

## PLANT–POLLINATOR INTERACTIONS FROM FLOWER TO LANDSCAPE

# Direct interactions between invasive plants and native pollinators: evidence, impacts and approaches

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### Summary

1. Invasive non-native plants form interactions with native species and have the potential to cause direct and indirect impacts on those species, as well as the functioning of invaded ecosystems.
2. Many entomophilous invasive plants form interactions with resident pollinators; sometimes, these interactions are necessary for the reproductive success of the invader. However, the direct role native pollinators play in plant invasion is not well understood and varies according to invasive plant traits, including breeding system and pollination syndrome.
3. The majority of studies addressing impacts on plant–pollinator mutualisms have focussed on the indirect impacts of plant invasion for native plant pollination. Fewer studies have focussed on the direct effects of invasive plants on native flower visitors.
4. Impacts of invasive plants on native pollinators can occur at a range of scales: from the individual flower visitors (in terms of nutrition, health and fitness), to populations (size, density and growth rates), communities (richness, diversity and composition) and community-level interactions (insect–flower interaction networks). Most research to date has focussed on community-level impacts, with almost nothing known about the effects of invaders on native flower visitor individuals or populations.
5. Invasive plant traits, including reward quantity and quality, spatial and temporal availability and accessibility, modulate effects on native flower visitors, and thus, different plant species have different impacts. Similarly, flower visitors do not all respond in the same way to invasive plants. Thus, generalizations are difficult to make, but understanding impacts at the individual and population level for different visitor taxa is key to explaining community-level impacts.
6. There have been varied approaches to determining impacts, with most studies attempting to compare invaded vs. non-invaded habitats. The pros and cons of different approaches are discussed.
7. Since it is impractical to study every invasive plant in every ecological context in which it occurs, we recommend a better understanding of relevant individual-level traits to predict direct interactions between invasive plants and native pollinators.

**Key-words:** community, experimental design, flower visitors, nutrition, plant invasion, plant–pollinator interaction network, pollination

### Introduction

Non-native invasive plants (henceforth ‘invasive plants’) are widely considered to have an adverse effect on the ecosystems they invade, resulting in biodiversity loss and

changes in ecosystem functioning (Mack *et al.* 2000). However, studies so far have not universally supported this theory; impacts are likely to be strongly context dependent and vary according to the traits of the invaders and the invaded community (Pyšek *et al.* 2012). Over the past 15 years, there has been particular focus on interactions between invasive plants and their mutualists (stimulated by Richardson *et al.* 2000 and others), especially pollinators (e.g. Stout & Morales 2009; Schweiger *et al.* 2010). The

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majority of studies to date on invasive plant–pollinator mutualisms have focussed on the indirect impacts of plant invasion for native plant pollination, testing hypotheses of competition and facilitation between native and invasive plants (Traveset & Richardson 2006; reviewed in Morales & Traveset 2009; and see Table S1, Supporting Information). Overall, these studies have shown largely negative effects of invasive plants on reproduction in co-flowering native species, particularly when the former are more abundant (Morales & Traveset 2009; Dietzsch, Stanley & Stout 2011). But these effects vary according to the traits of the invader (Thijs *et al.* 2012), the scale at which studies are conducted (Jakobsson, Padrón & Traveset 2009) and are context dependent. Fewer studies have focussed on the direct effects of invasive plants on native flower visitors or on the role native pollinators play in plant invasion (Fig. 1). These gaps in the literature are particularly surprising given that these direct interactions can influence the fitness of both the invasive plants and the flower visitors with which they interact. However, there are inherent difficulties in studying mobile, small and, in many cases, unknown flower-visitor taxa, which may partially explain the relative paucity of literature on direct interactions.

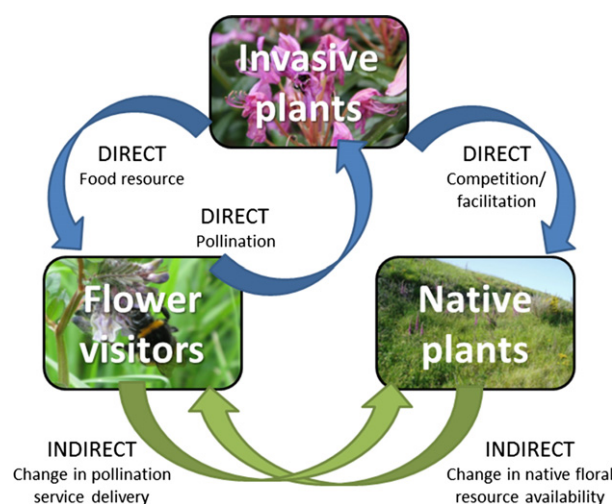
In this paper, we will review the state of knowledge on direct interactions between invasive plants and pollinators, critique approaches to determine effects, and identify gaps for future study.

