

Geographic mosaics of interactions via heterospecific pollen transfer may contribute to shape local and global patterns of plant diversity

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January 6, 2021

Abstract

Studies that aim to understand the processes that generate and organize plant diversity in nature have a long history in Ecology. Among these, pollinator-mediated plant-plant interactions that occur by altering pollinator floral preferences have been at the forefront in this field. Current evidence however indicates that plants can interact directly via heterospecific pollen (HP) transfer, that these interactions are ubiquitous, and can have strong fitness effects with implications for floral evolution, speciation and community assembly. Hence, interest in understanding their role in the diversification and organization of plant communities is rapidly rising. The existence of geographic mosaics of species interactions and their role in shaping patterns of diversity is also well recognized. However, after 40 years of research, the importance of geographic mosaics in HP intensity and effects remain poorly known, thus ignoring 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 geographic mosaics in HP transfer interactions and outline future directions in this field.

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 & Jordano 2002, Bascompte et al. 2003, Kaiser-Bunbury et al. 2017). Hence, the study of plant-plant interactions via their effects on pollinator choice (i.e. pre-pollination) and patterns of pollinator visitation (e.g. pollinator competition) has been a prolific area of study in ecology and evolutionary biology. Their study has rendered important insights on the mechanisms of floral diversification (Mitchell et al. 2009, Phillips et al. 2020) and the processes that mediate community assembly (Sargent & Ackerly 2008). It is thus also not surprising that the study of pre-pollination interactions has remained at the forefront in the fields of pollination biology and community ecology for over 100 years (Robertson 1985, Phillips et al. 2020). However, the ultimate outcome of pre-pollination interactions (via changes in pollinator visitation patterns) can be determined by plant-plant interactions that take place via pollen on the stigma (i.e. post-pollination) long after pollinators leave a flower (Morales & Traveset 2008, Ashman et al. 2020), nonetheless these have been far less studied. It is thus imperative that we integrate the complexity of heterospecific pollen (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 & Traveset 2008, Fang & Huang 2013, Tur et al. 2016, Arceo-Gómez et al. 2019a). Recent studies for instance, have shown that HP transfer is widespread across taxonomic (217 species; 88% of all species evaluated), geographic (five continents) and phylogenetic scales (52 plant families; Arceo-Gómez et al. 2019a), with some species averaging up to 368.5 HP grains per stigma (average of 11.83 ± 2.15 across species) and receiving HP in 50-100% of their flowers (Ashman & 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 (Morales & Traveset

2008, Ashman & Arceo-Gómez 2013), even if HP receipt occurs in small amounts (1% HP; Thomson et al. 1982a). For instance, a meta-analysis of 20 HP donor-recipient pairs revealed a 20% average decrease in seed production as a result of HP deposition (Ashman & Arceo-Gómez 2013). Given the pervasive nature of these interactions and its strong fitness effects, interest in understanding its role in the diversification (e.g. Hopkins & Rausher 2012, Armbruster et al. 2014, Ashman & Arceo-Gómez 2013, Moreira-Hernandez & Muchhala 2019) and organization of plant communities is rapidly rising (e.g. Eaton et al. 2012, Tur et al. 2016, Arceo-Gómez et al. 2019a).

The existence of complex geographic mosaics of species interactions and their role in shaping broad patterns of diversity has also been well-recognized (Thompson 1999, Gomulkiewicz et al. 2000, Thompson & Cunningham 2002). The most central tenet of these studies is that the intensity and outcomes of interactions between a pair, or group of species, can differ greatly across the geographic landscape, such that different traits are favored in different communities (Thompson 1999, Singer & McBride 2012). Geographic mosaics of species interactions have been observed in plant-pollinator (e.g. Thompson & Cunningham 2002), plant-herbivore (e.g. Singer & McBride 2012), plant-microbiome (e.g. Andonian et al. 2012), predator-prey (e.g. Toju & Sota 2006) and host-parasite interactions (e.g. Gandon & Nuismer 2009) among others. 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 geographic mosaics of plant-plant interactions via HP transfer (intensity and effects) remains poorly understood. The ecological, environmental and genetic landscape on which HP transfer interactions occur changes constantly (see below). Thus, the intensity and outcomes of these interactions are likely to fluctuate and elicit different evolutionary responses in different populations (e.g. Hopkins & Rausher 2012, Arceo-Gómez & Ashman 2014a, Arceo-Gómez et al. 2016a), potentially contributing to local and global patterns of plant diversification and assembly.

