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VIEWPOINT

Spatial variation in the intensity of interactions via heterospecific pollen transfer may contribute to local and global patterns of plant diversity

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- **Background:** Studies that aim to understand the processes that generate and organize plant diversity in nature have a long history in ecology. Among these, the study of plant–plant interactions that take place indirectly via pollinator choice and floral visitation has been paramount. Current evidence, however, indicates that plants can interact more directly via heterospecific pollen (HP) transfer and that these interactions are ubiquitous and can have strong fitness effects. The intensity of HP interactions can also vary spatially, with important implications for floral evolution and community assembly.
- **Scope:** Interest in understanding the role of heterospecific pollen transfer in the diversification and organization of plant communities is rapidly rising. The existence of spatial variation in the intensity of species interactions and their role in shaping patterns of diversity is also well recognized. However, after 40 years of research, the importance of spatial variation in HP transfer intensity and effects remains poorly known, and thus we have ignored its potential in shaping patterns of diversity at local and global scales. Here, I develop a conceptual framework and summarize existing evidence for the ecological and evolutionary consequences of spatial variation in HP transfer interactions and outline future directions in this field.
- **Conclusions:** The drivers of variation in HP transfer discussed here illustrate the high potential for geographic variation in HP intensity and its effects, as well as in the evolutionary responses to HP receipt. So far, the study of pollinator-mediated plant–plant interactions has been almost entirely dominated by studies of pre-pollination interactions even though their outcomes can be influenced by plant–plant interactions that take place on the stigma. It is hence critical that we fully evaluate the consequences and context-dependency of HP transfer interactions in order to gain a more complete understanding of the role that plant–pollinator interactions play in generating and organizing plant biodiversity.

Key words: Adaptation, community assembly, competition, diversity, heterospecific pollen, natural selection, pollen transfer, pollination.

INTRODUCTION

Generalization in plant–pollinator interactions, where pollinators visit more than one plant species and plants are visited by more than one pollinator, is widespread in nature (e.g. Herrera, 1988; Waser *et al.*, 1996; Olesen and Jordano, 2002; Bascompte *et al.*, 2003; Kaiser-Bunbury *et al.*, 2017). Hence, the study of plant–plant interactions via their effects on pollinator choice and floral visitation (i.e. pre-pollination) has been a prolific area of study in ecology and evolutionary biology (e.g. pollinator competition; Mitchell *et al.*, 2009). Their study has rendered important insights on the mechanisms of floral diversification (Mitchell *et al.*, 2009; Phillips *et al.*, 2020) and community assembly (Sargent and Ackerly, 2008). It is thus also not surprising that the study of pre-pollination interactions (via pollinator visitation) has remained at the forefront in the fields of pollination biology and community ecology for over 100 years (e.g. Robertson, 1895; Ghazoul, 2006; Sargent and Ackerly, 2008; Phillips *et al.*, 2020). However, the ultimate outcome of these interactions can be determined by post-pollination interactions via heterospecific pollen (HP) transfer, which take place on the stigma long after pollinators leave a flower (Morales and Traveset, 2008; Ashman *et al.*, 2020*a*, *b*); nonetheless, these have been less studied. It is hence imperative that we integrate the complexity of HP transfer into our understanding of pollinator-mediated interactions in order to fully uncover their ecological and evolutionary consequences in nature. This is particularly important as the ubiquity of HP transfer interactions is becoming increasingly more evident (e.g. Morales and Traveset, 2008; Fang and Huang, 2013; Tur *et al.*, 2016; Arceo-Gómez *et al.*, 2019*a*). Recent studies have shown that HP transfer is widespread across taxonomic (217 species; 88 % of all species evaluated), geographic (five continents) and phylogenetic (52 plant families; Arceo-Gómez *et al.*, 2019*a*) scales. Some species can average up to 368.5 HP grains per stigma and receive HP in 50–100 % of their flowers (Ashman and Arceo-Gómez, 2013). Detrimental male (e.g. Muchhala *et al.*, 2010; Muchhala and Thomson, 2012) and female fitness effects of HP receipt have also been widely demonstrated (~20 % decrease in seed production; Morales and Traveset, 2008; Ashman and Arceo-Gómez, 2013), even if HP receipt occurs in small amounts (1 % HP; Thomson *et al.*, 1982*a*). Given the pervasive nature of these interactions and its strong fitness effects, interest in understanding its role in the diversification (e.g. Hopkins and Rausher, 2012; Armbruster *et al.*, 2014; Ashman and Arceo-Gómez, 2013; Moreira-Hernandez and Muchhala, 2019) and organization of plant communities is rapidly rising (e.g. Eaton *et al.*, 2012; Tur *et al.*, 2016; Arceo-Gómez *et al.*, 2019*a*).

The role that spatial variation in the intensity of species interactions plays in shaping broad patterns of diversity has also been well recognized (e.g. Thompson, 1999; Gomulkiewicz *et al.*, 2000; Agrawal, 2001; Moeller, 2005; Chamberlain *et al.*, 2014). The most central tenet of these studies is that the intensity and outcomes of species interactions can vary across the landscape, such that different traits are favoured in different populations (Thompson, 1999; Agrawal, 2001; Singer and McBride, 2012). Spatial mosaics of species interactions have been observed in plant–pollinator (e.g. Moeller, 2005), plant–herbivore (e.g. Singer and McBride, 2012), plant–microbiome (e.g. Andonian *et al.*, 2012), predator–prey (e.g. Toju and Sota, 2006) and host–parasite (e.g. Gandon and Nuismer, 2009) interactions. Surprisingly however, after 40 years of research (Morales and Traveset, 2008; Ashman and Arceo-Gómez, 2013), the extent as well as the ecological and evolutionary consequences of among-population variation in plant–plant interactions via HP transfer (intensity and effects) remains poorly understood. The ecological, environmental and genetic context in which HP transfer interactions occur varies widely (see below). Thus, the intensity and outcomes of these interactions can fluctuate and elicit different evolutionary responses in different populations (e.g. Hopkins and Rausher, 2012; Arceo-Gómez and Ashman, 2014*a*; Arceo-Gómez *et al.*, 2016*a*), potentially contributing to shaping patterns of plant diversification and assembly.

