Ashman *et al.* 2004; Gomez and Zamora 2006). Furthermore, a trait that is advantageous for pollinator attraction or seed production may be disadvantageous for other life stages, such as seedling survival. For example, increased seed set is often associated with a decreased maternal investment per individual seed, potentially leading to decreased seedling survival (Gomez and Zamora 2006). Density-dependent processes, such as seed or seedling predation and intraspecific competition, can also eliminate any positive effect of increased pollination services (Ashman *et al.* 2004).

Pollen limitation. Most studies stress the importance of pollen limitation as a precondition for environmental effects on plant reproduction. In general, pollen-limited plants are expected to be more sensitive to changes in the pollination regime, since any change in pollinator type, abundance or behavior may influence the amount and/or quality of seeds sired. Furthermore, maternal selection for traits that reduce pollen limitation have been shown to vary positively with the intensity of the phenomenon (Harder and Aizen 2010). However, differences in the quality of seeds may also appear in plants that are seed- or resource-limited. For example, a plant that compensates for low visitation rates by delayed selfing can still achieve full seed set and remain pollen-unlimited, but if the species has a high rate of late-acting inbreeding depression, most of the progeny will not reach maturity, and fitness will decline (Harder and Aizen 2010). Furthermore, pollen-unlimited plants that experience increased visitation frequencies (e.g. because of facilitation by an invasive plant) can also increase their fitness, by reducing their investment in advertizement and/or reward or by reducing flower longevity, and reallocating resources to other physiological processes (Harder and Aizen 2010).

Magnitude of alien species' invasion. Plant populations that are likely to adapt to species invasions are those that experience, on both spatial and temporal scales, significant and prolonged negative or positive effects due to these invasion events, such as pollen or resource limitation, and pollinator usurpation or facilitation (Harder and Aizen 2010). Thus, the entire plant population should be affected by the invasive species acting as a selective agent, and there should be relatively little gene flow from adjacent populations which are not under such influence. Therefore, adaptation is most likely where species invasion follows a uniform pattern across large areas, rather than a patchy pattern, as well as in well-isolated stands of the native species upon which selection can act.

Population size. The size and density of the plant population are of the utmost importance in determining its fate in the event of invasion. Small plant populations occupying anthropogenically transformed habitats, where alien species often predominate, are particularly prone to decline. Small populations are subject to Allee effects, which may also manifest in pollination, by reduced pollinator attraction, increased interspecific pollen movement, decreased mating opportunities, and increased inbreeding (Ashman *et al.* 2004). Furthermore, the smaller genetic reservoir available for small populations reduces their chances of successfully adapting to their changing environment. Thus, adaptive evolution is less likely to salvage small populations that are on the brink of extinction from the detrimental effects of species invasions.

Factors influencing the direction of adaptation

Among the different available adaptive mechanisms that optimize biotic pollination, adaptations that increase plant attractiveness to pollinators or compensate for illegitimate reward consumption often require increased allocation of resources to the floral tissues. However, the availability of such resources can be severely limited in habitats invaded by some alien species, especially plants (Levine *et al.* 2003). Furthermore, many showy invasive plants maintain an unusually high attractiveness to a wide range of pollinator species, which often far outcompetes that of native plant

species (Morales and Traveset 2009); in some cases, rates of nectar or sugar production differ by an order of magnitude between natives and aliens (e.g. Chittka and Schürkens 2001). Under such harsh competitive conditions, it is unlikely that any modest increase in advertizement or reward in the native species will prevent pollinator usurpation by the alien. Rather, usurpation of pollinators by a highly attractive alien plant is more likely to select for an increasing investment in animal-independent reproductive modes, possibly coupled with a reduction in the amount of advertizement and reward.

Among the animal-independent reproductive adaptations, evolution of autonomous selfing is one of the most common transitions during angiosperm history (Harder and Aizen 2010), and is one of the chief paths that species subjected to pollen or resource limitation are likely to take. Several explanations can be given for why this adaptation is so common. To name only two, selfing strategies have a twofold advantage over outcrossing strategies in the rates of genetic transmission; and autonomous selfing is a "safe bet" in most environments, since it does not depend on any outside vector for efficient pollination. Therefore, the genetic sequences that code for autonomous selfing may remain largely conserved within lineages, even after prolonged periods when they are not in use. Evolution of autonomous selfing is especially likely in invaded habitats, if both adequate pollen vectors and potential mates are in short supply (Eckert *et al.* 2009). A recent study estimated that increased selfing may evolve about three to four times more often than increased outcrossing in response to anthropogenic disturbance, especially in short-lived herbs (Harder and Aizen 2010).

Which type of selfing mechanism is most likely to evolve? According to some recent models, prior selfing is more likely to evolve than delayed selfing under pollen limitation, especially in annual species, and even with strong inbreeding depression (Harder and Aizen 2010). However, in species that have already acquired delayed selfing, when pollination services are improved and the opportunities for outcrossing increase, the presence of delayed selfing may slow down selection towards the optimal mating system, which should then rely more upon outcrossing (Harder and Aizen 2010).