Changes in the intensity of HP donation and receipt can result from spatial variation in conspecific flower density (Thomson et al. 2019) and changes in plant and pollinator community assemblages across the landscape (Arceo-Gómez & Ashman 2014a, Johnson & Ashman 2019). Variation in HP effects on the other hand, can fluctuate as a result of variation in resource availability (Celaya et al. 2005), pollen donor-recipient species co-existence history (Arceo-Gómez et al. 2016a) or genetic architecture (i.e. selfer vs outcrosser; Arceo-Gómez & Ashman 2014b). 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), and its fitness effects tested under constant greenhouse conditions (reviewed in Morales & Traveset 2008, Ashman & Arceo-Gómez 2013; but see Briggs et al. 2015). Thus, to this day, the degree to which the intensity and effects of HP receipt varies across broad spatial scales is virtually unknown for any species (but see Waites & Agren 2004). Hence, we have so far ignored the potential for geographic variation in HP transfer interactions in contributing to shape plant communities in nature.

Community-level changes in the intensity of HP transfer may also lead to differences in its importance as a driver of diversification and as a mediator of co-flowering community assembly at larger spatial scales. For instance, different HP transfer interaction landscapes, where the incidence and intensity of HP transfer varies across communities (e.g. Johnson & Ashman 2019, Tur et al. 2016) or geographic regions (Arceo-Gómez et al. 2019a), may result in evolutionary hotspots (high HP transfer; as in Thompson 1999). Heterospecific pollen receipt has been shown to influence the evolution of floral traits (e.g. Armbruster et al. 1994, Muchhala & Thomson 2012), mating systems (Fishman & Wyatt 1999, Randle et al. 2018), flowering time (Waser 1978) and even play a role in reinforcing speciation (e.g. Hopkins & Rausher 2012). Thus, HP-mediated evolutionary hotspots may have the potential to foster global patterns of plant diversification (Arceo-Gómez et al. 2019a, Moreira-Hernandez & Muchhala 2019). The existence of geographic mosaics of species interactions has been proposed as an important contributor to the diversification and organization of life (Thompson 1999), and interactions via HP transfer may not be the exception. Here, I outline a conceptual framework and summarize existing evidence for the causes and potential ecological and evolutionary consequences of geographic variation in HP transfer interactions and propose future directions in this field.

Geographic mosaics of HP transfer interactions

Drivers of spatial variation in patterns of HP receipt

While there is a growing body of literature describing among-species differences in the intensity and diversity of HP receipt (reviewed in Morales & Traveset 2008, Ashman & Arceo-Gómez 2013, Arceo-Gómez et al. 2019a), little has been done to understand the extent and potential drivers of within-species variation in HP receipt across spatial scales. 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 (Fig. 1a-b) are related to the abundance and spatial distribution of the HP recipient, whereas the remaining two (Fig. 1c-d) are related to changes in the surrounding plant and pollinator community.

I and II. Density and fine-scale spatial arrangement of conspecific flowers - I) It is well known that variation in conspecific flower density can influence pollinator attraction, flower visitation rate, conspecific pollen deposition and overall reproductive success (e.g. Rathcke 1983, Kunin 1997, Hegland & Boeke 2006, Spigler & Chang 2008). What has been less explored, however, is how variation in conspecific flower density influences pollen transfer dynamics with co-flowering species, i.e. HP donation and receipt (Waal et al. 2015, Thomson et al. 2019; Fig. 1a). For instance, as conspecifics decrease in density across the landscape 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). Waal et al. (2015) found support for this prediction in an experimental study with South African daisies. They found an increase in HP receipt with decreasing conspecific density leading to reduced fecundity in populations of low relative abundance (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 direction of the relationship between conspecific density and HP receipt may thus depend on the pollination system (wind vs animal-pollinated) of the main HP donor. These predictions however, require further testing.