Plant populations can differ in the intensity of HP receipt as well as in the magnitude of its effects. For instance, among-population variation in HP receipt can result from changes in conspecific flower density and/or population size (flower abundance; e.g. Spigler, 2018; Thomson *et al.*, 2019), or from changes in the surrounding plant and pollinator community composition (Arceo-Gómez and Ashman, 2014*a*; Johnson and Ashman, 2019; Smith *et al.*, 2021). Variation in HP effects, on the other hand, can fluctuate as a result of variation in plant resource availability (i.e. water and nutrients; Celaya *et al.*, 2015), pollen donor–recipient species co-existence history (i.e. varying history of exposure to HP receipt; Arceo-Gómez *et al.*, 2016*a*) or plant mating system (i.e. selfer versus outcrosser; Arceo-Gómez and Ashman, 2014*b*; discussed in detail below). In spite of this, the intensity of HP receipt in any given species has been typically evaluated at a single location (but see Emer *et al.*, 2015; Tur *et al.*, 2016; Spigler, 2018), and its fitness effects have been tested under constant greenhouse conditions (reviewed in Morales and Traveset, 2008; Ashman and Arceo-Gómez, 2013; but see Briggs *et al.*, 2016; Smith *et al.*, 2021). Thus, to this day, the degree to which the intensity and effects of HP receipt varies among populations across broad spatial scales is virtually unknown for any species (but see Waites and Agren, 2004). Hence, we have so far ignored the potential for geographic variation in HP transfer interactions to contribute to the shaping of plant communities in nature.

While the intensity and effects of HP receipt can vary among populations of a single species, it is also possible for plant communities as a whole to experience differences in average HP transfer and receipt depending on their broad geographic location (e.g. temperate versus tropical systems; Arceo-Gómez *et al.*, 2019*a*). These community-wide differences could result in HP transfer hotspots, where all or most species in a community will be exposed to high levels of HP transfer (Arceo-Gómez *et al.*, 2019*a*). Heterospecific pollen receipt has been shown to influence the evolution of floral traits (e.g. Armbruster *et al.*, 2014; Muchhala and Thomson, 2012), mating systems (Fishman and Wyatt, 1999; Randle *et al.*, 2018) and flowering time (Waser, 1978), and even to mediate speciation processes (e.g. Hopkins and Rausher, 2012). Although circumstantial, this evidence suggests the potential for HP-mediated evolutionary hotspots that could partially contribute to the shaping of global patterns of plant diversification (Arceo-Gómez *et al.*, 2019*a*; Moreira-Hernandez and Muchhala, 2019). However, to my knowledge, no study has rigorously evaluated the relative contribution of HP transfer to plant diversification, particularly compared with other well-studied drivers of biodiversity (but see Moreira-Hernandez and Muchhala, 2019 and references therein). Spatial variation in the intensity and outcomes of biotic interactions has been proposed as an important contributor to the diversification and organization of life (e.g. Thompson, 1999; Agrawal, 2001; Moeller, 2005; Chamberlain *et al.*, 2014), and interactions via HP transfer may not be the exception.

In this Viewpoint, I first outline different mechanisms and summarize existing evidence for how the intensity and effects of HP receipt can vary among populations of the same species, and how this can generate different selective pressures across populations. Then, I briefly discuss the potential for community-wide differences in HP transfer regimes and the existence of HP transfer hotspots that contribute to global patterns of plant diversity. Finally, I outline future directions in this field.

DRIVERS OF WITHIN-SPECIES VARIATION IN PATTERNS OF HP RECEIPT ACROSS SPACE

While there is a growing body of literature describing between-species differences in the intensity and diversity of HP receipt (reviewed in Morales and Traveset, 2008; Ashman and Arceo-Gómez, 2013; Arceo-Gómez *et al.*, 2019*a*), little has been done to understand the extent and potential drivers of within-species variation in HP receipt across populations. Here I briefly outline and provide evidence for four non-mutually exclusive and likely interlinked sources of within-species variation in HP receipt (Fig. 1). The first two are related to the abundance and spatial distribution of the HP recipient (Fig. 1A, B), whereas the remaining two (Fig. 1C, D) are related to changes in the surrounding plant and pollinator community.

Density and fine-scale spatial arrangement of conspecific flowers

It is well known that variation in conspecific flower density can influence pollinator attraction, flower visitation rate,

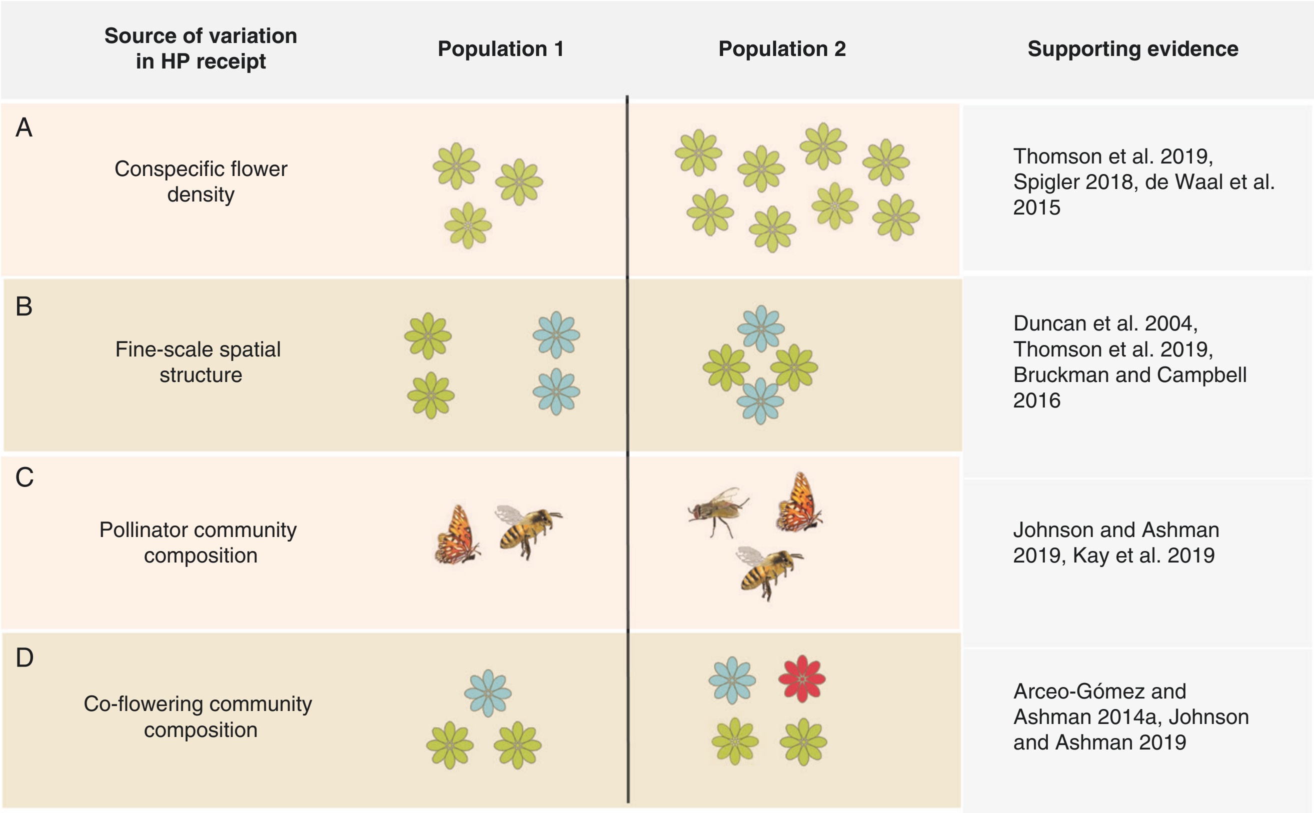


FIG. 1. Four predicted sources of within-species variation in HP receipt across space: (A) conspecific flower density (low versus high); (B) fine-scale spatial plant distribution within a site (isolated versus intermingled); and (C) pollinator and (D) co-flowering community composition (low versus high species richness). Spatial variation is represented here as two different populations that differ in each one of all four sources of variation. Examples of studies providing supporting evidence for the role of each source of variation in mediating HP transfer dynamics are also presented.

