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Impacts of plant invasions in native plant–pollinator networks

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Summary

The disruption of mutualisms by invasive species has consequences for biodiversity loss and ecosystem function. Although invasive plant effects on the pollination of individual native species has been the subject of much study, their impacts on entire plant–pollinator communities are less understood. Community-level studies on plant invasion have mainly focused on two fronts: understanding the mechanisms that mediate their integration; and their effects on plant–pollinator network structure. Here we briefly review current knowledge and propose a more unified framework for evaluating invasive species integration and their effects on plant–pollinator communities. We further outline gaps in our understanding and propose ways to advance knowledge in this field. Specifically, modeling approaches have so far yielded important predictions regarding the outcome and drivers of invasive species effects on plant communities. However, experimental studies that test these predictions in the field are lacking. We further emphasize the need to understand the link between invasive plant effects on pollination network structure and their consequences for native plant population dynamics (population growth). Integrating demographic studies with those on pollination networks is thus key in order to achieve a more predictive understanding of pollinator-mediated effects of invasive species on the persistence of native plant biodiversity.

I. Introduction

Understanding community-level responses to human-mediated disturbances such as species invasions is critical to prevent further biodiversity loss and ensure ecosystem function (Ehrenfeld, 2010; Kaiser-Bunbury *et al.*, 2010; Thebault & Fontaine, 2010; Evans *et al.*, 2013; Tylianakis & Morris, 2013). Developing a predictive understanding of invasive species effects on pollination services is particularly important given its role in human well-being and in the overall maintenance of biodiversity (Pejchar & Mooney, 2009; Burkle & Alarcón, 2011; Tylianakis, 2013; Kaiser-Bunbury *et al.*, 2017; Ramos-Jilberto *et al.*, 2020). As a result, there is large body of literature on the effects of invasive species on the pollination of individual native plant species (reviewed in Morales & Traveset, 2009; Vilá *et al.*, 2011; Charlebois & Sargent, 2017). The drivers and consequences of species invasions on entire plant–pollinator communities however are less understood (Morales & Traveset, 2009; Valdovinos *et al.*, 2009; Charlebois & Sargent, 2017; Stout & Tiedeken, 2017; van Kleunen *et al.*, 2018; Valdovinos, 2019). This underscores the need for studies that scale invasive species effects from species-pair interactions to whole interaction networks in order to more fully understand the consequences of the rapidly increasing invasion of plant species around the world (Ghazoul, 2002; van Kleunen, 2018). Work in this field has so far focused on two main areas (1) understanding the factors that mediate the 'integration' of invasive species into native plant–pollinator communities (Fig. 1a) and (2) evaluating their subsequent effects on these communities (Fig. 1b,c). However, we find there is a need to integrate knowledge within and across these two areas of study. In particular, there is a need to clearly define and integrate different aspects of the invasive species 'integration process' (discussed later), and to evaluate effects on aspects of plant fitness that more directly relate to plant reproductive success (e.g. pollen transfer dynamics, seed production) and population growth (e.g. seed germination and establishment). Here we briefly summarize the main findings in these aspects of plant invasion and outline potential future directions in this field. In doing so, we hope to elucidate ways to achieve a more predictive understanding of the drivers and effects of invasive species on native plant–pollinator communities. For simplicity, when referring to invasive plant species, here we include those that have been characterized as exotic, alien or invasive (see Richardson *et al.*, 2011 for a detailed discussion).

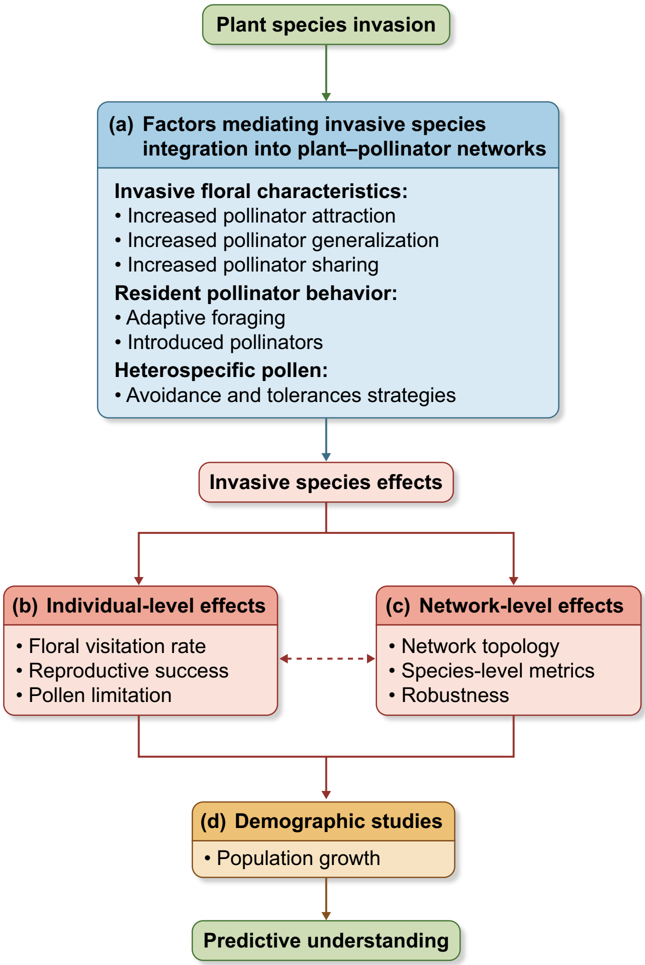

Fig. 1 Summary of current understanding for the causes and consequences of plant species invasion in native plant–pollinator communities. (a) Factors predicted to facilitate the integration of invasive plants into plant–pollinator networks. Effects of invasive species on resident communities evaluated at the level of (b) individual species and at the level of (c) entire communities (network approaches). Understanding of invasive species integration processes and its effects need to be combined with (d) demographic studies to fully assess the long-term effects on native populations.

