ANNUAL REVIEWS

Annual Review of Ecology, Evolution, and Systematics

Importance of Pollinator-Mediated Interspecific Pollen Transfer for Angiosperm Evolution

Juan Isaac Moreira-Hernández and Nathan Muchhala

Department of Biology and Whitney R. Harris World Ecology Center,
University of Missouri–St. Louis, St. Louis, Missouri 63121, USA;
email: juan.moreira@gmail.com, muchhalan@umsl.edu

Annu. Rev. Ecol. Evol. Syst. 2019. 50:191–217

First published as a Review in Advance on
July 23, 2019

The *Annual Review of Ecology, Evolution, and Systematics* is online at ecolsys.annualreviews.org

https://doi.org/10.1146/annurev-ecolsys-110218-024804

Keywords

reproductive interference, plant competition, hybridization, reproductive isolation, floral evolution, plant speciation

Abstract

Understanding how pollen moves between species is critical to understanding speciation, diversification, and evolution of flowering plants. For co-flowering species that share pollinators, competition through interspecific pollen transfer (IPT) can profoundly impact floral evolution, decreasing female fitness via heterospecific pollen deposition on stigmas and male fitness via pollen misplacement during visits to heterospecific flowers. The pollination literature demonstrates that such reproductive interference frequently selects for reproductive character displacement in floral traits linked to pollinator attraction, pollen placement, and mating systems and has also revealed that IPT between given pairs of species is typically asymmetric. More recent work is starting to elucidate its importance to the speciation process, clarifying the link between IPT and current and historical patterns of hybridization, the evolution of phenotypic novelty through adaptive introgression, and the rise of reproductive isolation. Our review aims to stimulate further research on IPT as a ubiquitous mechanism that plays a central role in angiosperm diversification.

1. INTRODUCTION

Pollen grains from approximately 300,000 species worldwide, corresponding to 87.5% of angiosperms, are transported by a variety of animal pollinators (Ollerton et al. 2011). When pollinators alternate foraging visits between co-flowering, co-occurring plant species, pollen may be transferred interspecifically (Morales & Traveset 2008). Interspecific pollen transfer (IPT) has long been recognized in the pollination literature as a form of reproductive interference—a type of competitive interaction that decreases fitness for at least one of the interacting species (Campbell 1985; Mitchell et al. 2009; Rathcke 1983; Waser 1978a, 1983). This fitness decrease can be due to either heterospecific pollen deposition on stigmas, which can reduce seed set by clogging stigmas or usurping ovules (Ashman & Arceo-Gómez 2013, Briggs et al. 2015, Jakobsson et al. 2008), or pollen misplacement during foraging on heterospecific flowers, which reduces successful pollen export to conspecific stigmas (Minnaar et al. 2019, Muchhala & Thomson 2012, Thomson et al. 2018). IPT dictates patterns of interspecific gene flow when species are closely related (Campbell et al. 2002, Harder et al. 1993, Kay 2006, Natalis & Wesselingh 2012a); thus, the study of IPT is also critical to understanding plant diversification in terms of the speciation process, reproductive isolation, adaptive introgression, and hybridization.

A decade ago, Morales & Traveset (2008) contributed the first and only comprehensive review on IPT, carefully laying out evidence for the occurrence of IPT in nature and the expected ecological and evolutionary consequences. Prior to this seminal publication, IPT tended to receive less attention than other forms of competition between co-flowering plants, such as competition for pollinator attraction (Ashman & Arceo-Gómez 2013, Mitchell et al. 2009, Muchhala & Thomson 2012). However, pollinator sharing and generalization are widespread in pollination networks (Arceo-Gómez et al. 2016a, Bascompte et al. 2006), and multiple recent community-level studies have shown that IPT is more common than previously thought (Arceo-Gómez et al. 2018, Fang & Huang 2013, Johnson & Ashman 2019, Tur et al. 2016). In addition, IPT interactions have recently been highlighted as one of the major sources of pollen loss along the paternity pathway from pollen production to ovule fertilization (Minnaar et al. 2019), underscoring its importance for plant reproduction and floral evolution. This growing recognition has stimulated a burgeoning literature, including studies on the mechanics of IPT in terms of how the presence of competitors affects pollen export and receipt (Flanagan et al. 2009, Minnaar et al. 2019, Muchhala & Thomson 2012, Thomson et al. 2018), the evolutionary consequences of IPT in terms of selection for specialization on pollinators (Armbruster et al. 2014, Muchhala et al. 2010), character displacement in floral phenotype (Eaton et al. 2012, Grossenbacher & Stanton 2014, Muchhala et al. 2014), and the evolution of mating systems (Briscoe Runquist & Moeller 2014, Randle et al. 2018). Importantly, the movement of pollen between species and its evolutionary costs have been repeatedly shown to be highly asymmetric (Briscoe Runquist 2012, Natalis & Wesselingh 2012a, Randle et al. 2018, Zhang et al. 2016). Inspired by this intensified interest in IPT as a ubiquitous process in nature, here we review our current understanding of its implications for angiosperm ecology and evolution.

Our first main goal is to present a critical synthesis of our current understanding of IPT and its consequences. In Section 2, we review the fitness costs of pollen misplacement and heterospecific pollen deposition, and in Section 3, we explore the implications of these costs for floral divergence, specialization, and mating system evolution. Our second main goal is to explore the intersection between the pollination ecology perspective of IPT and the evolutionary implications of IPT in terms of how it affects gene flow during early plant diversification. In Section 4, we outline the expected outcomes of pollen transfer between a pair of species, based on the time since they shared a common ancestor, and the consequences for reproductive isolation and the transfer of adaptive genetic variation. We conclude by emphasizing the emerging patterns in an evolutionary context and highlighting underexplored issues particularly deserving of future research.

2. EFFECTS OF INTERSPECIFIC POLLEN TRANSFER ON FLORAL FITNESS

From the plant perspective, the fitness of a flower is maximized by increasing pollen dispersal to conspecific flowers and by ensuring the receipt of sufficient conspecific pollen to fertilize its ovules (Mitchell et al. 2009, Morales & Traveset 2008). These components of floral fitness correspond to the male and female functions, respectively. The degree to which a pollinator maximizes male and female fitness is termed pollinator effectiveness, and it can be further subdivided into quantity and quality components (Ne'eman et al. 2010). The quantity component refers to the number of visits a pollinator makes, whereas quality refers to the amount of pollen that is transported per visit as well as the genetic attributes of this pollen (in terms of the diversity of sires and the amount of outcross pollen versus self pollen; Mitchell et al. 2009, Ne'eman et al. 2010). Both components of pollinator effectiveness are typically thought to be determined by factors intrinsic to the vector, including foraging behavior, floral fidelity, visitation behavior, and visitation rates (Armbruster 2014, Flanagan et al. 2009, Muchhala et al. 2009, Ne'eman et al. 2010), but this perspective overlooks the fact that pollinator effectiveness may fundamentally change in the presence of competitor plant species (an extrinsic factor) if this leads to increased heterospecific pollen transfer (negatively affecting female fitness) and/or pollen misplacement (negatively affecting male fitness; Mitchell et al. 2009, Muchhala & Thomson 2012). Such effects may be highly asymmetric, affecting one competitor more than the other, due to idiosyncrasies of pollinator preference, floral morphology, spatial arrangement, species abundances, and postpollination reproductive barriers (Muchhala & Thomson 2012, Natalis & Wesselingh 2012b, Thomson et al. 2018). In the following subsections, we review evidence for negative effects of pollen misplacement on male fitness followed by negative effects of heterospecific pollen deposition on female fitness.

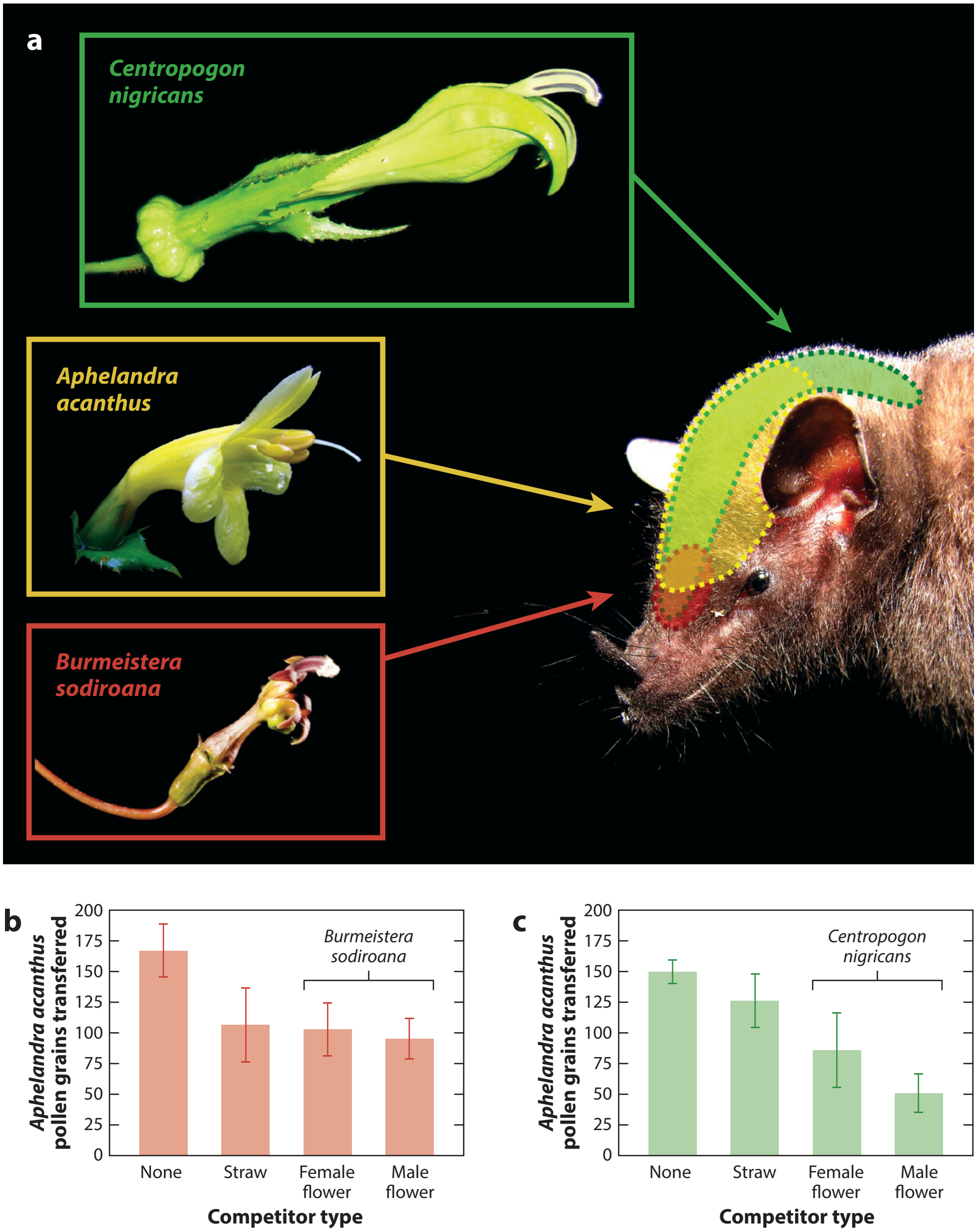
2.1. Pollen Misplacement

Male fitness in plants requires efficient pollen transport from the anthers, where it is produced, to conspecific stigmas, where it can germinate, produce a pollen tube, reach the ovary, and deploy the sperm cells that will ultimately effect ovule fertilization (Minnaar et al. 2019, Mitchell et al. 2009, Morales & Traveset 2008). Mounting evidence shows that pollen loss during transport is arguably the largest factor affecting male fitness, as the vast majority of pollen never reaches conspecific stigmas (Minnaar et al. 2019). Throughout this review, we use pollen misplacement to refer specifically to competitive costs due to the loss of pollen during visits to competitor species; this includes pollen deposited on foreign stigmas or other plant structures as well as pollen lost from pollinators' bodies due to passive detachment or active grooming (Muchhala & Thomson 2012). We prefer the term pollen misplacement to conspecific pollen loss (Morales & Traveset 2008) because of the referential difficulties of the latter term—pollen lost during visits to foreign flowers is not merely conspecific to the source flower, it was produced by it (Muchhala & Thomson 2012).

A critical first step in the pathway to paternity, which can have important implications for pollen misplacement, involves the deposition of pollen on pollinators' bodies (Minnaar et al. 2019). The interaction between a plant's traits, including its morphology (e.g., anther size and orientation, corolla constriction, tube length) and the nature of its floral rewards (e.g., position in the flower and quantity), and the pollinator's traits (including size, shape, and visitation behavior) together determine the amount of pollen placed, its position on the pollinator's body, and the total area it covers (Armbruster et al. 2009, Huang & Shi 2013, Muchhala 2007). Two co-flowering plant species that place pollen in the same region of a pollinator's body will be at risk of losing pollen every time the vector misplaces it onto the reproductive organs of its competitor (Muchhala & Potts 2007, Muchhala & Thomson 2012, Natalis & Wesselingh 2012a). For a more thorough discussion of intra- and interspecific competition for pollen placement on pollinator bodies, we refer readers to the excellent review by Minnaar et al. (2019).

