

Senses and signals: evolution of floral signals, pollinator sensory systems and the structure of plant–pollinator interactions

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Communication of any sort is complex and communication between plants and animals is particularly so. Plant–pollinator mutualisms are amongst the most celebrated partnerships that have received a great deal of attention for many centuries. At the outset, most pollination studies focused on phenotypic matches and invoked co-evolution to explain plant–pollinator interactions, which gave rise to the concept of pollination syndromes. A few centuries later, there has been a substantial shift in the way we view these mutualistic interactions. In a significant departure from a co-evolutionary framework, numerous studies subsequently showed that there is usually only a loose, non-exclusive matching between flowers and their pollinators. Concurrently, the global prevalence of generalized pollination systems was demonstrated repeatedly. However, our understanding of the evolutionary processes that underlie these mutualisms is still limited. Here, we provide a concise review of the state of our knowledge on the evolution of floral traits and pollinator sensory perception and how these together shape the structure and organization of pollination networks.

Keywords: Floral odours, Olfaction, pollination syndromes, pollinator vision, sensory bias, signal evolution.

Introduction

MUTUALISMS between plants and pollinators have long dominated the literature and can be traced back to the 17th century starting with Sprengel's seminal work on floral biology¹ and Darwin who linked floral form and function within a co-evolutionary framework². The diversity in floral form is lauded as the most remarkable feature in the evolution and radiation of angiosperms. Considered evolutionary counterparts of secondary sexual characteristics in animals, angiosperm flowers perform the singular function of enhancing the plant's reproductive success by enticing pollinators to export and deposit pollen. Pollinators derive benefits such as food, mating sites and brood sites which are usually advertized to them using conspicuous floral signals. The immobility of

plants limits the effectiveness of floral signals, which rapidly dampen with distance. Therefore, it is imperative that floral traits and sensory capabilities of pollinators are tuned to each other for this mutualism to persist.

Flowers vary in multiple features such as colour, pattern, shape, size and odour contributing to the complexity in floral signals. Since plant fitness is dependent on perception and appropriate behaviours that these signals elicit in pollinators, floral signals will be under strong selection to improve detection and attractiveness to diverse pollinator species. A long-held notion is that the main basis for the selective diversification of angiosperm flowers is the dependency of plants on different pollinator species, thereby implying pollinator-mediated evolution of floral displays^{1–7}. This idea has survived, though phylogenetic constraints, exaptation, pleiotropy and genetic drift have also been proposed as causes of angiosperm diversification^{8–13}. Though we solely consider the role of pollinators in this review, it is important to remember that multiple agents of selection are known to act on the evolution of floral traits. Pollinators apart, the thrust of several other non-pollinating agents such as abiotic stress factors, florivores and herbivores are significant^{14–18}.

Two major components of the interaction between plants and their pollinators include floral traits on the one hand and neural and sensory systems of pollinators on the other. The diverse and complex nature of floral traits reflects a combination of selective pressures exerted by the sensory abilities of pollinators, as well as selection on plant species themselves to converge their signals to exploit pollinator senses, and yet diverge sufficiently from competing plant species to ensure pollinator fidelity and constancy^{19–22}. Floral displays are broadcasted multimodally using visual, olfactory, tactile, thermal and even acoustic stimuli^{23–29}. This complexity makes it interesting to study the evolution of signals using flowers as 'models' and floral traits as 'signals'. Recent insights from the foraging ecology of pollinators^{30,31}, neurophysiology of pollinator sensory systems^{32,33}, angiosperm phylogeny and floral development^{34–37} have considerably advanced our knowledge of floral traits and pollinator sensory perception from both mechanistic and evolutionary perspectives. Here, we review our understanding of the evolution of complex floral signals, corresponding sensory adaptations

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in insect pollinators, and the contribution of signals and senses to the structure and organization of plant–pollinator interactions ranging from specialization to generalization.

