**Research review**

When mutualism goes bad: density-dependent impacts of introduced bees on plant reproduction

**Author for correspondence:** Marcelo A. Aizen  
Tel: +54 294 442 3374  
Email: maizen@comahue-conicet.gob.ar

Received: 25 March 2014  
Accepted: 10 June 2014

**Marcelo A. Aizen¹, Carolina L. Morales¹, Diego P. Vázquez²,³, Lucas A. Garibaldi⁴, Agustín Sáez¹ and Lawrence D. Harder⁵**

¹Laboratorio Ecotono-CRUB, Universidad Nacional del Comahue and INIBIOMA-CONICET, 8400 San Carlos de Bariloche, Río Negro, Argentina; ²Instituto Argentino de Investigaciones de las Zonas Áridas, CONICET, CC 507, 5500 Mendoza, Argentina; ³Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Cuyo, Centro Universitario, 5502 Mendoza, Argentina; ⁴Sede Andina, Universidad Nacional de Río Negro and CONICET, 8400 San Carlos de Bariloche, Río Negro, Argentina; ⁵Department of Biological Sciences, University of Calgary, Calgary, AB T2N 1N4, Canada

**Summary**

Invasive, alien plants and pollinators have varying effects on their interaction partners, ranging from highly beneficial to strongly detrimental. To understand these contrasting impacts, we review the benefits and costs associated with plant–pollinator interactions and enquire as to how the presence of abundant invaders affects the benefit–cost balance. We provide a conceptual framework that predicts that mutualism shifts to antagonism when invaders increase disproportionally in abundance relative to their interaction partners. This outcome is illustrated by an empirical example of a crop in which flower damage and an associated reduction in fruit quality represent interaction costs of intense visitation by invasive bees. More generally, the extremely high density of invasive flower visitors, such as *Apis mellifera* and *Bombus terrestris*, might have population- and community-level consequences by hampering reproduction of native plants while promoting reproduction of alien plants. Furthermore, modification of the structure of pollination networks resulting from intense visitation of native plants by superabundant alien flower visitors in highly invaded communities could predict accentuated interaction costs for many native plants. Owing to their high density and the exclusion of native pollinators, invasive bees, originally introduced for honey production and crop pollination, may negatively impact both the native biota and agriculture.

**Introduction**

The pollination mutualism is critical for the maintenance of terrestrial biodiversity, because most species of flowering plants depend on flower-visiting animals for pollen transfer and hence seed set (Ollerton et al., 2011). In turn, thousands of insect species and hundreds of vertebrate species either rely on or benefit from food and other resources provided by flowers (Kearns et al., 1998). This mutualism is also pervasive, as it occurs on all continents except Antarctica.

Pollination mutualisms are typically generalized, with most plant species pollinated by a diversity of animals and most pollinators rewarded by flowers from a variety of plant species (Waser et al., 1996). The diffuse nature of pollination systems facilitates the turnover of interaction partners following natural or anthropogenic species range expansions or retractions. Thus, both alien plants and flower-visiting animals transported far from their native ranges can profit from their interaction with the indigenous fauna and flora, respectively (Aizen et al., 2008; Ollerton & Watts, 2012). Humans also benefit from the generalized nature of this mutualism by cultivating many pollinator-dependent crops outside of their ancestral ranges, and artificially selecting and engineering new crop varieties that interact readily with naturally occurring pollinator assemblages (Garibaldi et al., 2013). Humans additionally profit by managing generalist pollinators for honey production and pollination supplementation of crops. The classical example is the honey bee, *Apis mellifera*, which is native to Eurasia and Africa and has been introduced to the Americas, Australia and many islands, and which forages well on crops, weeds and native vegetation (Villanueva-Gutierrez & Roubik, 2004). However,
from the perspective of an indigenous species, partner replacement or inclusion of additional interaction partners need not lead to the same mutualistic outcome.

Mutualisms involve both benefits and costs to the interacting species, so that the interaction is mutually beneficial only if benefits exceed costs for both participants (Bronstein, 2001; Holland et al., 2004; Morris et al., 2010). Thus, despite benefiting alien partners and facilitating their invasion, the interaction between alien and native plants and pollinators can range from beneficial to highly detrimental to the native partners, depending on their life-history and demographic traits (Morales & Aizen, 2006; Aizen et al., 2008). For instance, in Australia, invasion of A. mellifera decreased seed output by Grevillea barklyana, as a consequence of the replacement of nectar-feeding birds that provide more efficient pollination (Vaughton, 1996). Even replacement of taxonomically related and functionally equivalent pollinators, such as endemic subspecies of bumble bees by introduced Bombus terrestris in Japan, may reduce fruit set of native plant species (Kenta et al., 2007).