conspecific pollen deposition and overall reproductive success (e.g. Rathcke, 1983; Kunin, 1997; Hegland and Boeke, 2006; Spigler and Chang, 2008). What has been less explored, however, is how variation in conspecific flower density influences pollen transfer dynamics between co-flowering species, i.e. HP donation and receipt (Duncan *et al.*, 2004; de Waal *et al.*, 2015; Spigler, 2018; Thomson *et al.*, 2019; Fig. 1A). For instance, as conspecific density decreases HP receipt can be expected to increase as a result of increasing pollinator visits to heterospecific flowers (Thomson *et al.*, 2019; Ashman *et al.*, 2020*a*). de Waal *et al.* (2015) found support for this prediction in an experimental study in populations of South African daisies. They found an increase in HP receipt with decreasing conspecific density leading to reduced fecundity in populations of low relative abundance (de Waal *et al.*, 2015). However, it has also been proposed that HP receipt may increase with increasing conspecific flower density as plants become larger and/or more frequent targets for HP delivery, particularly from wind-pollinated HP donors (Parra-Tabla *et al.*, 2020). The relationship between conspecific density and HP receipt may thus depend on the pollination system (wind- versus animal-pollinated) of the main HP donor. These predictions however, require further testing.

It has also been shown that density-dependent effects on HP receipt can be influenced by plant species' dispersion within a site, particularly when pollinators respond to fine-scale (within metres) spatial patterns of flowering species distribution (e.g. intermixed versus isolated; Fig. 1B; Thomson *et al.*, 1982*b*, 2019; Hanoteaux *et al.*, 2013). For instance, experimental studies have shown that within-species patterns of HP transfer dynamics can vary significantly between isolated, patchy and intermixed arrays of plants (Bruckman and Campbell, 2016; Thomson *et al.*, 2019), with HP receipt typically increasing in intermixed arrays. de Waal *et al.* (2015) even show evidence suggesting that the spatial aggregation of plants can buffer against the increasing incidence of HP receipt that occurs at low conspecific densities. It has further been shown that within-species variation in the diversity and intensity of HP receipt can be more than two times higher than the variation among species (Arceo-Gómez *et al.*, 2016*b*), thus supporting the idea that fine-scale spatial drivers of HP receipt (or plant trait differences such as size or age) may be at play. For instance, a recent experimental study with artificial flowers (hence controlling for plant/flower traits) showed that dispersion patterns of co-flowering plants within a sub-metre scale strongly influence patterns of HP transfer and receipt (Thomson *et al.*, 2019). Overall, the evidence so far suggests that within-species patterns of HP receipt can vary extensively across populations, generating complex mosaics of HP transfer and receipt. Population-level differences in pollen transfer dynamics may in turn lead to a mosaic of adaptive landscapes (discussed below) if population differences in HP receipt persist over time (e.g. Arceo-Gómez *et al.*, 2016*a*; Fang *et al.*, 2019). However, to my knowledge, very few studies have evaluated the extent and drivers of among-population variation in HP receipt within a species, which has limited our understanding of its potential evolutionary consequences.

Co-flowering and pollinator community composition

The intensity and diversity of HP receipt for any single species may also vary with varying pollinator species composition (identity and diversity) across populations (e.g. Herrera, 1988, 1995), as pollinators vary in the size and diversity of HP loads they transfer (Fig. 1C; e.g. King *et al.*, 2013; Arceo-Gómez *et al.*, 2016*b*; Minnaar *et al.*, 2019*b*). For instance, Johnson and Ashman (2019) showed that 70 % of variation in the composition of HP loads transferred among plants, across 13 communities in Hawaii, was the result of differences in pollen loads transported by *Apis mellifera*. As a result, most of the site-to-site variation in HP receipt within a species was attributed to differences in the abundance of this introduced pollinator species (Johnson and Ashman, 2019). In another study Kay *et al.* (2019) showed that hawkmoths vary extensively in the amount of HP transferred among *Clarkia* species, suggesting that the presence/absence of this pollinator in any given population can have large effects on overall HP transfer dynamics. Changes not only in the identity, but also in the overall diversity of the pollinator community among populations, have also been predicted to lead to extensive changes in patterns of HP receipt (e.g. Arceo-Gómez *et al.*, 2016*b*; Ashman *et al.*, 2020*a*; Smith *et al.*, 2021), with HP load size predicted to increase with increasing pollinator diversity at a site (Arceo-Gómez *et al.*, 2016*b*).

