

Pollinator-mediated evolution of floral signals

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Because most plants rely on animals for pollination, insights from animal sensory ecology and behavior are essential for understanding the evolution of flowers. In this review, we compare and contrast three main types of pollinator responses to floral signals – receiver bias, ‘adaptive’ innate preferences, and associative learning – and discuss how they can shape selection on floral signals. We show that pollinator-mediated selection on floral signals can be strong and that the molecular bases of floral signal variation are often surprisingly simple. These new empirical and conceptual insights into pollinator-mediated evolution provide a framework for understanding patterns of both convergent (pollination syndromes) and advergent (floral mimicry) floral signal evolution.

Pollinators and selection on flowers

The diversity of flowers is one of the most striking features of the angiosperm radiation. Like the secondary sexual displays of animals, floral displays are products of sexual selection for traits that enhance mating success. However, unlike those in animals, the sexual displays of plants usually signal to animal intermediaries that act as couriers of male gametes. This means that an understanding of the evolution of floral signals requires additional insights from animal sensory ecology [1–5]. Floral displays vary in color, pattern, shape, and scent, which alone or in combination can act as signals for attraction of animal pollinators [1]. Selection favors signals that exploit the preferences and perceptual abilities of pollinators that are locally abundant and/or effective [6]. Thus, pollinator perception and its associated behavior constitutes a key selective environment for floral traits because it mediates the relationships between floral signals and pollen receipt and export. Recent insights into the mechanisms and evolutionary origins of pollinator preferences, the strength and shape of pollinator-mediated selection on floral signals, and their molecular bases make it now timely to update our understanding of the proximate and ultimate mechanisms of floral signal evolution.

In this review, we bring together insights from fields as diverse as insect sensory ecology, floral biology, and plant molecular and evolutionary biology to explain the processes and patterns of floral signal evolution. We first consider

the roles that various combinations of innate and learned preferences have played in the evolution of floral signals. We put particular focus on new insights into preferences that have not evolved in the context of flower visitation, so-called receiver bias, because it provides important insights into the evolution of floral signals that are not directly linked to floral rewards. We then focus on pollinator-mediated selection on floral signaling and how it can drive diversification. We show that the molecular basis of floral signal variation is often simple, enabling evolutionary lability. Finally, we discuss the selective factors that have shaped two important evolutionary patterns of floral signals; namely, floral convergence among unrelated plants (pollination syndromes), which arises when unrelated plants adapt to the same functional group of pollinators, and advergent floral evolution (floral mimicry), which arises when plants mimic the signals of key food plants, animal mating partners, or oviposition sites. Thus our review provides a single conceptual framework for understanding these two well-known patterns of floral signal evolution. We conclude by highlighting some of the current frontiers of research on the evolution of floral signals.

Types of pollinator response to floral signals

Receiver biases

The cognitive basis of pollinator attraction to floral signals is dependent on both innate behavioral responses and on learning, as well as on interactions between these factors. Innate sensory preferences have often been considered to be the outcome of unilateral adaptation of pollinators to flowers or reciprocal adaptation leading to coevolution [7,8]; however, recent investigations suggest that some of these preferences have not evolved in the context of flower visitation. For example, some bees show spontaneous preferences for radiating stripes, dark centers, and peripheral dots and such preferences are likely to have evolved in the context of finding nest burrows or of aggregation or mate-seeking behavior [9–11]. Such receiver biases [12] can be sensory, such as the ability to detect signals with a given efficiency, but can also be based on neuronal or higher cognitive processes in the perceiver's brain [5,13,14]. Most of the work on receiver biases has related to animal communication in the context of sexual selection, but this concept has recently also been applied to the evolution of mutualisms, including plant–pollinator interactions [5,15]. The general term ‘receiver bias’ used here includes phenomena such as perceptual bias, pre-existing bias, and sensory traps, each having a slightly

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Box 1. Coevolution and pre-existing bias in floral signaling

The hypothesis of trait coevolution makes the assumption that selection leads to reciprocal adaptive evolution in interacting partners. For example, pollinators should evolve effective detection of floral signals associated with the highest reward and plants should produce signals that exploit the sensory abilities of their most effective pollinators. On a macroevolutionary scale, traits should evolve congruently in taxa that interact with each other. Key factors for microevolution of signal perception and floral signaling are the fitness effects that these can have on the respective partners in the interaction. Whereas the link between floral signals and reproductive fitness in plants is well established, surprisingly few studies have addressed the fitness consequences of sensory abilities and innate preferences in pollinators. Raine and Chittka [24] showed that innate preferences in bumblebees are variable and can lead to more efficient nectar foraging when corresponding to the most rewarding colors present in the plant community. This suggests that signaling and signal perception could potentially coevolve at the population level. Such coevolution has, however, not been corroborated by macroevolutionary studies that tested for patterns of coevolution in sensory

abilities and floral signals. Traits like trichromatic color vision and preferences for given 'floral' scent compounds in insects evolved before these insects started to visit flowers and thus clearly pre-date the evolution of the matching floral color and the respective floral scent compounds [17–19] (Figure 1). This pattern thus suggests that attractive floral signals evolve under pre-existing bias. The seemingly contradictory findings of micro- and macroevolutionary studies can be reconciled, however, by distinguishing between the kinds of traits expected to evolve at different hierarchical levels. Major innovations, like olfactory or color receptors, or the ability to learn signals might have evolved in a context other than pollination, perhaps through sexual selection, and thus be more constrained as adaptations for flower visitation. However, fine-tuning of sensory and perceptual abilities as well as some innate preferences might show more adaptability and hence coevolve with floral signaling at the population level. Highly specialized brood-site mutualisms, such as those between figs and fig wasps, are among the most promising systems for identifying coevolution between plant signals and pollinator sensory preferences.

