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Ecology and evolution of floral volatile-mediated information transfer in plants

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Summary

Floral volatiles are complex, multi-functional signals that are often used by pollinators in combination with other signals, such as color. Floral visitors use floral scent to estimate the amount of reward present in flowers, to facilitate the identification of a specific host flower or as signals that chemically resemble those important for pollinator insects in other ecological contexts. There is good evidence that floral scent evolves under selection imposed by both mutualists and antagonists. Antagonists may often limit the amount of scent emitted by flowers, thus contributing to spatial population variation, and select for phenotypic plasticity after enemy attack. Floral scent is also an important component of pollinator-mediated reproductive isolation, as it often co-varies with color and morphology in sister species with different pollination systems.

I. Introduction

Floral signals are sexual signals, much like the flamboyant sexual displays found in many animals. However, floral signals do not directly address the sexual partner, but a vector (pollinator) that transfers the male gametes (Raguso, 2008; Schiestl & Johnson, 2013). Therefore, floral signals evolve under selection mediated by pollinators, often insects or birds, as well as by antagonistically interacting organisms that can eavesdrop on these signals. In the last decade, amazing progress has been achieved in our understanding of the functions and evolution of floral scent. A major component of this success has been achieved through functional studies that have essentially turned the field of 'fragrance research' from overly descriptive to largely experimental. Often, these studies include

electrophysiological analyses (gas chromatography with electroantennographic detection, GC-EAD) and bioassays with synthetic scent compounds or manipulation of floral volatile organic compounds (VOCs) *in situ*. Such studies have highlighted the multi-functional nature of floral scent, ranging from the attraction of mutualists to the deterrence of antagonists (Junker & Blüthgen, 2010; Kessler *et al.*, 2013), as well as direct defense through toxicity (Huang *et al.*, 2012). Some floral VOCs are, however, likely by-products of various biosynthetic processes and may not have evolved under adaptive evolution; nonetheless, they can be used as 'cues' (in a non-adaptive sense) by antagonistic flower visitors. Therefore, floral scent evolves as a mosaic, with different VOCs facing different selection and, to some degree, independent evolutionary fates.

Despite the fact that floral scent is of key importance for plant fitness, it should nonetheless be investigated in the context of other signals emitted by flowers. In many cases, pollinators find their host plant most efficiently when using both visual and olfactory signals, as recently demonstrated in systems involving generalist bees (Dötterl *et al.*, 2014), specialized bees (Burger *et al.*, 2010; Milet-Pinheiro *et al.*, 2012), cetoniid beetles (Steenhuisen *et al.*, 2013) and hawkmoths (Klahre *et al.*, 2011). An interesting additional aspect is the change in signal use when foraging pollinators gain experience with flowers. Some pollinators become broader in the type of volatiles they use (Burger *et al.*, 2012; Milet-Pinheiro *et al.*, 2013), whereas others switch their preference from olfactory to visual signals (Dötterl *et al.*, 2011). In this review, based primarily on papers published during the last 2 yr, I focus on the ecology and evolutionary origin of floral volatiles in different pollination systems, the conflicting selection mediated by mutualists and antagonists, and the component of reproductive isolation mediated by floral scent.

II. Why do pollinators use floral scent?

In a strict sense, no plant tissue is scentless, because volatiles can be a by-product of plant metabolism, and even the ubiquitous plant cuticular wax layer contains volatile components. It is clear, however, that in many flowers, certain volatiles have specifically evolved as signals, under selection imposed by pollinators. Below, I discuss three major factors in the pollinator's ecology and neurobiology that select for the production of volatile signaling in flowers. These three factors may often broadly overlap, and thus influence floral scent evolution in a combined way.