Even when pollen is deposited on and picked up from different portions of a pollinator's body, it may still be lost during visits to competitor flowers (Flanagan et al. 2009, Muchhala & Thomson 2012). For example, Murcia & Feinsinger (1996) found no effect of floral morphological similarity (which corresponds with overlapping pollen placement) on pollen losses by foraging hummingbirds alternating between competitor flowers but still found that visits to competitors decreased the pollen transferred to conspecific stigmas by as much as 76%. Most of this pollen loss appeared to be from the corollas of competitor flowers scraping pollen off of the birds' bills (Murcia & Feinsinger 1996). Another study showed that increased grooming frequency by bumblebee pollinators during visits to the invasive competitor *Lythrum salicaria* (Lythraceae) was the main contributor to pollen misplacement in *Mimulus ringens* (Phrymaceae) (Flanagan et al. 2009). Very little pollen was transferred to heterospecific stigmas, but pollen misplacement due to grooming while visiting competitor flowers was sufficient to limit seed set of *M. ringens*, showing that male fitness costs can carry over and depress female fitness of a population as well (Flanagan et al. 2009). Finally, Muchhala & Thomson (2012) found that, although competitor species with similar sites of pollen placement on bats' bodies suffered the greatest pollen losses, all pairs of species suffered significant amounts of pollen misplacement relative to the amount of pollen transferred without intervening visits to a competitor, demonstrating the importance of losses from pollinators' bodies due to passive detachment or active grooming (**Figure 1**). Regardless of how exactly pollen is misplaced, studies such as those mentioned above and others in natural and experimental populations show that pollen misplacement can often entail larger overall fitness losses than those incurred through heterospecific pollen deposition (Campbell & Motten 1985, Muchhala & Thomson 2012, Thomson et al. 2018). Despite its high contribution to overall fitness, pollen misplacement has been much less explored than heterospecific pollen deposition, likely due to the difficulties associated with accurately tracking pollen grains' fate and/or distinguishing between pollen from closely related species (Minnaar et al. 2019, Morales & Traveset 2008). Fortunately, in the last decade, powerful methods of pollen tracking and identification have emerged, such as individual grain genotyping (e.g., Hasegawa et al. 2015) and biolabeling (Minnaar & Anderson 2019), which should greatly facilitate the study of male fitness, competition for pollination, and floral evolution (Minnaar et al. 2019).

We know very little about the magnitude and prevalence of pollen misplacement in nature, but recent evidence shows that it can be as common as heterospecific pollen deposition. One detailed study on the structure of a pollen transfer network of 57 species from an alpine community in China revealed that plant species exported pollen to stigmas of 5.5 [±5.4 standard deviation (SD)] other species on average and received pollen in their stigmas from 7.2 (±5.0 SD) other species (Fang & Huang 2013). Interestingly, the number of recipient species per donor species was positively correlated with the total number of pollen grains exported, as were the number of donor species per recipient species and the total number of heterospecific pollen grains received in stigmas (Fang & Huang 2013). In other words, most species suffered extensive pollen misplacement, experienced high rates of heterospecific pollen deposition from a diversity of sources, or had a minor participation in the network overall. These results and those from other IPT network studies typically show that separate subsets of species regularly experience high rates of pollen misplacement or of heterospecific pollen deposition (Arceo-Gómez et al. 2016a, Fang & Huang 2013, Johnson & Ashman 2019, Tur et al. 2016). However, because they use only stigmatic loads to build IPT networks, these studies underestimate the magnitude of pollen misplacement, as they do not account for passive or active pollen detachment during the intervening visits (e.g., Murcia & Feinsinger 1996). Overall, the imbalance in the amount of research on pollen misplacement versus heterospecific pollen deposition has precluded a more complete understanding of the importance of IPT interactions in nature.



(Caption appears on following page)

Figure 1 (*Figure appears on preceding page*)

Example of interspecific pollen transfer interactions among three sympatric bat-pollinated flowers that exhibit distinct but overlapping pollen placement patterns on their shared bat pollinators (e.g., *Anoura geoffroyi*, Phyllostomidae). Panel *a* shows the pollen placement location for each species indicated by dashed lines and colors: *Centropogon nigricans* (Campanulaceae) (*green*), *Aphelandra acanthus* (Acanthaceae) (*yellow*), and *Burmeistera sodiroana* (Campanulaceae) (*red*). Panel *b* shows the number of pollen grains (± standard error) from focal species *A. acanthus* that were transferred by bats to conspecific stigmas following four treatments: without any intervening visit and after an intervening visit to either a plastic straw (control), a female *B. sodiroana* flower, or a male *B. sodiroana* flower bearing pollen. Panel *c* shows the results of the experiments in which the competitor was *C. nigricans*. Together, both sets of experiments show that greater overlap in pollen placement promotes higher rates of pollen misplacement during alternating visits, therefore diminishing male fitness as a result of competition. In addition, intervening visits to male flowers caused the bats to deposit large amounts of foreign pollen in *A. acanthus* stigmas (95.4 grains from *B. sodiroana* and 115.7 grains from *C. nigricans*, on average) (Muchhala & Thomson 2012). Such heterospecific pollen deposition would further impact fitness through the female floral function. Figure adapted with permission from Muchhala & Thomson (2012).

2.2. Heterospecific Pollen Deposition

In contrast to the male function, the fitness costs for female function in the form of heterospecific pollen deposition are much better understood. As with pollen misplacement, the extent to which a species may experience heterospecific pollen deposition depends on spatial and temporal flowering overlap with competitors, the degree of pollinator sharing (simultaneously determined by plant and pollinator traits influencing attraction and pollen deposition/pickup from the pollinator bodies), relative floral abundances, pollinator preference, and visitation behavior (Arceo-Gómez & Ashman 2014, Mitchell et al. 2009, Morales & Traveset 2008, Thomson et al. 2018). In combination, all of these factors determine the quantity and diversity of foreign pollen a flower receives. Below, we review the cascade of negative effects foreign pollen may have on female fitness and then review our understanding of how the quantity and diversity of these foreign pollen loads modulate these negative effects.

Following the arrival of foreign pollen on a stigma, the first potential negative effects occur on the stigmatic surface. Foreign grains may interact with conspecific grains or with the stigma itself, interfering with conspecific pollen adhesion and germination (Ashman & Arceo-Gómez 2013, Brown & Mitchell 2001). Studies that applied foreign pollen either before, after, or at the same time as conspecific pollen demonstrate the importance of timing: Although several studies found that seed set was decreased only when the foreign pollen was applied beforehand (Caruso & Alfaro 2000, Kohn & Waser 1985, Waser & Fugate 1986), one study found that applying foreign pollen before or after had no effect and seed set was decreased only when foreign and conspecific pollen were applied together (Bruckman & Campbell 2016). The mechanisms by which foreign pollen affects conspecific pollen adhesion and germination can vary and may include stigma clogging (Galen & Gregory 1989), foreign pollen allelopathy (Murphy & Aarssen 1995, Thomson et al. 1982), induction of the mechanical closure of the stigma (Waser & Fugate 1986), or the triggering of incompatibility reactions in the stigma surface that also impact conspecific grains (reviewed in Ashman & Arceo-Gómez 2013).

A second set of negative effects can occur if the foreign pollen germinates and forms pollen tubes. This is more likely among closely related species, as they may have similar pollen–pistil compatibility. The foreign pollen tubes may reduce seed set through stylar clogging as they physically crowd the stylar tissue. This idea makes intuitive sense and is supported by the fact that several hand-crossing studies using a single self-incompatible (SI) species have shown that mixing incompatible pollen (i.e., self pollen) with compatible pollen reduces seed set via stylar clogging (Palmer et al. 1989, Scribailo & Barrett 1994, Shore & Barrett 1984). However, we are not aware of a study clearly showing stylar clogging in crosses between pairs of species. The strongest evidence for such an effect comes from crosses between the congeners *Impatiens capensis* and *I. pallida* (Randall & Hilu 1990). This study found that seed set was reduced only when *I. capensis* was the recipient and that *I. pallida* pollen tubes can reach the ovaries in *I. capensis* styles, whereas *I. capensis* pollen fails to adhere to *I. pallida* stigmas (Randall & Hilu 1990). This finding would seem to implicate stylar clogging but does not rule out the possibility that negative effects may be due solely to interactions on the stigmatic surface.

Finally, assuming it successfully germinates on the stigma and forms a pollen tube capable of reaching the ovules, foreign pollen from closely related species may release sperm and fertilize ovules, causing the recipient plant to waste precious maternal resources (Jakobsson et al. 2008). Such usurped ovules are no longer available for conspecific fertilization, a fitness cost termed interspecific seed discounting (Burgess et al. 2008) that may lead to seed or whole fruit abortion (Fishman & Wyatt 1999, Montgomery et al. 2010, Wang & Cruzan 1998, Wolf et al. 2001), seed germination failure (Natalis & Wesselingh 2012b), or the production of unfit or sterile offspring (Goodwillie & Ness 2013).

Now that we have outlined the various negative effects heterospecific pollen can have on female fitness, we consider how quantity and diversity of heterospecific pollen loads can modulate these effects. In terms of quantity, heterospecific pollen has been found to account for up to 74% of total pollen receipt in nature (Arceo-Gómez et al. 2016a, Ashman & Arceo-Gómez 2013). How does increasing heterospecific pollen quantity affect the fitness costs? Unfortunately, few studies directly address this question. Most examine heterospecific pollen deposition by applying a 50:50 ratio of conspecific to heterospecific pollen to stigmas (Ashman & Arceo-Gómez 2013). In one study that varied this ratio, no amount of heterospecific pollen from invasive nightshade *Solanum elaeagnifolium* (Solanaceae) decreased seed production (50–70 seeds per fruit, on average) in the poppy relative *Glaucium flavum* (Papaveraceae) as long as some conspecific pollen was present (Tscheulin et al. 2009). In four other cases involving pairs of closely related hybridizing species, the relative proportion of heterospecific pollen was inversely correlated with seed production, although the strength of this relationship varied across the different recipient species (Harder et al. 1993, Montgomery et al. 2010, Ramsey et al. 2003, Wang & Cruzan 1998). In an additional study, the proportion of heterospecific pollen did not affect total seed set but predicted the proportion of hybrid seeds produced (Alarcon & Campbell 2000). Finally, we are aware of only one study to examine effects of variable amounts of heterospecific pollen on seed set in natural settings (rather than experimental hand-pollinations): For the herb *Delphinium barbeyi*, receipt of greater amounts of heterospecific pollen dampened the positive interaction between conspecific pollen receipt and seed set (Briggs et al. 2015). Thus, overall, the evidence to date tends to support the conclusion that greater amounts of heterospecific pollen lead to lower conspecific seed set.

Similar to the above question about the effects of quantity, how does diversity of heterospecific pollen loads affect the fitness costs? We know of only one study that directly addressed this question. For the monkey flower *Mimulus guttatus* (Phrymaceae), seed set decreased with increasing number of foreign pollen donor species, although the effect size of this pattern varied depending on donor identity (Arceo-Gómez & Ashman 2011). Pollen from one species, the sunflower *Helianthus exilis* (Asteraceae), was capable of reducing *M. guttatus* seed set by the same magnitude as its congener *Mimulus nudatus* and also equaled the combined effect from a mixture of *M. nudatus* and the mint relative *Stachys albens* (Lamiaceae) (Arceo-Gómez & Ashman 2011). The authors hypothesized that the strong negative effect *H. exilis* had on *M. guttatus* seed set was due to a combination of the large size and spiny surface of its pollen grains, its ability to germinate in *M. guttatus* stigmas, and possibly additional allelopathic effects decreasing conspecific pollen germination. *M. nudatus*, however, reduced seed production at a later stage by usurping ovules and promoting seed abortion. The negative effects of *S. albens* on *M. guttatus* seed set were weak unless in combination with pollen from the other two competitors (Arceo-Gómez & Ashman 2011). Although this remains the only study of its kind that we are aware of, it suggests that female fitness responses to diverse heterospecific pollen loads may be highly species- and context-specific. Given the extreme variability in the amount of foreign pollen receipt found within and among plant communities (Arceo-Gómez et al. 2016a, Fang & Huang 2013, Johnson & Ashman 2019, McLernon et al. 1996, Tur et al. 2016), the fitness consequences to diverse heterospecific pollen deposition represent an exciting avenue for future research.

3. EVOLUTIONARY RESPONSES TO INTERSPECIFIC POLLEN TRANSFER

Angiosperms have evolved a wide range of strategies to reduce the impact of IPT on fitness, which can be categorized into three main types. The first involves adaptations to prevent IPT from occurring in the first place (prepollination isolation), which can reduce both pollen misplacement and heterospecific pollen deposition, thus improving male and female fitness (Armbruster et al. 1994, Kay et al. 2019, Muchhala et al. 2014). The second involves adaptations to counteract foreign pollen germination and performance after heterospecific pollen arrives on stigmas (gametic isolation), which limits negative effects on female fitness (Arceo-Gómez et al. 2016b, Kay & Schemske 2008, Natalis & Wesselingh 2012b). A third type of evolutionary response to IPT involves an increase in autonomous self-pollination rates, which allows conspecific (selfed) seed set even when foreign pollen is deposited (Briscoe Runquist & Moeller 2014, Randle et al. 2018, Smith & Rausher 2008).

Before discussing these three responses to IPT, we would first like to clarify pertinent terminology. By prepollination isolation, here we mean any reproductive barriers that act to reduce IPT and thus arrival of foreign pollen to stigmas. Gametic isolation refers to barriers that occur as the gametes interact, from the point at which heterospecific pollen arrives at the stigmas until ovule fertilization occurs (Coyne & Orr 2004). Both are forms of prezygotic isolation, whereas any barriers that serve to reduce gene flow after ovules are fertilized are here referred to as postzygotic isolation. It is important to note that we still consider prepollination and gametic barriers as forms of reproductive isolation, regardless of whether gene flow can actually occur between a pair of species, because they still serve to limit reproductive interference. Any evolutionary increases in prepollination barrier strength in response to pollen transfer between species in sympatry is termed reproductive character displacement, whether or not the species are already fully reproductively isolated through postpollination barriers, whereas a special form of reproductive character displacement termed reinforcement occurs when natural selection favors increased prezygotic isolation in the face of ongoing gene flow (Beans 2014, Hopkins 2013, Kay & Schemske 2008). In the following three subsections, we explore how plants may respond to competition through IPT, with or without accompanying gene flow, through evolutionary increases in prepollination isolation, gametic isolation, or selfing rates.