The nature of plant–pollinator interactions

Early ‘syndromization’ of pollination

Pollination is the first crucial interaction in the lifecycle of a plant and is a vital ecosystem service³⁸. Early pollination studies were cast in a co-evolutionary framework and assumed that flowers are specialized for their most efficient pollinators; this resulted in the categorization of convergent floral traits of unrelated species into ‘pollination syndromes’^{4,39}. Some common syndromes include melitophily (bee-pollination), cantharophily (beetle-pollination), myophily (fly-pollination), sphingophily (hawkmoth-pollination) and ornithophily (bird-pollination). For example, sphingophilous flowers are described to be mostly white in colour, with strong odour, long corolla tubes and nocturnal anthesis⁴⁰. However, later studies recurrently showed that interactions between plants and their pollinators range from being highly specialized to generalized. While some studies found support^{41–43}, others did not find any or much evidence for pollination syndromes^{44–46}. In a meta-analysis of six communities, Ollerton *et al.*⁴⁶ found support for pollination syndromes in only 30% of the plant species studied. In a more recent meta-analysis of 417 plant species, Rosas-Guerrero *et al.*⁴⁷ suggested that the concept of pollination syndrome still holds, indicating convergent evolution driven by adaptation to the most effective pollinators. However, no study so far has evaluated the role and spread of such ‘syndromization’ in explaining diversity of floral traits by comprehensively examining suites of multiple floral traits and pollinator assemblages in multiple plant communities. In the absence of such information the concept of pollination syndromes remains debatable.

Generalization dominates plant–pollinator interactions

Generalization in which both plants and pollinators interact with multiple mutualistic partners is prevalent, and is the rule rather than the exception in pollination systems^{44,48}. This marks a significant departure from the early co-evolutionary models of plant–pollinator mutualisms. From the perspective of the pollinator, generalization is beneficial when floral rewards are similar across species, travel between plants is expensive, pollinator lifespans are longer than flowering of individual species⁴⁴ or when flowering phenology is highly seasonal, short or irregular. From the plant’s perspective, visits by diverse pollinators insures against pollination deficiency and reproductive failure. Fontaine *et al.*⁴⁹ tested the significance

of functionally diverse plants and pollinators for long-term persistence of plant communities, and showed that functional diversity of pollinators positively influences seed set in plants.

There is considerable asymmetry in the generalized interactions between the two partners, in which the extent of dependency varies in strength and degree. Such asymmetry can confer resilience and buffer against unfavourable conditions^{50–53}, when compared to specialization. For plants, fitness is a consequence of both the quantity and quality of pollen transferred^{54–56}. Effective pollinators can therefore shape the evolution of floral characters and contribute to plant reproduction^{57–60}. Thus, floral specialization has often been attributed to their effective pollinators⁴. However, such specialized floral phenotypes are products of fitness trade-offs and require strong selection pressures^{61,62}. Generalized floral phenotypes on the other hand, could possibly be the result of selection imposed by diverse pollinators and are often considered to be optimally adapted to them^{63,64}. Quite naturally, evolution of floral signals and pollinator senses is often examined in specialized systems (for e.g. between fig and fig wasps⁶⁵, yucca and yucca moths⁶⁶), which are much less complex in structure and easier to characterize than are generalized scenarios. However, given the predominance of generalization, the role of diverse pollinators and their sensory preferences in shaping floral traits is undeniable.

Diversity of rewards and the multiplicity of signalling in flowers

In any communication system, signal design and evolution are tightly coupled to enhance detection and attractiveness to intended receivers while deterring or avoiding antagonistic agents^{67,68}. Floral signals transmit a range of information advertizing their rewards to intended animal receivers^{27,69}. In order to elicit the desired response in pollinators, the design of these signals, their quantity and quality are crucial^{70,71}. Floral rewards (such as nectar and pollen) are packaged in diverse ways to attract pollinators, to ensure pollen transport and pollinator fidelity, with ultimate benefits to plant fitness. In order to access these rewards, pollinators are forced to contact reproductive structures during a visit. Moreover, variations in the quality and quantity of rewards are often signalled through variations in floral traits. Occasionally, rewards themselves function as attractants. Pollen-packed anthers and pollen grains can function as visual⁷² and olfactory signals^{73,74} advertizing reward availability. Similarly, presence of scented nectar in some flowers can function to draw in pollinators^{75,76}. Apart from such nutritive rewards as pollen and nectar, flowers also provide non-nutritive rewards such as brood sites, sleeping sites, mating sites, sexual attractants, heat sources, and nesting materials such as oils, resins and waxes^{77–82}.