Thus, substitution of efficient native mutualists by less efficient, or even antagonistic, alien species (e.g. legitimate pollinators by habitual nectar robbers or pollen thieves) can be an important cause of pollination disruption (Goulson, 2003; Dohzono & Yokoyama, 2010). Disproportionate differences in abundance between native and alien partners can also challenge mutualism integrity, determining a shift from a mutualistic (Fig. 1a) to an antagonistic (Fig. 1b) plant–animal interaction. Released from many regulatory processes present in their native ranges, alien plants and flower-visiting animals can reach densities in their introduced range that predispose them to overexploit their novel partners and compete for mutualists with their native counterparts (Morales & Traveset, 2009). In particular, high-density alien flower-visiting animals may aggravate interaction costs for low-density native plants, when this relative density difference imposes extreme visitation frequencies (Morris et al., 2010). Analogous increases in interaction costs can exist for native pollinators when diverse communities of flowering plants are replaced by species-poor communities dominated by one or a few mass-flowering invasive species, particularly because of adults rearing larvae on a low-quality, monotypic pollen diet (Praz et al., 2008; Tasei & Aupinel, 2008). Moreover, differences in abundance may explain why alien plants are stronger competitors for pollinators than their native counterparts (Fig. 1c). Despite considerable evidence consistent with such indirect, pollination-mediated competition (Morales & Traveset, 2009; Holzschuh et al., 2011), there is less evidence and consensus on the density-dependent consequences of direct interactions between native plants and alien flower visitors or alien plants and native flower visitors.

In this contribution, we focus on this latter direct effect, an overlooked aspect of the impact of species invasions on the pollination mutualism. Specifically, we hypothesize that an antagonistic twist of an otherwise mutualistic plant–animal interaction is especially prevalent when partners have disparate relative densities. Here we develop a conceptual framework focused specifically on the density-dependent effects of alien flower visitors on the pollination interaction, primarily from the perspective of indigenous plants, but which also applies to crops and invasive weeds. Building on previous arguments (Bronstein, 2001; Holland et al., 2004; Morris et al., 2010), we first consider the plant–pollinator interaction as a benefit–cost relation, which can be mutualistic or antagonistic, depending on whether the net benefits are positive or negative. Then, we analyze how an increase in the relative abundance of one of the partners shifts the balance of benefits and costs for the other. We close by providing examples of invasive bees that have become superbundant, and discuss the individual, population and community consequences of such a shift in the benefit–cost balance. Although recognition of the plant–pollinator interaction as a benefit–cost relation is far from novel (Bronstein, 2001), to our knowledge, its implications for varying responses of pollination mutualisms to species invasion have not been addressed previously. The conceptual framework we propose has both theoretical and practical relevance, and can assist in conservation and agricultural management.

**Conceptual framework**

Mutualism exists when the benefits from an interaction exceed the costs for all partners; otherwise the interaction becomes antagonistic (Bronstein, 2001; Holland et al., 2004; Morris et al., 2010). Although the respective benefits of pollination mutualisms are obvious, the maximum benefits realized by interacting partners can be limited by different factors. For plants, the capacity to take advantage of abundant, efficient pollinators depends on either the number of ovules available for fertilization or the resources available.
for seed development, whichever of the two is most limiting (Harder et al., 2008). Correspondingly, the capacity for animals to capitalize on abundant floral resources from a single plant species depends on the time available for foraging (Stephens & Krebs, 1986), the quality of the plant resources (Pranz et al., 2008), and the availability and diversity of other essential resources (Tasei & Aupinel, 2008). The most apparent and direct costs involve the production and maintenance of attractive structures and reward production for plants (Southwick, 1984; Ashman & Baker, 1992), and foraging time and energy for animals (Stephens & Krebs, 1986). In addition, both plants and pollinators experience other direct and indirect costs related to the interaction itself, including flower damage, pathogen transmission, and increased exposure to herbivores and predators (Morris et al., 2010).