3.1. Prepollination Isolation

When IPT occurs, selection may favor divergence in several aspects of floral phenotype to increase prepollination isolation, thus reducing the fitness costs arising from pollen misplacement and heterospecific pollen deposition. One response to IPT, termed temporal isolation, occurs when competing species diverge in phenology, flowering at different times of the day or of the year (Borchsenius et al. 2016, Hipperson et al. 2016, Martin & Willis 2007, Paudel et al. 2018, Waser 1978b, Yang et al. 2007, Zhang et al. 2016). In such instances, if flowering overlap is not completely eliminated, the later-flowering species might still experience low but detectable fitness costs when its first-flowering individuals are at a large numerical disadvantage versus earlier-flowering competitors (e.g., Waser 1978b). Similarly, among hybridizing species, the later-flowering species might suffer asymmetric hybridization from its earlier-flowering relative (Martin & Willis 2007, Zhang et al. 2016). To date, no studies have found support for either reproductive character displacement or reinforcement of temporal isolation when comparing sympatric and allopatric populations (Christie & Strauss 2018, Kay 2006, Paudel et al. 2018), but it is possible that flowering time differences evolve as an initial step following secondary contact, yet quickly relax after other barriers to IPT evolve (Christie & Strauss 2018).

A second response to IPT, termed floral isolation, involves diverging in the use of pollinators to reduce the amount of pollen they transfer between species. Floral isolation can be divided into two subcomponents: ethological isolation, which involves differences in floral traits affecting pollinator preference and thus reducing interspecific pollinator movements, and mechanical isolation, which involves differences in traits that influence the mechanical fit between flower and pollinator during visits (Grant 1994, Schiestl & Schlüter 2009). For the former, the most direct way to achieve ethological isolation is for competing species to specialize on different pollinator types by diverging in traits influencing attraction (e.g., color, scent) or access to rewards (e.g., morphology), thus reducing interspecific pollinator movements (Muchhala et al. 2010, Rodríguez-Gironés & Santamaría 2007). A less obvious way to achieve ethological isolation involves increasing floral constancy, or the degree to which individual pollinators remain constant to one single flower type during foraging bouts instead of switching between types (Amaya-Márquez 2009, Waser 1986). This can lead to, for example, a bumblebee being classified as generalized on a species or colony level despite individuals being highly specialized to different species of flowering plant and thus not contributing to competition via IPT (Oyama et al. 2010). There are three proposed mechanisms by which shifts in floral traits could improve constancy. First, if accessing nectar rewards is complicated, this may encourage constancy to one flower type due to constraints on the ability to learn and remember how to manipulate multiple types (Chittka et al. 1999, Gegear & Laverty 2005, Laverty 1994). Second, differences in floral traits could reinforce search images used to locate flowers during foraging (Goulson 2000, Heinrich 1975, Wilson & Stine 1996). For instance, bat-pollinated *Burmeistera* flowers present extreme interspecific variation in the size, shape, and orientation of the leaf-like calyx lobes at the base of their flowers (Muchhala 2006), which likely reflect echolocation calls very differently; when multiple species co-occur, this may encourage individual bats to learn and remain constant to a single species. A third mechanism to encourage floral constancy involves differences that encourage and reinforce social hierarchies among pollinators that aggressively defend resources, which may cause dominant individuals to visit different subsets of flowers than those visited by subordinate individuals (Muchhala et al. 2014). Experiments with hummingbirds and artificial flowers in flight cages support this idea. When provided with two flower types with either high- or low-nectar rewards, dominant male and subordinate female *Eulampis jugularis* visited both types indiscriminately, but when the same types had different colors, the sexes partitioned the resource, with males sticking with the high-reward flowers and vice versa (Temeles et al. 2017). Although more work is needed to understand the extent to which these three mechanisms contribute to floral constancy, all three lead to similar patterns, in that they all favor diverging from sympatric competitors in floral traits (e.g., De Jager et al. 2011, Takahashi et al. 2016, Weber et al. 2018).

Mechanical isolation, the other subcomponent of floral isolation, can be achieved through changes in the length, shape, or orientation of the floral reproductive parts or of other aspects of floral morphology that affect the pollinator positioning and mechanical fit during visits, causing divergence in pollen placement (Armbruster et al. 1994, Huang & Shi 2013, Huang et al. 2015, Kay et al. 2019, Muchhala & Potts 2007). In fact, many studies on IPT and floral evolution have shown that small trait adjustments can have large impacts on pollinator efficiency in terms of pollen transport and delivery (Castellanos et al. 2003, More et al. 2007, Muchhala 2007). However, it is important to note that even a total shift in pollen placement on shared pollinators may fail to eliminate male fitness costs from pollen misplacement. As long as pollinators move between species, pollen may still be lost to grooming or may be scraped off of the pollinator's body during intervening visits to competitors (Flanagan et al. 2009, Muchhala & Thomson 2012); thus, ethological isolation is more effective at preventing pollen misplacement. On the other hand, mechanical isolation can effectively eliminate costs to female fitness from heterospecific pollen deposition.

3.2. Gametic Isolation

The costs to female fitness from IPT can be reduced by various forms of gametic isolation, including stigma incompatibility and suppression of pollen tube growth rate (Ashman & Arceo-Gómez 2013). Stigmas can evolve to increase incompatibility with foreign pollen by altering stigma structure (Arceo-Gómez & Ashman 2011, Caruso & Alfaro 2000), the chemical composition of stigma exudates (Kay & Schemske 2008), or the factors controlling pollen recognition and self-incompatibility (Bedinger et al. 2017). These three mechanisms need not be mutually exclusive, and they usually suffice to prevent germination of pollen among distantly related species (but see Arceo-Gómez & Ashman 2011). Although few studies have determined the precise isolating mechanisms operating at the stigma surface (Bedinger et al. 2017), the importance of the self-incompatibility pathway can be seen in instances of asymmetric rejection of pollen from self-compatible (SC) species on stigmas of SI relatives (Ashman & Arceo-Gómez 2013, Brandvain & Haig 2005; see Section 3.3).

Differential pollen tube performance in the style constitutes the other main form of gametic isolation that can evolve in response to IPT interactions, and it typically acts only among close relatives, given that pollen from more distantly related species typically fails to germinate in each other's stigmas. Interestingly, for crosses between a given pair of species, the relative ability of one species to germinate, form pollen tubes, and fertilize ovules of the other is typically significantly asymmetric (Tiffin et al. 2001). Two main mechanisms have been proposed to explain such asymmetry. The first, termed conspecific pollen precedence (Howard 1999), results from incompatibility reactions elicited by foreign pollen such that conspecific pollen performs better in terms of germination, pollen tube growth rates, access to the ovary, and ovule fertilization relative to heterospecific pollen (Lyu et al. 2016, Montgomery et al. 2010). Because the various ways in which heterospecific pollen is suppressed can differ between pairs of closely related species, asymmetry often occurs across pairs in pollen tube performance and/or hybridization (Figueroa-Castro & Holtsford 2009, Fishman et al. 2008, Harder et al. 1993, Lyu et al. 2016, Montgomery et al. 2010; but see Alarcon & Campbell 2000, Natalis & Wesselingh 2012b). The second main mechanism for gametic isolation involves a mismatch between host style length and foreign pollen grain size. Because grain size often determines the maximum pollen tube length it can attain (Brothers & Delph 2017, Carney et al. 1996), smaller-grained pollen from short-styled species often cannot effect fertilization in long-styled species, whereas the opposite can occur unimpeded (Carney et al. 1996, Diaz & Macnair 1999, Kay 2006, Wolf et al. 2001).

3.3. Evolution of Mating Systems

In SC plant populations, the mating system of a particular population is defined as the relative proportion of seeds sired by self pollen versus those sired by outcross pollen from other conspecific individuals (Barrett & Harder 2017). Flexibility in a plant's mating system allows outcrossing when outcross pollen is not a limiting factor while providing reproductive assurance through self-pollination when outcross pollen is not readily available (Cheptou 2019, Karron et al. 2012). Shifts in mating systems to higher selfing rates are typically thought to represent a response to low or unpredictable pollination services (Cheptou 2019), but many studies have shown that they can also occur if IPT diminishes the availability of outcross pollen (Bell et al. 2005, Fishman & Wyatt 1999, Randle et al. 2018, Smith & Rausher 2008). IPT can favor selfing regardless of whether the competing species are closely related or not; for example, one study found that extensive pollen misplacement by foraging bumblebees resulted in much greater probabilities for stigmas to receive self pollen rather than outcross pollen in *Mimulus ringens* plants growing in experimental arrays with the distantly related competitor *Lobelia siphilitica* (Bell et al. 2005).

In many cases, selfing may occur toward the end of the flower's life span as a last resort if little or no outcross pollen was received (Lloyd 1992). However, this does not prevent heterospecific pollen deposition or pollen misplacement from diminishing outcrossing rates; thus, selection for delayed selfing should not occur if IPT is the main factor influencing the mating system (Goodwillie & Ness 2013, Randle et al. 2018). Preemptive selfing, conversely, takes place before the floral bud opens (Lloyd 1992, Sicard & Lenhard 2011), thus securing pollination before any IPT can occur (Randle et al. 2018). Such extreme transitions to a predominantly or fully selfing mating system are also commonly accompanied by a suite of characters termed the selfing syndrome, including smaller flowers, highly reduced anther–stigma separation distance (herkogamy), lower pollen-to-ovule ratio, diminished pollen production, and limited secretion of nectar and scent (Sicard & Lenhard 2011). Divergence in these floral traits among closely related species is well documented in several angiosperm taxa (Briscoe Runquist & Moeller 2014, Grossenbacher & Whittall 2011, Kalisz et al. 2012, Vallejo-Marín et al. 2014). In one clear example of selfing in response to IPT, Fishman & Wyatt (1999) found that *Arenaria uniflora* populations exhibited preemptive selfing, smaller flowers, and reduced herkogamy in regions of sympatry with its congener *A. glabra*, and that outcrossing *A. uniflora* individuals placed in arrays with *A. glabra* faced significant decreases in conspecific seed set. A similar study with three *Centaurium* species that exhibit a range of mating systems demonstrated that the earlier that selfing occurs in a flower's life span, the more effective it is in reducing costs of IPT from congeners (Brys et al. 2016). For two of these species that overlap greatly in their native and invaded habitats in mainland Europe and the United Kingdom (*C. erythraea* and *C. littorale*), a separate study found that herkogamy rates decreased and selfing increased, depending on which species first colonized the site, suggesting that the reproductive assurance value of selfing is higher for late-arriving species as it simultaneously counters any abundance disadvantage and prevents the production of unfit hybrid progeny (Schouppe et al. 2017).

The outcome of IPT interactions between selfers and outcrossers also depends greatly on the differences in their pollen competitive ability in each other's pistils, and these differences almost invariably favor the outcrosser (Brandvain & Haig 2005). Pollen from outcrossing species is well adapted to compete in a wide range of pistil environments, whereas pollen from selfers typically fails in outcrossers' flowers. Similarly, stigmas and styles from SI outcrossing species present much stronger barriers to pollen from SC species than vice versa (collectively termed the SI × SC rule) (Brandvain & Haig 2005, Goodwillie & Ness 2013, Harder et al. 1993). Thus, species that begin to shift toward selfing due to IPT competition with more outcrossing relatives may face a snowballing selective pressure for such selfing, as their pollen loses its competitive ability.

Wide interpopulation variation in mating systems was found to be common across angiosperms in an extensive survey covering 741 populations of 105 species from 80 genera and 44 plant families

(Whitehead et al. 2018). This variation could be due to differences across a species' distribution in pollinator environments, IPT interactions with co-flowering plants, or both (Karron et al. 2012). We know of only two cases in which researchers attempted to disentangle the importance of these factors. The first involves two recently diverged subspecies of *Clarkia xantiana* (Onagraceae): the outcrosser subsp. *xantiana* and the selfer subsp. *parviflora*. Briscoe Runquist & Moeller (2014) found that (*a*) pollen limitation was higher and selfing more advantageous in regions where these subspecies co-occurred, (*b*) the selfer's herkogamy and flower size were significantly reduced in these regions of sympatry, and (*c*) contrasting pollinator environments did not explain the differences detected between allopatric and sympatric sites (Briscoe Runquist & Moeller 2014). A follow-up study further established that, despite pollen transfer being reduced due to low flowering overlap and a stronger pollinator preference for the outcrosser, gametic isolation barriers were weaker for the selfer, making it prone to greater costs from maladaptive hybridization with its congener as predicted by the SI × SC rule (Briscoe Runquist et al. 2014). A second striking example found high flowering overlap and pollinator sharing between the sister species *Collinsia linearis* and *C. rattanii* in zones of sympatry but also found that interspecific movements by pollinators caused highly asymmetric pollen flow from *C. linearis* to *C. rattanii* (Randle et al. 2018). In line with this observation, *C. rattanii* (and not *C. linearis*) displayed significantly earlier preemptive selfing in sympatry (Randle et al. 2018). Although variation in mating systems does not always correlate with co-occurrence patterns among close relatives (Grossenbacher et al. 2016, Matallana et al. 2010, but see Whitton et al. 2017), substantial evidence suggests that increased selfing rates in sympatry can facilitate coexistence and may be a common evolutionary response to IPT-driven pollen limitation.

4. POLLEN TRANSFER DYNAMICS AND GENE FLOW DURING EARLY DIVERSIFICATION

Although IPT typically causes fitness reductions and selection for floral divergence, its impacts can vary among more closely related species if it leads to interspecific gene flow. Among interfertile plant species, IPT is in fact the means by which genes are exchanged. We believe that the classical competition-based view of IPT prevalent in the pollination literature has limited the understanding of its evolutionary importance in angiosperm diversification in terms of speciation and introgression. Hybridization as a consequence of IPT was recognized by Morales & Traveset (2008) but only in the context of gene flow between alien and native species and between genetically modified crops and their wild relatives. However, rapid advances in our ability to detect and quantify interspecific gene flow using modern genomic and statistical tools (Ellstrand 2014, Payseur & Rieseberg 2016) have revealed widespread evidence of hybridization across many levels of the Tree of Life. Speciation and reproductive isolation are now known to commonly occur despite ongoing gene flow (Abbott et al. 2013, Baack et al. 2015), and modern phylogenetic thinking has shifted to embrace reticulation (Mallet et al. 2016). Furthermore, evidence suggests that gene flow has contributed significantly to the evolution of many plant clades through adaptive introgression (Ellstrand 2014, Schmickl et al. 2017). Finally, our rapidly changing world is bringing about increasing opportunities for gene exchange via IPT due to range shifts among formerly allopatric plant species (Vallejo-Marín & Hiscock 2016), making it particularly urgent that we study and understand the effects of IPT on patterns of gene movement between species.