Floral scent as an honest signal

Honest floral signals are quantitatively associated with the quantity or quality of rewards offered by a flower, comparable with animal sexual signals that are correlated with mate quality. Honest floral signals can be the outcome of constraints as a result of the costs

involved in signal and reward production, or the product of selection as a result of the avoidance of cheaters by pollinators. Honest signals are thus expected to evolve when plants are: pollinated by generalist visitors that can switch to other food sources; and dependent on multiple, repeated visits by pollinators (Raguso, 2008). This is the case, for example, when pollen transfer is inefficient, flowering is sequential and prolonged, or when plants are self-incompatible (Knauer & Schiestl, 2015). It has been known for some time that bees are good learners of floral signals. They quickly form associations between rewards and a particular signal (Wright & Schiestl, 2009). Recently, it has been shown that bees can also assess the correlation between the strength of an olfactory signal and the amount of reward offered by a flower, which may be especially important in plants in which the amount of nectar is highly variable (Knauer & Schiestl, 2015). Because many studies on the learning of flower signals by generalist bees have been conducted with artificial flowers, we know surprisingly little about the actual signals used by generalist bees in a natural flower visitation context, which floral signals are (the most) honest ones, and whether bees preferentially use honest over dishonest signals. In some plants, visual signals (i.e. flower size) have been found to be honest signals (Gomez & Perfectti, 2010); however, few studies have compared visual and olfactory signals. A recent study that has done so found one floral scent compound to be more strongly associated with nectar sugar than flower size, at least on a per flower basis (Knauer & Schiestl, 2015). The finding that the salience of a stimulus impacts on its likelihood of being learned by bumble bees suggests that sensory exploitation (see below) can also have an impact on the learning of (honest) signals by pollinators (Katzenberger *et al.*, 2013).

Recognition of a specific host flower

Many pollinators are specialized on a given (group of) plant(s) and are thus dependent on signals or cues to efficiently identify them. Floral color may rarely be sufficiently specific to serve as an identifying token for a specialized visitor (Fig. 1). For example,

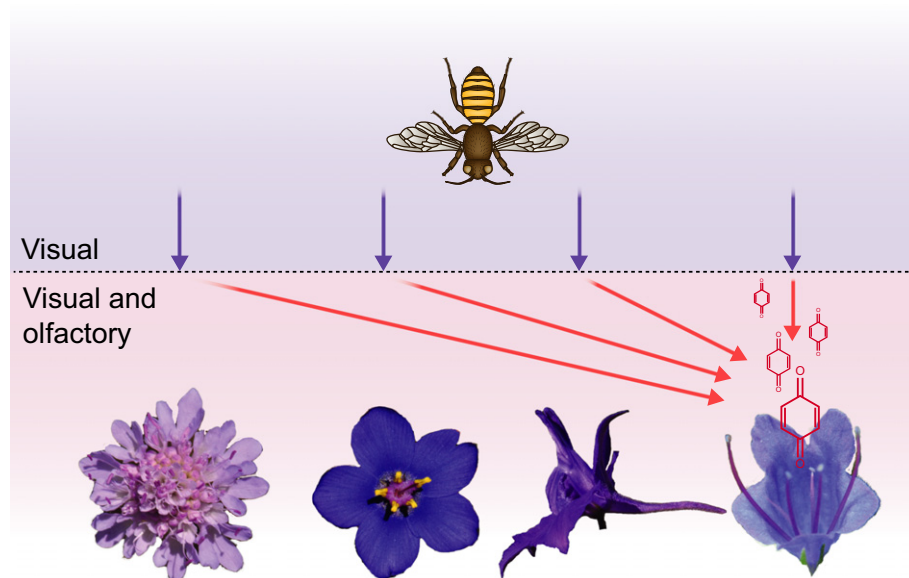


Fig. 1 Floral scent as a specific recognition signal/cue for specialized pollinators. A pollinator may use floral color as a general attractant, but specific volatiles to recognize its host plant. This strategy has been shown recently for *Hoplitis adunca* bees which use 1,4-benzoquinone as an *Echium*-specific recognition cue (Burger *et al.*, 2010, 2012).

