

Research review

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

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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 disproportionately 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

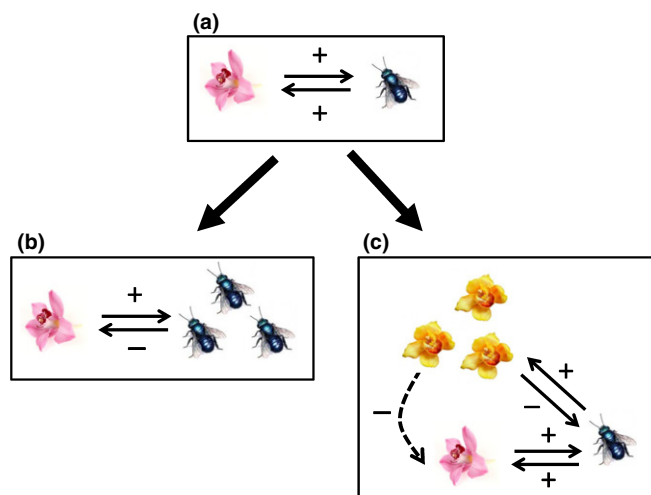


Fig. 1 Density-dependent shift of a plant–pollinator mutualism into antagonism. (a) Reciprocal benefits arise when animals visit flowers primarily for food (typically nectar and/or pollen) and secondarily for other resources (e.g. resins as building materials) and incidentally transfer compatible pollen from anthers to stigmas, improving siring success, ovule fertilization, and seed production. (b) However, when relative abundances become too unequal, one partner (e.g. a flower-visiting animal) can overexploit the other (e.g. the plant). In such cases, the interaction remains profitable for the high-abundance partner, but it can become less so or even detrimental for the low-abundance partner, if interaction costs equal or exceed interaction benefits. (c) A highly abundant plant species may have nonreciprocal effects on a low-abundance animal partner, also causing negative (but indirect) effects (dashed arrow) as a competitor for pollinators, if in its presence a low-abundance plant species incurs lower net interaction benefits.

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 superabundant, 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 (Praz *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_1) 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_2) 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-tongued 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).