Along the continuum of evolutionary divergence, populations, lineages, and species become gradually differentiated (De Queiroz 2011), and the effects of IPT and resulting gene flow also change with increasing differentiation. Pollen transfer will closely approximate gene flow in early stages of divergence, but they progressively decouple during intermediate and late stages as reproductive isolation increases, until eventually heterospecific pollen fails to produce any hybrid progeny. Below, we discuss impacts of IPT in three main stages of the divergence continuum.

4.1. Early Divergence: Homogenizing Gene Flow and Gene Flow–Selection Balance

With little evolutionary divergence and a lack of isolating barriers, IPT should lead to homogenizing gene flow: Pollen is transferred and fertilizes ovules, and genes are thus exchanged. The expectation is that the populations will fuse together or form a stable hybrid zone in the point of contact (Abbott et al. 2013, Payseur & Rieseberg 2016). Differences in abiotic and biotic environmental conditions outside of the point of contact may favor the formation of a stable hybrid zone due to a balance between selection and gene flow, depending on the rate of IPT and the fitness of hybrids relative to parental populations (Arnold et al. 2008, Campbell et al. 1998). Absence of such selection outside of the point of contact would make fusion of the two gene pools more likely (Buerkle et al. 2003).

What role do pollinators play in preventing or promoting such fusion of gene pools? Manipulative studies across multiple populations are needed to understand if local adaptation to pollinator availability and/or IPT dynamics can generate the initial levels of floral and genetic divergence needed to restrict gene flow to some extent. For example, how do fitness costs associated with pollen transfer between populations initially arise and drive incipient reproductive isolation? Do local pollen transfer dynamics and the competitive environment promote local adaptation of pollen–pistil compatibilities that restrict gene flow between populations? Does specialization to different pollinator environments across a plant's range (ecotypes) (e.g., Anderson et al. 2010, Newman et al. 2015) result in floral isolation between subpopulations? These questions have only recently begun to be explored by a handful of studies, for example, in North American *Clarkia* with generalized pollination (Briscoe Runquist & Moeller 2014, Briscoe Runquist et al. 2014, Kay et al. 2019, Miller et al. 2014), in bee-pollinated *Mimulus* (Grossenbacher & Stanton 2014), in South African hawkmoth–pollinated *Gladiolus* (Anderson et al. 2010), and in long-proboscis fly–pollinated *Nerine* (Newman et al. 2015) and *Lapeirousia* (Anderson et al. 2016). Unfortunately, comparable multisite studies are lacking for other biogeographic regions, most notably from the species-rich tropics.

One of these relevant studies, by Kay et al. (2019), examined the role of pollinators in floral isolation between populations of the sister species *Clarkia concinna* (Onagraceae) and *C. breweri* via experimental sympatry (**Figure 2*a***). The authors' primary objective was to evaluate whether the shift to hawkmoth pollination by *C. breweri* conferred floral isolation from the pollinator generalist *C. concinna*. Common garden experiments revealed remarkable variation in IPT between *C. breweri* and four different ecotypes of *C. concinna* (**Figure 2*b***). Specifically, hawkmoths transferred very little pollen from any of the *C. concinna* ecotypes to *C. breweri*, nor from *C. breweri* to three of the *C. concinna* ecotypes, yet transferred strikingly large amounts from *C. breweri* to the coastal ecotype of *C. concinna* (Kay et al. 2019) (**Figure 2*b***). Thus, this coastal form of *C. concinna* would be very likely to suffer hawkmoth-mediated asymmetric pollen transfer from *C. breweri* (and possibly associated fitness costs) if they co-occurred together. Notably, another *C. concinna* ecotype (see South in **Figure 2*a***) parapatric with *C. breweri* shows all of the traits typical of the selfing syndrome described in Section 3.3, suggesting a shift to selfing might have been favored by IPT interactions with *C. breweri* (Kay et al. 2019).

What does this study tell us about early divergence and how initial reproductive isolation might arise? Results demonstrate that floral isolation remains incomplete between *C. breweri* and *C. concinna* in either direction, that potential IPT would be mostly asymmetric (*C. breweri* → *C.*

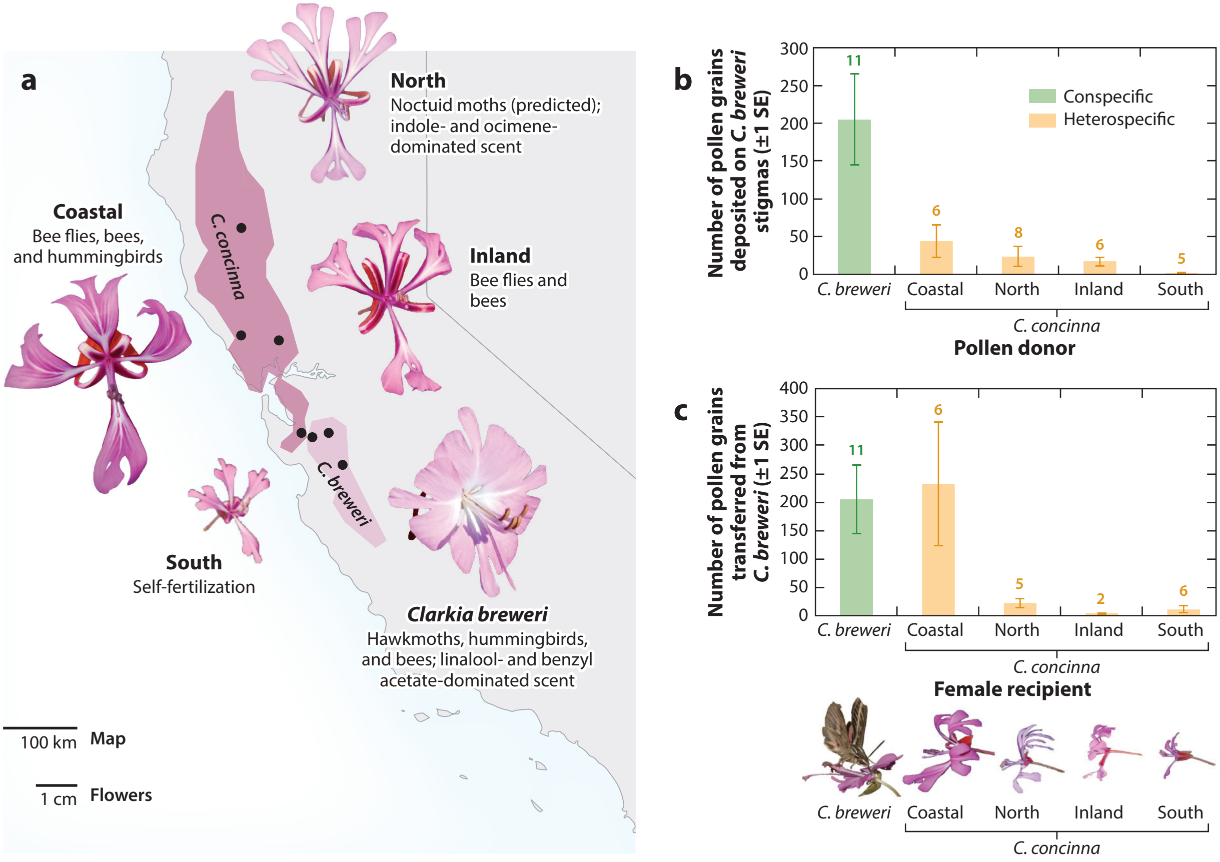


Figure 2

Pollen transfer interactions and floral isolation in experimental sympatry for two recently diverged *Clarkia* species (Onagraceae) from California. Panel *a* shows the geographic occurrence, floral morphology, and pollinators of focal *C. breweri* and four ecotypes of its close relative, *C. concinna*. Panels *b* and *c* show pollen deposition per stigma for different floral arrays with *C. breweri* as the female recipient or pollen donor, respectively, alongside the four floral ecotypes of *C. concinna*. Numbers above the bars represent the number of experimental arrays including each floral ecotype. Abbreviation: SE, standard error. Figure adapted with permission from Kay et al. (2019).

concinna), and that the various populations of *C. concinna* are not all equally isolated from their congener. This and similar studies (Grossenbacher & Stanton 2014, Newman et al. 2015) show that selection to local pollinator environments across a species' range might confer ecotypes with different degrees of susceptibility to IPT with close relatives and even with other intraspecific ecotypes. Over enough time, the selective effects of local pollinator environments and local competition via IPT could lead to floral divergence and associated reproductive isolation, which would then restrict gene flow among subpopulations and potentially lead to speciation.

One intriguing hypothesis is that even in the absence of differences in habitat, pollinators, or competitors across a species' geographic range, strong sexual selection alone may drive intraspecific divergence and thus ultimately promote speciation. Specifically, outcrossing species constantly face intraspecific competition between males when pollen from multiple males is deposited on stigmas, such that males with pollen that germinates and reaches ovules faster will enjoy higher levels of paternity. At the same time, females may benefit from leveling the playing field between competing males to maximize the diversity of sires among their offspring. Such sexual conflict can lead to local adaptation of compatibility between pollen and stigmas/styles, thus potentially promoting reproductive isolation among the various subpopulations within a species (Ortiz-Barrientos et al. 2009). Costly maladaptive hybridization with sympatric congeners might further select for such local adaptation between conspecific pollen and stigmas/styles, as a byproduct of increasing gametic isolation from these congeners. This mechanism of local adaptation to conspecific mating environment might similarly carry over a disruption of compatibility with individuals from other conspecific populations (Ortiz-Barrientos et al. 2009). Unfortunately, to our knowledge, this interplay between local conspecific mating environment and IPT among diverging species remains unexplored to date.

4.2. Intermediate Divergence: Reinforcement and Adaptive Introgression

At an intermediate stage of divergence, gene flow will be restricted to some extent but IPT dynamics among two species will still affect patterns of gene flow between them (Campbell et al. 1998, Natalis & Wesselingh 2012b, Surget-Groba & Kay 2013, Zhang et al. 2016). Even if gametic or postzygotic isolation serves to limit gene flow, or constrain it to small parts of the genome (Payseur & Rieseberg 2016), IPT will still influence whether gene flow occurs. Evolutionarily speaking, it is during this stage when IPT-driven gene flow might have the most profound impacts for plant evolution (Ellstrand 2014), leading to the merging of gene pools, the reinforcement of barriers separating them, and/or adaptive introgression between the species.

If hybrids formed by IPT exhibit particularly low fitness relative to parental species, reinforcing selection may favor strengthening of prezygotic barriers to gene flow (Hopkins 2013, Ortiz-Barrientos et al. 2009). This can include the same adaptations outlined in Section 3: temporal isolation via reduced flowering overlap (Martin & Willis 2007, Zhang et al. 2016), floral isolation via the attraction of different pollinators (Hopkins & Rausher 2012) or differential pollen placement (Kay & Schemske 2008), gametic isolation via increased pollen–pistil incompatibilities (Arceo-Gómez et al. 2016b), or transitions toward self-pollination (Rausher 2017, Schouppe et al. 2017). Such reinforcement of reproductive barriers will ultimately determine the evolutionary course of hybridization and the resulting pattern of gene exchange between the interacting species.

As mentioned previously, it is unlikely that these various isolating mechanisms evolve at the same rate between pairs of species; thus, we might often expect barriers and associated gene flow between pairs to be asymmetric. In fact, previous assessments of reproductive isolation among angiosperms have found asymmetry to be the norm (Lowry et al. 2008, Tiffin et al. 2001). A survey of 19 species pairs found that prezygotic barriers were on average twice as strong as postzygotic ones but that the latter were almost three times more asymmetric (Lowry et al. 2008). Among the prezygotic barriers evaluated, pollinator-mediated isolation (i.e., floral isolation) showed the greatest asymmetry: almost twice as high as the other prezygotic barriers and roughly half as high as the postzygotic ones (Lowry et al. 2008). Regrettably, no quantitative assessments of the extent to which asymmetry in barrier strength correlates with gene flow among diverging species have been made. As a preliminary assessment of this relationship, in **Table 1** we review 10 instances of congeneric species pairs for which the following is available from the literature: (*a*) clear evidence for IPT between the pair, via pollinator sharing, interspecific pollinator movements, and/or transfer of pollen or analogs; (*b*) sufficient data to quantify asymmetry in the strength of prepollination and gametic isolation (following Sobel & Chen 2014); and (*c*) additional data on gene flow between the pair. For 4 species pairs (*Helianthus*, *Iris fulva–Iris brevicaulis*, *Mimulus*, and *Phlox*) prepollination and gametic barriers were asymmetric in the same direction and correctly predicted the direction of introgression. For 3 others (*Ipomopsis*, *Iris fulva–Iris hexagona*, and *Silene*), only

Table 1 Asymmetries in pre- and postpollination isolation and gene flow among 10 diverging species pairs