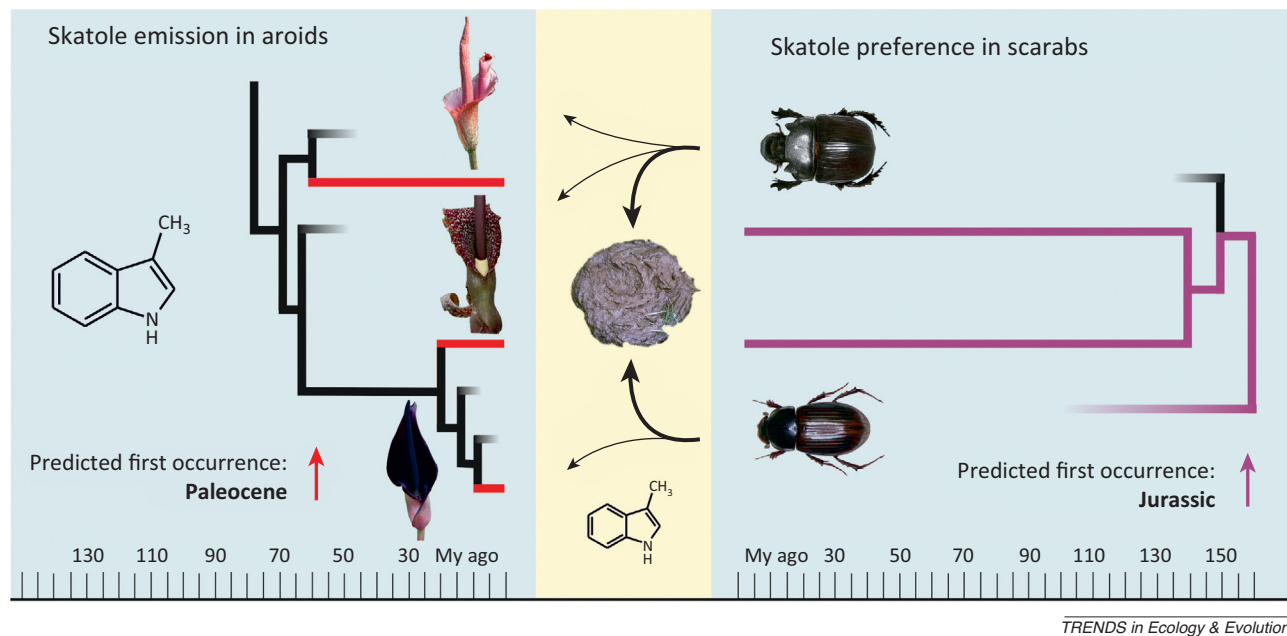


Figure 1. The emission of skatole in mimetic Araceae has evolved through pre-existing bias. The three aroid genera *Amorphophallus*^a, *Sauromatum*^a, and *Arum*^b (from top to bottom in the left panel) comprise species with skatole emission (red branches in left phylogeny) that mimic dung and thereby attract coprophagous insects as pollinators. Skatole emission is a key signal in this floral mimicry, because it is usually emitted from dung and attracts dung beetles. The right panel shows a reconstruction of preference for skatole (purple branches in phylogeny) in scarab beetles. The figure shows species of the genera *Heliocopris*^c (top) and *Aphodius*^c (bottom) that pollinate dung-mimicking aroids in *Amorphophallus*, *Sauromatum*, and *Arum*, respectively. Dated phylogenies suggest that preferences for skatole in the beetles evolved at least 150 Mya, whereas the emission of skatole in aroids evolved comparatively recently, approximately 60 Mya [19]. Picture credits: ^aAlex Bernhard, ^bSeán O'Hara, ^cUdo Schmidt.

different meaning [12]. The insight that receiver bias often existed before its current context, a phenomenon known as pre-existing bias, has been gained through phylogenetic studies [16]. Several recent studies support this scenario in plant–pollinator interactions by showing that pollinator preferences for floral signals are evolutionarily older than the floral signals themselves [17–19]. Floral mimicry provides a prime example of floral evolution through pre-existing bias (Box 1), but this phenomenon is by no means limited to mimetic plant–pollinator systems.