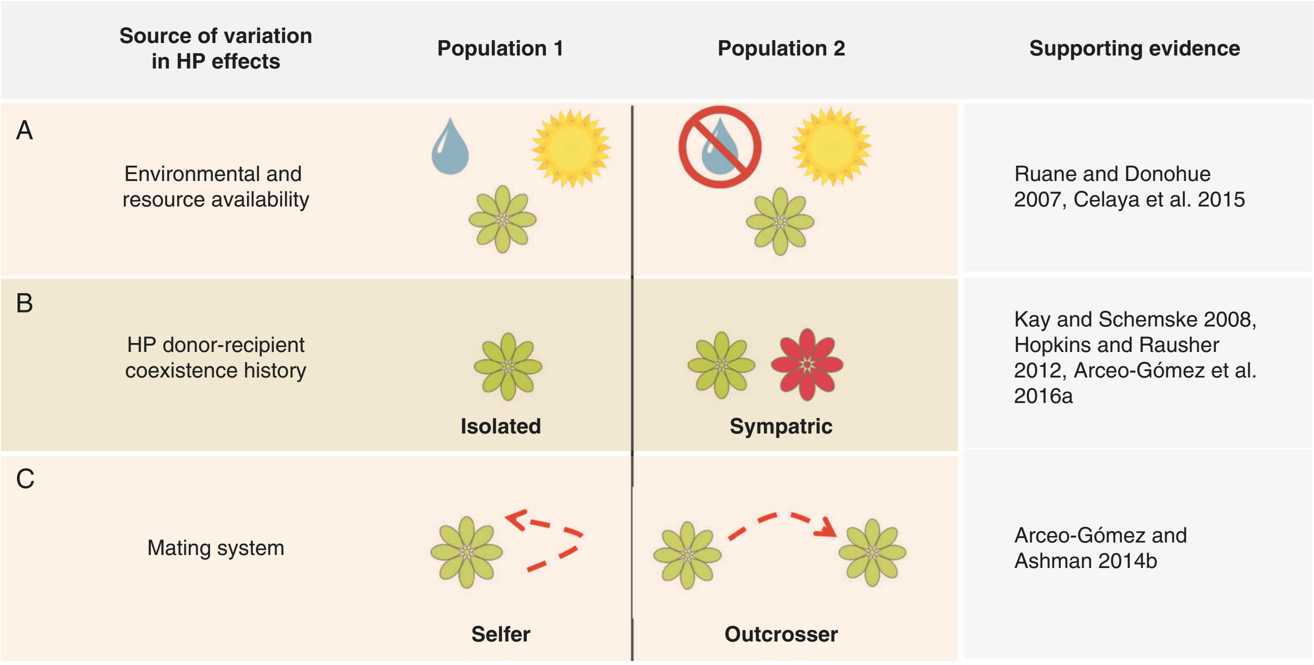
Among-population variation in species composition of the co-flowering neighbourhood can also have large impacts on patterns of HP receipt (load size, diversity and identity of HP interactions; Fig. 1D). Variation in HP receipt can be mediated by among-population variation in surrounding co-flowering species identity, diversity and even functional trait composition (e.g. floral trait similarity; Eaton *et al.*, 2012). For instance, Arceo-Gómez and Ashman (2014*a*) showed that *Mimulus guttatus* populations receive up to four times more HP depending on the diversity of the co-flowering community where they occur. Another study showed that the presence of one (invasive) species (*Cirsium arvense*) caused a rearrangement of HP transfer interactions, such that some HP transfer interactions disappeared while new ones emerged (Daniels and Arceo-Gómez, 2020). This reorganization of HP transfer interactions could have the potential to alter species' evolutionary trajectories (Ashman and Arceo-Gómez, 2013). What is evident from these studies is that the intensity, diversity and identity of HP loads on individual recipient species can vary extensively across populations as a result of changes in the surrounding plant and pollinator community, including the addition of non-native plants and pollinators. Even when the surrounding plant and pollinator community remains relatively constant across populations, the identity of pairwise plant–plant interactions via HP transfer could still vary, as has been shown in plant–pollinator interaction networks (Carstensen *et al.*, 2014). It is evident that individual plant species can experience large among-population variation in the surrounding plant (e.g. Arceo-Gómez and Ashman, 2014*a*; Albor *et al.*, 2019) and pollinator (Herrera, 1988; Cosacov *et al.*, 2008) community, and evidence suggesting this plays a key role in mediating variation in HP transfer dynamics is rapidly accumulating (e.g. Arceo-Gómez and Ashman, 2014*a*; Ashman and Johnson and Ashman 2019; Kay *et al.*, 2019; Smith *et al.*, 2021). In spite of this, and although studies have evaluated spatial changes in overall pollen transfer network structure (e.g. Emer *et al.*, 2015; Tur *et al.*, 2016), to my knowledge no study has documented the extent to which changes in the surrounding species composition mediate within-species variation in HP receipt across a wide geographic scale.

DRIVERS OF WITHIN-SPECIES VARIATION IN HP FITNESS EFFECTS ACROSS SPACE

While many studies have documented the existence of fitness effects of HP receipt (reviewed in Morales and Traveset, 2008; Ashman and Arceo-Gómez, 2013; Moreira-Hernandez and Muchhala, 2019), little work has been done evaluating the extent and potential drivers of within-species variation (i.e. among populations) in these effects. Here I outline and provide existing evidence to support three potential sources of among-population variation in HP effects (Fig. 2).

Environmental and resource variability

It is known that variation in resource conditions (e.g. water and nutrients) can have strong effects on fertilization success (e.g. Herrera, 1995; Lush *et al.*, 1998; Feng *et al.*, 2000). Specifically, the availabilities of water (Lush *et al.*, 1998), light (e.g. Feng *et al.*, 2000; Campbell *et al.*, 2001) and temperature (Lankinen, 2001) have been shown to affect conspecific pollen germination and pollen tube growth. For instance, conspecific pollen germination rate decreased with decreasing water and light availability in *Nicotiana alata* (Lush *et al.*, 1998). It has also been shown that changes in soil composition can alter style chemistry, which in turns affects conspecific pollen performance (Searcy and Macnair, 1990). If among-population variability in abiotic resources and environmental conditions affects conspecific pollen performance on the stigma/style, then we can expect that this would also affect pollen's ability to compete and succeed in the face of HP interference (Fig. 2A). If this is the case, then it is likely that the effects of HP receipt may vary among populations across a species' distribution range. In spite of this possibility, the great majority of studies have evaluated HP effects under constant greenhouse conditions (reviewed in Morales and Traveset, 2008; Ashman and Arceo-Gómez, 2013), and results from these studies have been used to make wide-ranging inferences of overall species' HP tolerance or susceptibility. Plant populations, however, often experience a wide range of environmental conditions in nature (e.g. Chapin *et al.*, 1987; Davis *et al.*, 2000; Toräng *et al.*, 2010), and thus HP effects derived from greenhouse studies may lead to an incomplete understanding of such effects in natural populations (Celaya *et al.*, 2015). To my knowledge, only one study



	Source of variation in HP effects	Population 1	Population 2	Supporting evidence
A	Environmental and resource availability			Ruane and Donohue 2007, Celaya et al. 2015
B	HP donor-recipient coexistence history	Isolated	Sympatric	Kay and Schemske 2008, Hopkins and Rausher 2012, Arceo-Gómez et al. 2016a
C	Mating system	Selfer	Outcrosser	Arceo-Gómez and Ashman 2014b

Fig. 2. Three predicted sources of within-species variation in the intensity of heterospecific pollen (HP) effects across space: (A) environmental and resource availability (high versus low resources); (B) HP donor–recipient coexistence history (no coexistence versus long history of coexistence); and (C) plant mating system (mostly selfer versus outcrosser). Spatial variation is represented here as two different populations that differ in each one of all three sources of variation. Examples of studies providing supporting evidence for the role of each source of variation in mediating HP effects are also presented.

has evaluated the role of resource availability in mediating HP effects on reproductive success (Celaya *et al.*, 2015; but see Ruane and Donohue, 2007 for environmental effects on hybridization). In this study, Celaya *et al.* (2015) showed that HP effects are stronger (reduced pollen tube growth) under stressful abiotic conditions; that is, when the availability of water, light or both is low. Interestingly, they did not observe any effects of HP receipt when both water and light availabilities were high (Celaya *et al.*, 2015). These conditions of 'unlimited' resources, however, represent the conditions under which most greenhouse studies on HP effects have been conducted, suggesting that HP effects could be underestimated for some species or at least in some populations. Such limitations could ultimately obscure our understanding of the real effects and consequences of HP transfer in nature. Here I thus argue that the outcome of HP transfer interactions is likely context-dependent, and strongly depends on the particular abiotic conditions where these interactions take place. Among-population variation in resource-mediated HP effects may in turn lead to spatial variation in selective pressures associated with HP receipt. For instance, selective pressure for HP avoidance (discussed below) may be stronger (or only present) under low resource availability, as HP fitness effects would be stronger in these conditions and not present when resource availability is high. However, to my knowledge, this prediction has not been explored.