II) It has also been shown that density-dependent effects on HP receipt can be influenced by plant species' spatial distribution within a site, particularly when pollinators respond to fine-scale (within meters) spatial patterns of flowering species distribution (e.g. intermixed vs isolated; Fig. 1b Thomson et al. 1982, Hanoteaux et al. 2013, Thomson et al. 2019). 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 within a site (Bruckman & Campbell 2016, Thomson et al. 2019), with HP receipt typically increasing in intermixed arrays. 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 with decreasing conspecific density. 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 among-species variation within a single community (Arceo-Gómez et al. 2016b), thus supporting the idea that fine-scale spatial drivers of HP receipt are at play. Overall, the evidence so far suggests that within-species patterns of HP receipt can vary extensively within and across communities, generating complex geographic 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. 2016a, Fang et al. 2019). However, to my knowledge, very few studies have evaluated the extent and drivers of spatial variation in HP receipt within a species, which has limited our understanding of its potential evolutionary consequences.

III and IV. Co-flowering and pollinator community composition - III) The intensity and diversity of HP receipt in individual species may also vary with varying pollinator species composition across the landscape (identity, abundance and diversity; 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. 2016b, Minnaar et al. 2019b). 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 & 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 can have large effects on overall HP transfer dynamics. Changes not only in the identity, but in the overall diversity of the flower visiting insect community, have also been predicted to lead to extensive changes in patterns of HP receipt (e.g. Arceo-Gomez et al. 2016b, Ashman et al. 2020). With HP load size predicted to increase with increasing pollinator diversity (Arceo-Gomez et al. 2016b).

IV) Fluctuations in plant species composition have also been shown to have large impacts on patterns of HP receipt (Fig. 1d). These changes in HP receipt can be mediated by variation in plant species identity, diversity and even in the functional trait composition in a community (e.g. floral trait similarity; Eaton et al. 2012). For instance, the abundance of a single plant species in co-flowering communities in Hawaii significantly altered patterns of HP receipt, with plants receiving smaller HP loads and being less connected via HP transfer in sites where it was dominant (Johnson & Ashman 2019). In another study, Arceo-Gomez and Ashman (2014a) showed that *Mimulus guttatus* plants receive up to four times more HP depending on the overall diversity of the plant community where they occur. Changes in plant community composition may not only alter overall HP load size and diversity but also the identity of the interacting partners. For instance, a recent study showed that the presence of one (invasive) species (*Cirsium arvense*) causes a rearrangement of HP transfer interactions in the community, such that some HP transfer interactions disappear while new ones emerge (Daniels & Arceo-Gomez 2020). This reorganization of HP transfer interactions may also have the potential to alter species' evolutionary trajectories within a community (Ashman & Arceo-Gomez 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 the landscape as a result of changes in plant and pollinator community composition, including the addition of invasive and non-native plants and pollinators to native communities. Moreover, even in cases where plant and pollinator community composition remain relatively constant, the identity of pairwise plant-plant interactions via HP transfer could still vary across communities, as it has been shown in plant-pollinator interaction networks (Carstensen et al. 2014). It is evident that individual plant species can experience large variation in the surrounding plant (e.g. Arceo-Gomez & Ashman, 2014a, Albor et al. 2019) and pollinator community (Herrera 1988, Cosacov et al. 2008), and evidence suggesting this plays a key role in mediating within-species variation in HP transfer dynamics is rapidly accumulating (e.g. Arceo-Gomez & Ashman 2014a, Ashman & Johnson 2019, Kay et al. 2019). 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 community species composition mediate within-species variation in HP receipt across a wide geographical scale.