Focal group (RI references)	Diverging taxa	Prepollination isolation[a]				Gametic isolation[e]				Introgression[g] (gene flow references)
		Barriers	RI[b]	Asymmetry[c]	IPT direction[d]	Barriers	RI[b]	Asymmetry[c]	Crossing direction[f]	
Clarkia xantiana subspecies (Briscoe Runquist et al. 2014)	*C. xantiana* subsp. *parviflora*	FO, PS, IMP	0.991	0.045	S, very low	PTG, PC, HSS	0.528	0.411	A (*Cxx* → *Cxp*)	A (*Cxp* → *Cxx*) (BC) (Pettengill & Moeller 2012)
	C. xantiana subsp. *xantiana*		0.946	−0.045			0.939	−0.411		
Costus (Kay 2006)	*C. pulverulentus*	PS, PT	1.000	0.820	U (*Cp* → *Cs*)	PG, PTG, HSS	0.954	0.298	A (*Cp* → *Cs*)	S (BC) (Surget-Groba & Kay 2013)
	C. scaber		0.180	−0.820			0.656	−0.298		
Helianthus petiolaris ecotypes (Ostevik et al. 2016)	Dune	PS	0.550	0.190	A (dune → non-dune)	PC	0.380	0.260	A (dune → non-dune)	A (dune → non-dune) (Andrew et al. 2012, 2013)
	Non-dune		0.360	−0.190			0.120	−0.260		
Ipomopsis (Aldridge & Campbell 2006, 2007; Campbell & Waser 2007)	*I. aggregata*	IMP	0.578	0.027	S	PC	0.322	0.574	A (*Ia* → *It*)	A (*Ia* → *It*) (Wu & Campbell 2005
	I. tenuituba		0.551	−0.027			−0.252	−0.574		
Iris (Arnold et al. 1993, Burke et al. 1998, Carney et al. 1996, Emms & Arnold 2000)	*I. brevicaulis*	IMP	−0.333	0.698	A (*If* → *Ib*)	PC	−0.395	0.928	A (*If* → *Ib*)	A (*If* → *Ib*) (Arnold et al. 2010)
	I. fulva		0.365	0.698			0.534	−0.928		
Iris (Arnold et al. 1993, Burke et al. 1998, Carney et al. 1996, Emms & Arnold 2000)	*I. fulva*	IMP	0.264	0.000	S	PC, HSS	1.000	0.560	A (*If* → *Ib*)	A (*If* → *Ib*) (Arnold et al. 2010)
	I. hexagona		0.264	0.000			0.440	−0.560		
Mimulus aurantiacus ecotypes (Sobel & Streisfeld 2014)	Red	IMP	0.873	0.226	A (red → yellow)	PC, HSS	0.087	0.150	A (red → yellow)	A (red → yellow) (Sobel & Streisfeld 2014)
	Yellow		0.647	−0.226			−0.063	−0.150		
Phlox (Hopkins & Rausher 2012, Ruane & Donohue 2008)	*P. cuspidata*	IMP	0.160	0.320	A (*Pc* → *Pd*)	PC, HSS	0.743	0.350	A (*Pc* → *Pd*)	A (*Pc* → *Pd*) (Roda et al. 2017)
	P. drummondii		−0.160	−0.320			0.393	−0.350		

(*Continued*)

Table 1 ***(Continued)***

Focal group (RI references)	Diverging taxa	Prepollination isolation[a]				Gametic isolation[e]				Introgression[g] (gene flow references)
		Barriers	RI[b]	Asymmetry[c]	IPT direction[d]	Barriers	RI[b]	Asymmetry[c]	Crossing direction[f]	
Rhinanthus (Natalis & Wesselingh 2012a, 2012b, 2013)	*R. angustifolius*	PS, IMP, PT	0.449	0.805	A (*Ra* → *Rm*), very high	PTG, PC, HSS	0.408	0.006	A (*Ra* → *Rm*)	A (*Rm* → *Ra*) (BC) (Ducarme et al. 2010, Vrancken et al. 2012)
	R. minor		−0.356	−0.805			0.402	−0.006		
Silene (Karrenberg et al. 2018)	*S. dioica*	FO, PT	0.584	0.066	S, high	PC, HSS	0.247	0.243	A (*Sl* → *Sd*)	S range-wide; A (*Sl* → *Sd*) cpDNA in HZ (Minder et al. 2007, Muir et al. 2012)
	S. latifolia		0.650	−0.066			0.490	−0.243		

Abbreviations: A, asymmetric; BC, backcrossing; cpDNA, chloroplast DNA; FO, flowering overlap; HSS, hybrid seed set; HZ, hybrid zone; IMP, interspecies movements by pollinators; IPT, interspecific pollen transfer; PC, pollen competition; PG, pollen germination; PS, pollinator sharing; PT, direct counts of pollen transferred (or pollen analog, e.g., fluorescent dye); PTG, pollen tube growth; RI, reproductive isolation; S, bidirectional symmetric; U, unidirectional.

[a] Here, prepollination barriers that reduce IPT are defined by estimates from sympatric populations or by using experimental arrays in sympatry.

[b] Cumulative isolation for that reproductive stage estimated following Sobel & Chen (2014). An RI value of 1 equals a gene flow probability of zero (full assortative mating), whereas an RI value of −1 specifies a gene flow probability of 1 (complete disassortative mating), and an RI value of 0 indicates a gene probability of 0.5 (random mating). Raw data, calculations, and references provided in **Supplemental Table 1**.

[c] Estimated as the absolute value of the difference in isolation for that stage as in Lowry et al. (2008).

[d] Expected prevailing direction of IPT based on the asymmetry of prepollination barriers (*arrows*).

[e] Includes only barriers to fertilization and siring success (postpollination prezygotic). Postzygotic barriers were also estimated in most cases when relevant data were available but not included here (see **Supplemental Table 1**).

[f] Expected prevailing crossability direction based on the asymmetry of postpollination barriers (*arrows*).

[g] Estimated direction of interspecies gene flow found during follow-up studies in the same locations or populations and by the same research group. Direction is shown with the same notation as in footnotes *d* and *f*.

Supplemental Material >

gametic isolation was asymmetric and again correctly predicted the direction of introgression. In 1 pair (*Costus pulverulentus* and *C. scaber*), prepollination and gametic barriers were asymmetric in the same direction, but inferred gene flow was symmetric. This mismatch may be due to fertile F_1 hybrids crossing equally well with either parental species, nullifying the asymmetry found in pure parental crosses (Surget-Groba & Kay 2013). In the final 2 pairs (*Clarkia* and *Rhinanthus*), gene flow actually followed a pattern opposite to the isolating barriers. Evidence suggests a similar explanation for this mismatch in the case of *Rhinanthus*, in that backcrossing via fertile hybrids is asymmetrical in the opposite direction (Natalis & Wesselingh 2012b). Thus, despite some exceptions due to backcrossing, overall the direction of asymmetry in prepollination isolation (which equals asymmetry in IPT) and in gametic isolation between pairs of species seems to predict the direction of gene flow, with gametic barriers typically more closely related to gene flow patterns.

In this stage of intermediate divergence between species, IPT-mediated gene flow can also play a profound role in plant evolution by increasing genetic variation and/or by allowing exchange of adaptive traits across species boundaries (Abbott et al. 2013, Schmickl et al. 2017). Such adaptive introgression has been shown for traits related to drought tolerance (Campbell & Waser 2007, Whitney et al. 2010) and floral color (Stankowski & Streisfeld 2015). In some extreme cases, repeated hybridization and backcrossing can lead to the formation of new species reproductively isolated from its parental relatives (Clay et al. 2012, Renaut et al. 2014, Vallejo-Marín et al. 2016).

Despite the large amount of research devoted to the evolution of reproductive isolation and how it restricts gene flow during divergence, many questions remain unanswered. For example, the relationship between IPT and gene flow is expected to be positive during early divergence as more pollen flow leads to more genes exchanged, but how does the relationship change as different isolation processes are reinforced at the pre- and postpollination stages? Do more highly asymmetric IPT dynamics influence how fast isolating barriers arise? And does the degree of asymmetry in IPT between a pair of species tend to decrease over time, as the species facing greater IPT evolves stronger prepollination barriers? Finally, the relative contribution of postpollination (i.e., gametic and postzygotic isolation) versus prepollination barriers to total reproductive isolation is expected to increase with increasing evolutionary divergence (Christie & Strauss 2018, Kostyun & Moyle 2017); how do IPT dynamics and resulting gene flow change across these stages of speciation? We argue that the relationship between IPT and gene flow during speciation represents an exciting and underexplored topic in need of further research.

4.3. Late Divergence: Reproductive Character Displacement

Finally, the third stage represents IPT between pairs of species that are already completely reproductively isolated via gametic and/or postzygotic barriers. In these cases, competition through IPT will still negatively impact floral fitness via reproductive interference by wasting gametes and resources for the plants and decreasing seed set (Morales & Traveset 2008). These costs will select for reproductive character displacement that shifts barriers to earlier-acting stages of reproductive isolation. In other words, if only postzygotic barriers are present, gametic isolation will be favored (to prevent styles from being clogged and ovules from being usurped), and if only postpollination barriers are present, prepollination barriers will be favored to increase temporal isolation, floral isolation (ethological or mechanical), or selfing rates (as described previously in Section 3).

5. CONCLUDING REMARKS AND FUTURE DIRECTIONS

Although much research has focused on elucidating the effects of competition for pollination in plant ecology and evolution, a common outcome of this competition, IPT, has received little attention until relatively recently. Our understanding of these competitive interactions will only improve as more research is devoted to the fitness consequences of heterospecific pollen deposition and pollen misplacement in natural plant populations under diverse ecological and evolutionary contexts. In particular, the extent to which IPT affects plant reproduction must be evaluated on multiple pollinator community contexts across species' ranges, over a breadth of phylogenetic distances, and at different spatial scales and habitat configurations. Experimental manipulations must also be employed whenever feasible to improve our mechanistic understanding of factors influencing IPT dynamics and their outcomes.

The role of IPT and the extent to which it matches gene flow during early plant diversification also warrants more attention. Genomic tools, modeling approaches, and species-level phylogenies readily available for several plant groups constitute valuable resources to investigate the influence of IPT on reproductive isolation and floral evolution. Patterns of recent and ongoing gene flow mediated by IPT and its effects can inform our knowledge about the evolution of reproductive isolation and the maintenance of species boundaries, patterns of adaptive introgression, the rise of floral phenotypic novelty, and shifts in mating systems. One particularly informative approach to examine early divergence involves using experimental sympatry (sensu Kay et al. 2019) to examine the importance of various pre- and postpollination barriers in preventing gene flow should allopatric subpopulations or incipient species come into secondary contact.

We also need to expand the breadth of plant–pollinator systems studied, as most research involves bee- and bird-pollinated systems in temperate zones. Large-sized pollinators with hairy body surfaces and high vagility, such as hawkmoths and bats, often carry large pollen loads from multiple plant species (Johnson & Raguso 2016, Muchhala & Jarrín-V 2002), but the extent to which they drive IPT interactions has been explored by only a few studies (Ippolito et al. 2004, Muchhala & Potts 2007, Muchhala & Thomson 2012, Muchhala et al. 2009). Small-bodied bees and flies are similarly understudied, as are tropical plants, in terms of studies of competition for pollination generally and IPT interactions more specifically (but see Feinsinger & Tiebout 1991, Muchhala 2008, Muchhala & Thomson 2012, Muchhala et al. 2014). The only exhaustive and complementary set of studies on pollination, reproductive isolation, gene flow, and speciation among closely related tropical plants was conducted in the Neotropical spiral ginger genus *Costus* (Kay 2006, Kay & Schemske 2008, Surget-Groba & Kay 2013).

Finally, more attention to the magnitude and importance of IPT in natural communities will greatly improve our understanding of plant species coexistence and community assembly. This in turn can inform both pure and applied aspects of pollination biology (Mitchell et al. 2009), especially with regard to human-modified environments and plant invasion scenarios, in which novel evolutionary interactions between plants and pollinators are taking place (Albrecht et al. 2016, Johnson & Ashman 2019, Vallejo-Marín & Hiscock 2016). Further ecological and evolutionary research on IPT dynamics is necessary to better understand plant–pollination interactions in our rapidly changing world and will have profound implications for biodiversity conservation and the provisioning of ecosystem services enjoyed by human societies.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

LITERATURE CITED

Abbott R, Albach D, Ansell S, Arntzen JW, Baird SJE, et al. 2013. Hybridization and speciation. *J. Evol. Biol.* 26:229–46

Alarcon R, Campbell DR. 2000. Absence of conspecific pollen advantage in the dynamics of an *Ipomopsis* (Polemoniaceae) hybrid zone. *Am. J. Bot.* 87(6):819–24

Albrecht M, Ramis MR, Traveset A. 2016. Pollinator-mediated impacts of alien invasive plants on the pollination of native plants: the role of spatial scale and distinct behaviour among pollinator guilds. *Biol. Invasions* 18(7):1801–12

Aldridge G, Campbell DR. 2006. Asymmetrical pollen success in *Ipomopsis* (Polemoniaceae) contact sites. *Am. J. Bot.* 93:903–9

Aldridge G, Campbell DR. 2007. Variation in pollinator preference between two *Ipomopsis* contact sites that differ in hybridization rate. *Evolution* 61:99–110

Amaya-Márquez M. 2009. Floral constancy in bees: a revision of theories and a comparison with other pollinators. *Rev. Colomb. Entomol.* 35:206–16

Anderson B, Alexandersson R, Johnson SD. 2010. Evolution and coexistence of pollination ecotypes in an African *Gladiolus* (Iridaceae). *Evolution* 64(4):960–72

Anderson B, Pauw A, Cole WW, Barrett SCH. 2016. Pollination, mating and reproductive fitness in a plant population with bimodal floral-tube length. *J. Evol. Biol.* 29:1631–42

Andrew RL, Kane NC, Baute GJ, Grassa CJ, Rieseberg LH. 2013. Recent nonhybrid origin of sunflower ecotypes in a novel habitat. *Mol. Ecol.* 22:799–813

Andrew RL, Ostevik KL, Ebert DP, Rieseberg LH. 2012. Adaptation with gene flow across the landscape in a dune sunflower. *Mol. Ecol.* 21:2078–91

Arceo-Gómez G, Abdala-Roberts L, Jankowiak A, Kohler C, Meindl GA, et al. 2016a. Patterns of among- and within-species variation in heterospecific pollen receipt: the importance of ecological generalization. *Am. J. Bot.* 103(3):396–407

Arceo-Gómez G, Alonso C, Ashman TL, Parra-Tabla V. 2018. Variation in sampling effort affects the observed richness of plant–plant interactions via heterospecific pollen transfer: implications for interpretation of pollen transfer networks. *Am. J. Bot.* 105(9):1601–8

Arceo-Gómez G, Ashman TL. 2011. Heterospecific pollen deposition: Does diversity alter the consequences? *New Phytol*. 192(3):738–46

Arceo-Gómez G, Ashman T-L. 2014. Coflowering community context influences female fitness and alters the adaptive value of flower longevity in *Mimulus guttatus*. *Am. Nat*. 183(2):E50–63

Arceo-Gómez G, Raguso RA, Geber MA. 2016b. Can plants evolve tolerance mechanisms to heterospecific pollen effects? An experimental test of the adaptive potential in *Clarkia* species. *Oikos* 125(5):718–25

Armbruster WS. 2014. Floral specialization and angiosperm diversity: phenotypic divergence, fitness trade-offs and realized pollination accuracy. *AoB PLANTS* 6(Sept.):plu003