### Role of pollinators in facilitating invasion of non-native plants

For many invasive plants world-wide, we know little about what pollinates them in their native range; if those species of pollinator or similar functional groups exist in their new range; which species of pollinator visit flowers in the new range; whether they are pollinator limited; how important

the quality of pollinator service is; or whether they are successful via other means of reproduction. The pollination ecology of a few species has been studied in both native and invasive ranges, for example *Hedysarum coronarium* in Spain, in populations where it is native on the mainland, and where it has been introduced to the Balearic islands (Montero-Castaño, Vilà & Ortiz-Sánchez 2014); *Rhododendron ponticum* in native populations in Spain and where it is introduced and highly invasive in Ireland (Stout *et al.* 2006); and *Nicotiana glauca* in its native habitats in South America and across its introduced range globally (Ollerton *et al.* 2012). In all cases, pollination in the non-native range is carried out by resident native pollinators belonging to similar functional groups as those pollinating plants in their native ranges. *Hedysarum coronarium* is pollinated in both native and introduced areas by some of the same species (Hymenoptera and Coleoptera), notably the honeybee *Apis mellifera* (Montero-Castaño, Vilà & Ortiz-Sánchez 2014); *R. ponticum* by large bees *Xylocopa violacea* and *Bombus* spp. in Spain and *Bombus* spp. in Ireland (Stout *et al.* 2006); and *N. glauca* by hummingbirds in the native range and specialized sunbirds in the parts of its invasive range where they occur (Ollerton *et al.* 2012). However, knowledge of pollination ecology in native and non-native regions is far from complete for most species, even those which have received a large amount of scientific and public attention. For example, *Impatiens glandulifera*, a notorious invader in the northern temperate regions, is pollinated by a variety of bee species in its invasive range (Valentine 1978; Starý & Tkalčů 1998; Nienhuis & Stout 2009), but little is known of its pollinators in native India, Pakistan and Nepal, except that *Bombus* spp. visit it for food (Saini, Raina & Khan 2013).

The role of pollinators in facilitating invasion in non-native ranges is similarly under-studied. Theoretically, the replacement of lost mutualists (including pollinators) from a plant's native range with new mutualist partners in the non-native range is key to the establishment and spread of invasive plants (mutualist facilitation hypothesis, Richardson *et al.* 2000). It follows that self-compatible plants that reproduce via asexual propagation and self-pollination would be better invaders; such plants are less likely to suffer from pollination limitation (i.e. reduced quantity and quality of pollination service in the new habitat) (Parker 1997; Goodell, McKinney & Lin 2010). Nevertheless, analyses of traits of invasive plants have revealed that a large proportion are biotically pollinated (Pyšek *et al.* 2011); for some species, high levels of autonomous self-pollination can enhance reproductive success and invasion, but so can visitation by generalist pollinators (Stout 2007; Powell, Krakos & Knight 2011). Even if suitable pollinators are present, the quality of pollination service is not assured. Visitors may not possess appropriate behaviour or phenology to deliver high quality pollination service resulting in heterospecific or low-quality pollen transfer. However, studies have shown that pollen limitation is both relatively uncommon and context specific in invasive plants (Pyšek



**Fig. 1.** Invasive plants interact with native flower visitors directly (blue arrows) and indirectly via effects on interactions with native plants (green arrows).

*et al.* 2011). Of course, factors other than pollination, such as herbivore pressure and genetic diversity in the introduced population, also contribute to reproductive success.