Drivers of spatial variation in HP effects

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

I. 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 availability 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 glauca* (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 & Macnair 1990). If variability in abiotic resources and environmental conditions affects conspecific pollen performance on the stigma/style, then we can expect that this variability would also affect its ability to compete and succeed in the face of HP interference (Fig. 2a). If this is the case, then it is likely effects of HP receipt may vary 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 & Traveset 2008, Ashman and Arceo-

Gomez 2013), and results from these studies have been used to make wide-ranging inferences of overall species' HP tolerance or susceptibility. Plants however, often experience a wide range of environmental conditions in nature (e.g. Chapin et al. 1987, Davis et al. 2000, Torang et al. 2010), and thus HP effects derived from greenhouse studies may lead to an incomplete understanding of such effects (Celaya et al. 2015). To my knowledge, only one study has evaluated the role of resource availability in mediating HP effects on reproductive success (Celaya et al. 2015; but see Ruane & 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 availability, 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 populations. Such limitations could ultimately obscure our understanding of the real effects and consequences of HP transfer in nature. Here I argue that the outcome of HP transfer interactions are likely to be context-dependent, and strongly depend on the particular abiotic conditions where these interactions take place. Interpopulation variation in HP effects may in turn lead to geographic mosaics of selection, as the strength of HP receipt as a selective pressure would vary (via female fitness) across the landscape (discussed below). However, to my knowledge, this prediction has not been explored.

II. 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 specie's 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 tolerance strategies to minimize its negative effects on reproductive success (Ashman & Arceo-Gomez 2013, Arceo-Gomez et al. 2016a). As a result, these populations would show little to no reproductive effects when exposed to HP compared to populations that typically receive minimal or infrequent amounts of HP (e.g. Arceo-Gomez et al. 2016a). 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 & Schemske 2008, Arceo-Gomez et al. 2016a), 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-Gomez et al. (2016a) 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-Gomez et al 2016a; also see Kay & 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-Gomez et al. 2016a). 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 & Arceo-Gomez 2013, Moreira-Hernandez & 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 plants typically exposed to high levels of HP transfer. However, if varying degrees of history/intensity of exposure lead to geographic mosaics of selection on stigmatic HP tolerance or conspecific pollen performance is yet to be determined.

III. Recipient mating system - Plant populations can vary substantially in their degree of selfing versus outcrossing, which has implications for their genetic diversity and architecture across their distribution range (e.g. Barrett & Husband 1990, Tamaki et al. 2009, Ness et al. 2010, Hargreaves & 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 is slower compared to outcross pollen (e.g.,

Weller & Ornduff 1977, Aizen & Searcy 1990, Cruzan & Barrett 1993, Kruszewski & 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 & Traveset 2008, Ashman & Arceo-Gomez 2013), self-pollen may be more susceptible to HP effects compared with outcross pollen (Arceo-Gomez & Ashman 2014b). 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 & Carr 2005), showed that HP has stronger effects when competing against self- compared to outcross conspecific pollen (Arceo-Gomez & Ashman 2014b). Specifically, HP reduced self-pollen tube growth by an additional 32% compared with outcross pollen (Arceo-Gomez & Ashman 2014b). Among-population variation in the degree of selfing can also take place as a result of breakdown in self-incompatibility systems (e.g. Reinartz & Les 1994, Nasrallah et al. 2004, Busch & 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 & Dickinson 1993, Murfett et al. 1996, Bedinger et al. 2011). 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 & Arceo-Gomez 2013). Thus, variation not only in the mating system (ratio of self/outcross pollen), but in the strength of self-incompatibility mechanisms, could mediate 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 realized mating system by favoring outcross pollen grains (i.e. HP has greater effects on self-pollen; Arceo-Gomez and Ashman 2014b), or if increased selfing provides reproductive assurance in the face of high HP receipt (Ashman et al. 2020). 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.

Geographic mosaics of selection.