One example is the evolution of floral scent under selection imposed through the pre-existing bias of pollinators for compounds used in their own chemical communication channels. Indeed, floral fragrances often show

chemical similarities to compounds involved in insect chemical-communication systems [20]. Some flowers produce insect sex or aggregation pheromones to attract pollinators; others produce alarm pheromones to ward off unwanted visitors [21]. Other evidence suggests that floral color evolved long after insect color vision. The most common form of color vision in insects, the presence of three color receptors sensitive for UV, blue, and green, has been shown to be ancestral in the insects as a whole, and basal insect lineages are much older than flowering plants [17]. Therefore, floral color seems to have evolved under the broad perceptual bias imposed by insect color-vision systems. In addition, large floral displays have been shown to be attractive to many pollinators [13,22]. Although such

preferences might have evolved because larger displays can reflect greater rewards, they can also be explained simply by better detection of larger, colored objects [23] or by higher cognitive processes in the brain [13] that would have been present before the evolution of flowers.

Adaptive innate preferences

In contrast to receiver biases, innate sensory preferences in pollinators can also reflect the outcome of selection for efficient usage of the most rewarding flowers in a given habitat. Such preferences have been shown to increase the efficiency of foraging in bumblebees [24], although these generalist insects have traditionally been considered to rely mainly on associative learning for flower choices. Innate preferences have even been shown to vary among populations of bumblebees, possibly in relation to the signals produced by the most important food plants [2]. Although innate preferences of naive bees might seem relevant only for the first few flower visitations, they have also been shown to persist after associative learning, when bees have to choose among colors sufficiently different from the learned colors [25].

Oligolectic bees specialized for certain host plants for pollen collection often show innate sensory preferences for host-plant signals, such as petal color or particular floral scent compounds [26,27]. Such preferences are thought to have a genetic basis and can be pronounced, leading to the rejection of potentially suitable pollen sources in a given community, even in the absence of the host plants [8]. Floral preferences of oligolectic bees can even constrain host switching during bee diversification. In the genus *Chelostoma*, for example, host use is highly conserved and related species often use flowers of similar shape and color, sometimes of unrelated plant lineages [28].

Several pollinators show innate behavioral responses to the yellow color of pollen or its contrast to petal colors, relating to their use of pollen as food [29]. Many plants produce yellow spots or patterns on petals, which are thought to exploit innate pollinator preferences for signals associated with pollen [30]. Pollen imitation might not only increase the attractiveness of a flower to pollinators, but can also decrease male fitness costs inferred by pollen collection by pollinators. Whether an innate sensory preference confers fitness benefits to a pollinator thus depends on the context of floral visitation, because plants can readily exploit these preferences without providing rewards.

Associative learning

Sensory preferences of pollinators can quickly be altered by associative learning, leading to a preference for the signal associated with the highest reward in any given plant community [31–33]. For example, the sphingid moth *Manduca sexta* learns to feed from bat-adapted *Agave* flowers through olfactory conditioning, but then easily switches to moth-adapted *Datura* flowers as they become more common in the community [34]. Even learning, however, can be subject to receiver bias; that is, in the form of a shifted response away from a rewarded stimulus (peak shift) [14,35]. Learning of floral signals enables floral constancy by the pollinators – the short-term specialization of

Box 2. Rewards and floral signals

The quantity (and quality) of floral rewards and local abundance of plant species have important consequences for pollinator-mediated selection on floral signals. Highly rewarding plants that are common in a community should be selected to produce unique signals. These signals encourage pollinators to establish constancy on flowers of these species, leading to fitness advantages in terms of increased receipt and export of intraspecific pollen and reduced clogging of stigmas with incompatible pollen [80]. Plants that are either too rare or insufficiently rewarding to induce constancy can nevertheless attract pollinators by imitating signals of other rewarding plants, either in a nonspecific sense, known as generalized food deception, or in the more specific sense of floral mimicry [81] (Figure 2). There is probably stronger selection for floral mimicry in deceptive species because they are more likely than rewarding species to be pollen limited [82]. Floral mimicry is indeed strongly associated with deception, but some mimics are also rewarding (Müllerian mimicry) [73,83,84].

Floral deception is a common strategy among plants, particularly in orchids where it occurs in approximately 40% of species [85]. Pollination by deception is thought to be maintained by selection when inbreeding depression is high and pollinators are abundant [86]. Most deceptive plants deploy generalized food deception, indeed lack of specialization in pollinators, particularly bees, is thought to be the major constraint on the evolution of mimicry (Figure 2). Receiver bias of pollinators is likely to explain the evolution of the large floral displays associated with generalized food deception. However, pollinator learning has been implicated in the evolution of floral color polymorphisms in food-deceptive orchids [87]. It has been suggested that rare color morphs are favored by negative frequency-dependent selection, because pollinators would learn to avoid the dominant color morph and switch to visiting flowers of other colors. The evidence for this mechanism is equivocal, with at least one study finding no association between morph frequency and fruit set [88]. Selection imposed through avoidance learning by pollinators might more commonly lead to a continuum of variability in floral signals, rather than discrete polymorphisms [89,90]. In the case of scent signals, avoidance learning can lead to reduced emissions because scent is a particularly powerful learning cue [91].

pollinators on flowers of a given type – which can have important consequences for floral evolution [36]. Whether pollinators establish floral constancy depends on the rewards offered by flowers and the uniqueness of their floral signals in a community context. Plants with poor or no rewards relative to the rest of the community will not induce constancy and are likely to be selected to mimic the signals of more rewarding plants (Box 2) and thus share their pollinators. By contrast, plants that are highly rewarding are likely to undergo selection, through pollinator associative learning, for distinctive signals, leading to floral constancy by pollinators. Selection for traits that induce floral constancy might underlie the processes of character displacement and reinforcement and thus play an important role in maintaining or establishing reproductive isolation [36].