To become successful invaders, there are several options available to biotically pollinated plants. First, their pollinators may be introduced with them, either at the same time, or subsequently. For example, this occurred in both Florida and New Zealand, where *Ficus* spp. became invasive after host-specific pollinating fig wasps were introduced and viable seed production started to occur (Kaufmann *et al.* 1991; Richardson *et al.* 2000). In other cases, introduced generalist pollinators may facilitate pollination, either because there are no suitable native pollinator species or because plant and pollinator have pre-existing adaptations which promote their interaction. For example, European honeybees *A. mellifera* and *Bombus* spp. introduced to New Zealand, are frequent pollinators of introduced European plants there, for example *Trifolium pratense* and *Echium vulgare* (Goulson & Hanley 2004). Similarly, introduced *A. mellifera* is a major pollinator of *Lythrum salicaria*, *Cirsium vulgare* and *Rosa multiflora* in North America, invasive species also of European/Eurasian origin (Brown, Mitchell & Graham 2002; Jesse, Moloney & Obyrcki 2006; Powell, Krakos & Knight 2011). Given the extent to which *A. mellifera* and *Bombus* spp. are introduced into agricultural areas for crop pollination world-wide, they have the potential to facilitate invasion by a wide range of plant species with which they have co-evolved.

Secondly, non-native plants may form novel interactions with pollinators already present in the new habitat, co-opting them into a pollination role (Pyšek *et al.* 2011). In many cases, these pollinators are native generalists of the same species or functional groups as pollinators in the plant's native range, for example *Hedysarum coronarium*, *R. ponticum* and *N. glauca* (mentioned above). In other cases, these pollinators are non-native generalists which have not co-evolved with the non-native plant, but with close relatives of it. Again, generalist bees, such as *Apis* and *Bombus* spp., introduced for crop pollination purposes, provide good examples of this: *Lupinus arboreus* is pollinated by introduced bees (*A. mellifera* and *B. terrestris*) in Australia (Stout, Kells & Goulson 2002), which do not occur in the species' native range, but which are functionally similar to *L. arboreus*'s native pollinators, and pollinate native *Lupinus* species in Europe (Williams 1987). There are also cases where plants with a relatively specialized pollination system may be pollinated by resident species; for example, invasive *Lilium formosanum* is pollinated by a widespread hawkmoth pollinator in South Africa (Rodger, van Kleunen & Johnson 2010). Furthermore, non-native plants may form relationships with pollinators from different functional groups. For example, the bird-pollinated *Fuchsia magellanica* is pollinated by insects in parts of its introduced range (Valentine 1978), whilst *Lantana camara*, one of the most widespread and invasive species of the old-world tropics, which is presumed to be butterfly and/or bird pollinated in its native central and

southern America (Barrows 1976; Mathur & Ram 1986), forms an alliance with introduced honeybees *A. mellifera* in Australia (Goulson & Derwent 2004).

The third route by which biotically pollinated plants have become invasive in the absence of a suitable pollinator is by possessing a mixed mating strategy, enabling them to produce seeds and fruit via autonomous self-pollination in the absence of pollinators (Moodley *et al.* 2016). Plants may evolve higher rates of self-compatibility (SC) and/or self-pollination in the invasive range. Some species have been reported to be self-incompatible (SI) in their native range, but SC in the invasive range (Rambuda & Johnson 2004; Ward, Johnson & Zalucki 2012), suggesting that post-introduction selection has driven the evolution of SC, which could be due to inadequate pollinator attention. *Nicotiana glauca* plants, introduced into areas which lack specialized flower-visiting birds, have evolved shorter anther-stigma distances and seed production occurs as a result of selfing (Ollerton *et al.* 2012). However, other studies have found little support for SC in introduced species (Sutherland 2004; Colautti, White & Barrett 2010). This could be due to species traits (annuals vs. perennials, Petanidou *et al.* (2012)) and/or time since introduction (Pyšek *et al.* (2011)).

Finally, some biotically pollinated plant species have become invasive independently of sexual reproduction, and spread via vegetative means in their invasive range. For example, the widespread invasive *Fallopia japonica*, which reproduces sexually in North America (Forman & Kesseli 2003), relies entirely on clonal spread in parts of its European range (Hollingsworth & Bailey 2000). In this case, lack of sexual partners (male fertile individuals) rather than lack of pollinators has driven this phenomenon. *Oxalis pes-caprae* is another example of a species which spreads via clonal production of bulbs in parts of its invasive range in the Mediterranean Basin (Vilà *et al.* 2006; but see Ferrero *et al.* 2015).