Despite the seemingly large spatial variation in the intensity and effects of HP receipt the potential role of HP transfer interactions as a force generating geographic mosaics of selection is mostly unknown (but see Kay & Schemske 2008, Hopkins & Rausher 2012, Arceo-Gomez et al. 2016a). HP receipt can act as a selective force driving the evolution of floral strategies that mitigate female (Morales & Traveset 2008) and male fitness costs (conspecific pollen loss; Moreira-Hernandez & Muchhala 2019). Examples include adaptations to enhance pollen placement (e.g. Armbruster et al. 1994, Minnaar et al. 2019a), shifts in flowering phenology (e.g. Waser 1978) and adaptations to minimize pollinator sharing such as flower trait divergence (e.g. Hopkins & Rausher, 2012), pollinator specialization (Muchhala et al. 2010) and increased selfing (e.g. Fishman & Wyatt, 1999). Specifically, Ashman and Arceo-Gomez (2013) proposed two main evolutionary strategies to mitigate female fitness effects, i.e. tolerance or avoidance of HP receipt. Although these strategies were proposed as a means to explain among-species variation in HP receipt (Ashman & Arceo-Gomez 2013), plants within the same species that are exposed to different HP transfer environments may experience the same evolutionary pressures and outcomes. For instance, Hopkins and Rausher (2012) showed evidence for divergent selection pressures on flower color 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 & Rausher 2012), or maybe even direct HP effects on reproductive success (e.g. stigma clogging), thus generating spatial mosaics 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 geographic mosaics of selection on HP tolerance strategies (also see Arceo-Gomez et al. 2016a). Furthermore, *Mimulus guttatus* 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-Gomez & Ashman 2014a). 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-Gomez & Ashman 2014a). Evolutionary adaptations that minimize male fitness costs have also been shown and these include traits that enhance accuracy in pollen placement (e.g. Muchhala & Potts 2007, Armbruster et al. 2014), increase in pollinator specialization (e.g. Muchhala et al. 2010) and floral constancy (Moreira-Hernandez & 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 favor mechanisms that increase the degree of autonomous self-pollination in order to preemptively minimize HP effects (e.g. Fishman & Wyatt 1999, Randle et al. 2018). For instance, Fishman and Wyatt (1999) demonstrated that selection favored selfing and selfing-related traits only in *Arenaria uniflora* populations that grew in sympatry with congeneric *A. glabra*. They further show that HP transfer rather than pollinator competition was the main driver of selection (Fishman & Wyatt 1999). Thus, HP transfer not only has the potential for generating geographic mosaics of selection in floral traits, but also on patterns of mating system evolution.

Changes in HP transfer dynamics as a result of changes in community species composition (e.g. Arceo-Gomez & Ashman 2014a, Johnson & Ashman 2019) can further contribute to generate selection mosaics via diffuse selection (e.g. Iwao & Rausher 1997; Stinchcombe & Rausher 2001). For instance, Iwao and Rausher (1997) proposed that diffuse co-evolution would occur if, 1) susceptibility 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. So far, we know that at least one of these conditions is likely violated in the context of HP receipt. Specifically, Arceo-Gomez 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 recipient's self-incompatibility system, that is, self-compatible plants may be similarly susceptible to a wide array of HP donors (violating condition one; Hiscock & 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 two stated above (Johnson & Ashman 2019, Daniels & Arceo-Gomez 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 & Rausher 2001). While the role of multispecies interactions in mediating diffuse evolutionary processes is a topic of ongoing study (Johnson & 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 geographic mosaics of selection remains largely unexplored.