Given limited potential benefits, fitness maximization by both partners will commonly involve reducing their own costs while increasing the costs of their interacting partners (Bronstein, 2001). For instance, whereas plants benefit from limiting rewards to increase pollen transfer by reducing pollen loss and geitonogamy and encouraging pollinator movement, pollinators benefit from minimizing costly movement by choosing highly rewarding plants (Klinkhamer & de Jong, 1993; Waser et al., 1996). Despite mechanisms that prevent overexploitation of mutualisms (Holland et al., 2004), an extreme increase in the density of one of the partners can change the benefit–cost balance, tipping the mutualism into an antagonism (Morris et al., 2010). From the plant perspective, net benefits peak at intermediate visitation frequencies if costs increase continuously with visitation, but gross benefits level off (Klinkhamer & de Jong, 1993; Harder et al., 2001). For instance, in raspberry (Rubus idaeus), c. 10 bee visits during a flower’s lifetime deliver sufficient pollen to maximize the number of drupelets per fruit (Chagnon et al., 1991), a measure of fruit quality, but additional visits become increasingly detrimental (Fig. 2). Specifically, variation in flower visitation by bees, particularly the alien B. terrestris, which accounted for >50% of the visits among raspberry fields in northwest Patagonia, directly affects the proportion of damaged styles per flower (Fig. 2a,b), which in turn reduces drupelet number (Fig. 2c) because early style damage precludes ovule fertilization and drupelet development (Fig. 2d). The finding of declining net benefits with increased pollinator visits in excess of an optimum number was also the outcome of eight out of the 10 benefit–cost models proposed by Morris et al. (2010), based on biologically reasonable assumptions about the nature of benefits and costs of generic pollination mutualisms. An intermediate visit frequency that maximizes seed output was also a common feature of these models, despite different shapes of the benefit and cost curves, because interaction benefits are expected to saturate faster than costs with increasing visitation (Morris et al., 2010).

To illustrate this shift from mutualistic to antagonistic interactions, consider a plant with gross benefits (B), in terms of seed output and/or siring success, that increase asymptotically with increasing visitation (Aizen & Harder, 2007; Fig. 3, blue curve). This asymptote exists for female function because of limits on either ovule number or the resources available for seed production, and for male function because of limited pollen production. Although costs (C) eventually also saturate with increasing number of visits, mostly because of resource depletion (Morris et al., 2010), assume for simplicity that costs increase linearly over the same range of flower visitation (Fig. 3, red curve; see also Simms & Rausher, 1987). Mutualism requires that benefits exceed costs, which is true at low to moderate visitation; however, because of the different relations of benefits and costs to visitation, at some visitation frequency, a plant’s interaction cost exceeds its benefits and the interaction becomes antagonistic (Fig. 3). Although benefits and costs are measured proximally in different currencies (e.g. seed siring and production vs sugar production, respectively, in the case of a nectar-rewarding plant interacting with nectar-foraging pollinators), costs ultimately involve expended resources that can compromise present and future reproductive success via reduced growth and/or survivorship (Obeso, 2002). For instance, continuous nectar removal, and thus induced nectar replenishment, in bird-pollinated Blandfordia nobilis has a large effect on seed set (Pyke, 1991), demonstrating a tradeoff between B and C. Thus, the net benefits in terms of seed contributions are maximized (i.e. \( B − C \)max in Fig. 3) at the number of visits \( (I) \) for which the first derivative of the benefit curve equals the slope of the cost function, whereas mutualism switches to antagonism at a threshold interaction frequency \( (I_d) \) beyond which costs exceed benefits, and thus reproduction falls to zero (Fig. 3, black curve). For instance, in Capparis atamisquea, fruit production is maximized at approx. six to seven visits per flower and decreases to almost zero at >10 visits, although the nature of the costs involved is unknown (Morris et al., 2010).

Two bee examples

Despite claims of global pollinator decline (Potts et al., 2010), some bee species introduced in many regions of the world for honey production and (or) crop pollination have become exceptionally successful invaders, reaching abundances not observed in their native regions or among their native counterparts (Goulson, 2003; Stout & Morales, 2009). One such species is the Africanized honey bee, Apis mellifera scutellata, which monopolizes many floral resources in the Neotropics, particularly in fragmented subtropical and tropical dry forests (Vital et al., 2012). For example, visits by Africanized honey bees to the brush-like inflorescences of Prosopis nigra in small fragments of Chaco forest (<1 ha) exceeded visits by all other insects by c. 12-fold (Aizen & Feinsinger, 1994). Another ‘weedy’ pollinator is B. terrestris, a short-tonged bumble bee native to Eurasia and northern Africa that is reared commercially and has been introduced intentionally into Japan, New Zealand, and South America for crop pollination and unintentionally into Tasmania. This species was released in avocado fields in Chile in 1997, invaded northwestern Patagonia, Argentina, during 2006, and is still spreading towards the southernmost end of the continent (Morales et al., 2013). Its current density in Patagonia is at least three times the previous density of its now almost extinct congener, Bombus dahlbomii, the only bumble bee native to southern Chile and Argentina (Morales et al., 2013). As a consequence, in cultivated raspberry fields in northwestern Patagonia, flowers experience up to c. 150 visits d\(^{-1}\) by B. terrestris alone (Fig. 2).
Such extreme abundances of invasive *A. mellifera* and *B. terrestris* could cumulatively increase interaction costs. Although both species can effect pollination, high visit frequency can reduce reproductive success via increasing pollen theft (Hargreaves *et al.*, 2009), nectar robbery (Kenta *et al.*, 2007), and flower damage (Combs, 2011). These examples illustrate that the exceptional abundances reached by at least some flower visitors can translate into visitation frequencies that both saturate gross benefits and increase interaction costs, potentially shifting the interaction from mutualism toward the antagonism threshold.