Pollen donor–recipient co-existence history

Another potential driver of within-species variation in HP effects is variation in a population's history of exposure to HP receipt (Fig. 2B). As mentioned above, within-species variation in the intensity of HP receipt can be large and driven by various sources (Fig. 1) across a species' distribution range. With this in mind, we could predict that plant populations that have been continually exposed to high levels of HP receipt (i.e. large history of exposure) will be more likely to evolve avoidance/tolerance strategies to minimize its negative effects on reproductive success (Ashman and Arceo-Gómez, 2013; Arceo-Gómez *et al.*, 2016*a*). As a result, these populations would show little to no reproductive effects when exposed to HP compared with populations that typically receive minimal or infrequent amounts of HP (e.g. Arceo-Gómez *et al.*, 2016*a*). However, whether plant populations can evolve tolerance mechanisms to HP receipt is not fully known. Nevertheless, if this level of local adaption to HP effects occurs (e.g. Kay and Schemske, 2008; Arceo-Gómez *et al.*, 2016*a*), then variation in the history/intensity of exposure to HP transfer could underlie population divergence in HP tolerance. For instance, in one of the few studies to date, Arceo-Gómez *et al.* (2016*a*) showed evidence indicating that *Clarkia xantiana* populations vary in their level of HP tolerance according to their history of exposure to HP. Specifically, *Clarkia* pollen from populations with no history of HP exposure had lower reproductive success when subjected to HP hand-pollination treatments compared with populations that had been naturally exposed to HP for more than 30 years (Arceo-Gómez *et al.*, 2016*a*; also see Kay and Schemske, 2008). This study also suggested that local adaption to different HP exposure regimes may not only occur in response to selective pressures on female (stigma/style) fitness, but that selective pressures could act on male (pollen) fitness as well (Arceo-Gómez *et al.*, 2016*a*). For instance, conspecific pollen grains may be locally adapted to succeed in highly competitive stigmatic environments (large and diverse HP loads), resulting in enhanced pollen performance (i.e. higher pollen germination and pollen tube growth; Ashman and Arceo-Gómez, 2013, Moreira-Hernandez and Muchhala, 2019), analogous, perhaps, to the effects of conspecific pollen competition on the evolution of pollen tube growth rates (Mazer *et al.*, 2010). Such local adaptation of male gametophytes (pollen) could lead to lower HP effects in plant populations typically exposed to high levels of HP transfer. However, whether varying degrees of history/intensity of exposure lead to spatial variation in selection pressures on stigmatic HP tolerance or conspecific pollen performance is yet to be determined.

Recipient mating system

Plant populations can vary substantially in their degree of selfing versus outcrossing, which has implications for their genetic diversity across their distribution range (e.g. Barrett and Husband, 1990; Tamaki *et al.*, 2009; Ness *et al.*, 2010; Hargreaves and Eckert, 2014). For instance, a recent study showed large interpopulation mating system variation in 105 species across 44 families (Whitehead *et al.*, 2018). Furthermore, numerous studies have demonstrated that self-pollen is typically less competitive, as germination and pollen tube growth are slower compared with outcross pollen (e.g. Weller and Ornduff, 1977; Aizen *et al.*, 1990; Cruzan and Barrett, 1993; Kruszewski and Galloway, 2006). Since both of these components of the pollination process (pollen germination and tube growth) are commonly affected by the presence of HP (Morales and Traveset, 2008; Ashman and Arceo-Gómez, 2013), self-pollen may be more susceptible to HP effects compared with outcross pollen (Arceo-Gómez and Ashman, 2014*b*). If this is the case, then population susceptibility to HP effects may covary with a population's mating system (Fig. 2C). To my knowledge, this prediction has not been explored for any species. For instance, a hand-pollination experiment in *Mimulus guttatus*, a species with high interpopulation mating system variation (Ivey and Carr, 2005), showed that HP has stronger effects when competing against self-pollen compared with outcross conspecific pollen (Arceo-Gómez and Ashman, 2014*b*). Specifically, HP caused a decrease in self-pollen-tube growth by an additional 32 % compared with outcross pollen (Arceo-Gómez and Ashman, 2014*b*). Among-population variation in the degree of selfing can also take place as a result of breakdown in self-incompatibility systems (e.g. Reinartz and Les, 1994; Nasrallah *et al.*, 2004; Busch and Schoen, 2008; Encinas-Viso *et al.*, 2020). It has been proposed that HP effects may depend on self-incompatibility mechanisms in the HP recipient, since self-incompatible plants could co-opt mechanisms involved in rejection of self-pollen to reject HP (e.g. Hiscock and Dickinson, 1993; Murfett *et al.*, 1996; Bedinger *et al.*, 2011). That is, the same or similar mechanisms used for active rejection of self-pollen (e.g. match of pollen and pistil alleles) may be used to reject/tolerate HP effects (e.g. prevent HP germination; reviewed in Ashman and Arceo-Gómez, 2013). In this case, styles of self-incompatible populations would be predicted to be more tolerant to the negative effects of HP receipt compared with populations where self-incompatibility mechanisms have broken down or are less effective (Ashman and Arceo-Gómez, 2013). Thus, variation not only in mating system (ratio of self/outcross pollen) but also in the strength of self-incompatibility mechanisms could mediate among-population variation in the outcome of HP interactions in nature. Furthermore, in mixed-mating populations (plants that receive self- and outcross pollen), HP receipt may have the potential to influence the realized mating system by favouring outcross pollen grains (i.e. HP has greater effects on self-pollen; Arceo-Gómez and Ashman, 2014*b*), or if increased selfing provides reproductive assurance in the face of high HP receipt (Spigler, 2018; Ashman *et al.*, 2020*b*). Both of these mechanisms could ultimately influence mating system evolution and genetic diversity in plant populations. Thus, HP receipt could have far-reaching consequences that go beyond what has been proposed, but these intriguing ideas remain untested.