II. Invasive plant species integration into plant–pollinator networks

So far, the main criteria used to evaluate invasive species effective 'integration' into native plant–pollinator networks (PPNs) have been related to their capacity to establish interactions (e.g. floral visits) with resident pollinators (e.g. Aizen *et al.*, 2008; Traveset & Richardson, 2014). As a result, a wide array of metrics related to invasive use of resident pollinators have been used to describe their 'integration' into PPN (Table 1). For instance, invasive plants have been considered well-integrated when they share pollinators with native plants, and/or if they receive equal or higher visitation rates than natives (e.g. Aizen & Morales, 2008; Maruyama *et al.*, 2016; Montero-Castaño & Vilà, 2017; Seitz *et al.*, 2020; Table 1). However, these metrics only describe one component of invasive plant 'integration', i.e. their degree of pollinator use in invaded communities. A second component of invasive 'integration' however relates to pollinator efficiency and invasive reproductive success, which ultimately determines invasive long-term persistence (and hence integration) in invaded communities. For instance, many invasive plants are animal-pollinated (Richardson *et al.*, 2000; Traveset & Richardson, 2006; Richardson & Pyšek, 2012), but even when they are visited by one or very few pollinators, they can still achieve a high reproductive success compared to natives (Thompson & Knight, 2018). Few studies, however, have described successful 'integration' by also quantifying invasive plant reproductive success (e.g. fruit and seed production, seedling establishment) in invaded communities (Barthell *et al.*, 2001; Stokes *et al.*, 2006; Kaiser-Bunbury *et al.*, 2011; Thompson & Knight, 2018; and see van Kleunen *et al.*, 2008; Table 1). A third component of invasive 'integration' refers to the role that invasive plants play within native plant–pollinator communities. That is, whether invasives help maintain PPN structure, or if invasive species' role within a network is equivalent to that of natives. The answer to these questions can only be evaluated by assessing invasive species effects within the context of PPNs (Table 1). For instance, well-integrated invasive plants have been defined as those that have dominant roles (e.g. core or hub species) or are highly connected within the network (e.g. Bartomeus *et al.*, 2008a; Vilà *et al.*, 2009; Larson *et al.*, 2016; Table 1). Other studies have also used simulated extinction models (while accounting for interaction rewiring) to assess invasive species role in PPN structure (e.g. nestedness) and robustness, compared to that of natives (Parra-Tabla *et al.*, 2019; also see Albrecht *et al.*, 2014; Corcos *et al.*, 2020). However, these different components of invasive 'integration' are rarely differentiated and specifically defined, even though they describe very different processes that relate to the invader's ability to

Table 1 Examples of response variables used to characterize the integration of invasive plant species into native plant–pollinator communities.

	Response variable used	Pattern observed	References
(a) Species-level descriptors			
Patterns of pollinator use	Flower visitor richness	Same as natives	Bartomeus *et al*. (2008); Aizen & Morales (2008); Montero-Castaño & Vilà (2017); Thompson & Knight (2018)
		Higher than natives	Vilá *et al*. (2009); Maruyama *et al*. (2016); Seitz *et al*. (2020)
	Species composition	Same as natives	Parra-Tabla *et al*. (2019)
Pre-pollination success	Pollinator visitation rate	Same as natives	Vilà *et al*. (2009); Montero-Castaño & Vilà (2017); Parra-Tabla *et al*. (2019)
		Higher than natives	Lópezaraiza-Mikel *et al*. (2007); Bartomeus *et al*. (2008a); Morales & Aizen (2008); Morales & Traveset (2009); Kaiser-Bunbury *et al*. (2011); Seitz *et al*. (2020)
Post-pollination success	Pollen limitation	No pollen limitation	Pyšek *et al*. (2011); Thompson & Knight (2018)
	Fruit and seed-set	Same or higher as natives	Kaiser-Bunbury *et al*. (2011)
(b) Network and species level descriptors			
Invasive species functionality within plant–pollinator networks	Species roles within pollination networks[1]	Core species role	Lópezaraiza-Mikel *et al*. (2007); Vilà *et al*. (2009); Bartomeus *et al*. (2008a)
		Hub species role	Albrech *et al*. (2014); Larson *et al*. (2016)
	Interactions properties[2]	Higher interactions strength than natives	Aizen *et al*. (2008); Bartomeus *et al*. (2008a); Maruyama *et al*. (2016)
		Higher linkage level than natives	Bartomeus *et al*. (2008a); Vilá *et al*. (2009); Kaiser-Bunbury *et al*. (2011)
Invasive species effects on network structure	Nestedness/connectance	No change	Bartomeus *et al*. (2008a); Vilá *et al*. (2009); Padrón *et al*. (2009); Stouffer *et al*. (2014); Tiedeken & Stout (2015)
	Robustness	No change	Albrecht *et al*. (2014); Parra-Tabla *et al*. (2019); Corcos *et al*. (2020)

Response variables used to describe successful integration include (a) species-level descriptors of invasive species pollinator use and reproductive success in invaded communities and (b) descriptors of the role invasive species play in plant–pollinator networks. References are provided as examples of the use of each response variable.

[1] Species roles: core species, highly connected species; hub species, species that received many visits to other well connected species.

[2] Interactions properties: strength, frequency of interactions; linkage, number of species interactions per species.

(1) use the pollinator resource available, (2) reproduce efficiently and achieve sustainable population growth and (3) perform meaningful roles in maintaining PPN structure. In fact, most studies typically used the term 'integration' interchangeably to describe these three processes (e.g. Bartomeus *et al.*, 2008a; Aizen & Morales, 2008; Vilà *et al.*, 2009; Montero-Castaño & Vilà, 2017; Parra Tabla *et al.*, 2019). Thus, we still lack a unified framework and a set of unique criteria to characterize and assess successful invasive plant species 'integration' into native communities.