**Individual, population, and community consequences**

Increasing interaction costs arising from the ‘mass effect’ associated with species invasions predict impacts at different levels of biological organization. Most immediately, diminishing net benefits associated with increasing costs decrease individual fitness. Secondly, to the extent that these costs involve many individuals and persist over time, they could affect population growth rate. Lastly, eroded mutualism as a result of increasing interaction costs could be reflected by changes in the structure and functioning of interaction networks. We now discuss and illustrate some of these invasion-driven, density-dependent interaction costs for individuals, populations, and communities.

As interspecific interactions involve individuals, their associated costs should first be evaluated at that level. For plants, the physiological costs of flowering include the fixed cost of flower construction, the daily cost of flower maintenance, and several possible costs that tend to increase with visitation frequency and thus the density of their animal partners. The latter may include the cost of nectar replenishment (Pyke, 1991), direct and indirect effects of nectar and pollen theft (Hargreaves *et al.*, 2009), and costs...
of flower damage (Traveset et al., 1998). In addition, receipt of excessive pollen may precipitate extreme pollen-tube competition, depressing seed production below that resulting from more moderate pollen receipt (Young & Young, 1992). Parasitic castration of flowers by fungi (Antonovics, 2005) and reduced nectar quality as a result of yeast infection (Herrera et al., 2008) are also interaction costs inflicted by pollinator-transmitted pathogens. Importantly, these visitation-dependent costs can co-occur. For instance, visits to *Fuchsia magellanica* by passerine birds, rather than hummingbirds, can impose both a direct cost via ovary damage and indirect costs associated with nectar robbery and replenishment (Traveset et al., 1998). This example also illustrates the potential for cost interactions, because the indirect effects of nectar robbing on reproductive success should diminish as the direct effect of ovary damage increases.

The nature and magnitude of density-related interaction costs have seldom been documented, except for the unusual mutualisms involving pollinator larvae that consume seeds (e.g. figs and fig wasps, *Yucca* and *Tegeticula*, senita cactus and senita moth; Bronstein, 2001; Holland et al., 2004), and, to our knowledge, they have not been examined in the context of biological invasions. For instance, short-tongued *B. terrestris* can be a legitimate pollinator or a major robber of long-tubed flowers, and increased nectar theft has not been examined in the context of biological invasions. For instance, visits to *Fuchsia magellanica* by passerine birds, rather than hummingbirds, can impose both a direct cost via ovary damage and indirect costs associated with nectar robbery and replenishment (Traveset et al., 1998). This example also illustrates the potential for cost interactions, because the indirect effects of nectar robbing on reproductive success should diminish as the direct effect of ovary damage increases.

Being generalists, abundant alien pollinators could also alter the structure of plant–pollinator networks. Such networks involve plant and animal species that represent ‘nodes’ linked by species interactions, with the cluster of highly connected nodes constituting the ‘core’ of the network. The composition and structure of this core largely determine the ecological and evolutionary dynamics of the whole network (Bascompte & Jordano, 2014). In general, alien mutualists integrate well into existing local networks, with limited to strong effects on their structure (Memmott & Waser, 2002; Viå et al., 2009; Kaiser-Bunbury et al., 2011; Santos et al., 2012). In particular, Aizen et al. (2008) found no effect of invaders on the
Review

or native (green curves). In the left-hand panels, the focal species was a plant, nonreciprocal dependence of the focal on the target species. The target equivalent dependence; and a value close to 1 represents strong nonreciprocal dependence of the target on the focal species; 0 indicates V was estimated as the difference in mutual dependence (i.e. proportion of forests of northwestern Patagonia (data from Aizen et al., 2008). Asymmetry was estimated as the difference in mutual dependence (i.e. proportion of total interaction frequency) between the focal and target species, following Vázquez et al. (2007). An asymmetry index close to −1 implies strong nonreciprocal dependence of the target on the focal species; 0 indicates equivalent dependence; and a value close to 1 represents strong nonreciprocal dependence of the focal on the target species. The target species was native in all cases, but the focal species could be alien (red curves) or native (green curves). In the left-hand panels, the focal species was a plant, whereas in the right-hand panels the focal species was an animal. N, number of interactions.