Honest and dishonest floral signals

Generally speaking, floral signals have evolved to be an honest representation of rewards with exceptions being cases of pollination by deceit^{83–96}. For example, a change in flower colour with decreasing nectar and pollen levels occurs in several species such as *Lantana camara*, *Lupinus argenteus*, *Streptosolen jamesonii*^{88–91}, which functions to direct visits towards the more rewarding unpollinated flowers⁹¹. Scent signals might also be associated with reward status. In *Datura wrightii*, naive *Manduca sexta* moths based their foraging decisions on the association of reduced nectar with a decrease in carbon dioxide emission^{92,93}. Multiple floral signals broadcasted by a flower can range from being synergistic to complementary to redundant^{27,87}. Multimodal signals increase the accuracy of signal detection, and such coupling of rewards with one or more sensory cues assists associative learning in pollinators and improves pollination efficiency^{94–97}.

Though floral signals tend to be honest usually, deceptive floral signals have evolved in approximately 7500 angiosperm species⁹⁸. For reasons not known, more than 85% of known deceptively pollinated plant species belong to the family Orchidaceae⁸⁵. Various deceptive strategies including food deceptive mimicry, generalized food deception, brood-site mimicry, shelter mimicry, pseudoantagonism, rendezvous attraction and sexual deception are known^{84,99}. Deceptive systems can be based on visual or olfactory cues and usually involve just one or a few specialist receivers¹⁰⁰.

Pollinators frequently encounter transiently empty flowers and this has likely resulted in the lack of strong selection pressure against rewardlessness. Rewardless mimics or deceptive flowers are maintained by negative frequency dependence, where they are rare compared to rewarding model species¹⁰¹. Rewardlessness confers fitness benefits such as redirecting resources for increased seed production^{99,102,103}, and increased outcrossing since pollinators visit fewer flowers on a plant when rewards are absent^{85,104–106}. Unisexual flowers of some monoecious and dioecious species produce differential rewards in which females produce very low or no rewards for pollinators (Batesian mimicry)^{107–109}. While in Mullerian mimicry, rewardless species mimic highly rewarding and attractive species¹¹⁰. The persistence of such deceit pollination primarily relies on the perceptual biases of pollinators. The evolution of deceptive pollination systems is a topic that has received little attention and will benefit from an understanding of the phylogenies of rewardless flowers¹¹¹ and pollinators, as well as an analysis of the costs incurred by the pollinator.

Sensory ecology of pollinators

The remarkable diversity in floral traits such as colour, pattern, shape and scent are thought to reflect pollinator-

mediated selection pressures^{3,4,112–117}. Therefore, knowledge of the sensory ecology of pollinators and their cognitive abilities is essential to gain an understanding of how pollinators impact the evolution of floral signals^{28,118–121}. The match between floral signals and the sensory systems of pollinators have been most often examined in specialist pollination systems. However, insights from pollinator learning, and sensory biases in pollinators appear promising in understanding the links between signals and senses in generalized pollination systems.

The role of innateness, learning and sensory biases in pollinator foraging decisions

The responses that floral signals elicit in pollinators can be explained by a combination of pre-existing sensory biases (receiver bias), innate preferences and their associative learning abilities⁶⁸. While the role of innate and learnt preferences has been widely addressed in relation to the evolution of floral traits, more recently pre-existing sensory biases in pollinators have gained interest and are being studied extensively^{68,120,122,123}.