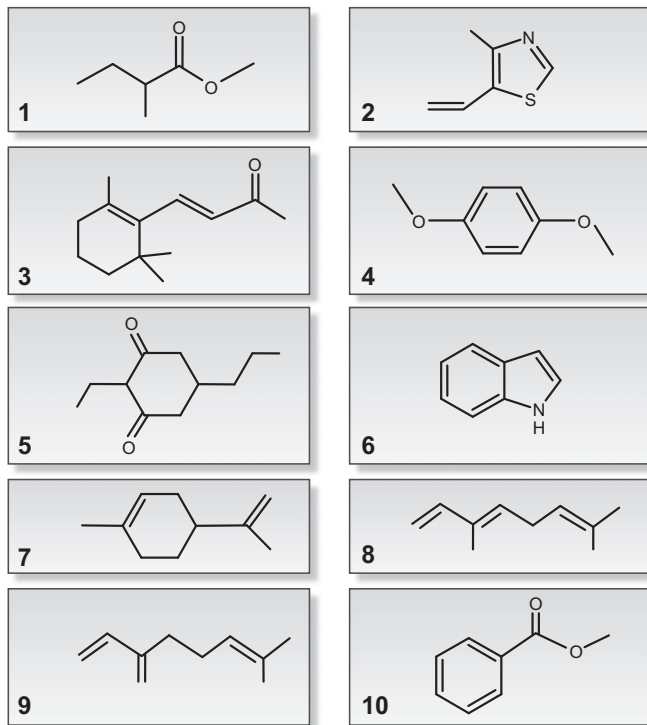


Fig. 2 Structures of volatile organic compounds (VOCs) introduced in the text. The names of the VOCs are: **1**, methyl 2-methyl butyrate; **2**, 4-methyl-5-vinylthiazol; **3**, dihydro- β -ionone; **4**, 1,4-dimethoxybenzene; **5**, chiloglottone; **6**, indole; **7**, limonene; **8**, ocimene; **9**, myrcene; **10**, methyl benzoate.

Hoplitis adunca bees, specialized on *Echium* flowers, are more strongly attracted by the blue color of their host flowers than by their smell. Only the combination of visual and olfactory signals, however, leads to discrimination between host and nonhost plants by the bees (Burger *et al.*, 2010). In *Macropis* bees that collect floral oil and pollen from *Lysimachia*, naive individuals prefer olfactory

over visual signals when foraging (Dötterl *et al.*, 2011). Arguably one of the most striking examples of specialized olfactory communication in plant–pollinator interactions are cyclocephaline scarab beetles, the nocturnal pollinators of several neotropical Araceae and members of other plant families. A recent breakthrough in the identification of behaviorally active floral VOCs in these systems was the identification of methyl 2-methyl butyrate (Fig. 2, **1**) as the *Cyclocephala*-attracting volatile in *Magnolia ovata* (Gottsberger *et al.*, 2012), and 4-methyl-5-vinylthiazol (**2**) as the key attractive volatile in several other cyclocephaline-pollinated plants (Maia *et al.*, 2012). Other specific floral VOCs used by cyclocephaline scarabs are (*S*)-2-hydroxy-5-methyl-3-hexanone (Fig. 3), dihydro- β -ionone (**3**) and a number of methoxylated aromatic compounds (Dötterl *et al.*, 2012; Maia *et al.*, 2012, 2013; Pereira *et al.*, 2014). Interestingly, in all cyclocephaline-pollinated taxa analyzed so far, the attractive scent compounds are not only produced in exceptionally large amounts, but also encompass the major components of the total bouquet, and are often emitted in combination with thermogenesis. This is in strong contrast with the pollination systems involving specialized bees, in which the attractive chemical signals seem to be much more cryptic. 1,4-Benzoquinone and spiroacetals (Fig. 3), the ‘bioactive’ VOCs emitted by *Echium* and *Campanula*, respectively, are emitted in trace amounts only and typically comprise <5% of the total bouquet (Fig. 3; Burger *et al.*, 2012; Milet-Pinheiro *et al.*, 2013). With such small amounts, these compounds resemble (non-adaptive) cues used by herbivores to find their host plants, such as cucurbitacins or isothiocyanates (Kuehnle & Mueller, 2011).