average number of interactions between native pollinator and plant species in lightly invaded communities, but a great reduction in highly invaded communities. In the latter communities, native species interacted predominately with alien species, which concentrated most of the interaction links and total interaction frequency. Comparable relative densities between interacting partners should promote similar mutual dependence (i.e. symmetrical interactions), and lower interaction costs, than when a superabundant species overexploits its partner. Thus, because of great differences in abundance, native species could engage in more asymmetric interactions with alien partners than with any other native partner before invasion. For example, differential dependence of native plants on abundant alien flower visitors increased overall network asymmetry in highly invaded communities of the forests of northwestern Patagonia (Aizen et al., 2008). This resulted specifically from native plants interacting more asymmetrically with alien flower visitors during late-invasion stages than with native flower visitors during early-invasion stages (Fig. 4; the red curve in the lower-right panel is lower than the green curve of the upper-right panel). Although the functional consequences of such changes in interaction asymmetry are still unknown, comparisons of seed output for a set of common plant species between lightly and highly invaded communities could offer an insight into the impact of superabundant alien flower visitors within plant assemblages. In particular, increased interaction costs should decrease seed set for native plants compared with alien plants, contributing to vegetation change in invaded communities.

Concluding remarks

Despite an apparent global pollinator decline (Potts et al., 2010), invasive pollinators could paradoxically increase total pollinator abundance, and thus visitation frequency, compared with pre-invasion conditions, at least in some regions and for some plant species. Africanized honey bees and B. terrestris provide clear examples. Among nonbee invasive flower visitors, the less well-studied syrphid fly Eristalis tenax, omnivorous wasp Vespula germanica, and cabbage butterfly Pieris rapae might provide other examples (Memmott & Waser, 2002; Morales & Aizen, 2006). These invasions may greatly increase flower visitation by less diversified pollinator assemblages, which could in turn aggregate interaction costs and eventually reduce plant reproductive success and crop yield (Fig. 2). For this reason, future pollinator introductions outside their native ranges should be discouraged. Although the density-dependent effects of pollinator invasions on seed set are little studied, the raspberry example indicates that, at the least, bees introduced for crop pollination can have the opposite effect of that intended when they become superabundant. We propose that pollinator introductions also frequently intensify mutualism costs among native plants, a proposition that needs to be tested in future studies. The conceptual framework provided here should prove useful in motivating and guiding this research.

Acknowledgements

The authors thank editor Amy Austin, Martín Nuñez, and three anonymous reviewers for useful comments and suggestions. This work was supported by the National Research Council of Argentina (PIP 01623 to M.A.A.), the National Fund for Scientific and Technological Research (PICT 2007–01300, PICT 2007–01464, and PICT 2012–3015 to M.A.A. and C.L.M., and PICT 2010–2779 to D.P.V.), the Universidad Nacional de Río Negro (UNRN–PI 40–B–259 to L.A.G.), a Rufford Small Grant to C.L.M., and a Discovery Grant from the Natural Sciences and Engineering Research Council of Canada to L.D.H.

References


Fig. 4 Rankings of the asymmetry of interactions between pairs of focal and target species consolidated for four lightly invaded (upper panels) and four heavily invaded plant–pollinator networks (lower panels) from temperate forests in northwestern Patagonia (data from Aizen et al., 2008). Asymmetry was estimated as the difference in mutual dependence (i.e. proportion of total interaction frequency) between the focal and target species, following Vázquez et al. (2007). An asymmetry index close to −1 implies strong nonreciprocal dependence of the target on the focal species; 0 indicates equivalent dependence; and a value close to 1 represents strong nonreciprocal dependence of the focal on the target species. The target species was native in all cases, but the focal species could be alien (red curves) or native (green curves). In the left-hand panels, the focal species was a plant, whereas in the right-hand panels the focal species was an animal. N, number of interactions.
Research review