Although a widespread mechanism, there are situations in which autonomous self-pollination is less likely to develop. The presence of strong inbreeding depression can prevent selection towards autonomous selfing (Harder and Aizen 2010). Some strategies of sex segregation are also unlikely to revert to allow selfing, especially dioecy and dicliny (flower unisexuality) (Culley *et al.* 2002; Friedman and Barrett 2009). Indeed, other modes of animal-independent reproduction are often associated with increased sex segregation. Thus, apomictic reproduction is especially important in self-incompatible, dioecious, and heterostylous taxa (Bicknell and Koltunow 2004; Barrett *et al.* 2008); and dioecious and diclinous lineages usually shift to wind pollination instead of autonomous selfing (Culley *et al.* 2002; Friedman and Barrett 2009). These adaptations may be viewed as alternative modes of reproductive assurance (Friedman and Barrett 2009).

The various adaptive paths followed by different plant species are determined to a certain degree also by the evolutionary history of the clade (Harder and Aizen 2010). Species are more likely to shift toward pollination modes that are common among their closely related taxa. However, phylogenetic evidence suggests that some

transitions between reproductive modes tend to be irreversible. In general, shifts from partial or obligate animal pollination to obligate uniparental reproduction or wind pollination are rarely reversed (Harder and Aizen 2010; Culley *et al.* 2002). Moreover, being an absorbing state with reduced genetic diversity and accumulation of deleterious mutations, obligate selfing lineages, like obligate asexual lineages, are often short-lived and prone to frequent extinctions (Holsinger 2000; Harder and Aizen 2010). The shift from short-tongued to long-tongued pollination is also often irreversible (Harder and Aizen 2010). Thus, plants adapted for bird pollination that are visited by alien honeybees, for instance, are likely to resist radical shifts of their pollination syndrome, and be more susceptible to chronic pollen limitation. However, some degree of adaptation to the alien visitor may still be possible in such instances.

Conclusions

We have delineated different paths of adaptation that are available for native plant populations. Which of these alternative paths will be "chosen" by a given plant species suffering decreased reproductive output due to the invasion of aliens? As a rule of thumb, we suggest that plant species that are highly dependent on pollinator visits to achieve significant seed set, exhibit strong sexual segregation and/or inbreeding depression, and enjoy abundant abiotic resources and potential mating individuals, will maintain a reproductive mechanism that is dependent upon external vectors such as animals or wind, and will undergo selection to achieve optimal biotic or wind pollination; of these, wind pollination will prevail in dioecious and diclinous species with exposed sexual organs. On the other hand, species that are capable, to some extent, of reproducing without the aid of external pollen vectors (or have close relatives that do so), and occupy habitats that are severely resource-limited and with a low density of potential mates, will tend to increasingly rely on uniparental reproductive strategies, such as autonomous self-pollination, vegetative growth, and apomixis (see also Eckert *et al.* 2009).

Not all native plant species will survive the environmental changes induced by species invasions. Adaptive evolution can allow some plant species to meet their biotic pollination needs, thus protecting them from decline. Other species, especially those suffering high levels of competition or herbivory, will not be able to allocate enough resources to attract sufficient visitors in light of increased competition for pollinators. In some scenarios, wind pollination can provide a suitable alternative for these species. In other cases, adaptation will favor modes of reproduction that do not involve outcrossing, with consequent reductions in effective population size. Small, isolated populations, species with heavy inbreeding depression and those with strong self-incompatibility mechanisms, are expected to suffer the severest declines, with some populations and species reaching extinction. The reduction in gene flow among individuals in these instances will further limit the capacity to adapt to invaded environments. In the minority of cases, populations will increase due to facilitative effects of species invasions.

Pollination constitutes only one step in the life cycle of plants. The more limiting the pollination step on the species' reproduction and survival, the more significant will be any change in the pollination regime induced by alien species. In addition to changing pollination regimes, alien species exert many other direct and indirect effects on

native plants, such as interspecific competition, herbivory, and habitat modification (Levine *et al.* 2003; Crooks 2002). Many native plant populations have been affected by such processes, some reaching the brink of extinction (Coblentz 1990; Mooney and Cleland 2001). Efforts to overcome negative impacts by evolutionary adaptation are more likely to occur in populations that have maintained some genetic variability, and not in the weakest, most threatened ones. However, the potential for the occurrence of adaptive processes across different native taxa and invaded ecosystems has not been studied yet. Assessing which native plant species and communities have the capacity to adapt to species invasions, and which adaptation mechanisms are most likely to occur under different circumstances, should be a major goal for future research. Research in this field will improve our ability to manage pivotal pollination services and maintain functioning ecosystems.