Sensory exploitation

Sensory exploitation (sensory drive, pre-existing bias) suggests that pollinators select for VOCs that are primarily used in ecological contexts other than flower visitation (Fig. 4; Schiestl & Johnson, 2013). For example, methoxylated aromatic compounds have been

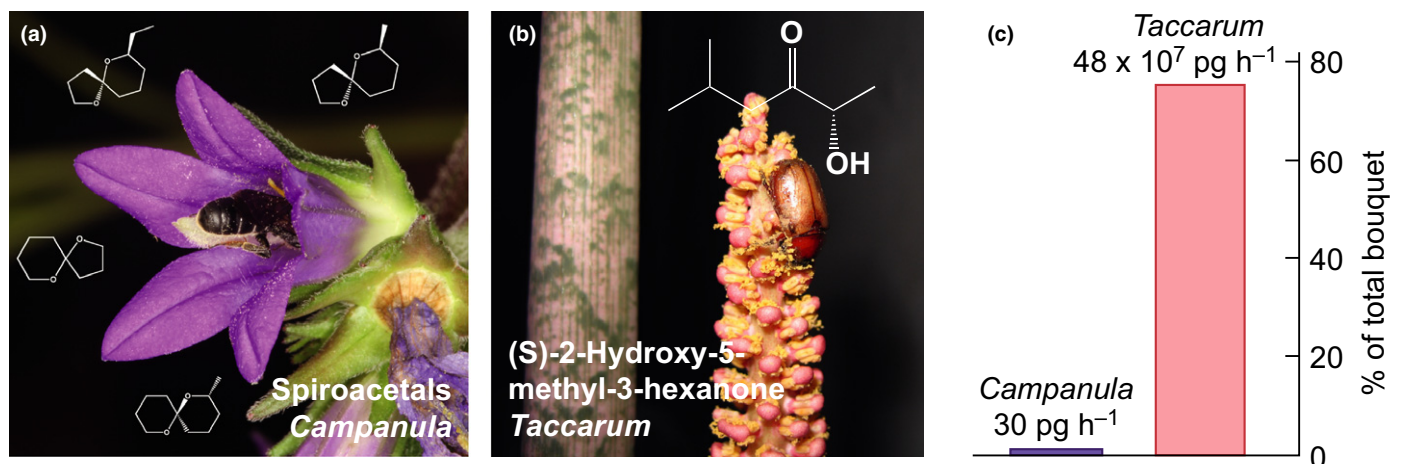


Fig. 3 Two examples of specific floral volatiles with extreme differences in the amounts emitted: (a) *Campanula glomerata* attracting *Chelostoma* bees with floral color and spiroacetals (photograph courtesy of Paulo Milet-Pinheiro), and (b) *Taccaurum ulei* attracting a *Cyclocephala* beetle with (*S*)-2-hydroxy-5-methyl-3-hexanone (photograph courtesy of Clemens Schindwein). In (c), the relative amounts of the active compounds as a percentage of the total bouquet in the two plant species are shown (left, spiroacetals in *Campanula*; right, (*S*)-2-hydroxy-5-methyl-3-hexanone in *Taccaurum*; Maia *et al.*, 2013; Milet-Pinheiro *et al.*, 2013). The numbers above the bars are the approximate mean absolute amounts emitted by a functional floral unit (flower or inflorescence).