Floral signals as targets of selection and their molecular basis

To drive evolutionary change in floral signals, pollinators must impose selection on traits that show heritable variation. On the one hand, pollinator-mediated selection has been detected through classical phenotypic selection studies in natural plant populations [20,31,37,38]; on the other hand, signals impacting on pollinator behavior have been identified through functional studies involving

Box 3. Plant antagonists and floral signals

Besides pollinators, plant antagonists can also influence the evolution of floral signals, either through direct fitness effects via destruction of flowers or indirectly through allocation trade-offs between defense (survival) and reproduction. Volatiles emitted by reproductive structures of plants are in fact likely to have evolved as primarily defensive traits in the ancestors of flowering plants [20,92]. Plants that attract animals as pollen vectors face a 'signaling dilemma' of how to attract pollinators yet deter antagonist visitors. A possible solution to the signaling dilemma is the production of specific volatiles that attract pollinators, in addition to others that deter antagonists [93,94]. Such functional division among volatiles can explain the evolution of chemically complex floral scent bouquets. An even more elegant adaptation was shown in *Acacia* flowers, where *E,E*- α -farnesene seems to both attract pollinators and repel ants that interfere with pollinator visitation [21]. When the attractive and defensive functions of floral signals interfere with each other, a trade-off between defense and pollinator attraction is the outcome. Such signaling trade-offs are supported by negative pollinator-mediated selection on certain floral volatiles in *Gymnadenia odoratissima* [95] and the finding of a deterrence effect of strong floral emission of 2-phenylethanol to both ant larcenists and bumblebee pollinators in *Polemonium viscosum* [45]. These studies suggest that balancing selection, depending on herbivore pressure, can contribute to high variation in floral signals. One way that signaling trade-offs are moderated is when changes in floral signals are induced only on herbivore attack. Such phenotypic plasticity is predicted to evolve under herbivore-mediated selection, as in the examples of decreased petal size or altered floral fragrance emission after herbivore attack, reducing attractiveness to pollinators [96–98]. However, herbivory can also increase floral attractiveness [99], possibly through increased emission of pollinator-attracting floral volatiles [100]. This can lead to compensation of fitness losses imposed by herbivory through increased pollination success [99]. As yet, we know little about whether induced changes in floral signaling are pleiotropic consequences of direct or indirect plant defenses or adaptive strategies to avoid destruction of reproductive organs or compensate biomass losses. More knowledge on the molecular details and signaling pathways of induced changes, as well as assessments of fitness consequences, will shed more light on the evolutionary origins of antagonist-mediated floral signaling.

manipulation of signals [39] (Box 3). Taking into account the sensory abilities of pollinators, such as their visual systems, has often been proven to be of key importance for identifying the functions of floral signals [40,41]. In the case of floral scent, electrophysiological detection combined with behavioral assays has led to the identification of specific pollinator-attracting volatile compounds, allowing researchers to decipher precisely part of the chemical language used by plants in their interaction with pollen vectors [42,43]. Adding floral scent compounds to flowers and removing individual compounds through gene silencing has revealed their functions in attracting and repelling mutualistic and antagonistic visitors, respectively [44–46].