Thus, we propose that assessing successful invasive species integration into PPN requires defining and ideally integrating the three main criteria described earlier, (1) degree of native (or invasive) pollinator use, (2) invasive species reproductive success (i.e. fruit and seed production) and population growth, and (3) its impact on plant–pollinator interaction structure. We recognize, that in some instances these three criteria may occur independently from each other, as is the case for *Oxalis* spp. in Mediterranean communities, which can be visited by native pollinators (hence integrated into the network) but reproduce vegetatively (Hulme, 2004, and references cited therein). However, we consider this to be the exception rather than the rule as many invasive species depend, fully or partially, on animal vectors for successful reproduction (e.g. Richardson *et al.*, 2000; Traveset & Richardson, 2006; Richardson & Pyšek, 2012). It is also important to note that some components (e.g. reproductive success, function within invaded communities) of invasive species 'integration' are better assessed relative to the function (structural role within PPN) and reproductive success of native species in the community (see Hernández-Castellano *et al.*, 2020). Thus, studies that only describe invasive species' use of pollinators or degree of reproductive success would be insufficient (Bartomeous *et al.*, 2008a; Thompson & Knight, 2018). For instance, using PPNs, the degree of pollinator use (criteria (1) earlier) can be evaluated by comparing metrics that describe the number, diversity and intensity (strength and frequency) of invasive species interactions (e.g. network centrality, number of links, interaction strength; Vilà *et al.*, 2009; Blüthgen, 2010) with those of natives. In this same way, invasive species reproductive success (criteria (2) earlier) would need to be comparable to average native species' reproductive success (fruit-set, seed-set, pollen limitation; Kaiser-Bunbury *et al.*, 2011; Thompson & Knight, 2018). Demographic models can also be used to integrate pollination success with other life history attributes (e.g. germination and establishment) to assess its ultimate role in population growth of native and invasive species (discussed later; also see Stokes *et al.*, 2006; Paynter *et al.*, 2010). Finally, invasive species' role in network structure can be evaluated by comparing outcomes of simulated extinction scenarios of invasive and native species (e.g. Parra-Tabla *et al.*, 2019), and/or via experimental removal or introduction of species in the field (Lópezaraiza-Mikel *et al.*, 2007; Muñoz & Caviers, 2008; Nienhuis *et al.*, 2009; Russo *et al.*, 2019). The contribution of plant species to network structure (e.g. nestedness contribution) can also be compared directly between invasive and native species. For instance, nestedness contribution values measure the relative importance of each plant species to overall network nestedness (via pollinator generalization; Geslin *et al.*, 2017), which has been shown to be a key mediator of network resilience and robustness to environmental disturbances (see Bascompte *et al.*, 2003). Although we consider all these components to be critical in the process of invasive species 'integration' into native communities, to our knowledge no study has evaluated all three for any single community.

In spite of the absence of a unified framework a growing body of evidence, across a wide range of habitats, has so far suggested that invasive plant species successfully integrate into PPN (e.g. Olesen *et al.*, 2002; Aizen *et al.*, 2008; Padrón *et al.*, 2009; Kaiser-Bunbury *et al.*, 2011; Vilá *et al.*, 2011; Stoufer *et al.*, 2014; Maruyama *et al.*, 2016; Johnson & Ashman, 2018; Parra-Tabla *et al.*, 2019; but see Memmott & Waser, 2002). In order to integrate successfully, invasive plants must first solve the problem of replacing its original pollinators with those available in invaded communities (e.g. Vilà *et al.*, 2009; Pyšek *et al.*, 2011; Murayama *et al.*, 2016; and see Richardson *et al.*, 2000). Invasives must then co-opt existing pollinators in invaded communities, perhaps from similar functional groups as those existent in their natural ranges (e.g. Stout *et al.*, 2006; Stout, 2007; Tepedino *et al.*, 2008; Powell *et al.*, 2011; Pyšek *et al.*, 2011; Ollerton *et al.*, 2012; Montero-Castaño *et al.*, 2014; Maruyama *et al.*, 2016). Among the main factors proposed to facilitate this process are, (1) invasive plant floral characteristics (e.g. Bartomeous *et al.*, 2008a; Morales & Traveset, 2009; Gibson *et al.*, 2012), (2) changes in native pollinator behavior (i.e. adaptive foraging) (Richardson *et al.*, 2000; Valdovinos, 2019), and more recently (3) tolerance to changes in pollen transfer dynamics among plant species (heterospecific pollen (HP) transfer, e.g. Arceo-Gómez & Ashman, 2016, Parra-Tabla *et al.*, 2021) (Fig. 1a). Here we discuss these factors separately, however, it is important to point out that these factors are not mutually exclusive and may also depend on phylogenetic relationships between native and invasive plants (Rezende *et al.*, 2007; Aizen *et al.*, 2016; Peralta, 2016; Klecka *et al.*, 2018; Valdovinos, 2019).

1. Floral characteristics of invasive plants

Invasive species typically have large floral displays, showy flowers, and large amounts of floral rewards, thus making them highly attractive for resident pollinators and hence facilitating their 'integration' into PPN (e.g. Chittka & Schurkens, 2001; Brown *et al.*, 2002; Moragues & Traveset, 2005; Muñoz & Caviers, 2008; Kandori *et al.*, 2009; Pyšek *et al.*, 2011; but see Charlebois & Sargent, 2017). Specifically, floral traits can aid in invasive species 'integration' of PPN by increasing (1) overall pollinator attraction, (2) pollinator generalization, and/or (3) pollinator use overlap with native plant species (Fig. 1a). Empirical and experimental evidence has supported this prediction (e.g. Lopezaraiza-Mikel *et al.*, 2007; Padrón *et al.*, 2009; Kaiser-Bunbury *et al.*, 2011; Vilà *et al.*, 2011). For instance, invasive *Impatiens glandulifera* (Balsaminaceae) and *Opuntia* spp (Cactaceae), which offer large quantities of nectar and pollen, attract a large number of native pollinators that aid in their 'integration' into PPN (Lopezaraiza-Mikel *et al.*, 2007; Padrón *et al.*, 2009, respectively). The capacity of attracting a large number of pollinators is however predicted to be dependent on resident pollinators' ability to adjust their foraging decisions (i.e. adaptive foraging; Valdovinos, 2019; discussed later).