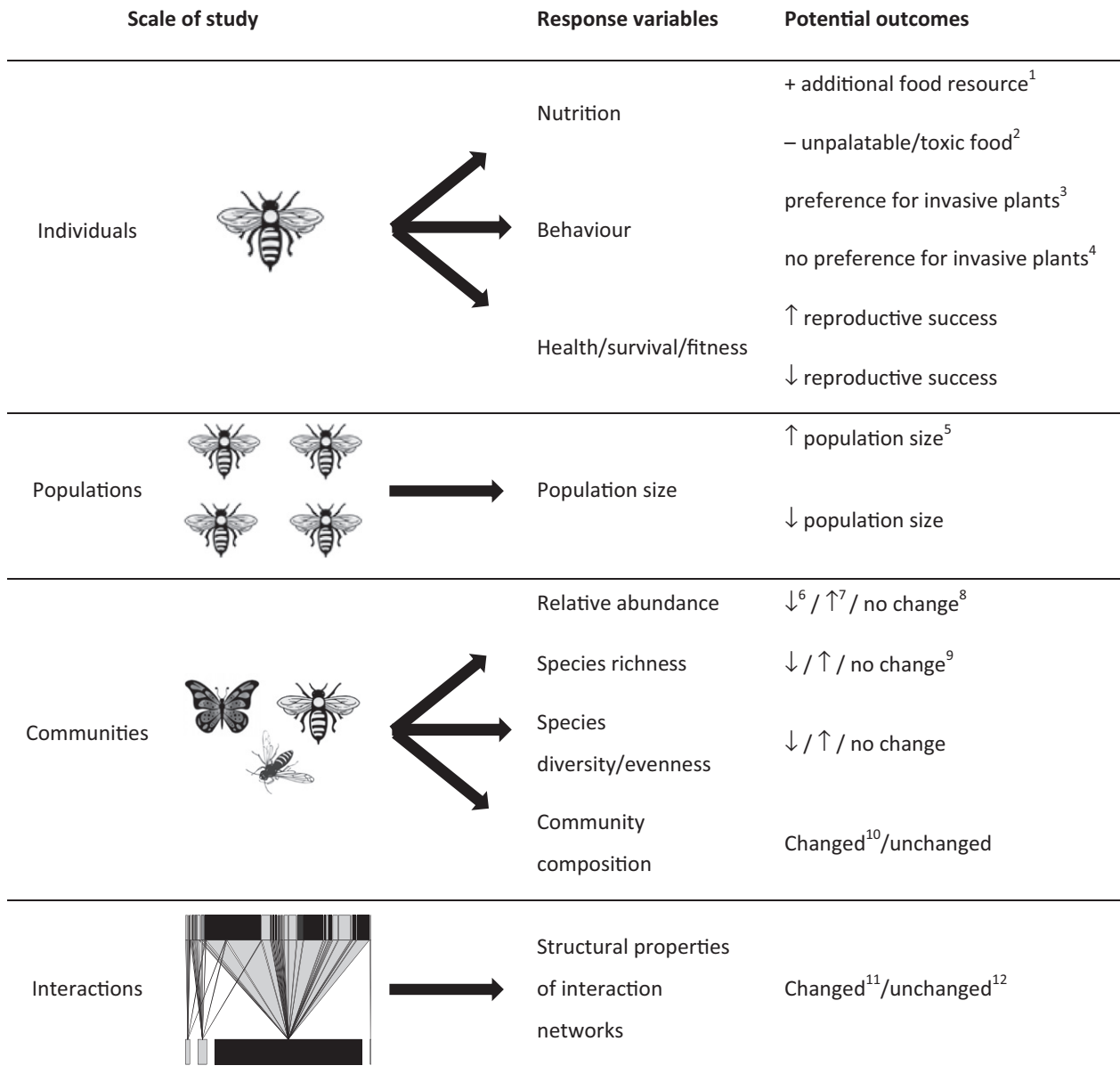
In summary, evidence to date shows that biotic pollination does not usually provide an effective barrier to invasion. Although some invasive plants circumvent the requirement for biotic pollination in their non-native ranges, many require or benefit from visitation and pollen transfer by animals, which can be provided by native or non-native animal pollinators. Biogeographical comparisons of the pollination ecology of invasive plants in their native and non-native regions present practical difficulties and are therefore infrequent, but this approach is critical for understanding the role pollinators play in the invasion process.