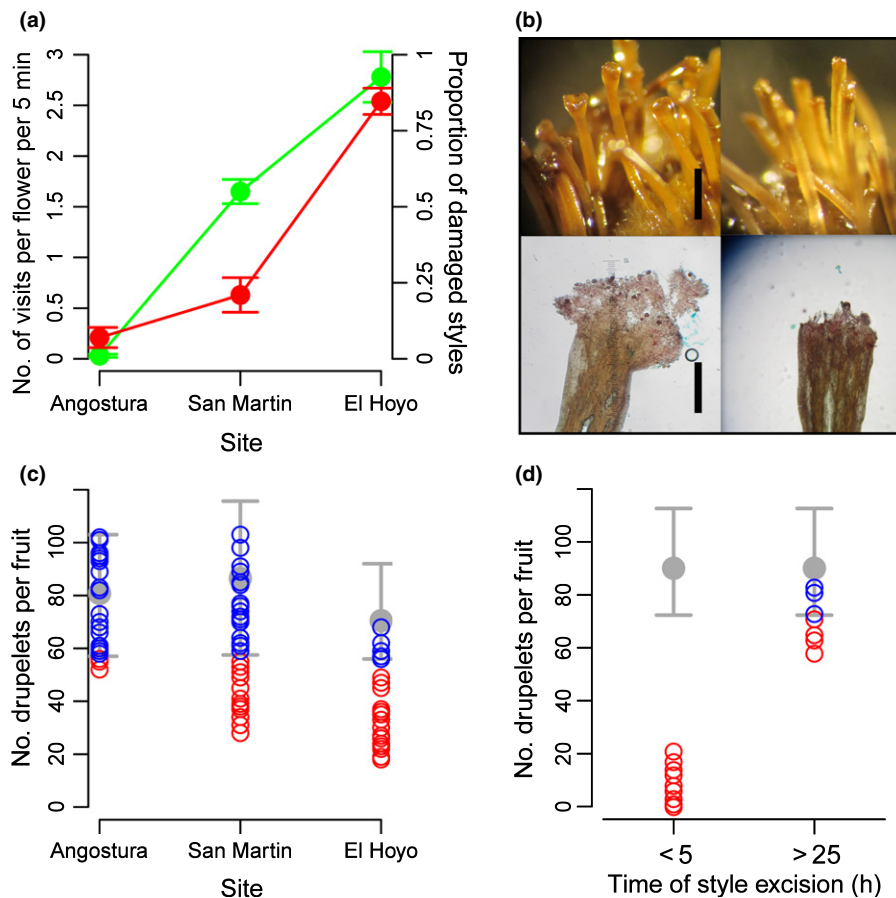


Fig. 2 Bee visitation to flowers, style damage, and drupelet set in raspberry (*Rubus idaeus* var. 'Autumn bliss') from three c. 0.5 ha commercial fields in northwestern Patagonia, Argentina (Angostura, 40°46'24"S, 71°39'35"W; San Martín, 40°07'29"S, 71°17'48"W; and El Hoyo, 42°02'49"S, 71°30'38"W). Raspberry produces insect-pollinated flowers, each with 60–110 pistils. A pollinated flower transforms into an aggregate fruit known as a polydrupe. (a) Mean (\pm SE) visit frequency to raspberry flowers (green circles and line segments) and incidence of damaged styles (red circles and line segments). Visit frequency was estimated from 20, 5-min pollinator observations to four to 10 flowers in each field during February 2012. The incidence of style damage was estimated based on the states of five pistils from each of 30 flowers per field. (b) Images of undamaged styles (left) and bee-damaged styles (right) at $\times 25$ (upper; bar, 1 mm) and $\times 100$ (lower; bar, 0.25 mm). Styles were classified as 'undamaged' if they were intact with stigmas present (left), or 'damaged' if they were broken, usually with missing stigmas (right). (c) Numbers of pistils per flower (gray symbol and bars representing the mean and 2.5 and 97.5 percentiles based on 30 flowers per field) and drupelets per fruit (open circles) at the three sampled fields. Drupelet numbers for fruits represented by blue circles fall within the central 95% of the distribution of pistil number, whereas drupelet numbers for fruits represented by the red circles fall below the 2.5 percentile. (d) Numbers of pistils per flower (gray bars; mean, 2.5 and 97.5 percentiles) and drupelets per fruit (open circles; colors as in c) from bagged flowers with styles excised experimentally 1–5 h or 25–30 h after hand pollination with cross pollen. Flowers last for c. 2 d. (A. Sáez, unpublished).

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

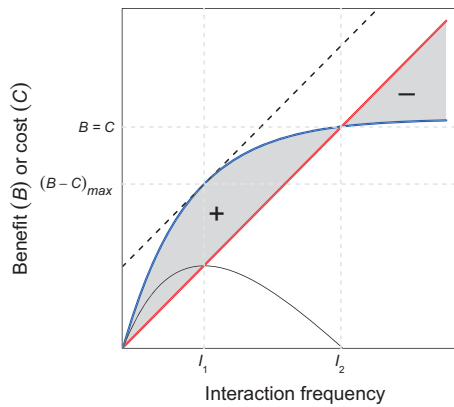


Fig. 3 The expected consequences of asymptotically increasing benefits (e.g. potential seed production; blue curve) and linearly increasing costs (e.g. flower damage; red curve) with elevated interaction frequency. Net benefits are maximized ($(B-C)_{\max}$) at the interaction frequency (I_1) for which the tangent (i.e. first derivative; black dashed line) to the benefit curve is equal to the slope of the cost function. From the perspective of the focal partner, the mutualism shifts to a net antagonism at the interaction frequency (I_2) at which the two functions intersect ($B = C$). According to this model, plant reproductive success should exhibit a hump-shaped relation to visitation frequency (black continuous curve).

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 been documented in invaded regions where it reaches high abundances (Kenta *et al.*, 2007; Combs, 2011). Although not a native crop, our studies of raspberry in northwestern Patagonia show that the proportion of damaged styles increases from 0 to almost 100% along a gradient of *B. terrestris* visitation, and as a consequence the number of drupelets per fruit declines by almost half (Fig. 2). Although *B. terrestris* also transfers pollen, these results suggest that above a relatively low number of visits, the antagonistic effect prevails over the mutualistic effect.