Community-level variation in patterns of HP receipt

The average intensity and diversity of HP that plants receive not only vary among populations of the same species but can vary among entire plant communities. Recent studies on HP transfer networks have shown that community-wide patterns of HP transfer can vary spatially (e.g. Tur et al. 2016, Johnson & Ashman 2019). For instance, a study across nine sand dune plant communities in the Yucatan showed large variation in average HP proportion (2.3% - 20.8%) and HP richness (2.3 - 5.5 HP donor species) that plants receive across communities (Parra-Tabla et al. 2020). A recent global study also showed that patterns of HP receipt (likelihood and intensity) correlate with latitudinal and altitudinal biodiversity gradients, suggesting that plants growing in highly diverse regions of the world are more likely to engage in HP transfer interactions (Arceo-Gomez et al. 2019a). Although it is evident that patterns of HP receipt vary across large spatial scales most studies to date have been limited to evaluate patterns of HP receipt within single communities (e.g. McLernon et al. 1996, Montgomery & Rathcke 2012, Fang & Huang 2013, Arceo-Gomez et al. 2016b). Wide differences in pollinator species composition across regions around the globe may further contribute to global trends in HP receipt (Arceo-Gomez et al. 2019a). 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 & Jarrin 2002, Muchhala & Thomson 2012) compared with invertebrate pollinators (e.g. beetles, bees, flies, butterflies) that are common in temperate areas (e.g. Barrett & Helenum 1987). These global differences in HP carriage and receipt may thus contribute to observed global patterns of floral diversification by imposing a wide-range of selective pressures via male (Moreira-Hernandez & Muchhala 2019) and female fitness (Morales & Traveset 2008, Ashman & Arceo-Gomez 2013). 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 & Muchhala 2019). In fact, the pollination literature has largely overlooked the potential contribution of post-pollination process (via HP transfer) to outcomes of pollinator-mediated selection. HP receipt has been shown to influence the evolution of morphological traits (e.g. flower color and size; Armbruster et al. 1994, Muchhala & Thomson 2012, Hopkins & Rausher 2012), physiological processes (e.g. Kay & Schemske 2008), mating systems (e.g. Fishman & Wyatt 1999, Randle et al. 2018) and flowering phenology (Waser 1978). Thus, differences in HP receipt mediated by variation in plant and pollinator community composition among geographic regions across the globe may have the potential to generate evolutionary hotspots (Thompson 1999) and contribute to shape 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 & Jayachandra 1980), we are just starting to unravel the complexity of its delivery (e.g. Fang & Huang 2013, Tur et al. 2016) and its effects (e.g. Muchhala et al. 2010, Arceo-Gomez & Ashman 2011, Arceo-Gomez et al. 2019b). Thus, much remains to be done in order to fully understand its ecological and evolutionary implications in natural communities. Here I outline a few avenues of future research that may help uncover the importance of HP in generating geographic mosaics of selection and its contribution to shaping patterns of plant diversity across local and global spatial 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 for a single species across spatial scales (e.g. compared to changes in pollen transfer network structure), and the spatial scales studied tend to be small (two or very few communities; e.g. Arceo-Gomez & Ashman 2014a, Arceo-Gomez et al. 2018; but see Waites & Agren 2004). So far, we have very little empirical evidence of the extent of within-species variation in HP receipt across natural communities. Such studies would constitute an important first in advancing our understanding of the relevance of geographic mosaics of HP transfer interactions in nature, as well as of its potential ecological and evolutionary consequences. Second, studies that evaluate the mediators of HP transfer dynamics (conspecific flower density, plant and pollinator community composition) and the directionality of their effects (increase or decrease HP receipt) are key if we aim to understand the underlying drivers generating geographic variation in HP interactions. This can be achieved via experimental studies, where flower density and plant and pollinator community composition are manipulated in the lab (e.g. Thomson et al. 2019) or field conditions (e.g. de Waal et al. 2015, Bruckman & Campbell 2016, Brosi et al. 2017), or by taking advantage of existing natural variation in the field (e.g. Arceo-Gomez & Ashman 2014a, 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 and spatial arrangement) 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 variation in HP transfer interactions. 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 these mediators in influencing 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 for simultaneous evaluation of multiple independent variables (e.g. structural equation modeling; Albor et al. 2019).

Third, when evaluating HP effects, it is important that we move beyond effects in species-pairs and start incorporating the complexity of HP interactions within natural communities by acknowledging the intricacies of HP loads (e.g. Arceo-Gomez et al. 2011) and the diversity of co-flowering species involved (e.g. Fang & Huang 2013, Arceo-Gomez et al 2019b). Along these same lines, it is also important to design studies that help understand how 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 conditions (e.g. Arceo-Gomez et al. 2016a). Such tests are necessary in order to gain a more complete understanding of the causes and consequences of HP receipt in natural communities and how these may contribute to generate geographic mosaics of selection.