Armbruster WS, Edwards ME, Debevec EM. 1994. Floral character displacement generates assemblage structure of Western Australian triggerplants (*Stylidium*). *Ecology* 75(2):315–29

Armbruster WS, Hansen TF, Pélabon C, Pérez-Barrales R, Maad J. 2009. The adaptive accuracy of flowers: measurement and microevolutionary patterns. *Ann. Bot.* 103(9):1529–45

Armbruster WS, Shi XQ, Huang S-Q. 2014. Do specialized flowers promote reproductive isolation? Realized pollination accuracy of three sympatric *Pedicularis* species. *Ann. Bot.* 113(2):331–40

Arnold ML, Cornman RS, Martin NH. 2008. Hybridization, hybrid fitness and the evolution of adaptations. *Plant Biosyst*. 142(1):166–71

Arnold ML, Hamrick JL, Bennett BD. 1993. Interspecific pollen competition and reproductive isolation in *Iris*. *J. Hered*. 84:13–16

Arnold ML, Tang S, Knapp SJ, Martin NH. 2010. Asymmetric introgressive hybridization among Louisiana iris species. *Genes* 1:9–22

Ashman TL, Arceo-Gómez G. 2013. Toward a predictive understanding of the fitness costs of heterospecific pollen receipt and its importance in co-flowering communities. *Am. J. Bot.* 100(6):1061–70

Baack E, Melo MC, Rieseberg LH, Ortiz-Barrientos D. 2015. The origins of reproductive isolation in plants. *New Phytol*. 207:968–84

Barrett SCH, Harder LD. 2017. The ecology of mating and its evolutionary consequences in seed plants. *Annu. Rev. Ecol. Evol. Syst.* 48:135–57

Bascompte J, Jordano P, Olesen JM. 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* 312(April):431–33

Beans CM. 2014. The case for character displacement in plants. *Ecol. Evol.* 4(6):852–65

Bedinger PA, Broz AK, Tovar-Mendez A, McClure B. 2017. Pollen-pistil interactions and their role in mate selection. *Plant Physiol.* 173(1):79–90

Bell JM, Karron JD, Mitchell RJ. 2005. Interspecific competition for pollination lowers seed production and outcrossing in *Mimulus ringens*. *Am. J. Bot.* 86(3):762–71

Borchsenius F, Lozada T, Knudsen JT. 2016. Reproductive isolation of sympatric forms of the understorey palm *Geonoma macrostachys* in western Amazonia. *Bot. J. Linn. Soc.* 182(2):398–410

Brandvain Y, Haig D. 2005. Divergent mating systems and parental conflict as a barrier to hybridization in flowering plants. *Am. Nat.* 166(3):330–38

Briggs HM, Anderson LM, Atalla LM, Delva AM, Dobbs EK, Brosi BJ. 2015. Heterospecific pollen deposition in *Delphinium barbeyi*: linking stigmatic pollen loads to reproductive output in the field. *Ann. Bot.* 117:341–47

Briscoe Runquist RD. 2012. Pollinator-mediated competition between two congeners, *Limnanthes douglasii* subsp. rosea and *L. alba* (Limnanthaceae). *Am. J. Bot.* 99(7):1125–32

Briscoe Runquist RD, Chu E, Iverson JL, Kopp JC, Moeller DA. 2014. Rapid evolution of reproductive isolation between incipient outcrossing and selfing *Clarkia* species. *Evolution* 68(10):2885–900

Briscoe Runquist RD, Moeller DA. 2014. Floral and mating system divergence in secondary sympatry: testing an alternative hypothesis to reinforcement in *Clarkia*. *Ann. Bot.* 113(2):223–35

Brothers AN, Delph LF. 2017. Divergence in style length and pollen size leads to a postmating-prezygotic reproductive barrier among populations of *Silene latifolia*. *Evolution* 71(6):1532–40

Brown BJ, Mitchell RJ. 2001. Competition for pollination: effects of pollen of an invasive plant on seed set of a native congener. *Oecologia* 129(1):43–49

Bruckman D, Campbell DR. 2016. Timing of invasive pollen deposition influences pollen tube growth and seed set in a native plant. *Biol. Invasions* 18(6):1701–11

Brys R, van Cauwenberghe J, Jacquemyn H. 2016. The importance of autonomous selfing in preventing hybridization in three closely related plant species. *J. Ecol.* 104(2):601–10

Buerkle CA, Wolf DE, Rieseberg LH. 2003. The origin and extinction of species through hybridization. In *Population Viability in Plants*, Vol. 165, ed. CA Brigham, MW Schwartz, pp. 117–41. Berlin: Springer

Burgess KS, Morgan M, Husband BC. 2008. Interspecific seed discounting and the fertility cost of hybridization in an endangered species. *New Phytol.* 177(1):276–84

Burke JM, Carney SE, Arnold ML. 1998. Hybrid fitness in the Louisiana irises: analysis of parental and F_1 performance. *Evolution* 52:37–43

Campbell DR. 1985. Pollen and gene dispersal: the influences of competition for pollination. *Evolution* 39(2):418–31

Campbell DR, Motten AF. 1985. The mechanism of competition for pollination between two forest herbs. *Ecology* 66(2):554–63

Campbell DR, Waser NM. 2007. Evolutionary dynamics of an *Ipomopsis* hybrid zone: confronting models with lifetime fitness data. *Am. Nat.* 169(3):298–310

Campbell DR, Waser NM, Pederson GT. 2002. Predicting patterns of mating and potential hybridization from pollinator behavior. *Am Nat.* 159(5):438–50

Campbell DR, Waser NM, Wolf PG. 1998. Pollen transfer by natural hybrids and parental species in an *Ipomopsis* hybrid zone. *Evolution* 52(6):1602–11

Carney SE, Hodges SA, Arnold ML. 1996. Effects of differential pollen-tube growth on hybridization in the Louisiana irises. *Evol. Evol.* 50(505):1871–78

Caruso CM, Alfaro M. 2000. Interspecific pollen transfer as a mechanism of competition: effect of *Castilleja linariaefolia* pollen on seed set of *Ipomopsis aggregata*. *Can. J. Bot.* 78(5):600–6

Castellanos MC, Wilson P, Thomson JD. 2003. Pollen transfer by hummingbirds and bumblebees, and the divergence of pollination modes in *Penstemon*. *Evolution* 57(12):2742

Cheptou PO. 2019. Does the evolution of self-fertilization rescue populations or increase the risk of extinction? *Ann. Bot.* 123(1):mcy144

Chittka L, Thomson JD, Waser NM. 1999. Flower constancy, insect psychology, and plant evolution. *Naturwissenschaften* 86:361–77

Christie K, Strauss SY. 2018. Along the speciation continuum: quantifying intrinsic and extrinsic isolating barriers across five million years of evolutionary divergence in California jewelflowers. *Evolution* 72(5):1063–79

Clay DL, Novak SJ, Serpe MD, Tank DC, Smith JF. 2012. Homoploid hybrid speciation in a rare endemic *Castilleja* from Idaho (*Castilleja christii*, Orobanchaceae). *Am. J. Bot.* 99(12):1976–90

Coyne JA, Orr HA. 2004. *Speciation*. Sunderland, MA: Sinauer

De Jager ML, Dreyer LL, Ellis AG. 2011. Do pollinators influence the assembly of flower colours within plant communities? *Oecologia* 166:543–53

De Queiroz K. 2011. Branches in the lines of descent: Charles Darwin and the evolution of the species concept. *Biol. J. Linn. Soc.* 103(Jan.):19–35

Diaz A, Macnair MR. 1999. Pollen tube competition as a mechanism of prezygotic reproductive isolation between *Mimulus nasutus* and its presumed progenitor *M. guttatus*. *New Phytol*. 144(3):471–78

Ducarme V, Vrancken J, Wesselingh RA. 2010. Hybridization in annual plants: patterns and dynamics during a four-year study in mixed *Rhinanthus* populations. *Folia Geobot*. 45:387–405

Eaton DAR, Fenster CB, Hereford J, Huang S, Ree RH. 2012. Floral diversity and community structure in *Pedicularis* (Orobanchaceae). *Ecology* 93:S182–93

Ellstrand NC. 2014. Is gene flow the most important evolutionary force in plants? *Am. J. Bot.* 101(5):737–53

Emms SK, Arnold ML. 2000. Site-to-site differences in pollinator visitation patterns in a Louisiana iris hybrid zone. *Oikos* 91:568–78

Fang Q, Huang S-Q. 2013. A directed network analysis of heterospecific pollen transfer in a biodiverse community. *Ecology* 94(5):1176–85

Feinsinger P, Tiebout HM III. 1991. Competition among plants sharing hummingbird pollinators: laboratory experiments on a mechanism. *Ecology* 72(6):1946–52

Figueroa-Castro DM, Holtsford TP. 2009. Post-pollination mechanisms in *Nicotiana longiflora* and *N. plumbaginifolia*: pollen tube growth rate, offspring paternity and hybridization. *Sex. Plant Reprod.* 22(3):187–96

Fishman L, Aagaard J, Tuthill JC. 2008. Toward the evolutionary genomics of gametophytic divergence: patterns of transmission ratio distortion in monkeyflower (*Mimulus*) hybrids reveal a complex genetic basis for conspecific pollen precedence. *Evolution* 62(12):2958–70

Fishman L, Wyatt R. 1999. Pollinator-mediated competition, reproductive character displacement, and the evolution of selfing in *Arenaria uniflora* (Caryophyllaceae). *Evolution* 53(6):1723–33

Flanagan RJ, Mitchell RJ, Knutowski D, Karron JD. 2009. Interspecific pollinator movements reduce pollen deposition and seed production in *Mimulus ringens* (Phrymaceae). *Am. J. Bot.* 96(4):809–15

Galen C, Gregory T. 1989. Interspecific pollen transfer as a mechanism of competition: consequences of foreign pollen contamination for seed set in the alpine wildflower, *Polemonium viscosum*. *Oecologia* 81:120–23

Gegear RJ, Laverty TM. 2005. Flower constancy in bumblebees: a test of the trait variability hypothesis. *Anim. Behav.* 69:939–49

Goodwillie C, Ness JM. 2013. Interactions of hybridization and mating systems: a case study in *Leptosiphon* (Polemoniaceae). *Am. J. Bot.* 100(6):1002–13

Goulson D. 2000. Are insects flower constant because they use search images to find flowers? *Oikos* 88:547–52

Grant V. 1994. Modes and origins of mechanical and ethological isolation in angiosperms. *PNAS* 91(1):3–10

Grossenbacher D, Briscoe Runquist RD, Goldberg EE, Brandvain Y. 2016. No association between plant mating system and geographic range overlap. *Am. J. Bot.* 103(1):110–17

Grossenbacher DL, Stanton ML. 2014. Pollinator-mediated competition influences selection for flower-color displacement in sympatric monkeyflowers. *Am. J. Bot.* 101(11):1915–24

Grossenbacher DL, Whittall JB. 2011. Increased floral divergence in sympatric monkeyflowers. *Evolution* 65(9):2712–18

Harder LD, Cruzan MB, Thomson JD. 1993. Unilateral incompatibility and the effects of interspecific pollination for *Erythronium americanum* and *Erythronium albidum* (Liliaceae). *Can. J. Bot.* 71(2):353–58

Hasegawa Y, Suyama Y, Seiwa K. 2015. Variation in pollen-donor composition among pollinators in an entomophilous tree species, *Castanea crenata*, revealed by single-pollen genotyping. *PLOS ONE* 10(3):1–15

Heinrich B. 1975. Bee flowers: a hypothesis on flower variety and blooming times. *Evolution* 29:325–34

Hipperson H, Dunning LT, Baker WJ, Butlin RK, Hutton I, et al. 2016. Ecological speciation in sympatric palms: 2. Pre- and post-zygotic isolation. *J. Evol. Biol.* 29(11):2143–56

Hopkins R. 2013. Reinforcement in plants. *New Phytol.* 197(4):1095–1103

Hopkins R, Rausher MD. 2012. Pollinator-mediated selection on flower color allele drives reinforcement. *Science* 335:1090–92

Howard DJ. 1999. Conspecific sperm and pollen precedence and speciation. *Annu. Rev. Ecol. Syst.* 30:109–32

Huang S-Q, Shi XQ. 2013. Floral isolation in *Pedicularis*: How do congeners with shared pollinators minimize reproductive interference? *New Phytol.* 199(3):858–65

Huang Z-H, Liu H-L, Huang S-Q. 2015. Interspecific pollen transfer between two coflowering species was minimized by bumblebee fidelity and differential pollen placement on the bumblebee body. *J. Plant Ecol.* 8(2):109–15

Ippolito A, Fernandes GW, Holtsford TP. 2004. Pollinator preferences for *Nicotiana alata*, *N. forgetiana*, and their F_1 hybrids. *Evolution* 58(12):2634–44

Jakobsson A, Padrón B, Traveset A. 2008. Pollen transfer from invasive *Carpobrotus* spp. to natives—a study of pollinator behaviour and reproduction success. *Biol. Conserv.* 141(1):136–45

Johnson AL, Ashman T. 2019. Consequences of invasion for pollen transfer and pollination revealed in a tropical island ecosystem. *New Phytol.* 221:142–54

Johnson SD, Raguso RA. 2016. The long-tongued hawkmoth pollinator niche for native and invasive plants in Africa. *Ann. Bot.* 117(1):25–36

Kalisz S, Randle A, Chaiffetz D, Faigeles M, Butera A, Beight C. 2012. Dichogamy correlates with outcrossing rate and defines the selfing syndrome in the mixed-mating genus *Collinsia*. *Ann. Bot.* 109(3):571–82

Karrenberg S, Liu X, Hallander E, Favre A, Herforth-Rahmé J, Widmer A. 2018. Ecological divergence plays an important role in strong but complex reproductive isolation in campions (*Silene*). *Evolution* 73:1–17

Karron JD, Ivey CT, Mitchell RJ, Whitehead MR, Peakall R, Case AL. 2012. New perspectives on the evolution of plant mating systems. *Ann. Bot.* 109(3):493–503