Plant species probably differ in their susceptibility to visitation-dependent mutualism breakdown, depending on their floral

characteristics. Most obviously, species with robust flowers, including large stigmas, and thick styles and stamen filaments should be less susceptible to physical damage caused by excessively frequent pollinator visits. In addition, pollination-induced floral senescence, which is relatively common among angiosperms (van Doorn, 1997), may buffer species against increased interaction costs by shortening exposure of individual flowers to repeated visits while allowing adequate pollination. Such responses would also reduce exposure to disease-carrying pollinators and the period for establishment of such diseases (Shykoff *et al.*, 1996). Nevertheless, many plant species do not exhibit these characteristics, and so should be vulnerable to the manifold negative effects of extremely high visitation.

Aggravated individual interaction costs associated with superabundant, invasive flower visitors can have demographic consequences, particularly when seed set decreases sufficiently to limit plant population growth (Turnbull *et al.*, 2000). Although no study has demonstrated such demographic effects in relation to pollinator invasion, excessive visitation by invasive *B. terrestris* may depress seed production in many native plants by causing severe flower damage and nectar robbery (Kenta *et al.*, 2007; Combs, 2011). A possible exception among natives could be represented by rarely visited and infrequently reproducing plants, such as early-flowering species with deceitful flowers, whose population growth could increase as a consequence of still infrequent but enhanced visitation associated with bee invasion (Sanguinetti & Bustos-Singer, 2014). Superabundant alien pollinators could also have indirect negative consequences for many native plant populations if their pollination of abundant, mass-flowering alien plants were to boost their invasion potential and competitive ability. This might be the case for *Cytisus scoparius*, a leguminous shrub of European origin, which has invaded regions of South and North America with Mediterranean climates. Demographic growth and spatial spread of this chronically pollination-limited shrub seem to be determined by the visitation of large bees capable of tripping its flowers (Parker, 1997). In northwestern Patagonia, the proportion of tripped flowers and consequently seed set increased with the density of *B. terrestris* (Morales *et al.*, 2014). Similarly, in Tasmania, *Lupinus arboreus*, a leguminous shrub native to California, is an aggressive invasive 'weed', but it is rarely visited by native bees, relying instead on pollination by alien *A. mellifera* and *B. terrestris* (Stout *et al.*, 2002). Thus, the formation of such 'invader complexes' could promote the invasion success of both alien partners (Olesen *et al.*, 2002; Morales & Aizen, 2006; Abe *et al.*, 2011).

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; Vilà *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

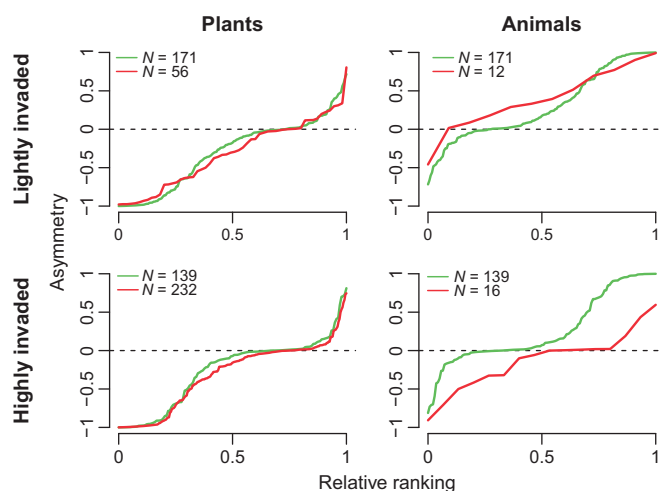


Fig. 4 Rankings of the asymmetry of interactions between pairs of focal and target species consolidated for four lightly invaded (upper panels) and four heavily invaded plant–pollinator networks (lower panels) from temperate forests in northwestern Patagonia (data from Aizen *et al.*, 2008). Asymmetry 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.

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 *Eristalix tenax*, omnivorous wasp *Vespa 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 aggravate 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.

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