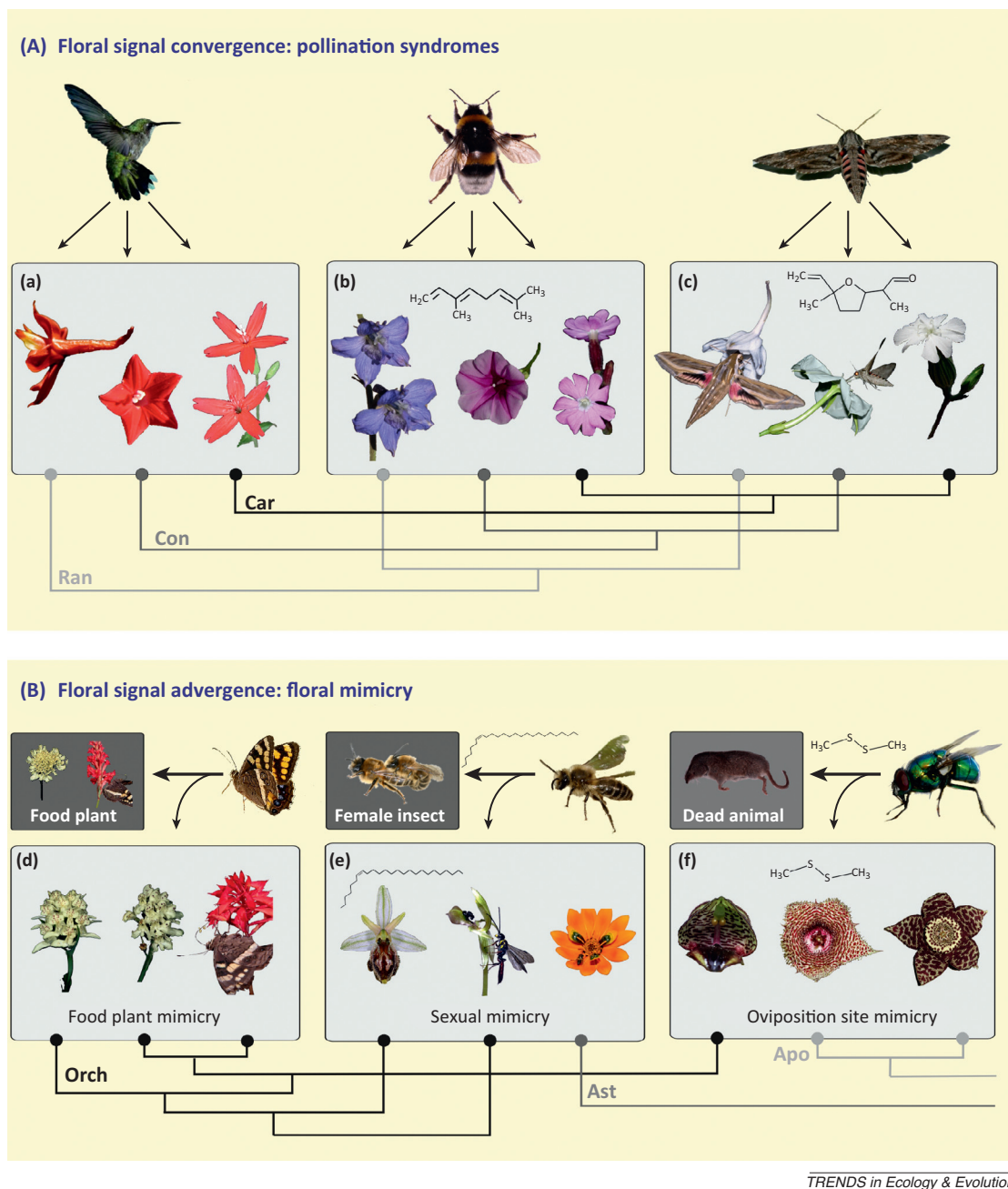
Phenotype manipulation experiments have shown that a change in floral signals, such as scent emission, can lead to the attraction of different pollinators [39] and thus contribute to reproductive isolation [47]. In some plants, pollinator differences between related species can be the most important prezygotic isolating barrier [48]. In the evolution of such floral isolation, the molecular basis of signal differences is an important factor for its emergence and potential fixation among populations (or species). Differences based on simple mutations are expected to arise more frequently, leading to higher adaptability. In

addition, adaptive signal variation based on a single locus or a few loci only is also more likely to be maintained under gene flow, because recombination is expected to break up coadapted complexes of multiple genes. Molecular investigations have indeed mostly demonstrated a simple genetic basis of floral color differences based primarily on expression differences in pigment-biosynthetic genes rather than coding-sequence differences in structural genes [49–53]. Such expression differences can be mediated by single transcription factors, for example through loss of function mutations [49], or by mutations in *cis*-regulatory elements of structural genes [53]. Although floral scent is often more complex than color, the molecular basis of its variation can also be simple, at least for suites of compounds arising from related biosynthetic pathways. In sexual mimics of the genus *Ophrys*, structural genes encoding biologically active scent compounds have recently been identified [54]. These genes form a gene family with different allele groups and, again, expression of different alleles is likely to be an important mechanism for the production of different scent bouquets [55]. The apparent genetic simplicity of alteration in floral signals might explain their common phylogenetic lability associated with shifts in pollination systems and suggests that variation in adaptive traits should emerge frequently through different mutational events [51].

Floral convergence leading to pollination syndromes

Unrelated plants pollinated by the same pollinators tend to exhibit convergence in their floral traits, including advertising signals [56]. These macroevolutionary associations between particular signals and pollinators (Figure 1) are usually based on qualitative measures of flower color and scent according to human perception. Nevertheless, an increasing number of quantitative studies show good support for signal convergence [1,57,58]. Convergent floral syndromes can be useful for generating hypotheses about traits under pollinator-mediated selection. For example, bat-pollinated plants show convergence in emission of sulfur-containing compounds [59]. Bats have been shown to be attracted to some of the compounds, providing an explanation for their evolution [60].