Acknowledgements

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Table 5.1. Summary of the effects of alien species on the abundance and behaviour of native pollinators, and the consequences for native plant pollination and seed set.

Invading organism	Effects on native pollinators	References	Effects on native plants	References
Alien plants	Pollen source	Moragues & Traveset 2005; Stubbs *et al.* 2007; Tepedino *et al.* 2008	Reduced visit frequencies	Chittka & Schürkens 2001; Brown *et al.* 2002; Moragues & Traveset 2005; Larson *et al.* 2006
	Nectar source	Chittka & Schürkens 2001; Moragues & Traveset 2005; Tepedino *et al.* 2008; Kandori *et al.* 2009	Increased visit frequencies	Moragues & Traveset 2005; Nielsen *et al.* 2008; Jakobsson *et al.* 2009
	Caterpillar forage host	Graves & Shapiro 2003	Increased visit lengths	Muñoz & Cavieres 2008
	Bee nesting substrate	Hurd 1978	Change in composition of visitor fauna	Ghazoul 2002; Muñoz & Cavieres 2008; Nienhuis *et al.* 2009; Tscheulin *et al.* 2009
	High flower attractiveness	Chittka & Schürkens 2001; Moragues & Traveset 2005; Vanparys *et al.* 2008; Kandori *et al.* 2009	Low flower constancy	Brown *et al.* 2002; Flanagan *et al.* 2009; Kandori *et al.* 2009
	Increased pollinator abundance / diversity	Stubbs *et al.* 2007	Reduced conspecific pollen deposition	Larson *et al.* 2006; Flanagan *et al.* 2009
	Reduced pollinator abundance / diversity	Johnson 2008; Moroń *et al.* 2009	Heterospecific pollen deposition	Grabas & Laverty 1999; Ghazoul 2002; Nielsen *et al.* 2008; Montgomery 2009
	Change in composition of pollinator fauna	Nienhuis *et al.* 2009	Increased seed set	Muñoz & Cavieres 2008
			Reduced seed set	Grabas & Laverty 1999; Chittka & Schürkens 2001; Brown *et al.* 2002; Muñoz & Cavieres 2008
Alien flower visitors	Reduced abundance / diversity of native pollinators	Roubik 1978	Reduced abundance / diversity of native / legitimate visitors	Dafni & Shmida 1996; Lach 2007, 2008a,b
	Physically deterring native pollinators from forage plants	Dafni & Shmida 1996; Gross & Mackay 1998; Hansen & Müller 2009	Increased frequencies of total legitimate visits	Osorio-Beristain *et al.* 1997; Madjidian *et al.* 2008
	Native pollinators shift their foraging to other plant species	Roubik & Villanueva-Gutiérrez 2009	Reduced visit frequencies of native / legitimate visitors	Dafni & Shmida 1996; Blancafort & Gómez 2005; Dohzono *et al.* 2008; Hansen & Müller 2009
	Competition for forage resources	Thomson 2004; Paini & Roberts 2005	Shortened visit lengths of native / legitimate visitors	Hingston & McQuillan 1999; Lach 2008a
	Competition for nest sites	Inoue *et al.* 2008	Reduced average efficiency per visit (illegitimate visits not included)	Osorio-Beristain *et al.* 1997; Hansen *et al.* 2002; do Carmo *et al.* 2004; Madjidian *et al.* 2008
	Competition through interspecific mating	Kanbe *et al.* 2008; Kondo *et al.* 2009	Nectar robbery	Dafni & Shmida 1996; Roberts & McGlynn 2004; Lach 2005; Dohzono *et al.* 2008
			Pollen robbery	Gross & Mackay 1998; do Carmo *et al.* 2004
			Nectar depletion	Dafni & Shmida 1996; Hingston & McQuillan 1999; Dupont *et al.* 2004; Roberts &

				McGlynn 2004
			Pollen depletion	do Carmo *et al.* 2004
			Damage to floral tissues	Kenta *et al.* 2007; Dohzono *et al.* 2008
			Reduced seed set	Gross & Mackay 1998; Roberts & McGlynn 2004; Dohzono *et al.* 2008; Hansen & Müller 2009
			Reduced pollinator movement among plants	Dupont *et al.* 2004
			Increased pollinator movement among plants	Celebrezze & Paton 2004
			Reduced outcrossing	England *et al.* 2001; Dick *et al.* 2003
			Increased gene flow distances	Dick *et al.* 2003
			Compensation for rare or extinct pollinators	Cox 1983; Lord 1991; Kelly *et al.* 2006
Alien herbivores	Reduced pollinator abundance / diversity	Spurr & Anderson 2004		
Alien predators	Reduced pollinator abundance / diversity	Kelly *et al.* 2006; Abe *et al.* 2010		
	Local or global pollinator extinction	Nogales & Medina 1996; Fritts & Rodda 1998		
Alien parasites & pathogens	Local or global pollinator extinction	Cox & Elmqvist, 2000		