Kay KM. 2006. Reproductive isolation between two closely related hummingbird-pollinated neotropical gingers. *Evolution* 60(3):538–52

Kay KM, Schemske DW. 2008. Natural selection reinforces speciation in a radiation of neotropical rainforest plants. *Evolution* 62(10):2628–42

Kay KM, Zepeda AM, Raguso RA. 2019. Experimental sympatry reveals geographic variation in floral isolation by hawkmoths. *Ann. Bot.* 123:405–13

Kohn JR, Waser NM. 1985. The effect of *Delphinium nelsonii* pollen on seed set in *Ipomopsis aggregata*, a competitor for hummingbird pollination. *Am. J. Bot.* 72:1144–48

Kostyun JL, Moyle LC. 2017. Multiple strong postmating and intrinsic postzygotic reproductive barriers isolate florally diverse species of *Jaltomata* (Solanaceae). *Evolution* 71(6):1556–71

Laverty TM. 1994. Costs to foraging bumble bees of switching plant species. *Can. J. Zool.* 72:43–47

Lloyd DG. 1992. Self- and cross-fertilization in plants. II. The selection of self-fertilization. *Int. J. Plant Sci.* 153:370–80

Lowry DB, Modliszewski JL, Wright KM, Wu CA, Willis JH. 2008. The strength and genetic basis of reproductive isolating barriers in flowering plants. *Philos. Trans. R. Soc. B* 363(1506):3009–21

Lyu N, Du W, Wang XF. 2016. Unique growth paths of heterospecific pollen tubes result in late entry into ovules in the gynoecium of *Sagittaria* (Alismataceae). *Plant Biol.* 19(2):108–14

Mallet J, Besansky N, Hahn MW. 2016. How reticulated are species? *BioEssays* 38(2):140–49

Martin NH, Willis JH. 2007. Ecological divergence associated with mating system causes nearly complete reproductive isolation between sympatric *Mimulus* species. *Evolution* 61(1):68–82

Matallana G, Godinho MAS, Guilherme FAG, Belisario M, Coser TS, Wendt T. 2010. Breeding systems of Bromeliaceae species: evolution of selfing in the context of sympatric occurrence. *Plant Syst. Evol.* 289(1–2):57–65

McLernon SM, Murphy SD, Aarssen LW. 1996. Heterospecific pollen transfer between sympatric species in a midsuccessional old-field community. *Am. J. Bot.* 83:1168–74

Miller TJ, Raguso RA, Kay KM. 2014. Novel adaptation to hawkmoth pollinators in *Clarkia* reduces efficiency, not attraction of diurnal visitors. *Ann. Bot.* 113(2):317–29

Minder AM, Rothenbuehler C, Widmer A. 2007. Genetic structure of hybrid zones between *Silene latifolia* and *Silene dioica* (Caryophyllaceae): evidence for introgressive hybridization. *Mol. Ecol.* 16:2504–16

Minnaar C, Anderson B. 2019. Using quantum dots as pollen labels to track the fates of individual pollen grains. *Methods Ecol. Evol.* 10(5):604–14

Minnaar C, Anderson B, de Jager ML, Karron JD. 2019. Plant–pollinator interactions along the pathway to paternity. *Ann. Bot.* 123(1):225–45

Mitchell RJ, Flanagan RJ, Brown BJ, Waser NM, Karron JD. 2009. New frontiers in competition for pollination. *Ann. Bot.* 103(9):1403–13

Montgomery BR, Soper DM, Delph LF. 2010. Asymmetrical conspecific seed-siring advantage between *Silene latifolia* and *S. dioica*. *Ann. Bot.* 105(4):595–605

Morales CL, Traveset A. 2008. Interspecific pollen transfer: magnitude, prevalence and consequences for plant fitness. *Crit. Rev. Plant Sci.* 27(4):221–38

More M, Sersic AN, Cocucci AA. 2007. Restriction of pollinator assemblage through flower length and width in three long-tongued hawkmoth-pollinated species of *Mandevilla* (Apocynaceae, Apocynoideae). *Ann. Mo. Bot. Gard.* 94(2):485–504

Muchhala N. 2006. The pollination biology of *Burmeistera* (Campanulaceae): specialization and syndromes. *Am. J. Bot.* 93:1081–89

Muchhala N. 2007. Adaptive trade-off in floral morphology mediates specialization for flowers pollinated by bats and hummingbirds. *Am. Nat.* 169(4):494–504

Muchhala N. 2008. Functional significance of interspecific variation in *Burmeistera* flower morphology: evidence from nectar bat captures in Ecuador. *Biotropica* 40(3):332–37

Muchhala N, Brown Z, Armbruster WS, Potts MD. 2010. Competition drives specialization in pollination systems through costs to male fitness. *Am. Nat.* 176(6):732–43

Muchhala N, Caiza A, Vizuete JC, Thomson JD. 2009. A generalized pollination system in the tropics: bats, birds and *Aphelandra acanthus*. *Ann. Bot.* 103(9):1481–87

Muchhala N, Jarrín-V P. 2002. Flower visitation by bats in cloud forests of Western Ecuador. *Biotropica* 34(3):387–95

Muchhala N, Johnsen S, Smith SD. 2014. Competition for hummingbird pollination shapes flower color variation in Andean Solanaceae. *Evolution* 68(8):2275–86

Muchhala N, Potts MD. 2007. Character displacement among bat-pollinated flowers of the genus *Burmeistera*: analysis of mechanism, process and pattern. *Proc. Biol. Sci.* 274:2731–37

Muchhala N, Thomson JD. 2012. Interspecific competition in pollination systems: costs to male fitness via pollen misplacement. *Funct. Ecol.* 26(2):476–82

Muir G, Dixon CJ, Harper AL, Filatov DA. 2012. Dynamics of drift, gene flow, and selection during speciation in *Silene*. *Evolution* 66:1447–58

Murcia C, Feinsinger P. 1996. Interspecific pollen loss by hummingbirds visiting flower mixtures: effects of floral architecture. *Ecology* 77(2):550–60

Murphy SD, Aarssen LW. 1995. Allelopathic pollen extract from *Phleum pratense L.* (Poaceae) reduces germination, in vitro, of pollen of sympatric species. *Int. J. Plant Sci.* 156:425–34

Natalis LC, Wesselingh RA. 2012a. Shared pollinators and pollen transfer dynamics in two hybridizing species, *Rhinanthus minor* and *R. angustifolius*. *Oecologia* 170(3):709–21

Natalis LC, Wesselingh RA. 2012b. Post-pollination barriers and their role in asymmetric hybridization in *Rhinanthus* (Orobanchaceae). *Am. J. Bot.* 99(11):1847–56

Natalis LC, Wesselingh RA. 2013. Parental frequencies and spatial configuration shape bumblebee behavior and floral isolation in hybridizing *Rhinanthus*. *Evolution* 67:1692–705

Ne'eman G, Jürgens A, Newstrom-Lloyd L, Potts SG, Dafni A. 2010. A framework for comparing pollinator performance: effectiveness and efficiency. *Biol. Rev.* 85(3):435–51

Newman E, Manning J, Anderson B. 2015. Local adaptation: mechanical fit between floral ecotypes of *Nerine humilis* (Amaryllidaceae) and pollinator communities. *Evolution* 69(9):2262–75

Ollerton J, Winfree R, Tarrant S. 2011. How many flowering plants are pollinated by animals? *Oikos* 120(3):321–26

Ortiz-Barrientos D, Grealy A, Nosil P. 2009. The genetics and ecology of reinforcement: implications for the evolution of prezygotic isolation in sympatry and beyond. *Ann. N.Y. Acad. Sci.* 1168:156–82

Ostevik KL, Andrew RL, Otto SP, Rieseberg LH. 2016. Multiple reproductive barriers separate recently diverged sunflower ecotypes. *Evolution* 70:2322–35

Oyama RK, Jones KN, Baum DA. 2010. Sympatric sister species of Californian *Antirrhinum* and their transiently specialized pollinators. *Am. Midl. Nat.* 164:337–47

Palmer M, Travis J, Antonovics J. 1989. Temporal mechanisms influencing gender expression and pollen flow within a self-incompatible perennial, *Amianthium muscaetoxicum* (Liliaceae). *Oecologia* 78:231–36

Paudel BR, Burd M, Shrestha M, Dyer AG, Li QJ. 2018. Reproductive isolation in alpine gingers: how do coexisting *Roscoea* (*R. purpurea* and *R. tumjensis*) conserve species integrity? *Evolution* 72(9):1840–50

Payseur BA, Rieseberg LH. 2016. A genomic perspective on hybridization and speciation. *Mol. Ecol.* 25(11):2337–60

Pettengill JB, Moeller DA. 2012. Tempo and mode of mating system evolution between incipient *Clarkia* species. *Evolution* 66:1210–25

Ramsey J, Bradshaw HD, Schemske DW. 2003. Components of reproductive isolation between the monkeyflowers *Mimulus lewisii* and *M. cardinalis* (Phrymaceae). *Evolution* 57(7):1520–34

Randall JL, Hilu KW. 1990. Interference through improper pollen transfer in mixed stands of *Impatiens capensis* and *I. pallida* (Balsaminaceae). *Am. J. Bot.* 77:939–44

Randle AM, Spigler RB, Kalisz S. 2018. Shifts to earlier selfing in sympatry may reduce costs of pollinator sharing. *Evolution* 72(8):1587–99

Rathcke BJ. 1983. Competition and facilitation among plants for pollination. In *Pollination Biology*, ed. L Real, pp. 305–29. New York: Academic

Rausher MD. 2017. Selfing, local mate competition, and reinforcement. *Am. Nat.* 189(2):87–104

Renaut S, Rowe HC, Ungerer MC, Rieseberg LH. 2014. Genomics of homoploid hybrid speciation: diversity and transcriptional activity of long terminal repeat retrotransposons in hybrid sunflowers. *Philos. Trans. R. Soc. B* 369(1648):20130345

Roda F, Mendes FK, Hahn MW, Hopkins R. 2017. Genomic evidence of gene flow during reinforcement in Texas *Phlox*. *Mol. Ecol.* 26:2317–30

Rodríguez-Gironés MA, Santamaría L. 2007. Resource competition, character displacement, and the evolution of deep corolla tubes. *Am. Nat.* 170:455–64

Ruane LG, Donohue K. 2008. Pollen competition and environmental effects on hybridization dynamics between *Phlox drummondii* and *Phlox cuspidata*. *Evol. Ecol.* 22:229–41

Schiestl FP, Schlüter PM. 2009. Floral isolation, specialized pollination, and pollinator behavior in orchids. *Annu. Rev. Entomol.* 54:425–46

Schmickl R, Marburger S, Bray S, Yant L, Henderson I. 2017. Hybrids and horizontal transfer: introgression allows adaptive allele discovery. *J. Exp. Bot.* 68(20):5453–70

Schouppe D, Brys R, Vallejo-Marín M, Jacquemyn H. 2017. Geographic variation in floral traits and the capacity of autonomous selfing across allopatric and sympatric populations of two closely related *Centaurium* species. *Sci. Rep.* 7(April):46410

Scribailo R, Barrett S. 1994. Effects of prior self-pollination on outcrossed seed set in tristylous *Pontederia sagittata* (Pontederiaceae). *Sex. Plant Reprod.* 7:273–81

Shore JS, Barrett SC. 1984. The effect of pollination intensity and incompatible pollen on seed set in *Turnera ulmifolia* (Turneraceae). *Can. J. Bot.* 62:1298–303

Sicard A, Lenhard M. 2011. The selfing syndrome: a model for studying the genetic and evolutionary basis of morphological adaptation in plants. *Ann. Bot.* 107(9):1433–43

Smith RA, Rausher MD. 2008. Experimental evidence that selection favors character displacement in the ivyleaf morning glory. *Am. Nat.* 171(1):1–9

Sobel JM, Chen GF. 2014. Unification of methods for estimating the strength of reproductive isolation. *Evolution* 68:1511–22

Sobel JM, Streisfeld MA. 2014. Strong premating reproductive isolation drives incipient speciation in *Mimulus aurantiacus*. *Evolution* 69:447–61

Stankowski S, Streisfeld MA. 2015. Introgressive hybridization facilitates adaptive divergence in a recent radiation of monkeyflowers. *Proc. R. Soc. B* 282(1814):20151666

Surget-Groba Y, Kay KM. 2013. Restricted gene flow within and between rapidly diverging Neotropical plant species. *Mol. Ecol.* 22(19):4931–42

Takahashi Y, Takakura KI, Kawata M. 2016. Spatial distribution of flower color induced by interspecific sexual interaction. *PLOS ONE* 11(10):e0164381

Temeles EJ, Mazzotta AR, Williamson A. 2017. Resource partitioning by color in a tropical hummingbird. *Behav. Ecol. Sociobiol.* 71:129

Thomson JD, Andrews BJ, Plowright RC. 1982. The effect of foreign pollen on ovule development in *Diervilla lonicera* (Caprifoliaceae). *New Phytol.* 90:777–83

Thomson JD, Fung HF, Ogilvie JE. 2018. Effects of spatial patterning of co-flowering plant species on pollination quantity and purity. *Ann. Bot.* 123(2):303–10

Tiffin P, Olson MS, Moyle LC. 2001. Asymmetrical crossing barriers in angiosperms. *Proc. R. Soc. B* 268(1469):861–67

Tscheulin T, Petanidou T, Potts SG, Settele J. 2009. The impact of *Solanum elaeagnifolium*, an invasive plant in the Mediterranean, on the flower visitation and seed set of the native co-flowering species *Glaucium flavum*. *Plant Ecol.* 205(1):77–85

Tur C, Sáez A, Traveset A, Aizen MA. 2016. Evaluating the effects of pollinator-mediated interactions using pollen transfer networks: evidence of widespread facilitation in south Andean plant communities. *Ecol. Lett.* 19(5):576–86

Vallejo-Marín M, Cooley AM, Lee MY, Folmer M, McKain MR, Puzey JR. 2016. Strongly asymmetric hybridization barriers shape the origin of a new polyploid species and its hybrid ancestor. *Am. J. Bot.* 103(7):1272–88

Vallejo-Marín M, Hiscock SJ. 2016. Hybridization and hybrid speciation under global change. *New Phytol.* 211:1170–87