Invasive species also often have highly generalized floral traits (e.g. flowers with radial symmetry), which allows them to use a wide range of pollinator taxa (e.g. Bartomeous *et al.*, 2008a; Vilà *et al.*, 2011; Emer *et al.*, 2015), including pollinator specialists (i.e. visit one or very few plant species; Stouffer *et al.*, 2014). Specifically, generalized floral traits may help avoid trait mismatches with resident pollinators, thus facilitating invasive species 'integration' (see Vázquez *et al.*, 2009; Valdovinos, 2019). For example, the large and radially symmetrical flowers of invasive *Carpobrotus afine acinaciformis* (Aizoaceae) and *Opuntia stricta* (Cactaceae) are visited by more than a third of the total insect taxa in Mediterranean communities (Bartomeous *et al.*, 2008a), while *Bidens pilosa* (Asteraceae) is visited by up to 60% of all the pollinators in coastal communities in the Yucatan (Parra-Tabla *et al.*, 2019). Furthermore, an analysis across multiple invaded and no invaded pollination networks showed that generalized invasive plants receive more visits and play more important network topological roles (i.e. network hubs) than specialized invasive species (Albrecht *et al.*, 2014). Increasing evidence further suggests that floral trait similarity between native and alien species may also help facilitate invasive species 'integration' into PPN (e.g. Vilà *et al.*, 2011; Gibson *et al.*, 2012; Parra-Tabla *et al.*, 2019). For instance, in highly invaded sand dune plant communities, high floral similarity between native and invasive plants (*c.* 80%) was predicted to facilitate the successful 'integration' of invasive species into pollination networks (Fig. 2; Parra-Tabla *et al.*, 2019). Likewise,

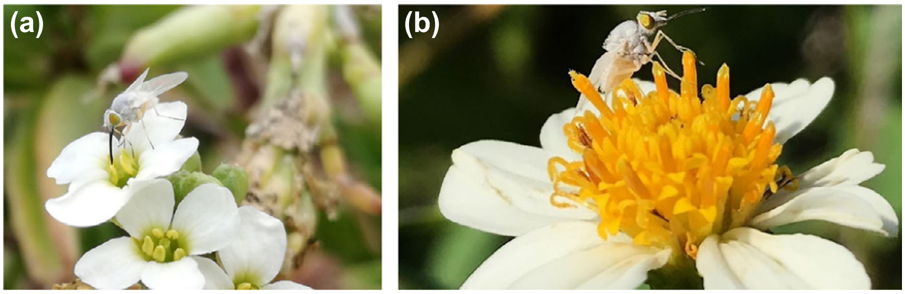

Fig. 2 Example of pollinator sharing between native and invasive species in coastal plant communities in the Yucatan. The endemic species (a) *Cakile edentula* (Brassicaceae) shares up to 35% of its pollinators with the invasive species (b) *Bidens pilosa* (Asteraceae). Of note is the high degree of floral trait similarity (size, color) between the two species (photograph credits: (a) Cristopher Albor and (b) Alexander Suárez-Mariño).

in sclerophyllous shrublands, floral similarity and high flower visitor overlap between native and invasive species facilitated the 'integration' of invasives into the resident community (Gibson *et al.*, 2012). Since shared evolutionary history often leads to increased floral trait similarity, phylogenetic relationships between invasive and native species can further help mediate invasive species 'integration' into native communities (see Rezende *et al.*, 2007; Carvalheiro *et al.*, 2014). However, to our knowledge, of the still limited number of studies that have evaluated invasive 'integration', few have evaluated whether integration into pollination networks is mediated by phylogenetic proximity with native species (but see Stouffer *et al.*, 2014).

Empirical studies have just begun to shed light on the role that floral traits play in mediating invasive species 'integration' into native co-flowering communities (Bartomeus *et al.*, 2008a; Vilà *et al.*, 2011; Gibson *et al.*, 2012; Parra-Tabla *et al.*, 2019). Thus, there is still an urgent need for experimental approaches that formally test the mechanistic hypothesis proposed to date. For instance, while theoretical studies have supported the role of invasive plant pollinator generalization (Romanuk *et al.*, 2009; Russo *et al.*, 2014) and floral traits in mediating its integration into PPN (Valdovinos, 2019), very few studies have tested these predictions experimentally. This could be achieved by conducting community-level experiments that manipulate the presence/absence of invasive/native plants (e.g. Lópezaraiza-Mikel *et al.*, 2007: Hernández-Castellano *et al.*, 2020), manipulate floral trait diversity and composition (e.g. generalized/specialized; see Seitz *et al.*, 2020) or that manipulate the degree of floral trait similarity between native and invasive species. For example, common garden experiments in which native species are grown alongside invasive species with similar and contrasting flowers traits (e.g. color, size or shape) would be useful in determining the role of floral similarity on invasive species integration into pollination networks (while controlling for phylogenetic relationships and abundance). Another possibility would be to remove highly generalist invasive species and evaluate their effect on the structure and rewiring of pollination networks compared to control (nonremoval) sites (Goodell & Parker, 2017; Biela *et al.*, 2019). Although logistically daunting, such community-wide experiments are necessary to fully understand the factors that mediate invasive plant integration into PPN, and their contribution to network structure (e.g. Lopezaraiza-Mikel *et al.*, 2007; Goodell & Parker, 2017; Hernández-Castellano *et al.*, 2020; Maia *et al.*, 2020; Seitz *et al.*, 2020).