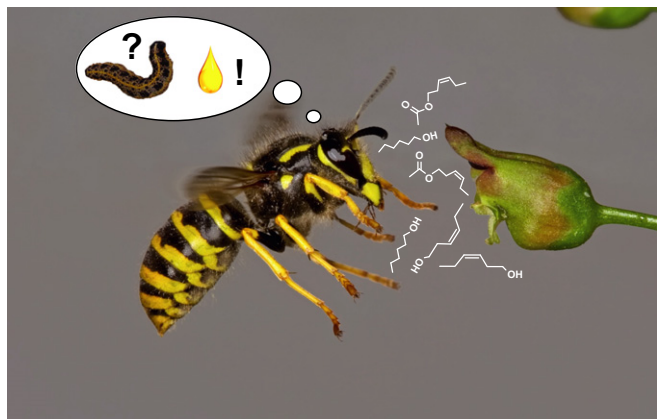


Fig. 4 Sensory exploitation in *Scrophularia* flowers pollinated by *Dolichovespula* social wasps (photograph courtesy of Heiko Bellmann). Flowers of *Scrophularia* produce green leaf volatiles (the figure shows (Z)-3-hexenyl acetate, hexan-1-ol and (Z)-3-hexen-1-ol) that are highly attractive for social wasps (Brodmann *et al.*, 2012). The same compounds are induced on herbivore attack by many plants, suggesting that wasps use these volatile organic compounds (VOCs) primarily when hunting for caterpillars (Brodmann *et al.*, 2008). *Scrophularia* and *Epipactis* have co-opted this signal to attract social wasps as pollinators by providing nectar as their reward.

identified as components of sex or aggregation pheromones in scarab beetles (Dötterl *et al.*, 2012), but also as attractive floral volatiles in cyclocephaline scarab-pollinated Araceae (Dötterl *et al.*, 2012; Schiestl & Dötterl, 2012). Such co-option of chemical

signals can be explained by sensory drive, namely through pollinator-mediated selection for volatiles for which olfactory receptors and/or preferences have not evolved in the pollination context. Because the pheromone functions of methoxylated aromatics are evolutionarily older than their occurrence as floral volatiles, this is an example of pre-existing bias (Schiestl & Dötterl, 2012). Other recent examples of floral VOCs that probably evolved under pre-existing bias are green leaf volatiles (GLVs, (Z)-3-hexenyl acetate, hexan-1-ol, (Z)-3-hexen-1-ol) emitted by *Scrophularia umbrosa* and *Epipactis helleborine* flowers, which are highly attractive to social wasps (Fig. 4; Brodmann *et al.*, 2008, 2012). Herbivore-induced GLVs are used by social wasps when hunting for caterpillars on plants, and have seemingly been co-opted to recruit these insects as pollinators through sensory exploitation. Although the flowers of both *S. umbrosa* and *E. helleborine* reward their visitors with nectar, those of *Epipactis veratrifolia* produce no reward, but emit terpenoids that constitute the alarm pheromone of aphids. This signal attracts hover flies that lay eggs on flowers (their larval stage feeds on aphids) and also pollinate the flowers (Stöckl *et al.*, 2011; Jin *et al.*, 2014). Thus, pre-existing bias can, but does not always, lead to the evolution of rewardless flowers. Sensory drive and pre-existing bias are also major factors leading to convergent signal evolution in plants, as exemplified by flowers employing brood site mimicry (Jürgens *et al.*, 2013). In these pollination systems, shared VOCs have evolved in five plant families, under similar selection imposed by insect pollinators specialized on dung, carrion or decaying plant matter as oviposition substrates.