Innate preferences for floral traits help in guiding pollinators towards potential food sources or the most rewarding flowers even without prior experience¹²². These preferences are hardwired and are guided by 'search images', which reflect evolutionary adaptations between floral signals and sensory-neural capacity of pollinators¹²⁴. For example, in four solitary species of megachilid bees, in the absence of host plants, innate preferences led to the rejection of non-host pollen, which is detrimental for their larval development^{125,126}. Although innate preferences are replaced as pollinators gain experience, it has been shown that when presented with novel stimuli, bumblebees revert to their innate colour preferences¹²⁷. Innate sensory preferences in pollinators such as butterflies, bumblebees and hawkmoths can change with experience and with associative learning, enabling them to maximize foraging benefits^{127–131}. Associative learning can confer benefits to pollinators since it can lead to better discrimination of rewarding flowers, and at the same time, it can induce floral constancy in pollinators with fitness benefits for plants.

The introduction of the concept of pre-existing sensory biases¹³² marked a departure from the earlier thinking that pollinator senses specifically evolved in response to angiosperm floral traits. Studies suggest that pollinator preferences have evolved in unrelated contexts and preceded the evolution of angiosperm flowers^{123,133,134}. Such pre-existing biases may be exploited by plants for attracting pollinators^{68,135–137}. It has been hypothesized that pollinator bias for non-floral features, such as dark-centred bee nest entrances, may have exerted strong selection on floral patterns such as stripes, dark centres and peripheral dots through convergent evolution¹³⁵. Such features can

facilitate efficient location of rewards. The bee fly *Usia bicolor* showed preference for artificial flowers with dissected outline, converging lines (which resemble nectar guides) and dark spots on petals over flowers that lack these features¹³⁸. Another study demonstrated that beetles preferred flowers with 'beetle marks' (dark spots or dark centres) over flowers without these marks¹³⁶.

Receiver biases can be sensory or based on the neuronal capacity of the receiver's brain^{120,139,140}. The idea that biases in pollinators may drive the evolution of floral traits is supported by recent theories such as: (i) Sensory drive, which proposes that the four steps involved in signalling systems, i.e. signal generation, transmission, reception and perception are interdependent, and a change in one of the components induces change in the others, and (ii) Sensory exploitation, which predicts that properties of the sensory system shape perception and preferences in a way that signals stimulating the sensory system most effectively are preferred⁸³.

Pollinator responses to visual signals

Visual signals are most explored in the context of evolution of floral traits. These signals assist in detection of flowers and learning by pollinators. Colour is an important multi-dimensional signal cue with properties such as contrast, hue, saturation and pattern, and acts as an effective releaser of responses in flower visitors²⁴. Pollinator colour vision and floral colours can be best described as an evolutionarily adapted signal-receiver system¹⁴¹. Visual cues other than colour, as well as olfactory and tactile cues help pollinators orient towards the flower^{23,142–145}, whereas colour triggers behavioural reactions^{146–148}.

Bees are amongst the most widespread and efficient pollinators in varied habitats. Research in honeybee vision has laid the foundations for understanding insect colour vision³¹. Peitsch *et al.*¹⁴⁹ tested the spectral sensitivities of the photoreceptors in 43 species of bees and found that they have trichromatic vision with maximal receptor sensitivities around 340, 430 and 535 nm (UV, blue and green respectively). This distribution of receptor sensitivities is believed to have derived from a basal visual system that predates the evolution of angiosperms^{133,150}. Molecular phylogeny of arthropod opsins has revealed the existence of trichromacy in the Devonian ancestor of insects providing evidence that the ancestors of flower visiting insects had fully functional trichromatic vision even before angiosperm radiation¹⁴⁸. Several models were developed to describe colour vision in honeybees such as colour opponent coding model^{151,152}, colour hexagon model¹⁵³ and RNL model¹⁵⁴. Interestingly, angiosperm flower colours are clustered rather than uniformly distributed in bee colour space (calculated using colour models). These clusters are distributed close to 400 and 500 nm where colour discrimination would be maximal,

as the discrimination is optimal at wavelengths closest to the position where spectrally different photoreceptors overlap^{149,155}. Very close fit was observed between wavelengths that bees best discriminate (400 and 500 nm), and spectral reflectances of flowers in two plant communities in Israel and in Australia, indicating optimal tuning between bee photoreceptors and floral colours^{147,156}.