It is generally assumed that convergence in floral signals among plants is due to 'hard-wired', innate sensory preferences of their shared pollinators. In particular, the premise is that these sensory preferences are similar within, and different between, various functional groups of related pollinators. The evidence for this is, however, weak and available data relate mostly to chemical communication. Some noctuid moths, for example, have shared innate preferences for scent compounds such as lilac aldehyde and phenylacetaldehyde [42,61], which are typical constituents of moth-pollinated flowers [59]. The evidence for hard-wired preferences for color is even weaker. Hummingbirds, for example, do not display innate preferences for red, although this color is predominant among flowers pollinated by these birds [62,63]. The visual system of a hummingbird species with red crown plumage in males has, however, been shown to be particularly sensitive to red, meaning that it would perceive red flowers as having a higher chromatic contrast to the background than flowers



TRENDS in Ecology & Evolution

Figure 1. Patterns of convergent and advergent evolution in floral signals in response to pollinator preferences. **(A)** The upper panels show three examples of pollination syndromes, where unrelated plant taxa show evolutionary convergence in their floral signals. The phylogenetic associations of the different taxa are shown below the pictures. (a) Hummingbird pollination, from left to right: *Delphinium nudicaule*, *Ipomoea quamoclit*^a, *Silene virginica*^b. (b) Bee pollination: *D. dasycaulon*, *I. pes-caprae*^c, *S. dioica*; the molecule shown is β -ocimene, a scent compound commonly found in bee-pollinated plants. (c) Moth pollination: *D. leroiyi* visited by *Hippotion celerio*, *I. alba*, *S. latifolia*; the molecule shown is lilac aldehyde, a scent compound that is attractive to moth species. **(B)** The lower panels show different floral mimicry systems, where mimics adverage towards different models (shown in the dark-shaded boxes) under selection mediated by the pollinators (the 'operators'). Phylogenetic relationships of the plant species are shown below the pictures. (d) Food-plant mimicry, models: *Scabiosa columbaria* and *Tritoniopsis triticea*; pollinator: the nymphalid butterfly *Aeropetes tulbaghia*; mimics: *Brownleea galpinii*, *Disa cephalotes*, *D. ferruginea*. (e) Sexual mimicry, model: a virgin female of the vernal bee, *Colletes cunicularius* (copulating with a male); pollinator: a male vernal bee, *C. cunicularius*^d; mimics: *Ophrys exaltata*, *Chiloglottis trapeziformis*^e visited by a male *Neozeleboria cryptoides*, *Gorteria diffusa*. The molecule shown is (Z)-7-pentacosene, a key component of the sex pheromone of *C. cunicularius*. (f) Oviposition mimicry, model: dead shrew; pollinator: a calliphorid fly; mimics: *Satyrion pumilum*, *Huernia hystrix*, *Orbea variegata*. The molecule shown is dimethyl disulfide, a key molecule in carrion mimicry. Ran, Ranunculaceae; Con, Convolvulaceae; Car, Caryophyllaceae; Orch, Orchidaceae; Ast, Asteraceae; Apo, Apocynaceae. Picture credits: ^aLorne Wolfe, ^bMichele Dudash, ^cRob Raguso, ^dNicolas Vereecken, ^eRod Peakall.

of other colors [64]. This suggests that red coloration in bird-pollinated flowers might have evolved through perceptual bias based on detectability.

Associative learning by pollinators in a community context can play an important role in the evolution of pollination syndromes. Hummingbirds, despite their lack

of innate preferences for red, quickly learn to associate colors with rewards [31] and in a community in which the dominant bird-pollinated plants have red flowers, plants that have red-flowered mutants will attract hummingbirds on account of their positive associative conditioning on this color.

Floral antagonists can also play a role in the convergence of floral signals. Bees, for example, often rob bird-adapted flowers of nectar and pollen. The red color of these flowers can discourage bee visits, because the bee visual system does not clearly distinguish the color red from the background [3,65]. When competing for floral rewards in a community context, bees prefer easily detectable flower colors such as blue [2]. Hummingbirds, by contrast, can detect red flowers easily and quickly learn to associate them with high rewards, leading to preferential visits to red flowers in the field [62,63,66,67]. In another example, convergent evolution of floral colors similar to those of background vegetation in a guild of plants pollinated by pompilid wasps has been attributed to selection for crypsis, because the exposed nectar of these flowers would otherwise attract insects such as bees and flies that are not morphologically suited to pollinate the flowers [68]. The wasp pollinators themselves can rely entirely on olfaction to locate the flowers [68].

Floral advergence leading to mimicry

Mimicry is the similarity of one organism (the mimic) to another (the model) that enhances the mimic's fitness through its effect on the behavior of a third party, the

operator. Because the mimic evolves to resemble a model, but the model is not necessarily shaped by the mimic, this is a form of adverbent evolution [69]. In floral mimicry, the operator is a pollinator and the models can be the flowers of rewarding plants [70], or even oviposition sites [71] or female insects [43,72] (Figure 1). Mimicry is most effective when behavioral responses to the signals of models are essential for the survival or reproduction of certain pollinators.