Vallejo-Marín M, Walker C, Friston-Reilly P, Solís-Montero L, Igic B. 2014. Recurrent modification of floral morphology in heterantherous *Solanum* reveals a parallel shift in reproductive strategy. *Philos. Trans. R. Soc. B* 369(1649):20130256

Vrancken J, Brochmann C, Wesselingh RA. 2012. A European phylogeography of *Rhinanthus minor* compared to *Rhinanthus angustifolius*: unexpected splits and signs of hybridization. *Ecol. Evol.* 2:1531–48

Wang J, Cruzan MB. 1998. Interspecific mating in the *Piriqueta caroliniana* (Turneraceae) complex: effects of pollen load size and composition. *Am. J. Bot.* 85(9):1172–79

Waser NM. 1978a. Interspecific pollen transfer and competition between co-occurring plant species. *Oecologia* 36(2):223–36

Waser NM. 1978b. Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. *Ecology* 59(5):934–44

Waser NM. 1983. Competition for pollination and floral character differences among sympatric plant species: a review of the evidence. In *Handbook of Experimental Pollination Biology*, ed. CE Jones, RJ Little, pp. 277–93. New York: Van Nostrand Reinhold

Waser NM. 1986. Flower constancy: definition, cause, and measurement. *Am. Nat.* 127:593–603

Waser NM, Fugate ML. 1986. Pollen precedence and stigma closure: a mechanism of competition for pollination between *Delphiniium nelsonii* and *Ipomopss aggregata*. *Oecologia* 70:573–77

Weber MG, Cacho NI, Phan MJQ, Disbrow C, Ramírez SR, Strauss SY. 2018. The evolution of floral signals in relation to range overlap in a clade of California Jewelflowers (*Streptanthus* s.l.). *Evolution* 72(4):798–807

Whitehead MR, Lanfear R, Mitchell RJ, Karron JD. 2018. Plant mating systems often vary widely among populations. *Front. Ecol. Evol.* 6(April):1–9

Whitney KD, Randell RA, Rieseberg LH. 2010. Adaptive introgression of abiotic tolerance traits in the sunflower *Helianthus annuus*. *New Phytol*. 187(1):230–39

Whitton J, Sears CJ, Maddison WP. 2017. Co-occurrence of related asexual, but not sexual, lineages suggests that reproductive interference limits coexistence. *Proc. R. Soc. B* 284(1868):20171579

Wilson P, Stine M. 1996. Floral constancy in bumble bees: handling efficiency or perceptual conditioning? *Oecologia* 106:493–99

Wolf PG, Campbell DR, Waser NM, Sipes SD, Toler TR, Archibald JK. 2001. Tests of pre- and postpollination barriers to hybridization between sympatric species of *Ipomopsis* (Polemoniaceae). *Am. J. Bot.* 88(2):213–19

Wu CA, Campbell DR. 2005. Cytoplasmic and nuclear markers reveal contrasting patterns of spatial genetic structure in a natural *Ipomopsis* hybrid zone. *Mol. Ecol.* 14:781–92

Yang CF, Gituru RW, Guo YH. 2007. Reproductive isolation of two sympatric louseworts, *Pedicularis rhinanthoides* and *Pedicularis longiflora* (Orobanchaceae): How does the same pollinator type avoid interspecific pollen transfer? *Biol. J. Linn. Soc.* 90(1):37–48

Zhang J-J, Montgomery BR, Huang S-Q. 2016. Evidence for asymmetrical hybridization despite pre- and post-pollination reproductive barriers between two *Silene* species. *AoB PLANTS* 8:plw032

Annual Review of Ecology, Evolution, and Systematics

Volume 50, 2019

Contents

Related Articles

From the ***Annual Review of Animal Biosciences***, Volume 7 (2019)

Functional Annotation of Animal Genomes (FAANG): Current Achievements and Roadmap
Elisabetta Giuffra, Christopher K. Tuggle, and The FAANG Consortium

Mammalian Sex Chromosome Structure, Gene Content, and Function in Male Fertility
Wan-Sheng Liu

Multiple Facets of Marine Invertebrate Conservation Genomics
Jose V. Lopez, Bishoy Kamel, Mónica Medina, Timothy Collins, and Iliana B. Baums

The Role of Reproductive Technologies in Amphibian Conservation Breeding Programs
Aimee J. Silla and Phillip G. Byrne

Tigers of the World: Genomics and Conservation
Shu-Jin Luo, Yue-Chen Liu, and Xiao Xu

From the ***Annual Review of Earth and Planetary Sciences***, Volume 47 (2019)

Seawater Chemistry Through Phanerozoic Time
Alexandra V. Turchyn and Donald J. DePaolo

Flood Basalts and Mass Extinctions
Matthew E. Clapham and Paul R. Renne

Soil Functions: Connecting Earth's Critical Zone
Steven A. Banwart, Nikolaos P. Nikolaidis, Yong-Guan Zhu, Caroline L. Peacock, and Donald L. Sparks

Marsh Processes and Their Response to Climate Change and Sea-Level Rise
Duncan M. FitzGerald and Zoe Hughes

The Mesozoic Biogeographic History of Gondwanan Terrestrial Vertebrates: Insights from Madagascar's Fossil Record
David W. Krause, Joseph J.W. Sertich, Patrick M. O'Connor, Kristina Curry Rogers, and Raymond R. Rogers

Droughts, Wildfires, and Forest Carbon Cycling: A Pantropical Synthesis
Paulo M. Brando, Lucas Paolucci, Caroline C. Ummenhofer, Elsa M. Ordway, Henrik Hartmann, Megan E. Cattau, Ludmila Rattis, Vincent Medjibe, Michael T. Coe, and Jennifer Balch

From the ***Annual Review of Environment and Resources***, Volume 44 (2019)

The State and Future of Antarctic Environments in a Global Context
Steven L. Chown and Cassandra M. Brooks

Island Biodiversity in the Anthropocene
James C. Russell and Christoph Kueffer

Mammal Conservation: Old Problems, New Perspectives, Transdisciplinarity, and the Coming of Age of Conservation Geopolitics
David W. Macdonald

The State of the World's Mangrove Forests: Past, Present, and Future
Daniel A. Friess, Kerrylee Rogers, Catherine E. Lovelock, Ken W. Krauss, Stuart E. Hamilton, Shing Yip Lee, Richard Lucas, Jurgenne Primavera, Anusha Rajkaran, and Suhua Shi

Status, Institutions, and Prospects for Global Capture Fisheries
Christopher Costello and Daniel Ovando

Illegal Wildlife Trade: Scale, Processes, and Governance
Michael 't Sas-Rolfes, Daniel W.S. Challender, Amy Hinsley, Diogo Veríssimo, and E.J. Milner-Gulland

Ecotourism for Conservation?
Amanda L. Stronza, Carter A. Hunt, and Lee A. Fitzgerald

Co-Producing Sustainability: Reordering the Governance of Science, Policy, and Practice
Carina Wyborn, Amber Datta, Jasper Montana, Melanie Ryan, Peat Leith, Brian Chaffin, Clark Miller, and Lorrae van Kerkhoff

Social Synergies, Tradeoffs, and Equity in Marine Conservation Impacts
David A. Gill, Samantha H. Cheng, Louise Glew, Ernest Aigner, Nathan J. Bennett, and Michael B. Mascia

From the ***Annual Review of Entomology***, Volume 64 (2019)

The Ecology of Collective Behavior in Ants
Deborah M. Gordon

Invasion Success and Management Strategies for Social *Vespula* Wasps
Philip J. Lester and Jacqueline R. Beggs

Invasive Cereal Aphids of North America: Ecology and Pest Management
Michael J. Brewer, Frank B. Peairs, and Norman C. Elliott

Movement and Demography of At-Risk Butterflies: Building Blocks for Conservation
Cheryl B. Schultz, Nick M. Haddad, Erica H. Henry, and Elizabeth E. Crone

Epigenetics in Insects: Genome Regulation and the Generation of Phenotypic Diversity
Karl M. Glastad, Brendan G. Hunt, and Michael A.D. Goodisman

Molecular Evolution of the Major Arthropod Chemoreceptor Gene Families
Hugh M. Robertson

Systematics, Phylogeny, and Evolution of Braconid Wasps: 30 Years of Progress
Xue-xin Chen and Cornelis van Achterberg

Water Beetles as Models in Ecology and Evolution
David T. Bilton, Ignacio Ribera, and Andrew Edward Z. Short

Phylogeography of Ticks (Acari: Ixodida)
Lorenza Beati and Hans Klompen

From the ***Annual Review of Genetics***, Volume 53 (2019)

Crossover Interference: Shedding Light on the Evolution of Recombination
Sarah P. Otto and Bret A. Payseur

Evolutionary Ecology of *Wolbachia* Releases for Disease Control
Perran A. Ross, Michael Turelli, and Ary A. Hoffmann

Living with Two Genomes: Grafting and Its Implications for Plant Genome-to-Genome Interactions, Phenotypic Variation, and Evolution
Brandon S. Gaut, Allison J. Miller, and Danelle K. Seymour

Standard Deviations: The Biological Bases of Transmission Ratio Distortion
Lila Fishman and Mariah McIntosh

The Microbiome and Aging
Bianca Bana and Filipe Cabreiro

Zebrafish Pigment Pattern Formation: Insights into the Development and Evolution of Adult Form
Larissa B. Patterson and David M. Parichy

From the ***Annual Review of Genomics and Human Genetics***, Volume 20 (2019)

The Genetics of Human Skin and Hair Pigmentation
William J. Pavan and Richard A. Sturm

Measuring Clonal Evolution in Cancer with Genomics
Marc J. Williams, Andrea Sottoriva, and Trevor A. Graham

The Causes and Consequences of Genetic Interactions (Epistasis)
Júlia Domingo, Pablo Baeza-Centurion, and Ben Lehner

Thinking About the Evolution of Complex Traits in the Era of Genome-Wide Association Studies
Guy Sella and Nicholas H. Barton

From the ***Annual Review of Marine Science***, Volume 11 (2019)

Planktonic Marine Archaea
Alyson E. Santoro, R. Alexander Richter, and Christopher L. Dupont

Arctic and Antarctic Sea Ice Change: Contrasts, Commonalities, and Causes
Ted Maksym

Biologically Generated Mixing in the Ocean
Eric Kunze

Climate Change, Coral Loss, and the Curious Case of the Parrotfish Paradigm: Why Don't Marine Protected Areas Improve Reef Resilience?
John F. Bruno, Isabelle M. Côté, and Lauren T. Toth

Marine Metazoan Modern Mass Extinction: Improving Predictions by Integrating Fossil, Modern, and Physiological Data
Piero Calosi, Hollie M. Putnam, Richard J. Twitchett, and Fanny Vermandele

From the ***Annual Review of Microbiology***, Volume 73 (2019)

Ecology and Evolution of Plant Microbiomes
Viviane Cordovez, Francisco Dini-Andreote, Víctor J. Carrión, and Jos M. Raaijmakers

Algal Sex Determination and the Evolution of Anisogamy
James Umen and Susana Coelho

The Ultimate Guide to Bacterial Swarming: An Experimental Model to Study the Evolution of Cooperative Behavior
Jinyuan Yan, Hilary Monaco, and Joao B. Xavier

Biogeography of the Oral Microbiome: The Site-Specialist Hypothesis
Jessica L. Mark Welch, Floyd E. Dewhirst, and Gary G. Borisy

Diversity, Genomics, and Distribution of Phytoplankton-Cyanobacterium Single-Cell Symbiotic Associations
Rachel A. Foster and Jonathan P. Zehr

Paleomicrobiology: Diagnosis and Evolution of Ancient Pathogens
Kirsten I. Bos, Denise Kühnert, Alexander Herbig, Luis Roger Esquivel-Gomez, Aida Andrades Valtueña, Rodrigo Barquera, Karen Giffin, Aditya Kumar Lankapalli, Elizabeth A. Nelson, Susanna Sabin, Maria A. Spyrou, and Johannes Krause

From the ***Annual Review of Plant Biology***, Volume 70 (2019)

Molecular Interactions Between Plants and Insect Herbivores
Matthias Erb and Philippe Reymond

A Molecular View of Plant Local Adaptation: Incorporating Stress-Response Networks
Acer VanWallendael, Ali Soltani, Nathan C. Emery, Murilo M. Peixoto, Jason Olsen, and David B. Lowry

Comparative and Functional Algal Genomics
Crysten E. Blaby-Haas and Sabeeha S. Merchant

CRISPR/Cas Genome Editing and Precision Plant Breeding in Agriculture
Kunling Chen, Yanpeng Wang, Rui Zhang, Huawei Zhang, and Caixia Gao

Risk Assessment and Regulation of Plants Modified by Modern Biotechniques: Current Status and Future Challenges
Joachim Schiemann, Antje Dietz-Pfeilstetter, Frank Hartung, Christian Kohl, Jörg Romeis, and Thorben Sprink

From the ***Annual Review of Phytopathology***, Volume 57 (2019)

Revisiting the Concept of Host Range of Plant Pathogens
Cindy E. Morris and Benoît Moury

Durability of Quantitative Resistance in Crops: Greater Than We Know?
Christina Cowger and James K.M. Brown

Molecular Dialog Between Parasitic Plants and Their Hosts
Christopher R. Clarke, Michael P. Timko, John I. Yoder, Michael J. Axtell, and James H. Westwood

Ecology and Evolution of the Sudden Oak Death Pathogen *Phytophthora ramorum*
Niklaus J. Grünwald, Jared M. LeBoldus, and Richard C. Hamelin

Understanding Adaptation, Coevolution, Host Specialization, and Mating System in Castrating Anther-Smut Fungi by Combining Population and Comparative Genomics
Fanny E. Hartmann, Ricardo C. Rodríguez de la Vega, Fantin Carpentier, Pierre Gladieux, Amandine Cornille, Michael E. Hood, and Tatiana Giraud

Surviving in a Hostile World: Plant Strategies to Resist Pests and Diseases
Samuel W. Wilkinson, Melissa H. Magerøy, Ana López Sánchez, Lisa M. Smith, Leonardo Furci, T.E. Anne Cotton, Paal Krokene, and Jurriaan Ton