### Impacts of invasive plants on pollinators

Whilst interactions with native pollinators may be beneficial for invasive plants, the opposite is thought (and sometimes assumed, i.e. Litt *et al.* 2014) to be true for impacts of invasive plants on native flower visitors. This could be because large stands of invasive non-native plants occupy

space which could otherwise contain native plants, which may be assumed to be more likely to provide a suitable resource. In addition, the invader could alter the behaviour of highly competitive flower visitors, resulting in additional indirect impacts of invasive plants on some taxa of flower visitors. Although it is more difficult to quantify the effects of invasive plants on native arthropods than on native plants (Ernst & Cappuccino 2005), due in part to their size, mobility and often taxonomic limitations, there have been several studies on the impacts of invasive plants on

non-pollinating taxa (reviewed in Tang *et al.* 2012; Litt *et al.* 2014). Litt *et al.* (2014) highlighted that there is a lack of understanding on how invasive plants influence habitat and dietary requirements of arthropods in general, not just flower-visiting insects. In terms of the studies of invasive plant impacts on native flower visitors, most have focussed on the abundance, species diversity and community composition of taxa in sites invaded by non-native plants; very few have addressed impacts at the individual or population level (Fig. 2).



**Fig. 2.** Studies on impacts of invasive plants on native pollinators have encompassed a range of scales and response variables. Potential outcomes and examples are given in the right hand column. <sup>1</sup>Chittka & Schurkens (2001), Olesen, Eskildsen & Venkatasamy (2002), Nienhuis, Dietzsch & Stout (2009); <sup>2</sup>Graves & Shapiro (2003), Tiedeken & Stout (2015); <sup>3</sup>Russo, Nichol & Shea (2015); <sup>4</sup>Williams *et al.* (2011); <sup>5</sup>Dietzsch (2009); <sup>6</sup>Valtonen, Jantunen & Saarinen (2006), Morón *et al.* (2009), Hanula & Horn (2011a), Fenesi *et al.* (2015); <sup>7</sup>Shapiro (2002), Tepedino, Bradley & Griswold (2008); <sup>8</sup>Nienhuis, Dietzsch & Stout (2009), Fenesi *et al.* (2015); <sup>9</sup>Bartomeus, Bosch & Vila (2008a), Bartomeus, Vilà & Steffan-Dewenter (2010); <sup>10</sup>Novotny *et al.* (2003), Ernst & Cappuccino (2005), Hanula & Horn (2011b), Elleriis, Pedersen & Toft (2015); <sup>11</sup>Kaiser-Bunbury *et al.* (2011), Albrecht *et al.* (2014); <sup>12</sup>Padrón *et al.* (2009), Vilà *et al.* (2009), Tiedeken & Stout (2015).

Studies which have examined the effects of invasive plants on the abundance of pollinators have come to contrasting conclusions. For example, some authors have reported positive impacts of invasive plants on the abundance of some species, for example generalist butterflies (Shapiro 2002) and bees (Tepedino, Bradley & Griswold 2008), whilst others have found invasive plants associated with decreased abundance of butterflies (Hanula & Horn 2011a), bees (Valtonen, Jantunen & Saarinen 2006; Hanula & Horn 2011b; Fenesi *et al.* 2015) and indeed entire pollinator communities (Morón *et al.* 2009). On the other hand, some studies have reported no impact on pollinator abundance (bees—Nienhuis, Dietzsch & Stout 2009; hoverflies—Fenesi *et al.* 2015). Whilst effects of invasive plants on pollinator species richness and diversity appear to be more consistently negative (Morón *et al.* 2009; Hanula & Horn 2011b), some studies have found no change in species richness following invasion (Bartomeus, Vilà & Santamaría 2008b; Bartomeus, Vilà & Steffan-Dewenter 2010). Several studies have reported that invasive plants affect not just the number of species, but the composition of communities in terms of the identity of the taxa present, and the relative abundance of individuals in each taxon. For example, Ernst & Cappuccino (2005) found that stands of the invasive vine, *Vincetoxicum rossicum*, supported low numbers of arthropods in general, and some feeding guilds were entirely absent, and very few pollinators were present.