2. The role of pollinators in invasive species integration

As noted previously, successful 'integration' of invasive plants may depend on the adaptive foraging abilities of resident pollinators (Richardson *et al.*, 2000; Stout *et al.*, 2006; Stout, 2007; Powell *et al.*, 2011; Montero-Castaño *et al.*, 2014) (Fig 1a). Adaptive foraging allows pollinators to switch their foraging decisions according to the quality and number of floral resources available (see Valdovinos, 2019). However, our understanding of the role of resident pollinators in the successful 'integration' of invasive plants is still limited (Olesen *et al.*, 2002; Stouffer *et al.*, 2014; and see Stout & Tiedeken, 2017; Thompson & Knight, 2018). What seems to be clear is that particular pollinator species can play a disproportional role in facilitating invasive plant species 'integration' (Olesen *et al.*, 2002; Stouffer *et al.*, 2014; Maruyama *et al.*, 2016). For instance, a study of invasive plant 'integration' on plant–hummingbird networks suggested that generalized short-billed hummingbirds play a key role in facilitating the 'integration' of invasive plants into native PPN (Maruyama *et al.*, 2016). Kaiser-Bunbury *et al.* (2011) also observed that *Apis mellifera* accounted for up to 80% of the visits to invasive plants in island plant communities while native pollinators visited at low frequencies (< 5%). Interestingly, invasive plants seem to highly benefit from the presence of introduced alien pollinators such as honeybees (e.g. Geslin *et al.*, 2017; Stout & Tiedeken, 2017, and references cited therein). This finding has lent support to the idea of 'invasive meltdowns', in which two invasive species facilitate each other's establishment in novel communities (Simberloff & Von Holle, 1999). This process might hence play an important role in invasive species 'integration' into PPN. For instance, exotic pollinators such as *Bombus terrestris* have been shown to have positive effects on population growth and rates of spread of invasive plant populations (Stokes *et al.*, 2006; and see Valido *et al.*, 2019). However, empirical evidence of the role of pollinators, including invasive ones, in mediating successful plant integration into local communities is still limited (Simberloff, 2006; Magrach *et al.*, 2017; Stout & Tiedeken, 2017; Herrera, 2020). Furthermore, most of the current evidence comes from data on floral visitation, and it is necessary to test if adaptive foraging also results in adequate pollinator service to invasive plants, thus securing its long-term 'integration' into resident communities. It is interesting to note, however, that invasive species that are animal-pollinated are not typically pollen limited, including those that establish few links with resident pollinators (see Pyšek *et al.*, 2011; van der Kleuken *et al.*, 2018; Thompson & Knight, 2018). This suggests that pollinator replacement via adaptive foraging may result in adequate fruit and seed production of invasive plants (or that most invasive plants possess mechanisms of reproductive assurance; Razanajatovo *et al.*, 2016). In spite of all these important advances, we join others (Kaiser-Bunbury *et al.*, 2011; Valdovinos *et al.*, 2013; Valdovinos, 2019) in emphasizing the need for more empirical and experimental studies to help more fully understand the role of particular pollinator species and/or pollinator adaptive foraging in mediating long-term invasive plant 'integration' into PPN.

3. Tolerance to effects of heterospecific pollen receipt

Pollen transfer among plant species is common (e.g. Fang & Huang, 2013; Tur *et al.*, 2016; Arceo-Gómez *et al.*, 2019) and prevalent in invaded co-flowering communities (e.g. Lopezaraiza-Mikel *et al.*, 2007; Bartomeus *et al.*, 2008b; Johnson & Ashman, 2018; Daniels & Arceo-Gómez, 2020; Parra-Tabla *et al.*, 2021; but see Emer *et al.*, 2015), with negative effects on plant fitness (e.g. Morales & Traveset, 2008; Arceo-Gómez & Ashman, 2016; Ashman *et al.*, 2020). For instance, a meta-analysis of 50 HP donor-recipient pairs showed strong negative effects on plant reproductive success (*c.* 20% decrease in seed production; Ashman & Arceo-

Gómez, 2013) across 21 HP donor and 22 recipient plant families (Arceo-Gómez & Ashman, 2016). Thus, reciprocal HP transfer between native and alien species may have the potential to influence invasive species 'integration' into PPN. For instance, in order to fully integrate into native PPN invasive plants may need to successfully avoid (minimize HP deposition on stigmas), or tolerate (minimize the reproductive cost of HP receipt), the negative effects of HP receipt (Fig. 1a; specific HP tolerance and avoidance mechanisms are reviewed in Ashman & Arceo-Gómez (2013); also see Arceo-Gómez & Ashman, 2016, Suárez-Mariño *et al.*, 2019, Parra-Tabla *et al.*, 2021). Evidence of HP tolerance or avoidance as a mechanism facilitating plant species invasion and 'integration' into PPN is still scarce. However, recent studies have shown some of the first empirical evidence suggesting a greater ability of invasive species in avoiding and tolerating negative HP fitness effects (Suárez-Mariño *et al.*, 2019; Parra-Tabla *et al.*, 2021). Interestingly, a meta-analysis of 56 study cases has also revealed that invasive HP donors tend to cause a stronger decrease in seed production compared to native HP donors (Arceo-Gómez & Ashman, 2016). It is important to note that floral trait similarity between native and invasive species is expected to facilitate invasive species 'integration' into PPN (see earlier). However, high floral trait similarity may also increase the probability of HP transfer by increasing pollinator sharing between native and invasive species (e.g. Lopezaraiza-Mikel *et al.*, 2007; Daniels & Arceo-Gómez, 2020). This in turn may help reinforce the role that HP avoidance or tolerance strategies play in plant invasion (Arceo-Gómez & Ashman, 2016). For instance, the ruderal *Bidens pilosa* (Asteraceae) which has invaded large portions of the coast of the Yucatan Peninsula over the last 30 yr, shares more than 35% of its pollinators with native plant species (Parra-Tabla *et al.*, 2019), but it is also significantly more tolerant to HP effects than native species (Fig. 2; Suárez-Mariño *et al.*, 2019). Thus, although still limited, the combined evidence so far suggests that HP tolerance and avoidance strategies may play a so far overlooked role in mediating the 'integration' of invasive species into native PPN (Arceo-Gómez & Ashman, 2016; Suárez-Mariño *et al.*, 2019; Parra-Tabla *et al.*, 2021).