WITHIN-SPECIES VARIATION IN HP-MEDIATED SELECTIVE PRESSURES ACROSS SPACE

Despite the seemingly large among-population variation in the intensity and effects of HP receipt, the potential role of HP transfer interactions as a force generating spatial variation in selective pressures is mostly unknown (but see Kay and Schemske, 2008; Hopkins and Rausher, 2012; Arceo-Gómez *et al.*, 2016*a*). Receipt of HP can act as a selective force driving the evolution of floral strategies that mitigate female (Morales and Traveset, 2008) and male fitness costs (conspecific pollen loss; Moreira-Hernandez and Muchhala, 2019). Examples include adaptations to enhance pollen placement (e.g. Armbruster *et al.*, 2014; Minnaar *et al.*, 2019*a*), shifts in flowering phenology (e.g. Waser, 1978) and adaptations to minimize pollinator sharing, such as flower trait divergence (e.g. Hopkins and Rausher, 2012), pollinator specialization (Muchhala *et al.*, 2010) and increased selfing (e.g. Fishman and Wyatt, 1999). Specifically, Ashman and Arceo-Gómez (2013) proposed two main evolutionary strategies to mitigate female fitness effects, i.e. tolerance or avoidance of HP receipt. Thus, differences in the strength of HP-mediated selection pressures may lead to the evolution of either tolerance or avoidance strategies in some populations (of the same species) but not in others (e.g. where HP fitness effects are negligible). For instance, Hopkins and Rausher (2012) showed evidence for divergent selection pressures on flower colour in *Phlox drummondii* populations as a result of HP transfer from *Phlox cuspidata.* Selective pressure on genes that affected floral pigmentation occurred only in sympatric *Phlox* populations to prevent hybridization (i.e. HP avoidance; Hopkins and Rausher, 2012), or maybe even direct HP effects on reproductive success (e.g. stigma clogging), thus generating spatial variation in the outcome of selection. In a similar study, Kay and Schemske (2008) found pollen–pistil incompatibilities had evolved only in sympatric populations of two *Costus* species, and not in isolated populations, thus providing evidence for among-population variation in selective pressures leading to the evolution of HP tolerance strategies (also see Arceo-Gómez *et al.*, 2016*a*). Furthermore, *Mimulus guttatus* populations growing in serpentine seeps in California showed an increase in flower longevity as an adaptive response to minimize effects of high levels of HP receipt with increasing co-flowering diversity (Arceo-Gómez and Ashman, 2014*a*). In this case, population-level differences in HP receipt likely led to changes in the adaptive value of flower longevity, hence influencing spatial patterns of floral evolution (Arceo-Gómez and Ashman, 2014*a*). Evolutionary adaptations that minimize male fitness costs have also been shown and these include traits that enhance accuracy in pollen placement (e.g. Muchhala and Potts, 2007; Armbruster *et al.*, 2014), increase pollinator specialization (e.g. Muchhala *et al.*, 2010) and floral constancy (Moreira-Hernandez and Muchhala, 2019). Nonetheless, evidence of within-species variation in these male-driven evolutionary responses across a species' distribution range is still limited. In addition to HP tolerance and avoidance strategies, selection can favour mechanisms that increase the degree of autonomous self-pollination in order to preemptively minimize HP effects (e.g. Fishman and Wyatt, 1999; Goodwillie and Ness, 2013; Brys *et al.*, 2016; Randle *et al.*, 2018; Spigler, 2018; Katsuhara and Ushimaru, 2019). For instance, Fishman and Wyatt (1999) demonstrated that selection favoured selfing and selfing-related traits only in *Arenaria uniflora* populations that grew in sympatry with congeneric *A. glabra.* They further showed that HP transfer rather than pollinator competition was the main driver of selection (Fishman and Wyatt, 1999). Thus, HP transfer has the potential for generating divergence not only in floral traits among populations, but also in patterns of mating system evolution.

DIFFUSE SELECTIVE PRESSURES MEDIATED BY HP TRANSFER

Changes in HP transfer dynamics as a result of changes in species composition in the community (e.g. Arceo-Gómez and Ashman, 2014*a*; Johnson and Ashman, 2019) can further contribute to the generation of among-population variation in selection pressures via diffuse selection (e.g. Iwao and Rausher, 1997; Stinchcombe and Rausher, 2001). In diffuse selection more than two species are involved in mediating the selection response (e.g. multiple interacting HP donors), while in pairwise evolution only two species are involved (e.g. one HP donor and one recipient) and thus the response to selection is independent of the presence of other species in the community (Iwao and Rausher, 1997; Stinchcombe and Rausher, 2001). For instance, Iwao and Rausher (1997) proposed that pairwise coevolution would occur only if (1) susceptibilities to different selective pressures (e.g. HP donors) are genetically uncorrelated, (2) the presence/absence of one species (e.g. HP donor) does not mediate the incidence of effects caused by another, and (3) the fitness effects of one species (e.g. HP donor) do not depend on the presence/absence of another. However, if any of these conditions are violated then diffuse selection can occur (Iwao and Rausher, 1997). So far, we know that at least one of these conditions is likely violated in the context of HP receipt. Specifically, Arceo-Gómez and Ashman (2011) showed that the fitness effects of HP receipt can strongly depend on the number and identity of HP donor species present on the stigma (violating condition three). Furthermore, it is possible that HP recipient susceptibilities to different HP donor species will be correlated if they all depend on the efficiency of the recipient's self-incompatibility system; that is, self-compatible plants may be similarly susceptible to a wide array of HP donors [violating condition (1); Hiscock and Dickinson, 1993; Murfett *et al.*, 1996]. It has also been shown that the presence of one species can cause a rearrangement of HP interactions in the community, mediating the incidence of HP effects from other species, and thus violating condition (2) stated above (Johnson and Ashman, 2019; Daniels and Arceo-Gómez, 2020). In other words, the effects and responses to selection via one HP donor are likely non-independent of the presence/absence of other HP donors in the community, thus setting the stage for diffuse selection (e.g. Stinchcombe and Rausher, 2001). While the role of multispecies interactions in mediating diffuse evolutionary processes is a topic of ongoing study (Johnson and Stinchcombe, 2007), the potential importance of diffuse selection via HP transfer interactions has been entirely overlooked. Nevertheless, the above evidence suggests that the potential for within-species variation in HP receipt to act as a driver of microevolutionary processes is strong. Yet its contribution to generating variation in selection pressures among plant populations remains largely unexplored.