Given that invasive plants can potentially directly or indirectly influence the relative abundance of different taxa, and thus the diversity and composition of pollinator communities, it is not surprising that several recent studies have attempted to characterize these changes by examining whether invasive plants result in functional changes in ecosystems. The most common approach to characterizing changes in plant–pollinator interactions has been to examine flower–visitor interaction network structure in invaded habitats. Whilst alien plants have become well integrated into interaction networks (Morales & Aizen 2006; Lopezaraiza-Mikel *et al.* 2007; Bartomeus, Bosch & Vila 2008a; Traveset *et al.* 2015; Maruyama *et al.* 2016), sometimes this has little effect on network structure metrics (Padrón *et al.* 2009; Vilà *et al.* 2009). In other cases however, invasive species significantly alter the structure of interaction networks, either by altering the interaction evenness (i.e. the distribution of interactions between species in the network) and linkage density (i.e. weighted links per species) (Kaiser-Bunbury *et al.* 2011), or by creating larger more connected modules within the network (Albrecht *et al.* 2014). The relative abundance of the invasive species in the network is likely to affect the magnitude of effects on network structure (Stout & Casey 2014). However, given the uncertainty regarding the functional implications of network structural properties, and the ability of networks to ‘rewire’ in the presence of invaders (e.g. Campos-Navarrete *et al.* 2013), there may not be a direct relationship between

changes in insect–flower network topology and ecosystem functioning.

Whilst there is a growing body of evidence for the effects of invasive plants on native flower visitor communities, there is still very little understanding of the causal mechanisms. The direct effects of invasive plants on individual organisms in terms of their nutrition, behaviour, health, survival and fitness, as well as the indirect effect via changes in behaviour of other flower-visiting species, are understudied. This is surprising given the attention currently afforded to drivers of pollinator decline, and the general consensus that availability of food resources is a key limiting factor (Goulson *et al.* 2015). However, the direct and indirect impacts of invasive plants on native foragers are complex and context specific. Invasive plants may offer an additional or alternative food resource for native animals, but only if native animals can access that food (i.e. depending on the trait complementarity of visitors and flowers of the invasive species (Nienhuis & Stout 2009), and only if that food is nutritionally valuable, and not detrimental to the health and fitness of individuals who consume it.

*Rhododendron ponticum* is one of the only invasive plants for which the effects of invasive plants on native flower visitors have been investigated at a range of scales, from individuals to populations to entire communities. A recent study highlighted the importance of species-level studies, and of studies investigating the nutritional impact invasive plants can have on native flower visitors: Tiedeken *et al.* (2016) found that secondary compounds, grayanotoxins, in the nectar of *R. ponticum*, are toxic for native honeybees and a solitary mining bee species, but not for a native bumblebee species. These findings demonstrate that only a portion of the native pollinator community will be able to utilize invasive *R. ponticum* as a floral resource, and that nectar chemistry modulates the direction and magnitude of the impact of invasion for these three bee species. In fact, further evidence suggests that two bumblebee species *B. lucorum* and *B. pascuorum* benefit from invasive *R. ponticum*; colonies of these two bee species occurred at higher density in invaded compared with uninvaded sites (Dietzsch 2009). Finally, community-level studies along invasion gradients (Stout & Casey 2014) and temporal comparisons of invaded sites during and after flowering of the invasive plant (Tiedeken & Stout 2015) have demonstrated that invasion by *R. ponticum* affects the composition of the flower-visiting community and affects diet breadth (generality) of flower-visiting insects. Overall, this body of work shows that differential impacts of floral resources on different visitor taxa, cascade up to explain community-level impacts: *R. ponticum* may be detrimental to some flower visitors, but not to bumblebees; thus, bumblebees appear to thrive in invaded sites (Stout *et al.* 2006). Understanding impacts at the individual and population level for different visitor taxa is key to explaining community-level impacts.