Future studies could then use novel pollen tracking techniques (see Anderson & Minnaar, 2020) to more fully understand patterns of reciprocal HP transfer between native and invasive species and its potential impacts on plant reproductive success. For instance, such techniques may allow to more quickly and accurately characterize patterns of pollen transfer among species, particularly in closely related species with strong similarities in pollen morphology. They may also allow to more precisely describe patterns of pollen movement as the location and number of pollen analogs can be manipulated (Anderson & Minnaar, 2020). Until now, only a couple of studies have evaluated HP transfer networks in invaded communities and both suggest important invasive species effects (Johnson & Ashman, 2018; Parra-Tabla *et al.*, 2021). Specifically, both studies show that invasive species are better pollen donors and play more central roles (i.e. hubs) within HP transfer networks than natives (Johnson & Ashman, 2018; Parra-Tabla *et al.*, 2021). One study also showed that native plants are more affected (stronger decrease in reproductive success) by HP than invasives (Parra-Tabla *et al.*, 2021). However, more studies are needed in order to fully assess the role of HP avoidance and tolerance in mediating invasive species integration into PPN.

III. Effects of invasive species on plant–pollinator networks

The effects of invasive plants on the pollination success of individual plant species have been well documented over the last 20 yr (Traveset & Richardson, 2006). These can include effects on pollinator community composition, visitation rate and native plant reproductive success (fruit and seed production), all of which have been discussed in a number of important reviews (Morales & Traveset, 2009; Charlebois & Sargent, 2017; Stout & Tiedeken, 2017) and thus are not considered here. However, recent interest has emerged on evaluating the effects of invasive plant species on the structure of entire plant–pollinator communities (Kaiser-Bunbury *et al.*, 2011; Vilà *et al.*, 2011; and see Maia *et al.*, 2020). For instance, in generalized plant–pollinator communities the impacts of invasive species on a single native plant can ripple throughout the whole community, as most species are directly or indirectly connected to each other (e.g. Rodriguez-Cabal *et al.*, 2013; Traveset *et al.*, 2017). In order to achieve this level of understanding studies have used constructs of network theory and analysis to evaluate the importance of three main invasive species effects on plant–pollinator communities. (1) Changes in patterns of species interactions (modularity, nestedness, connectance; Valdovinos *et al.*, 2009; Vilà *et al.*, 2009), (2) changes in the frequency and number of these interactions (interaction strength, degree; Bartomoues *et al.*, 2008a; Kaiser-Bunbury *et al.*, 2011) and (3) changes in the function that individual species play within the network (centrality, hubs; Aizen *et al.*, 2008; Martin-Gonzalez, 2010; Albrech *et al.*, 2014; Larson *et al.*, 2016).

These network metrics have in turn been used to make inferences regarding the resilience (i.e. the ability to quickly recover after disturbance) of communities to human-mediated disturbances (Kaiser-Bunbury *et al.*, 2017; Tylianakis & Morris, 2017). For instance, Vilà *et al.* (2009) found no changes in network connectance or nestedness resulting from plant species invasion across PPNs in Europe, hence leading to the conclusion that these communities are robust to the effects of invasive species. Other studies have even found that invasive species can increase community resilience (Aizen *et al.*, 2008; Albrecht *et al.*, 2014). The strength of plant–pollinator interactions in a network context has also been observed to be resilient to species invasion (e.g. Bartomeous *et al.*, 2008a). In some cases, alien species have even been found to be functionally equivalent to native species and contribute equally to network structure and robustness (Parra-Tabla *et al.*, 2019). The overall evidence so far hence suggests an apparent high robustness/resilience of plant–pollinator communities to the effects of plant species invasion (e.g. Padrón *et al.*, 2009; Vilà *et al.*, 2009; Albrecht *et al.*, 2014, Russo *et al.*, 2019; but see Bartomeous *et al.*, 2008a). Interestingly, the lack of invasive species effects on network structure has been observed despite a strong dominance of invasive species within PPNs, sometimes accounting for up to 42% of all visits and 24% of all interactions in a community (Vilà *et al.*, 2009; also see Bartomeus *et al.*, 2008a; Parra-Tabla *et al.*, 2019). This high network resilience could be at least in part attributed to high interaction rewiring within communities, wherein a redundancy of interactions leads to a rapid replacement of native interactions that are lost due to the introduction of invasive species (e.g. Fonseca & Ganade, 2001; Ramos-Jiliberto *et al.*, 2012; Sheykhali *et al.*, 2020; Vizentin-Bugoni *et al.*, 2020) (Fig. 3a). Most invasive species effects to date have thus only been observed via changes in the identity of species-pair interactions and in the role (e.g. connectors) individual species play within a community (Aizen *et al.*, 2008; see later).

Although the earlier-mentioned studies have so far played a key role in advancing our understanding of community-level effects they are limited in that they only describe patterns of pollinator visitation. For instance, per capita fitness effects in PPNs have been estimated based on the frequency of visits of a pollinator species to a given plant (e.g. Bascompte *et al.*, 2006). However, pollinator visitation is only one part of the pollination process and thus this approach omits potential post-visitation effects (e.g. pollen deposition, pollen tube growth, seed production). As such, these studies may not fully reflect the fitness effects that network changes can have on individual plant species (Valdovinos, 2019), and hence its full consequences for the permanence of plant–pollinator communities (Fig. 3b). Overall, we have very limited understanding of how structural network properties reflect fitness aspects of individual plant species in mutualistic communities (Okuyama & Holland, 2008; but see Vázquez, 2012; Kaiser-Bunbury *et al.*, 2017). Indeed, studies have shown that pollinator species can vary greatly in the amount and types of pollen delivered (King *et al.*, 2013; Minnaar *et al.*, 2019; Ashman *et al.*, 2020) and this can have severe implications for network structure (Fig 3b). For instance, a recent study showed that when pollinator efficiency (contribution to pollen transport and seed-set) is considered, PPN structure can be substantially different to those reflecting only visitation patterns (de Santiago-Hernández *et al.*, 2019). These tend to be less modular, less connected, more specialized and less nested (de Santiago-Hernández *et al.*, 2019). This study also showed that only half of pollinators and 27% of all interactions contribute to seed set, meaning that over 40% of insects and 70% of interactions do not contribute to plant fitness (de Santiago-Hernández *et al.*, 2019). Thus, even a small decrease in the number of efficient pollinators visiting native flowers as a result of plant invasion could have important consequences for native reproductive success. In another study, network nestedness and plant specialization were positively