COMMUNITY-WIDE DIFFERENCES IN HP TRANSFER DYNAMICS ACROSS GLOBAL GEOGRAPHIC REGIONS

The average HP intensity and diversity that plants receive can also vary among entire plant communities in predictable patterns across global latitudinal and altitudinal gradients (Arceo-Gómez *et al.*, 2019*a*). For instance, a recent global study showed that patterns of HP receipt (likelihood and intensity) correlate with latitudinal and altitudinal biodiversity gradients, suggesting that plants growing in communities that are located in highly diverse regions of the world are more likely to experience HP receipt (Arceo-Gómez *et al.*, 2019*a*). Recent studies on HP transfer networks also suggest that variation in patterns of HP transfer across communities may be widespread (e.g. Tur *et al.*, 2016; Johnson and Ashman, 2019; Parra-Tabla *et al.*, 2020). However, most studies to date have been limited to evaluating patterns of HP receipt within a single community (e.g. McLernon *et al.*, 1996; Montgomery and Rathcke, 2012; Fang and Huang, 2013; Arceo-Gómez *et al.*, 2016*b*). In fact, wide differences in pollinator species composition among broad regions around the globe could also contribute to the global trends in HP receipt observed (Arceo-Gómez *et al.*, 2019*a*). For example, large vertebrate pollinators common in tropical regions (e.g. bats and hummingbirds; Bawa, 1990) can carry larger and more diverse HP loads (e.g. Borgella *et al.*, 2001; Muchhala and Jarrin, 2002; Muchhala and Thomson, 2012) compared with invertebrate pollinators (e.g. beetles, bees, flies, butterflies) that are common in temperate areas (e.g. Barrett and Helenurm, 1987). These global differences in HP carriage and receipt could thus contribute to observed global patterns of floral diversification by imposing a wide range of selective pressures via male (Moreira-Hernandez and

Muchhala, 2019) and female (Morales and Traveset, 2008; Ashman and Arceo-Gómez, 2013) fitness. For instance, it has long been proposed that enhancing pollinator floral constancy is a strong force driving divergent evolution, but how much of this is due to HP avoidance versus competition for pollinator visitation is less known (e.g. Waelti *et al.*, 2008; also see Moreira-Hernandez and Muchhala, 2019). Receipt of HP has been shown to influence the evolution of floral traits (e.g. flower colour and size; Armbruster *et al.*, 1994; Hopkins and Rausher, 2012; Muchhala and Thomson, 2012), physiological processes (e.g. Kay and Schemske, 2008) and mating systems (e.g. Fishman and Wyatt, 1999; Randle *et al.*, 2018). Thus, differences in HP receipt among global geographic regions may have the potential to generate HP-mediated evolutionary hotspots and contribute to the shaping of global patterns of plant biodiversity.

FUTURE DIRECTIONS

Despite the fact that the study of HP receipt has a history of at least 40 years (Kanchan and Chandra, 1980), we are just starting to unravel the complexity of its delivery (e.g. Fang and Huang, 2013; Tur *et al.*, 2016) and its effects (e.g. Muchhala *et al.*, 2010; Arceo-Gómez and Ashman, 2011; Arceo-Gómez *et al.*, 2019*b*). Thus, much remains to be done in order to fully understand its ecological and evolutionary implications in nature. Here I outline a few avenues of future research that may help uncover the importance of HP in generating spatial variation in selection pressures and its contribution to shaping patterns of plant diversity across local and global scales.

Within-species variation in HP receipt and effects

First, future studies should more widely evaluate the variation in the intensity of HP receipt for one or multiple species across their geographic distributions. So far, very few studies have documented changes in the dynamics of HP receipt across populations of a single species (e.g. compared with changes in pollen transfer network structure), and the spatial scales studied tend to be small (e.g. Arceo-Gómez and Ashman, 2014*a*; Arceo-Gómez *et al.*, 2018; but see Waites and Agren, 2004). So far, we have very little empirical evidence of the extent of within-species variation in HP receipt. Such studies would constitute an important first step in advancing our understanding of the relevance of spatial variation in HP transfer interactions in nature, as well as of its potential ecological and evolutionary consequences. Second, studies that evaluate the underlying drivers of this variation (conspecific flower density, surrounding plant and pollinator community composition) and the directionality of their effects (increased or decreased HP receipt) are key. This can be achieved via experimental studies, where flower density and plant and pollinator community composition are manipulated in laboratory (e.g. Thomson *et al.*, 2019) or field conditions (e.g. de Waal *et al.*, 2015; Bruckman and Campbell, 2016; Brosi *et al.*, 2017), or by taking advantage of existing natural variation in the field (e.g. Arceo-Gómez and Ashman, 2014*a*; Albor *et al.*, 2019). It is also important to note that while some sources of variation are expected to vary inconsistently across the landscape (e.g. conspecific density) others may vary in a more predictable manner (e.g. species diversity, resource availability). This latter, more predictable type of variation (i.e. geographic gradients) could then be used to formulate and test specific predictions regarding the role of these drivers in mediating among-population variation in HP transfer and receipt. For instance, we could expect an increase in HP receipt with increasing co-flowering diversity and a decrease in HP effects with increasing resource availability. The importance of the mediators of HP transfer dynamics should also be evaluated singly and in combination (e.g. de Waal *et al.*, 2015; Thomson *et al.*, 2019). This is becoming more feasible with the development of powerful analytical techniques that allow simultaneous evaluation of multiple independent variables (e.g. structural equation modelling; Albor *et al.*, 2019).

Third, when evaluating HP effects, it is important that we move beyond effects in species pairs and start incorporating the more complex nature of HP interactions in natural communities, by acknowledging the intricacies of HP loads (e.g. Arceo-Gómez *et al.*, 2011) and the diversity of co-flowering species involved (e.g. Fang and Huang, 2013; Arceo-Gómez *et al.*, 2019*b*). Along these same lines, it is also important to design studies that help understand how HP effects revealed by greenhouse experiments may reflect expected outcomes in the field (e.g. Briggs *et al.*, 2016), and how these effects vary across a wide range of environmental (Celaya *et al.*, 2015) and biotic (e.g. Arceo-Gómez *et al.*, 2016*a*) conditions. Such tests are necessary in order to gain a more complete understanding of the causes and consequences of HP receipt and how these may contribute to the generation of spatial variation in selection pressures across populations.

Adaptive responses to HP receipt

Evaluation of the potential adaptive responses resulting from within-species variation in HP receipt across the landscape (Arceo-Gómez and Ashman, 2014*a*; Arceo-Gómez *et al.*, 2016*a*; Moreira-Hernandez and Muchhala, 2019) remains a promising field of study. Here, several avenues of research exist. First, studies that evaluate the potential for plant populations to adapt to different HP transfer regimes are still limited (e.g. Hopkins and Rausher, 2012; Arceo-Gómez *et al.*, 2016*a*). This can be achieved by evaluating the potential for natural selection on traits associated with HP tolerance or avoidance strategies under different HP transfer environments (e.g. Hopkins and Rausher, 2012; Tong and Huang, 2016), and/or via reciprocal transplant experiments that evaluate patterns of local adaptation (Arceo-Gómez and Ashman, 2014*a*). Hand-pollination studies that evaluate population-level variation in HP effects under controlled conditions would also be valuable to elucidate the potential for the evolution of HP tolerance strategies (e.g. Arceo-Gómez *et al.*, 2016*a*; Tong and Huang, 2016). Furthermore, few studies have measured traits and fitness in communities of varying co-flowering species composition (Johnson and Stinchcombe, 2007), thereby assessing the potential role of diffuse selection on species' evolutionary trajectory as a response to HP receipt.