A most striking example of the tuning of floral colour signals and pollinator vision is the UV reflectance of flowers. A common UV reflectance pattern includes areas of low UV reflectance (high absorbance) in the centre of the flower, surrounded by areas of high reflectance¹⁵⁷. Chittka *et al.*¹⁵⁸ proposed that blue and yellow hues are interfered by reflectance of the background, and decreases magnitude of colour contrast in the eye of a bee. On the other hand, flowers with UV reflectance are little affected by the background reflectance and appear vibrant to the bee eye, which enhances detection. A recent study demonstrated that pollinator visitation was severely disrupted in *Mimulus guttatus* flowers when its UV absorbing and reflecting parts were experimentally manipulated, indicating the prominent role of UV reflectance in the detection of flowers¹⁵⁹. Most pollinators are known to exhibit bias for certain colours; honeybees and bumblebees readily learn violet as a rewarding colour^{124,127,160}, whereas swallowtail butterflies and hawkmoths prefer blue over other colours¹⁶¹. The fact that very few non-flower objects fall within the blue–violet colour range in natural landscapes presumably guides pollinators to investigate these colours (flowers)^{122,162}.

Floral symmetry is another crucial visual trait where selection acts based on pollinator perception, their information processing and activity patterns^{163–165}. Insect pollinators detect and perceive symmetrical patterns, and such floral patterns were found to receive higher visitation rates and greater pollen transfer resulting in efficient pollination^{164,166}. Studies have demonstrated a spontaneous preference for disrupted patterns with high spatial frequency¹⁶⁷. It was later elucidated that bees use global features such as overall shape or size to discriminate patterns¹⁶⁸.

Pollinator responses to olfactory signals

Olfactory cues advertize reward properties to pollinators, often synergistically and in concert with visual cues^{28,169–171}. In the hawkmoth *Manduca sexta*, both visual and olfactory signals are required to elicit the full behavioural sequence associated with nectar feeding¹²⁴. Pollinators rely more on scents when visual cues are unreliable, as in flowers with nocturnal anthesis^{26,172}. Olfactory cues are learnt faster, and are chosen more accurately than colours and colour patterns, making it more resilient¹²⁰. Honeybees (*Apis mellifera*), for instance, can learn to rapidly associate an odour with nectar rewards with just one training trial resulting in the formation of long-term

memory¹⁷³. Bees can learn to associate any odour with reward, but they show preparedness to learn floral odours¹²⁴. Neural structures facilitating olfactory responses in insects are likely to have evolved due to the frequent association of odour with food, and the integration of gustatory and olfactory pathways, thus enabling organisms with food-related learning abilities¹⁷¹.

The ability of insects to associate nectar reward with scents by olfactory conditioning provides conclusive evidence for a pollinator's reliance on floral odours^{96,174}. Pollinators exert strong pressure on minimizing variations in odour compounds emitted, thus promoting better learning and floral constancy^{129,175,176}. Recent studies on the preferences of pollinators for floral Volatile Organic Compounds (VOCs) have shown widespread overlap between floral scent compounds and insect-produced VOCs, suggesting pollinator-mediated evolution and the presence of olfactory preferences^{28,177}. Evidence is accumulating that the use of VOCs by pollinators is evolutionarily older than the occurrence of VOCs in flowers, pointing to a scenario of sequential evolution, in which plants exploit the sensory biases of pollinators¹²⁴. Several cases of convergent evolution of scent compounds emitted by flowers with specialized groups of pollinator species have been reported^{39,62,178}. In obligate mutualistic interactions such as in fig–fig wasp nursery pollination systems, specific odourants released by the host fig direct the wasps towards them^{179–182}. Bat-pollinated flowers belonging to distinct plant families contain closely related sulphur compounds^{183,184}, moth-pollinated flowers contain oxygenated sesquiterpenes¹⁸⁵, and butterfly-pollinated flowers contain benzenoid and linalool derivatives¹⁸⁶. Several scent compounds emitted by flowers are similar to those involved in pollinators' communication system in non-feeding contexts^{187–189}. For example, *Clusia aff. sellowiana* attracts its rather unusual cockroach pollinator, *Amazonina platystylata* by emitting acetoin, which is also found in the male pheromones in many of these cockroach species¹⁷⁷, potentially exploiting sensory biases in female cockroaches.