Adaptive responses

Evaluation of the potential adaptive responses to within-species variation in HP receipt across the landscape (Arceo-Gomez & Ashman 2014a, Arceo-Gomez et al. 2016a, Moreira-Hernandez & 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 (e.g. Hopkins & Rausher 2012, Arceo-Gomez et al. 2016a). 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 & Rausher 2012, Tong & Huang 2016), and/or via reciprocal transplant experiments that evaluate patterns of local adaptation (Arceo-Gomez & Ashman 2014a). 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 in nature (e.g. Arceo-Gomez et al. 2016a, Tong & Huang 2016). Furthermore, few studies have measured traits and fitness in communities of varying species composition (Johnson & 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 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 & Arceo-Gomez 2013), to date very few studies have attempted to test these predictions (Tong & Huang 2016, Arceo-Gomez et al. 2019b). 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 and in altering the genetic architecture of plant populations, with so far unknown consequences (Arceo-Gomez & Ashman 2014b). For instance, higher levels of outcrossing as a result of greater HP receipt (Arceo-Gomez & Ashman 2014b), 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 & 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 across biological scales (from genes to communities).

Pre-conditions for selection

It would also be important to conduct studies that evaluate whether the pre-conditions for HP receipt to exert natural selection on traits that minimize HP effects in natural communities are met (i.e. opportunity for selection). One such condition for instance would be that HP transfer dynamics are relative stable over time (Ashman & Arceo-Gomez 2013). If HP transfer dynamics are highly stochastic over the years, or over

shorter periods of time, this would strongly limit the opportunity for selection on traits that minimize HP effects in a population. To my knowledge, the only study to date that has evaluated temporal stability in patterns of HP receipt has found good support for this pre-condition (Fang et al. 2019). Specifically, they 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). However, further research is necessary to determine whether this is the case for other communities or if patterns of HP remain constant over longer periods of time.

Another important test of the pre-conditions for natural selection would be to evaluate how variance in HP receipt is structured spatially 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 (see Herrera 2002, Arceo-Gomez et al. 2016c). 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-Gomez et al. 2016c), to my knowledge no study has evaluated how much of the variance in HP receipt is accounted for by within- versus among-plant, 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 for the opportunity of selection in natural communities. 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 community-level 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-Gomez & Ashman 2014a) and pollinator community composition (e.g. Johnson & 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-Gomez et al. 2016b) or spatial structuring within a site may play a more important role (Bruckman & 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 & Huang 2013, Arceo-Gomez et al. 2016b).

Conclusions

The drivers of variation discussed here may not be exhaustive, however, they illustrate the high potential for geographic 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-Gomez et al. 2019a; Fig. 3). Studies on HP transfer dynamics in highly diverse regions such as in Africa and South America are largely underrepresented (Fig. 3; Arceo-Gomez et al 2019a). Biases in studies of HP receipt are not only geographical but also phylogenetic as large groups of plants have also been poorly represented in these studies (e.g. monocotyledons; Arceo-Gomez et al. 2019a). 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.

Acknowledgments

The author thanks R. Raguso and V. Parra-Tabla for comments on an earlier version of this manuscript.

GAG was supported by NSF DEB 1931163. The author has no conflict of interests to declare.

Author contributions

GAG conceptualized the ideas and wrote the manuscript.

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Figure 1. Four predicted sources of within-species variation in HP receipt across spatial scales depicted here as two populations. Examples of studies providing supporting evidence for the role of each source of variation in mediating HP transfer dynamics are presented.

Figure 2 Three predicted sources of within-species variation in the intensity of HP effects across spatial scales depicted here as two populations. Examples of studies providing supporting evidence for the role of each source of variation in mediating HP effects are presented.

Figure 1

Source of variation in HP receipt	Population 1	Population 2	Supporting evidence
a) Conspecific flower density			Thomson et al. 2019, Waal et al. 2015
b) Fine-scale spatial structure			Thomson et al. 2019, Bruckman and Campbell 2016
c) Pollinator community composition			Johnson and Ashman 2019, Kay et al. 2019
d) Co-flowering community composition			Arceo-Gomez and Ashman 2014a, Johnson and Ashman 2019

Figure 2

Source of variation in HP effects	Population 1	Population 2	Supporting evidence
a) Environmental and resource variability			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-Gomez et al. 2016a
c) Mating system	 Selfer	 Outcrosser	Arceo-Gomez and Ashman 2014b

Figure 3 Global distribution of 26 studies (red circles) that have evaluated the intensity of HP receipt for 245 plant species across temperate and tropical regions between 1986 and 2017 (modified from Arceo-Gómez et al. 2019a).