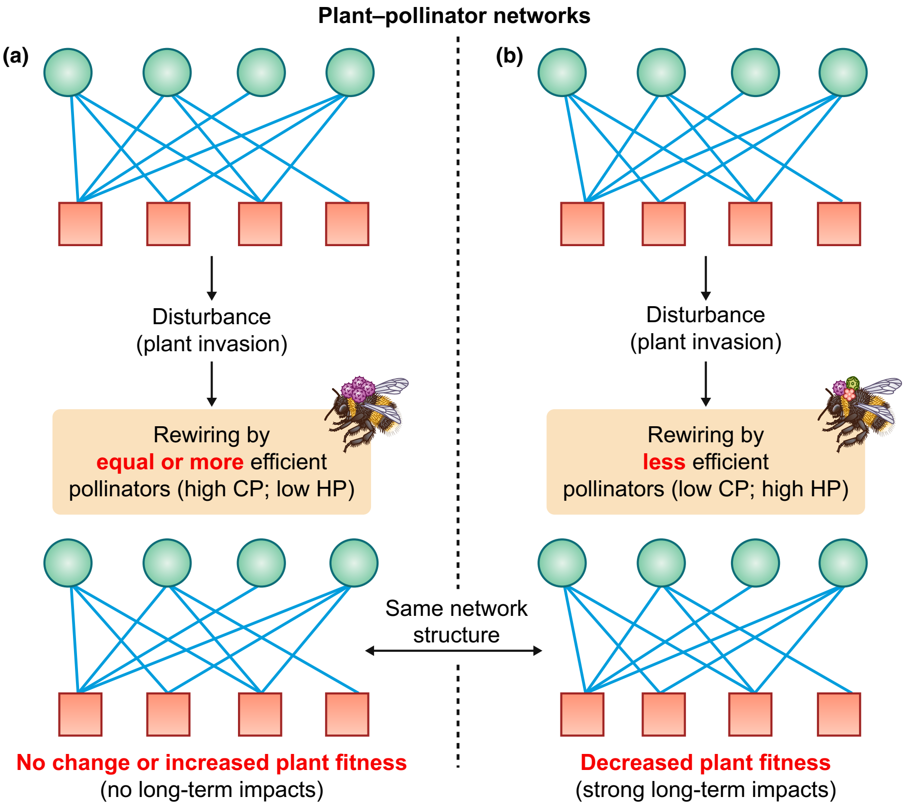

Fig. 3 Predicted effects of disturbance (plant invasion) on plant (red boxes)-pollinator (green circles) networks. After disturbance networks can undergo interaction rewiring by (a) similarly efficient (high conspecific pollen (CP; purple pollen grains) and low heterospecific pollen (HP) pollen loads) or by (b) less efficient pollinators (low CP loads and high HP (red and green pollen grains) loads). Overall effects on network structure and plant fitness are depicted when only considering (a) pollinator visitation patterns and when also considering (b) changes in pollinator efficiency as a result of rewiring. Note that while in both cases networks may retain their plant–pollinator visitation network structure changes in pollinator efficiency may lead to differences in plant species reproductive success with potential long-term impacts in plant communities (b). Rewiring by equally efficient pollinators (a) would result in no change in native plant reproductive success, but (b) rewiring by less efficient pollinators results in decreased native plant reproductive success.

associated with an increase in HP transfer, this because specialized species within nested networks tend to be visited by the most generalist pollinator species (Arceo-Gómez *et al.*, 2020). Thus, network metrics that only rely on visitation patterns may not accurately describe the potential reproductive impacts for native plant communities (de Santiago-Hernández *et al.*, 2019; Parra-Tabla *et al.*, 2021). Even if overall network structure remains unaffected, plant communities can still experience changes in patterns of pollen transfer dynamics that can directly impact plant reproductive fitness, e.g. as a result of rewiring (Fig. 3b; Montero-Castaño & Vila, 2017). For instance, changes in the behavior of only one pollinator species was shown to cause interaction rewiring of 92 other pollinator taxa (Montero-Castaño & Vila, 2017), with unknown consequences for pollinator efficiency and native plant reproductive success. Thus, even though pollinators may show plastic responses in foraging behavior that can help retain overall network structure (see earlier), the functional consequences of these responses remain largely unknown (Fig. 3) and its long-term effects have been mostly ignored (Gilljam, 2015).