Though pre-existing sensory biases in pollinators play an important role in determining floral preferences, both configural and elemental olfactory learning can occur in a floral context²⁸. Elemental learning suggests that animals treat components of a compound stimulus separately during the learning process, whereas configural models state that compound stimuli are learnt as novel entities, greater than the sum of their parts. Honeybees utilize configural learning to distinguish between four snapdragon cultivars (*Antirrhinum majus*) that share the same chemical composition but differ in compound ratios¹⁷⁶.

Other lesser known floral traits and pollinator response

Besides visual and olfactory properties of flowers, it has recently been shown that pollinators can respond to

hitherto little known cues such as the texture and electrical fields of flowers. Bees prefer flowers with conical cells in petals as it improves the perception of colour and provides better grip^{190,191}. In *Antirrhinum majus*, it has been shown that pollinator preference and seed set is greater in plants with conical petal cells than in plants with flat petal cells¹⁹². Insects usually possess positive electric charge^{193–197} in contrast to flowers which have a negative charge¹⁹⁷. Clarke *et al.*¹⁹⁸ have shown that electric field can act as a floral cue, by augmenting floral display aimed at pollinator senses, improving speed and accuracy of learning and facilitating the discrimination of rewarding resources in bumblebees. However, the importance of these novel cues in signal evolution and plant fitness needs to be verified empirically.

Conclusions and future directions

Plant–pollinator interactions have a long history of being cast in a co-evolutionary framework. In the recent times, this adaptationist viewpoint has been repeatedly criticized and questions have been raised regarding its importance in explaining plant–pollinator mutualisms. While a co-evolutionary scenario is appealing and may hold true at least for cases of specialized pollination, numerous studies have confirmed the rarity of specialization and the predominance of generalization. The loose fit between plants and pollinators involved in generalized partnerships is likely to have evolved via sensory preferences common to a group of pollinators and resulting in convergence of floral signals. However, it is unknown how these preferences evolve in pollinators themselves, though the role of pre-existing sensory biases in pollinators which are exploited by plants is gaining widespread support.

Some issues that mandate future studies include:

1. Potential roles of pollinators as well as antagonistic agents in shaping signal evolution in flowers.
2. While it is now well-appreciated that generalization is the norm in pollination systems, our understanding of how convergent floral signals address a diversity of pollinators with vastly differing sensory systems and biases, as well as differ in neuronal and cognitive abilities to perceive and process sensory stimuli, remains a challenging area of research in plant–pollinator interactions.
3. Most studies have dissected the various components of floral signals and examined their evolution in light of respective pollinator senses. An integrated approach encompassing the multimodality of signals and the parallel processing of these signals by the pollinators' sensory-neural systems will provide a comprehensive understanding of floral trait evolution.
4. Studies that have examined generalist pollination systems report that floral signals are optimized for being

- detected by the most effective pollinator. However, studies so far have by and large failed to take a more comprehensive view of what constitutes effective pollination. In most cases, this refers to species that carry away most number of pollen grains, or cause high pollination success. However, the effectiveness of pollinators in terms of flower constancy and spatial distance of gene flow is hardly considered, though they may well be implicated in steering the evolution of floral displays in several plant species.
5. Finally, studying the functioning of pollination systems in disturbed environments will contribute to our understanding of processes underlying floral signal evolution under rapidly changing habitat conditions.
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ACKNOWLEDGEMENTS. We acknowledge funds received by H.S. from the DST-Royal Society Seminar Series to organize an Indo-UK meeting on the ‘Biology of Pollination in the Tropics: From Individuals to Networks’, hosted by IISER, Thiruvananthapuram in February 2013.