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Perspective

The messenger matters: Pollinator functional group influences mating system dynamics

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The incredible diversity of plant mating systems has fuelled research in evolutionary biology for over a century. Currently, there is broad concern about the impact of rapidly changing pollinator communities on plant populations. Very few studies, however, examine patterns and mechanisms associated with multiple paternity from cross-pollen loads. Often, foraging pollinators collect a mixed pollen load that may result in the deposition of pollen from different sires to receptive stigmas. Coincident deposition of self- and cross-pollen leads to interesting mating system dynamics and has been investigated in numerous species. But, mixed pollen loads often consist of a diversity of cross-pollen and result in multiple sires of seeds within a fruit. In this issue of Molecular Ecology, Rhodes, Fant, and Skogen (2017) examine how pollinator identity and spatial isolation influence multiple paternity within fruits of a self-incompatible evening primrose. The authors demonstrate that pollen pool diversity varies between two pollinator types, hawkmoths and diurnal solitary bees. Further, progeny from more isolated plants were less likely to have multiple sires regardless of the pollinator type. Moving forward, studies of mating system dynamics should consider the implications of multiple paternity and move beyond the self- and cross-pollination paradigm. Rhodes et al. (2017) demonstrate the importance of understanding the roles that functionally diverse pollinators play in mating system dynamics.

KEYWORDS
ecological genetics, multiple paternity, plant mating systems, pollination

In a time of unprecedented climate change, evolutionary biologists are scrambling to understand the consequences that changing selection pressures can impose on plant mating systems. Declines as well as compositional changes in pollinator communities are widely reported, but unfortunately, we have a limited understanding of how such changes may influence mating system dynamics (Karron et al., 2012). It is entirely possible that pollination networks will maintain overall pollen delivery, as the greatest proportion of pollinators tend to be generalists within a network (Hegland, Nielsen, Lázaro, Bjerknes, & Totland, 2009). However, even in scenarios in which rates of cross-pollination may be maintained, we know little about how changes in the *composition* of pollinators—the abundance of particular pollinating animals—will influence mating dynamics within populations. For example, in a controlled experiment and in relatively few generations, functionally different pollinators exerted rapid divergent selection on floral traits in *Brassica rapa* (Gervasi & Schietl, 2017). One of the ways different pollinators can influence mating systems is by altering the number of pollen contributing parents, *that is*, changing patterns of multiple paternity. However, the evolutionary consequences of changes to multiple paternity are not well understood and have been examined to varying degrees in only a handful of species (e.g., Karron & Marshall, 1990). On the one hand, multiple paternity is hypothesized to lead to higher overall offspring fitness by providing a bet-hedging strategy in stochastic environments. Conversely, multiple paternity could lead to reduced fitness of progeny by increasing competition among maternal half-sibships, and increasing the potential for biparental inbreeding. How then, do functionally different pollinators influence patterns of multiple paternity?

Rhodes, Fant, and Skogen (2017) address this question in the Arkansas Valley evening primrose, *Oenothera harringtonii*, an endemic to the grasslands of Colorado. *Oenothera harringtonii* is visited by both hawkmoths and diurnal solitary bees, which exhibit different morphologies and foraging patterns (Figure 1). Hawkmoths forage shortly after flowers open in the evening whereas bees visit flowers in the morning before senescence (Rhodes et al., 2017; Skogen et al., 2016). Hawkmoths are not only larger-bodied, but forage deep into the corolla in search of nectar and do not groom pollen between foraging bouts. In comparison, solitary bees are much smaller, groom between floral visits, and when foraging pollen of *O. harringtonii*, do not necessary make contact with stigmas. Further, pollinator observations confirmed that visitation frequency and pollen dispersal distance did not differ between pollinator types, meaning that differences in paternity were likely due to pollinator behaviour and morphology (Rhodes et al., 2017). Using pollinator exclusion treatments and genetic analyses, the authors were able to isolate the effects of widely different pollinators, hawkmoths and bees, on multiple paternity.

They found overwhelming evidence that pollinator type had a strong influence on multiple paternity; seed families from bee-pollinated flowers had far fewer pollen donors and then both open- and hawkmoth-pollinated flowers (Rhodes et al., 2017). In fact, hawkmoths were ~3.7 times more likely to visit multiple flowers during a foraging bout compared to bees (Figure 1). One presumed benefit of multiple paternity is that it provides a bet-hedging strategy, as variable paternity increases the probability that favourable genes will occur in progeny (Mitchell, Karron, Holmquist, & Bell, 2005). Notably, the habitat of *O. harringtonii* exhibits annual environmental fluctuations (Skogen et al., 2016), providing conditions that might favour greater multiple paternity. If high levels of genetic diversity within fruits are beneficial to overall offspring survival in fluctuating years, then declines in the level of hawkmoth pollination would have a strong influence on mating system dynamics of *O. harringtonii*.