Recent studies have also shown that natives not only tend to receive more HP (80% more; Parra-Tabla *et al.*, 2021) compared to invasive species, but that they also experience stronger fitness effects (decrease in seed production and conspecific pollen tube growth; Parra-Tabla *et al.*, 2021; also see Suarez-Mariño *et al.*, 2019; Arceo-Gómez & Ashman, 2016). Thus, linking network properties to more direct metrics of pollination success and plant fitness is critical if we aim to fully understand the long-term impacts of invasive species on the permanence of native plant–pollinator communities. Although this may be challenging to achieve using whole network metrics (e.g. nestedness, modularity) due to the difficulty of achieving the amount of community-wide replication needed, studies that relate species-level metrics (linkage, degree, specialization, hub degree) with plant fitness may be feasible and informative (e.g. Arceo-Gómez *et al.*, 2020; Lazaro *et al.*, 2020). Such studies may also help uncover the mechanistic link between network structure and ecosystem function, which has so far been elusive (Tylianakis *et al.*, 2010). However, this would require that studies go beyond traditional estimates of pollinator visitation and include estimates of conspecific and HP deposition (Johnson & Ashman, 2018; Arceo-Gómez *et al.*, 2020; Parra-Tabla *et al.*, 2021), seed production and pollen limitation (e.g. Kaiser-Bunbury *et al.*, 2017; Thompson & Knight, 2018) for individual plant species within a community. These type of studies combined with experimental manipulations of communities and network attributes (e.g. Russo *et al.*, 2019) have enormous potential in this field. There is now a large body of modeling studies that have generated testable predictions regarding the consequences of species invasion on network structure (e.g. Memmott & Waser, 2002; Bascompte *et al.*, 2003; Aizen *et al.*, 2008; Valdovinos *et al.*, 2009; Vilà *et al.*, 2009; Kaiser-Bunbury *et al.*, 2011; Albrecht *et al.*, 2014; Russo *et al.*, 2014; Stouffer *et al.*, 2014; Parra-Tabla *et al.*, 2019). However, experimental research on community-wide responses to species invasion is still in its infancy, and thus most of these predictions remain untested in natural communities. We propose that the time is now ripe to test these predictions in the field in order to further advance our understanding of the impact of invasive species on the function and structure of plant–pollinator communities.

It is also important to consider that the effects and drivers described here could differ among the varying stages of the invasion process, from arrival to establishment (population build-up) and naturalization (Stout & Tiedeken, 2017; van Kleunen *et al.*, 2018). Changes in the drivers and effects of invasive species 'integration' into PPN may be largely driven by changes in invasive species abundance, which is expected to be low at arrival and the greatest after naturalization. Invasive plants for instance, may be less dependent on pollinators at the beginning stages of the invasion process (van Kleunen *et al.*, 2008; Razanajatovo *et al.*, 2016) and thus perhaps less 'integrated' compared to later stages. In one of the few studies to date, Pysek *et al.* (2011) evaluated pollination modes in more than 1100 invasive species and found that pollination modes of introduced species gradually change during the process of naturalization, becoming more similar to native species as they become naturalized. They also found that the number of insect pollinators increases with increasing residence time in an invaded area (Pysek *et al.*, 2011). These results suggest that invasive species at the late stages of invasion will be more 'integrated' into PPN compared to species that have been recently introduced. Geslin *et al.* (2017) also showed that massively introduced species (at high densities) are well integrated and tend to occupy central positions within PPN. Further suggesting that plant abundance, which varies across different stages of invasion, is a key determinant of invasive species 'integration' into PPN. Self-pollination modes, however, can still play a large role when invasive species spread to new locations (Pysek *et al.*, 2011). This lower reliance on pollinators (and hence low integration) at early stages of invasion has been commonly attributed to low population densities (e.g. Bakers Law; Baker, 1955), as suitable mates may be scarce or pollinators may display frequency dependent foraging strategies (Razanajatovo *et al.*, 2016). However, to our knowledge few studies have evaluated how the invasive 'integration' process as well as its potential effects on PPN structure change among different stages of invasion. Hence this remains a promising avenue for future research.

Finally, studies of plant–animal mutualistic networks often assume that changes on interaction patterns lead to population-level effects. This is a crucial simplifying assumption that so far lacks sufficient empirical evidence (Valdovinos, 2019). Acquiring this knowledge will require that studies link changes in network metrics with information on population dynamics (i.e. population growth) from demographic studies (Bond, 1994: Stinson *et al.*, 2006; Bennett *et al.*, 2018) (Fig. 1d). That is, that studies include changes in the relative abundances and other demographic parameters of native and invasive plants in invaded communities (e.g. Del Vechio *et al.*, 2015; Parra-Tabla *et al.*, 2018). For instance, Gómez *et al.* (2011) showed, using individual based networks, a positive relationship between network topology (nestedness and connectance) and per-capita production of juvenile plants, thus providing more direct evidence that changes in network structure can have consequences for the persistence of native plant populations. Another promising approach would be the use demographic models that integrate pollination efficiency with other life-history attributes to infer the potential consequences of pollination network changes on long-term population dynamics. These models could be used to assess the effects of variation in pollination efficiency (in a PPN context) on population growth rate (i.e. sensitivity/elasticity analysis; Stokes *et al.*, 2006). Alternatively, demographic models could retrospectively assess whether increased/decreased pollination efficiency contributes to changes in population growth rate (i.e. Life Table Response Experiment approach; e.g. Stokes *et al.*, 2006; Paynter *et al.*, 2010). For instance, Paynter *et al.* (2010) used a demographic modeling approach to assess the combined impacts of reduced pollination efficiency with other life history attributes (seed rain and seed destruction) on the growth and spread of an invasive plant. However, to our knowledge, this type of studies in the context of species invasion and PPN are lacking, even though the relevance of invasive species effects via pollination, from a conservation context, would only be relevant if these ultimately lead to a decrease in plant populations. Conducting these types of studies may be daunting, nonetheless they are essential to understand the long-term effects of PPN structural changes as a result of species invasion on the persistence of native plant populations.

IV. Conclusions

Although significant progress has been made in advancing our understanding of the causes and consequences of plant species invasion in plant–pollinator communities there is still much to be learned. In particular, the formulation of a more unified framework (like the one presented here) along with generating testable predictions via modeling studies, coupled with experimental tests of these predictions in the field, have great potential to advance our understanding in this field. We further highlight the need for more integrative studies that consider not only invasive species effects on patterns of pollinator floral visitation, but also include estimates of pollinator efficiency, native species reproductive success and population dynamics if we aim to fully understand the long-term impacts of invasive species on native plant communities.

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