### Variation in response among flower-visiting taxa

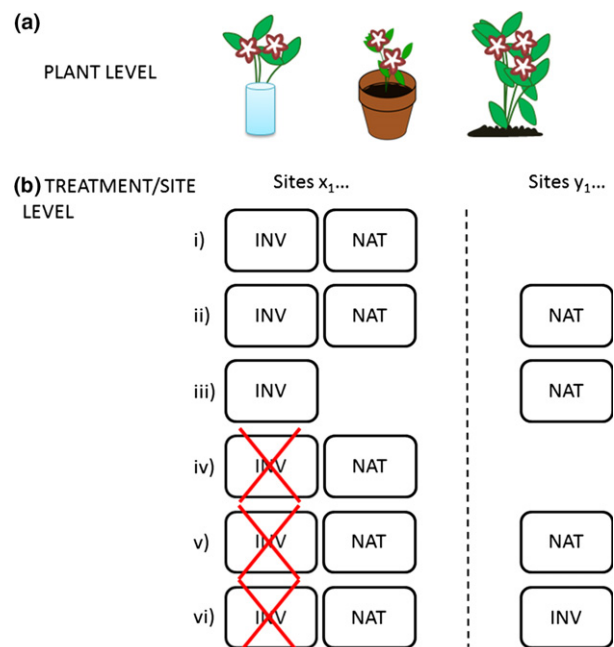
Although the effects of plant invasion on flower-visiting community abundance and diversity have been relatively well studied, we know less about the extent to which the invasive plant is incorporated into insect diets (Tang *et al.* 2012) and how this varies among insect taxa. Native flower visitors may vary in their response to plant invasion according to a number of factors, including the identity and traits of the invasive plant. Invasive plants are more likely to be utilized as a food source by native flower visitors if they are closely related to native plant species, represent a particular pollination syndrome or if they have similar chemistry (Graves & Shapiro 2003; Ernst & Cappuccino 2005). In the case of *R. ponticum*, susceptibility to floral secondary chemistry is a key modulator of the responses of native bee species to invasion (Tiedeken *et al.* 2016). Even if the secondary chemistry of invasive plants is compatible, the floral resources also have to be accessible for native pollinators to be able to utilize them. For example, Nienhuis, Dietzsch & Stout (2009) found that medium- and long-tongued *Bombus* spp. favoured the deep flowers of invasive *I. glandulifera* flowers, whilst short-tongued *Bombus* spp. preferred more shallow native flowers. In this case, the nectar provided by the invasive plant may only be available to native pollinators with physical traits that allow access to this forage resource (Nienhuis & Stout 2009). Time since introduction is another factor that can impact the effects an invasive plant has on native pollinators (Pyšek *et al.* 2011): long-established species may have evolved in response to their new habitat and may have exerted selection pressures on native flower visitors. The temporal scale at which studies are conducted also affects interpretation of findings: many studies are only conducted during the flowering period of the invader, and impacts outside this time may not be detected. Finally, the level of organization and spatial scale being studied can impact the observed response of native pollinators: although impacts from invasion may not be apparent for individual pollinator species, entire populations or communities may be affected, and over some distance from the site of invasion (Jakobsson, Padrón & Traveset 2009).

### Approaches to quantifying impacts on native pollinators

Several approaches have been used to determine impacts of invasive plants on native flower visitors (Fig. 3a). In some cases, cut branches or potted plants have been used to simulate invasion and to examine ecological consequences (e.g. Dietzsch, Stanley & Stout 2011). Most studies have been ‘natural experiments’, examining impacts in areas where invasive plants are established and growing naturally and comparing them to areas where they are not, with varying degrees of separation between such areas (de Groot, Kleijn & Jogan 2007; Jakobsson, Padrón &

Traveset 2009; Moroń *et al.* 2009; Bartomeus, Vilà & Stefan-Dewenter 2010; see also Kumschick *et al.* 2015). There are pros and cons to both approaches: in the first case, the effects of the sudden arrival of a new flowering species, and flower visitor response to that, can be monitored. However, effects on flower visitors are likely to be in terms of their behavioural response to the invader, rather than population/community-level responses. In the second case, there have been several approaches to designing ‘natural experiments’ (Fig. 3b).

Within a single site, flower visitor preference may be determined by monitoring visitation to invasive and native flowers with both present within a given site (Fig. 3b i), and comparing the two. Secondly, visitation could be recorded to both invasive and native flowers within a site, and comparing this with visitation to native flowers in the absence of the invader (Fig. 3b ii). This approach is most often used for analysing the effects of invasion on interaction networks (e.g. Vilà *et al.* 2009). Most studies have examined abundance/richness of taxa at invaded vs. control sites (e.g. de Groot, Kleijn & Jogan 2007), or at invasive plants vs. control plants (e.g. Ernst & Cappuccino 2005; Tepedino, Bradley & Griswold 2008) (Fig. 3b iii). Another approach is to remove the invader from a site and either examine the effect this has on the flower visitor community associated with the remaining native plants in that site (Fig. 3b iv) or compare this with corresponding communities in uninvaded (Fig. 3b v) or invaded (Fig. 3b



**Fig. 3.** Experimental approaches to testing impacts of invasive plants on native flower visitors (a) at the plant level; (b) at the treatment/site level, comparing sites  $x_1 \dots x_i$  (invaded) with sites  $y_1 \dots y_j$  (uninvaded). INV, invasive plants/invaded habitat; NAT, native plants/uninvaded habitat, red ‘X’ represents removal of the invader.

vi) sites (e.g. Lopezaraiza-Mikel *et al.* 2007; Nienhuis, Dietzsch & Stout 2009; Hanula & Horn 2011a,b).