Fruits fertilized by relatively more diverse pollen pools will exhibit decreased relatedness among individual seeds. Resource partitioning due to competition among half-sibs is predicted to result in a higher mean fitness relative to full-sibships (Karron & Marshall, 1990). Although Rhodes et al. (2017) did not measure potential consequences of competition among half-sibs, there is a fitness association with pollinator type in *O. harringtonii*. Flowers pollinated by bees set about a third-less seed than flowers pollinated by hawkmoths (Skogen et al., 2016) and there is a twofold reduction in number of effective pollen donors in bee-pollinated flowers (Rhodes et al., 2017). One interpretation of these findings is that increased fitness may be associated with greater numbers of pollen donors, a condition favoured by hawkmoths.

Interestingly, Rhodes et al. (2017) did not find significant biparental inbreeding in open-pollinated treatments, but seed families from both hawkmoth- and bee-pollinated seed families did have some biparental inbreeding. Understanding why exclusive pollinator types increase biparental inbreeding compared to open-pollinated plants requires further investigation. Nonetheless, in populations with inbreeding depression, biparental inbreeding results in reduced fitness of progeny. Ultimately, this will influence mating system

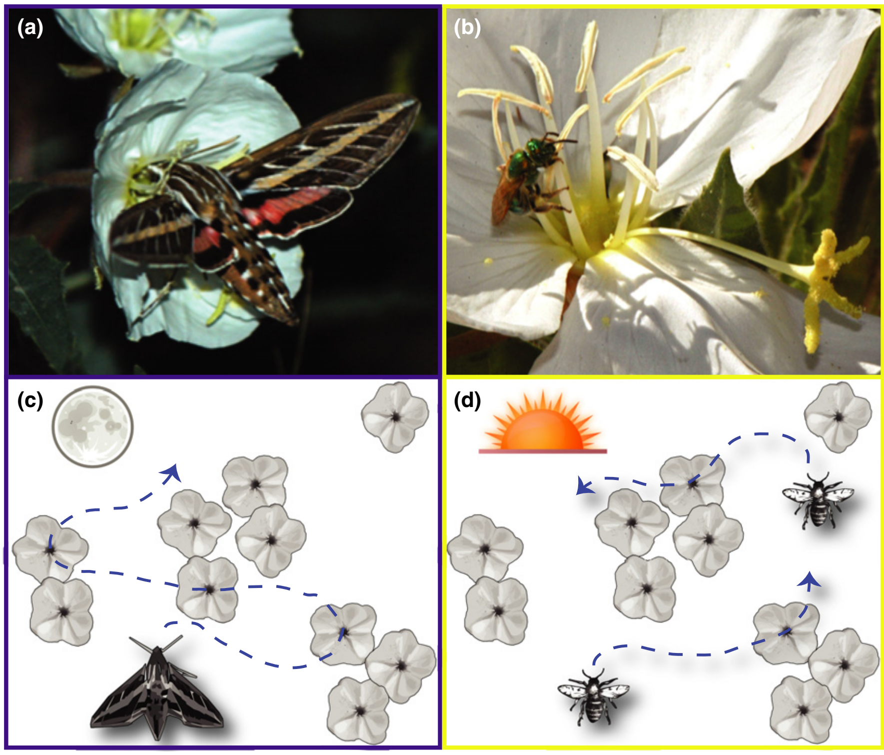

FIGURE 1 Two functionally diverse pollinators visit *Oenothera harringtonii*. Hawkmoths are larger-bodied, do not groom and forage deep into the corolla (a); solitary bees are smaller, groom between visits and can forage pollen without making stigmatic contact (b). Despite no differences in overall visitation frequency or pollen dispersal distance, hawkmoths are ~3.7 times as likely to visit multiple flowers on a single foraging bout and both pollinator types are less likely to visit isolated patches of flowers (c, d). Photograph credits: KA Skogen and SL Todd. Each dashed line depicts a foraging bout by an individual

dynamics by altering the potential consequences of inbreeding once deleterious alleles have been expressed in progeny. Given that pollinator treatments influenced levels of biparental inbreeding in *O. harringtonii* (Rhodes et al., 2017), more research is necessary to disentangle the relationship between biparental inbreeding and changes in pollinator composition.

We are currently challenged with understanding how ongoing changes in pollination ecology are influencing plant populations. Although the consequences of pollinator declines are worrisome, changes in the composition of pollinators can also impact plant mating systems. Differences in pollinator morphology and behaviour can influence selection on floral traits (e.g., Gervasi & Schietl, 2017), and the extent of multiple paternity among fruits (e.g., Rhodes et al., 2017). How changes in the composition of pollinator communities will impact the evolutionary trajectory of plant populations remains poorly understood and merits future research. Certainly, the enduring quest to understanding the intimate and fascinating relationship between plants and their insect pollinators is more important than ever.

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