To distinguish mimicry from chance similarity, the resemblance of a mimic to its model must be adaptive. Thus, in plant lineages, signals that confer similarity to a model would be expected to be not only functional, but also evolutionarily derived [73]. Floral mimics can be deceptive (no reward present, analogous to Batesian mimicry in palatable animals) or rewarding (analogous to Müllerian mimicry in unpalatable animals). Floral mimicry is mostly driven by the innate sensory preferences of the pollinator, but associative learning can also play a role, particularly in food-deceptive systems. In deceptive mimicry, the innate responses of a pollinator can be considered perceptual bias because they could not have evolved in the context of visits to the mimic (because such visits would not confer a fitness benefit). Therefore, the preferences of a pollinator for

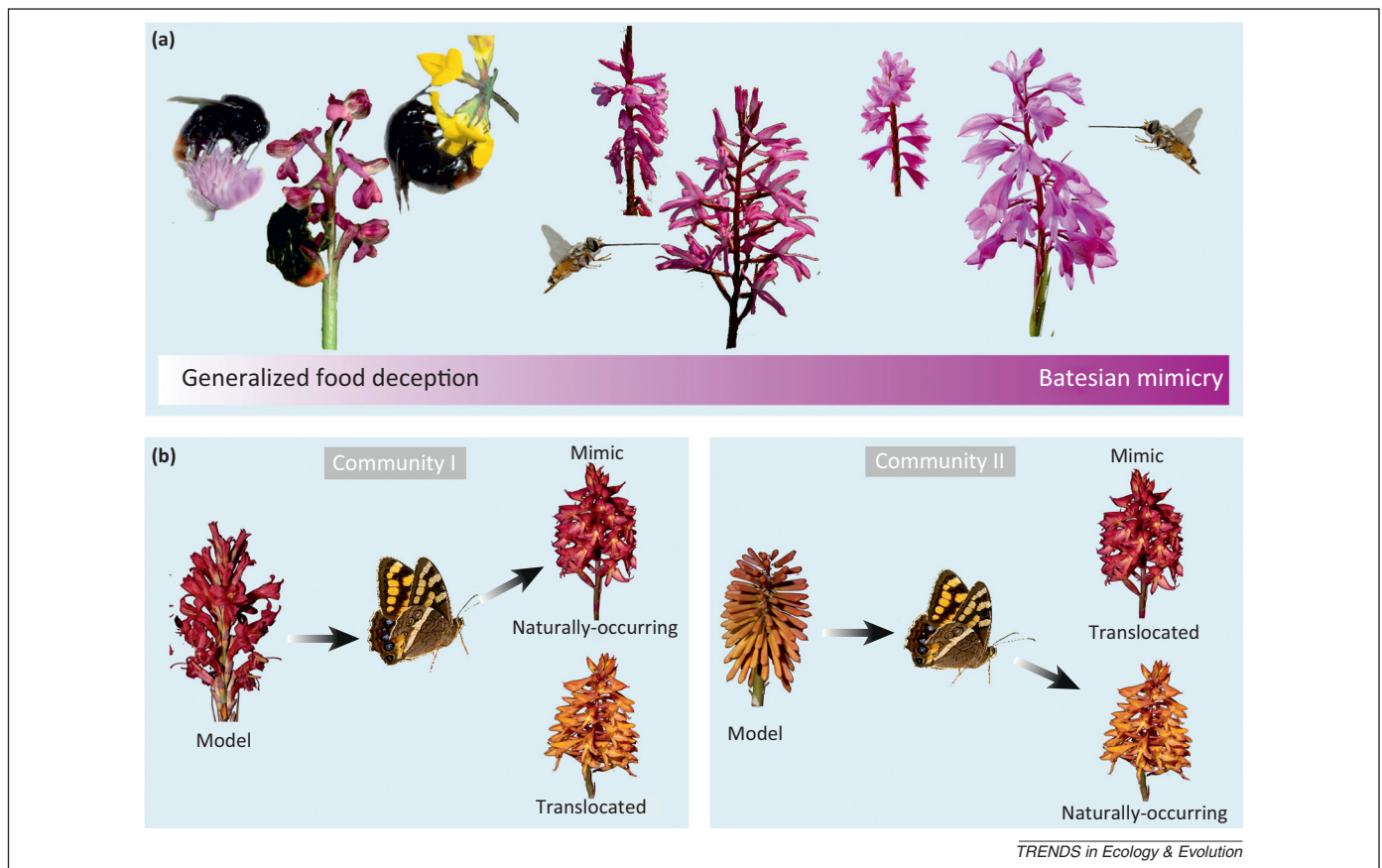


Figure 2. The evolution of floral signals in food-deceptive plants. **(a)** Signaling strategies used by non-rewarding plants to attract food-seeking pollinators show a continuum from generalized food deception to Batesian mimicry of the floral signals of particular rewarding plant species [76]. Generalized food deception exploits generalist pollinators and involves signals that cannot usually be traced to specific models, but there are species midway along the continuum that mimic the general signals of a guild of pollinator food plants. Floral Batesian mimicry exploits specialized interactions between pollinators and their food plants and typically involves close matching of the spectral reflectance and shape of the flowers of a particular model food plant. These strategies are illustrated (from left to right) by the orchids *Anacamptis* (= *Orchis*) *morio*, *Disa* *nervosa*, and *D. pulchra*, with plant species used as nectar sources by their pollinators shown above. **(b)** The evolution of flower color in Batesian mimics can depend on the community context. The deceptive orchid *D. ferruginea* occurs in two morphs: a red-flowered one in communities in which its butterfly pollinator (*Aeropetes tulbaghia*) obtains nectar from the red-flowered iris *Tritoniopsis triticea* (left panel) and an orange-flowered one in communities where the butterfly obtains nectar from the orange-flowered lily *Kniphofia uvaria* (right panel). Reciprocal translocation experiments have shown that, when offered a choice, the butterfly prefers to visit local morphs of the orchid that match the color of its nectar food plants [74].

