Editorial: Sensory ecology of plant-pollinator interactions

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Editorial on the Research Topic
Sensory ecology of plant-pollinator interactions

What explains the bewildering diversity of flowers in the natural world? This question has fascinated humans for centuries. Pollinator-mediated selection on floral traits is generally assumed to be the main driver of floral phenotypic divergence (Barth, 1991; Dyer et al., 2012; Schiestl and Johnson, 2013). Indeed, flowers could be considered "sensory billboards" (sensu Raguso, 2004), because they advertise their presence to pollinators *via* an enormous diversity in color, patterns, odor and shape. Pollinators perceive these signals *via* visual, olfactory and/or tactile mechanisms. How floral traits are produced and how they are perceived by pollinators hence is a central aspect in plant and pollination biology.

This Research Topic brings together a suite of papers on the sensory ecology of plant-pollinator interactions Figure 1. The papers can be categorized in the following groups, each of which we will discuss below: (i) inter- and intraspecific variation in floral traits; (ii) perception and learning of floral traits used as signals by pollinators; (iii) use of traits for deception by plants and pollinators, and (iv) variation in floral traits and perception as basis for the evolution of novel interactions.

Intra- and interspecific variation in floral traits

The extraordinary diversity in flower color is a quintessential visualization of plant diversity. Diversity in color is primarily created by different floral pigments, which differ in their absorption spectra and so create different colors. Narbona et al. investigated how three classes of floral pigment determine the visibility of flowers to different pollinators. They found that different pigment classes create colors that occupy separate parts of the visual space, and differences in visual conspicuousness between pigment classes were largely similar among pollinator groups. They also showed that carotenoids and the rarer aurones-chalcones create a higher contrast than the ubiquitous anthocyanins. In addition to the type of pigment, the amount of floral pigment is important for the degree of

FIGURE 1
A *Bombus pascuorum* bee visiting a *Nicotiana rustica* flower.
Image credit: Marjan Kraaij.

modulation of the reflected light. Combining an optical model of flowers and established vision models, van der Kooi showed that more pigment does not necessarily translate into a higher visibility to insect pollinators. Low amounts of pigment yield pale colors with low contrast, moderate amounts of pigment yield high contrast, but with high amounts of pigment, the flower's contrast to the background decreases. These findings dovetail with earlier work showing that bees prefer stimuli with intermediate pigment concentrations (Papiorek et al., 2013), and pave the way for explorations as to how the amount of floral pigment in natural species relates to the theoretical optimum of that species.

Several contributions investigated intraspecific floral trait variation and its consequences for the attraction of pollinators. Palmqvist et al. compared color and scent for diploid and polyploid *Chamerion angustifolium* plants. Flower reflectance was slightly different between cytotypes, but still similar to bee pollinators. Scent profiles, however, differed enough to enable discrimination by pollinator, which has potential implications for cytotype divergence. The South-African plant *Gerbera aurantiaca* showcases more salient flower color polymorphism. To uncover what determines the polymorphism, Johnson et al. charted the natural distribution of color morphs and

characterized soil type, climate and color preference of the main pollinator, a hopliine scarab beetle. A 5-year common garden experiment revealed that flower color is not plastic. Intriguingly, they found no clear association between morph color and any of the studied parameters. This contrasts with the case of color-polymorphic South-African *Drosera cistiflora* that is pollinated by related hopliine beetles (Johnson et al., 2020; von Witt et al., 2020). It seems unlikely that the color polymorphism in *G. aurantiaca* is purely coincidental, but what other factor(s) (e.g., floral scent) may determine the geographic pattern remains a question that begs to be answered. Bing et al. measured local adaptation in a suite of floral traits of a wild tobacco plant, *Nicotiana attenuata*. This is an interesting species, because it is primarily pollinated by hawkmoths, but it exhibits high floral trait divergence among populations. The authors showed that this divergence and the ratio of outcrossing vs. selfing can be partly ascribed to local adaptation to different pollinator fauna.

Floral trait divergence that is linked to different pollinator fauna is even more apparent in different varieties of the orchid *Neotinea ustulata* – a deceptive orchid from Central Europe, studied by Martel et al.. Bees and flies pollinate one variety, whereas only flies pollinate the other variety. They found that the two varieties differ in color, morphology and scent. Furthermore, the varieties are different in their emission of alkene scent compounds, which may mean that this species is not only food deceptive, but also (quasi-)sexually deceptive. Together, these works on *C. angustifolium*, *G. aurantiaca*, *N. attenuata* and *N. ustulata* add to the growing body of literature that highlights the vastness of trait variation within species and their implications for the interaction with pollinators and for trait evolution (e.g., Eisen et al., 2022; Venjakob et al., 2022).