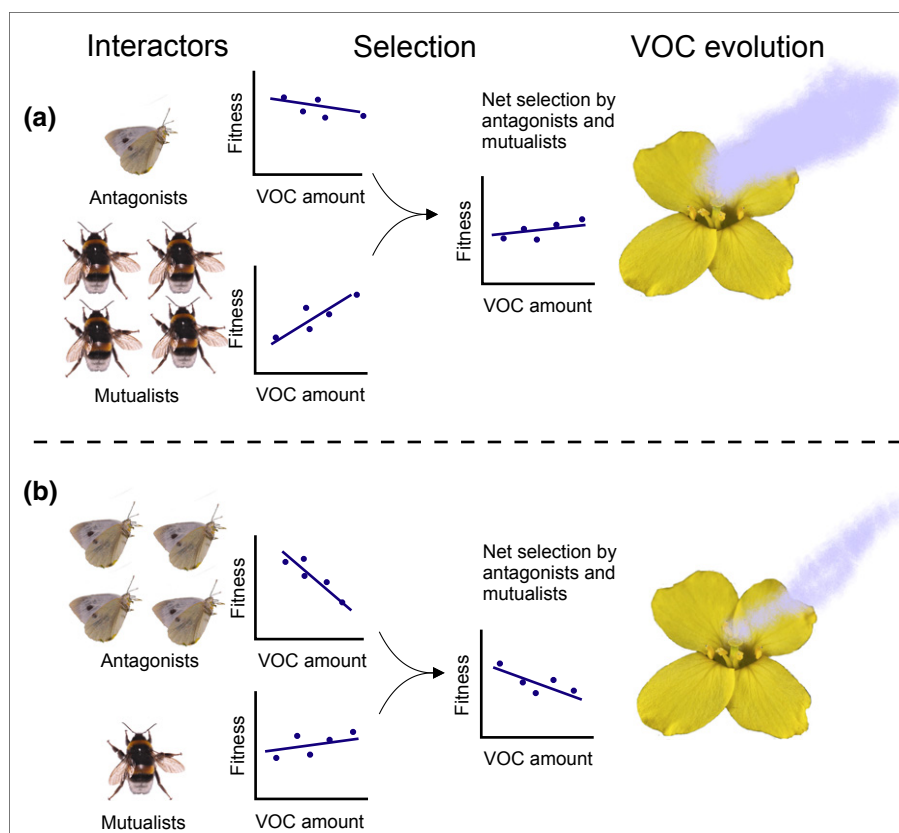


Fig. 5 Hypothetical example of selection on floral scent mediated by mutualists (pollinators) and antagonists (herbivores). Depending on the abundance of pollinators and herbivores, the net fitness outcome of volatile emission differs, leading to a spatially varying selection mosaic on floral scent. In (a), herbivores are rare, and thus the net selection on the volatile organic compound (VOC) is positive and strong scent emission evolves. In (b), herbivores are abundant, leading to net negative selection and the evolution of weakly scented flowers.

III. Conflicting selection imposed by mutualists and antagonists

Floral scent may rarely be detectable by mutualistic visitors only, but often also attracts antagonists, such as herbivores or florivores. Therefore, it can be assumed that VOCs evolve under conflicting selection for reproduction and survival, much like sexual signals in animals. This may explain the common observation of relatively small amounts of scent emitted by flowers, as well as often high geographic variation in scent emission (Galen *et al.*, 2011; Fig. 5). A scent compound known to attract both mutualists and antagonists of a single plant species is 1,4-dimethoxybenzene (Fig. 2, 4) emitted by *Cucurbita pepo* var *texana* flowers. This VOC is the major floral volatile and attracts specialized squash bees as pollinators, as well as striped cucumber beetles, a major herbivore and florivore of this plant (Theis & Adler, 2012). When this compound is enhanced artificially, increased beetle visitation, but not greater pollinator visitation was found, leading to decreased seed set. Generally, antagonists can select against 'showiness' in the sense of large amounts of floral VOCs. As the abundance of pollinators and herbivores varies in both space and time, geographically variable net selection on floral VOCs can be the outcome, possibly explaining some component of the high variation that typically characterizes floral volatile signaling (Fig. 5; Galen *et al.*, 2011). Although floral color variation is also known to be influenced by both pollinators and herbivores, we know very little about the combined effect of scent and color on the attraction of 'friends and foes' of plants (Ehrlen *et al.*, 2012).