There are pros and cons associated with each of these designs. If studies are conducted within a single site (Fig 3b i), with invaded and non-invaded patches in close proximity, highly mobile insect flower visitors may just move between patches, making it difficult to draw conclusions about impacts on populations or communities. However, this approach is useful for exploring the effects of invaders on individual flower-visitor behaviour, including floral preferences. One of the biggest challenges to designing studies which compare sites (Fig 3b ii–vi) is finding independent, comparable invaded and uninvaded sites; this is an issue common to studies of invasion across a range of taxa (Kumschick *et al.* 2015). Unless the habitat was recently invaded, there are usually confounding environmental factors between the invaded and uninvaded sites, so that sites differ in ways other than invasion status, even when a paired design is utilized. One approach to avoid this is to study change in flower visitor abundance through time: either before and after invasion (but long-term data on pollinators are rarely available, and other confounding factors come into play with this approach (Kumschick *et al.* 2015)), or through the season in invaded sites compared with uninvaded sites (Jakobsson & Padrón 2014). Another approach is to use a spatial gradient, with varying degrees of invasion in different sites (Dietzsch, Stanley & Stout 2011; Grass *et al.* 2013; Stout & Casey 2014). Removal of invaders is also problematic as this often reduces the total resource availability for flower-visiting insects. Due to their mobility, insects can disperse to alternative patches/sites to forage. This can potentially result in the false conclusion that invasive plants increase insect populations, and removal of invasive plants reduces them, whereas in reality, invasive plants may provide resources, but in their absence, insects disperse to find resources elsewhere.

An alternative approach to determine whether an invasive plant affects flower visitors because of its invasive status *per se* is to compare the role of a plant in ecosystems where it is invasive, compared to where it is native. This approach has not been attempted often, but may be desirable in terms of determining impacts, because it may simply be that an attractive plant species, which dominates interaction networks in its native habitats, may have similar effects when it is not native. Thus, we can move away from determining impacts of ‘invasive species’ to a more thorough ecological understanding of dominant plant species in ecological communities. Indeed, a recent study which compared the role of *R. ponticum* in both native and invasive habitats (E. J. Tiedeken and J. C. Stout, unpublished data) demonstrated that the impacts of the invader (*R. ponticum*) on insect–flower interaction networks were similar in both places: *R. ponticum* dominated networks and was highly linked in both its native and invasive range. Thus, biogeographical studies which investigate invasive species in their native as well as their

introduced range can provide useful insights into invasion ecology. However, since many of the impacts of invasive plants on flower visitors may be due to the fact they produce an abundance of flowers and thus are highly rewarding, an alternative approach would be to compare the impacts of invasive plants with the impacts of highly rewarding native ones. Then, we may begin to disentangle the effects of invasive non-native plants *per se* on flower visitors rather than just the effects of a highly rewarding species in the a system.

## Conclusions

Invasive plants often form interactions with native flower visitors, with their invasion sometimes dependent on these interactions. However, despite the assumption that invasive plants have generally negative impacts on native flower visitors, there is not a great deal of evidence to support this (Traveset & Richardson 2006). Perhaps unsurprisingly, given the difficulties associated with studying many flower-visiting taxa, the direct effects of invasive plants on individual flower visitor nutrition, health and fitness are poorly understood. Given the difficulty in conducting experiments to test effects, and the range of responses that can be measured, it is likely that we will only be able to determine impacts for a small proportion of the potentially affected species (most likely insect species which are commercially available and/or can be manipulated in a laboratory setting). Furthermore, since the impacts of invasive plants are likely to be plant species specific and ecological context specific, our understanding is likely to be limited to globally widespread, problematic plant species. However, by designing appropriate studies (Kumschick *et al.* 2015), and incorporating more knowledge of plant and insect species traits (including plant breeding system, pollination syndrome, nectar chemistry, insect body size and diet breadth), better prediction of impacts may be achieved. Thus, more studies of invasive plants and flower visitor ecology are required before generalizations about direct impacts can be made.

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## Data accessibility

This manuscript does not use data.

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## Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

**Table S1.** Examples of recent studies of the effects of non-native plants on native plant pollination.