signals emitted by the mimic can be expected to be evolutionarily older than the interaction between the two species (Box 1) [19]. Floral mimicry, in which, by definition, a specific model is imitated by a plant mimic, is likely to evolve when the relevant pollinators are specialized (Figure 2). For example, pollinators specialized on particular food plants are expected to have innate preferences for the floral signals associated with their hosts' flowers [26]. To attract such specialized pollinators, the mimic will be selected to match the signals of the host plant. In this situation, perceptual bias by the pollinator can lead to the evolution of mimicry. By contrast, the color preferences of pollinators of food-deceptive mimics can be shaped by the colors of flowers of local rewarding model plants [74] (Figure 2), suggesting a role for associative learning. Analysis of reflectance spectra in terms of the perceptual space of pollinators has shown that the flower colors of mimics and models are usually indistinguishable to their pollinators, although they sometimes differ in color according to the human eye [40,41]. The importance of color in food-deceptive mimicry systems is also evident from experimental studies showing that manipulation of behaviorally active components of the visual signals of mimics, such as their UV reflectance, results in a marked decline in pollinator visits [41].

In sexual mimicry (Figure 1) [11,43,72], plants exploit the responses of male insects to mating signals [75]. In this case, the receiver bias of male pollinators evolves in the context of sexual selection. Male insects are often under strong sexual selection to find conspecific females quickly and therefore typically show strong innate preference for signals, such as sex pheromones, emitted by receptive females. When effective as pollinators, male mate-searching insects impose selection that results in advergence of floral signals towards the mating signals of the female insects, which are the models in these systems.

Similar evolutionary dynamics occur in oviposition mimicry, where substrates usually used for egg laying, such as dung or carrion, serve as models (Figure 1) [71]. Female insects dependent on such substrates often show strong and specialized responses to the associated signals, which are typically volatile compounds. Plants exploiting these responses by female insects are selected to produce the same signals, leading to floral mimicry of model oviposition substrates in terms of both scent and visual signals (Figure 1).

Although most floral mimics are deceptive (non-rewarding), most deceptive plants are not specific mimics. Deception itself is thought to be maintained by selection because it reduces pollinator-mediated self-pollination by discouraging pollinators from lingering on plants, whereas mimicry increases the likelihood of pollinator visitation and, through its association with specialized pollinators, can also promote pollination efficiency [76]. Most food-deceptive plants have generalized pollinators and these do not select for mimicry because they lack non-variable innate preferences for the signals of a potential specific model and are also unlikely to be conditioned by the signals of a single rewarding plant species (Figure 2). Because receiver biases are a fundamental factor that shapes signal evolution in both mimetic and non-mimetic plant–insect interactions,

we do not view them as an alternative explanation for mimicry or mimicry-like phenomena [5,77]. Receiver biases in combination with associative learning underlie the pollinator-mediated selective processes that shape selection on signal evolution. By contrast, mimicry is a pattern of similarity between model and mimic that can emerge from these processes

Concluding remarks and outlook

Despite the striking variability in floral signals and a long history of research into their function [1], knowledge about factors that underlie their evolution remains limited. Little is known, for example, about the mechanisms of evolution of different sensory capabilities in pollinators. Why is it, for example, that many insect orders possess the basal set of color receptors for UV, green, and blue with little variation among them, whereas in lepidopterans additional red receptors have evolved independently at least four times [78]? Even less is known about variation in insect olfactory systems, which typically comprise a relatively large number of receptor types [79].

Despite recent advances in our understanding of the molecular basis of floral signals, little is known about the contribution of floral-signal genes to adaptive plant diversification. Thus, selection on these genes and their contribution to reproductive isolation should be quantified. This could be done using genetically modified plants in natural [44] or seminatural environments, such as a greenhouse with free-flying pollinators. Model systems, such as *Petunia* and *Nicotiana*, which have a diversity of floral adaptations to pollinators as well as being amenable to genetic transformation [44,51], are especially promising in this respect.

Floral-signal genes can also be informative for the question of whether signals evolve in a convergent or divergent way. In one such study of the evolutionary history of genes encoding wing patterns in a butterfly mimicry system, it was shown that red wing patterns in one species (*Heliconius melpomene*) adverged towards the pre-existing red wing pattern of another species (*H. erato*) [69]. The frequent finding of parallel molecular evolution in floral color signals [53] suggests that similar studies of pollination systems should be possible and could resolve questions about the historical sequence of adaptive floral evolution in guilds of plants that share pollinators.

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