Second, it is also important to design these studies in such a way that we can separate adaptive responses from the male (pollen) and female (style/stigma) perspectives in order to fully assess the adaptive potential of plants to HP effects. Such studies would also help to pinpoint the exact mechanisms mediating HP tolerance and avoidance. For instance, although several mechanisms/traits conferring HP tolerance have been proposed, such as longer styles or dry stigmas (reviewed in Ashman and Arceo-Gómez, 2013), to date very few studies have attempted to test these predictions (Tong and Huang, 2016; Arceo-Gómez *et al.*, 2019*b*). Thus, our understanding of the potential traits and mechanisms conferring HP tolerance is still very limited. Third, there is also evidence indicating that HP receipt may play an important role in mating system evolution, hence altering genetic diversity in plant populations and with so far unknown consequences (Arceo-Gómez and Ashman, 2014*b*). For instance, higher levels of outcrossing as a result of greater HP receipt (Arceo-Gómez and Ashman, 2014*b*) could increase genetic diversity and the rate of evolutionary change within populations (Hughes *et al.*, 2008). An increase in genetic diversity could also help generate and maintain species diversity at the community level via effects on population-level fitness (Vellend and Geber, 2005; Hughes *et al.*, 2008). In spite of these tantalizing possibilities, to my knowledge, this very promising avenue of research remains unexplored. Thus, studies that link within-species variation in patterns of HP receipt, outcrossing rates and levels of genetic diversity across populations with patterns of species diversity across communities could offer transforming insights on the role of HP receipt in shaping patterns of diversity not only across spatial but also across biological scales (from genes to communities).

Preconditions for natural selection and floral evolution

It would also be important to conduct studies that evaluate whether the preconditions for HP receipt to exert natural selection (i.e. opportunity for selection) and elicit evolutionary responses on traits that minimize HP effects in natural communities are met. One important test of the opportunity for selection would be to evaluate how variance in HP receipt is structured at different hierarchical levels of biological organization (populations, plants and individual flowers). For instance, from an evolutionary perspective we can expect that the fraction of total variance that is accounted for by within- and among-population differences in HP receipt would be more directly related to the potential for natural selection to act on traits that minimize HP effects (Herrera, 2002; Arceo-Gómez *et al.*, 2016*c*). On the other hand, a higher degree of within-plant variability will greatly reduce the opportunity for selection on such traits (Herrera, 2002), as flowers within the same plant will experience very different HP transfer regimes. Although a few studies have evaluated how variance in conspecific pollen deposition is partitioned among biological levels of organization (e.g. Herrera, 2002; Arceo-Gómez *et al.*, 2016*c*), to my knowledge no study has evaluated how much of the variance in HP receipt is accounted for by within- versus among-plant differences and among-population differences. Studies that partition the variability in HP receipt at the scale of populations and below (individual plants and flowers) are needed in order to gain a better understanding of the opportunity for selection in nature. Such studies can also provide insights into the factors underlying variation in HP receipt at different spatial scales. For instance, greater among-population variance would suggest that attributes such as conspecific flower density (e.g. de Waal *et al.*, 2015; Thomson *et al.*, 2019) or changes in co-flowering (e.g. Arceo-Gómez and Ashman, 2014*a*) and pollinator community composition (e.g. Johnson and Ashman, 2019) are key determinants of HP receipt. Greater among-plant variance, on the other hand, may indicate that within-species variation in intrinsic plant traits (e.g. flower size; Arceo-Gómez *et al.*, 2016*b*) or spatial structuring within a site may play a more important role (Bruckman and Campbell, 2016; Thomson *et al.*, 2019). If greater variance in HP receipt is observed among flowers within the same plants, then stochastic pollination events may be more important (Herrera, 2002; Fang and Huang, 2013; Arceo-Gómez *et al.*, 2016*b*).

A condition for an evolutionary response, on the other hand, would be that HP transfer dynamics are relative stable over time (Ashman and Arceo-Gómez, 2013). If HP transfer dynamics are highly stochastic over years, or over shorter periods of time, this would strongly limit the opportunity for evolutionary responses on traits that minimize HP effects in a population (even though natural selection via lifetime fitness may still occur each year). To my knowledge, the only study to date that has evaluated temporal stability in patterns of HP receipt has found good support for this precondition (Fang *et al.*, 2019). Specifically, Fang *et al.* (2019) showed constant patterns of HP receipt (HP load size and diversity) in up to 34 insect-pollinated species over three consecutive years. This result suggests that HP receipt may not vary stochastically over time and that HP tolerance or avoidance strategies could evolve in such communities (Fang *et al.*, 2019) as long as there are heritable traits that influence HP receipt (avoidance) or its effects (tolerance). It is important to note, however, that if resource heterogeneity within the same habitat and its associated fitness effects (discussed above) are strong, it could make these evolutionary responses more difficult. Thus, further research is necessary to determine whether this is the case and if patterns of HP remain constant over longer periods of time.

CONCLUSIONS

The drivers of variation discussed here may not be exhaustive; however, they illustrate the high potential for spatial variation in the intensity and effects of HP transfer interactions as well as in the evolutionary responses to HP receipt. So far, the study of pollinator-mediated plant–plant interactions has been almost entirely dominated by studies of pre-pollination interactions even though their outcomes are influenced by plant–plant interactions that take place on the stigma after pollen has been deposited. Therefore, it is paramount that we fully evaluate the causes, consequences and context-dependency of HP transfer interactions in order to gain a more complete understanding of the role that plant–pollinator interactions play in generating and organizing plant biodiversity. It is also important to acknowledge that the number of studies documenting patterns of HP receipt is still limited and strongly biased towards temperate systems (Arceo-Gómez *et al.*, 2019*a*). Studies on HP transfer dynamics in highly diverse regions such as in Africa and South America are largely underrepresented (see Fig. 1 in Arceo-Gómez *et al.*, 2019*a*). Biases in studies of HP receipt are not only geographic but also phylogenetic as large groups of plants have also been poorly represented in these studies (e.g. monocotyledons; Arceo-Gómez *et al.*, 2019*a*). Thus, there is an urgent need to evaluate patterns of variation in HP receipt at larger spatial and phylogenetic scales. Knowledge of wide-scale patterns of HP receipt may help uncover its potential role in shaping patterns of plant diversity at a global scale.

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