Plants often show great phenotypic plasticity, and thus a change in floral signaling of an individual after herbivore or pathogen attack seems possible. Such a change can take the form of induced emission of repellent volatiles in tomato (Kessler *et al.*, 2011), or decreased emission of attractive VOCs in *Brassica* (Schiestl *et al.*, 2014), both leading to reduced attractiveness of flowers to pollinators. Although, in tomato flowers, a herbivore-mediated decrease in attractiveness led to reduced seed production, in *Brassica*, no major impact of the reduction in floral volatiles on the reproductive fitness of the plants was detected. An interesting novel finding in this context was that parasitoids were less efficiently attracted to herbivore-attacked plants in the presence of floral volatiles; this effect was reduced by the decreased emission of floral volatiles after herbivore feeding, suggesting a trade-off between pollinator attraction and indirect defenses (Schiestl *et al.*, 2014). Collectively, a range of factors probably influence the evolution of floral signaling strategies in the context of defense and reproduction. Specialization in floral signaling can be important, as it may lead to a decreased number of antagonists able to eavesdrop on attractive signals. This may allow cyclocephaline-pollinated aroids to emit huge amounts of uncommon volatiles, not detectable by generalist herbivores. Mating system, pollinator limitation and life history are important additional factors requiring more attention in future studies (Campbell & Kessler, 2013).

IV. Floral scent and reproductive isolation

Floral signals often differ between closely related species, suggesting that their divergence plays a role in the establishment of reproductive isolation during speciation. In highly specialized pollination systems, such as those involving sexually deceptive orchids or aroids pollinated by cyclocephaline scarabs, floral scent may even be the prime mechanism for floral isolation in co-occurring species (Gottsberger *et al.*, 2013; Peakall & Whitehead, 2014). For example, in *Chiloglottis* orchids, the presence of different (combinations) of volatile 'chiloglottones' (Fig. 2, 5) defines pollinator specificity and is tightly linked to different haplotypes in completely compatible, partly sympatric orchid species (Peakall & Whitehead, 2014). This situation suggests that floral scent differences can be the primary mechanism for reproductive isolation during speciation. The prerequisites for such pollinator-mediated speciation are selection for pollinator switching, and new chiloglottones present in extant populations either as standing variation or through novel mutations. Selection for pollinator switches could be fueled by competition for pollinator access in these deceptive orchids with typically low pollination success.

In less specialized systems, however, pollinators might only rarely respond in a highly specific and consistent manner to given VOCs, because associative learning of an exploitable reward is often involved in food searching behavior (Schiestl & Johnson, 2013). Nevertheless, floral scent can also constitute an important component of the suite of traits used by pollinators to differentiate among flowers. In recent studies on pairs of sister species with different pollination systems, some of them classical research models for pollinator-mediated evolution, two common themes were found: the key differences in floral scent were relatively simple; and scent differences were combined with different color and morphology. With regard to floral scent composition, *Ipomopsis aggregata* (hummingbird pollinated) and *I. tenuituba* (moth pollinated) differ primarily in the nocturnal emission of indole (6), which was only found in *I. tenuituba* (Bischoff *et al.*, 2014). In the bumble bee-pollinated *Mimulus lewisii*, the three monoterpenes limonene (7), ocimene (8) and myrcene (9) play a key role in pollinator attraction, in contrast with the almost scentless, hummingbird-pollinated *M. cardinalis* (Byers *et al.*, 2014). Flowers of the moth-pollinated *Petunia integrifolia* emit methyl benzoate (10) in a significantly greater amount than those of the hummingbird-pollinated, almost scentless *P. exsecta* (Klahre *et al.*, 2011). Methyl benzoate is important for the initiation of upwind flight in moths and also influences their probing on flowers. The evident simplicity in floral scent differences in these systems, involving only few VOCs, suggests that scent differences mediating assortative pollinator visitation can evolve rapidly.

V. Conclusions

The gaining of comprehensive insights into the ecology and evolution of floral scent has been notoriously challenging, because of its functional complexity. Therefore, despite the recent advances in experimental studies, more functional studies on floral VOCs are

needed to highlight how individual organisms respond to different signals and how plants alter their signaling strategies when enemies strike. Even more promising are experiments that manipulate volatile compounds and monitor net fitness effects. Such studies can highlight both the functions of volatiles and potential selection regimes on VOCs. The investigation of floral scent in the context of both mutualistic and antagonistic plant–insect interactions, as well as the integration of scent and other sensory modalities, should also be a target of future research, as it will allow for a more comprehensive understanding of plant signaling.

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