A central question in pollination biology is how floral signals scale with rewards for pollinators. Signal "honesty" can occur at different ecological levels. It can occur at the species level, as has been shown in, for example, *Brassica rapa* (Knauer and Schiestl, 2015) and *Dalechampia* spp. (Armbruster et al., 2005; Pélabon et al., 2012), but it can also occur at the community level, when a set of co-flowering species with a shared trait (e.g. flower color or shape) are similarly rewarding for a certain pollinator. That "community-level honesty" was studied by Streinzer et al. in the Austrian alps. They found that blue flowers produce comparatively much nectar, but because pollinators learn that blue flowers are extra rewarding, they visit them disproportionally more, which cancels out the association in the field. The authors also investigated the importance of color contrast of the flower against the (green) background, which currently is considered the most realistic proxy for flower conspicuousness to pollinators (van der Kooi and Spaethe, 2022). They found that with increasing color contrast, flowers were less rewarding, which suggests that very conspicuous flowers get away with investing less into reward without negative impacts on fitness.

Perception and learning of floral traits used as signals by pollinators

Producing a signal is only one side of the coin of attracting to pollinators. To perceive floral stimuli, pollinators need to be equipped with appropriate sensory systems. Pollinators can sometimes exhibit a behavioral preference for a specific cue, such as a specific scent or color. The widespread (and sometimes notorious crop pest) *Pieris rapae* butterfly is an example of a species for which it was commonly assumed that it uses color vision to locate flowers, but nobody had explicitly tested that assumption. Arikawa et al. show that this butterfly indeed uses color vision to locate flowers, and that they innately prefer blue and yellow. Innate (color) preferences occur in numerous flower-visiting species (Lunau and Maier, 1995; Dyer et al., 2019) and can be a significant element in flower (color) evolution. Such a presence of a "hard-wired" flower template in the insect brain is also shown by Howard et al., who provided evidence of an innate bias toward visual stimuli with flower-like configurations. Both naïve and experienced honey bees (*Apis mellifera*) readily learn not only flower color but also flower shape. In addition to the chromatic component, the achromatic component (i.e., "brightness") conveys visual information. Behavioral experiments by van der Kooi and Kelber show that naïve hawkmoths prefer bright over dim stimuli, and a literature review suggests that achromatic contrast between flowers and their background may be more important for flies, butterflies and bees than commonly assumed. The ways *via* which floral pigments and structure determine the achromatic signal on different backgrounds is dissected using optical modeling. Particularly for pollinators foraging under dim light conditions, such as nocturnal and crepuscular bees, olfactory information plays an important role complementing or even replacing visual information (Wright and Schiestl, 2009), as highlighted by Martinez-Martinez et al..

Besides bees, flies and butterflies, beetles have played a pivotal role in the radiation of angiosperm and gymnosperm plants (Labandeira et al., 2007; Ollerton, 2017). Beetles are atypical pollinators, because although many species use color vision to locate flowers, they are generally dichromatic (they lack a blue photoreceptor type), unlike most other pollinator groups that are tri- or tetrachromatic. Sharkey et al. found that gene duplications in visual genes (opsins) underlying putative tri- and tetrachromatic color vision may be relatively common among beetles that strongly depend on floral resources and these gene duplications have evolved independently in multiple beetle lineages. Although duplications do not necessarily imply new photoreceptor sensitivities, the authors showed a marked increase in gene duplication in obligate flower visitors (74%) vs. non-flower visitors (28%).

In the noisy natural world, it probably requires a substantial amount of time and brainpower to perceive and process visual, olfactory and taste stimuli simultaneously presented by flowers. This may explain why several pollinators use only specific

sensory stimuli during specific foraging tasks. For example, Sculfort et al. found that *Bombus terrestris* bumblebees were unable to perceive three potentially toxic plant secondary metabolites (amygdalin, scopolamine, and sinigrin) in sugar solutions. Similarly, Ruedenauer et al. showed that honeybees focus taste perception on restricted nutrient groups, i.e., amino acids and fatty acids, but ignore others, i.e., sterols, when faced with complex chemical profiles as represented by pollen. Brandt et al. provided evidence for the evolutionary adaptation of olfactory perception in scent collecting male euglossine bees. The authors demonstrated that male bees showed highly species-specific patterns of antennal responses to various scent bouquets. More closely related species were more similar in their responses, indicating adaptation to those chemical compounds that typically occur in scent bouquets of their preferred perfume flowers.

Adaptation of sensory systems can result in marked differences between the actual and perceived stimulus and explain why final perception is highly species-, context- and occasionally individual-specific. Animals can use various sensory strategies to counteract limitations imposed by the physiological properties of their sensory system. For example, some animals, e.g., birds, increase the signal-to-noise ratio under dim illumination (Warrant, 1999). Taking into account the interaction between environmental complexity and species-specific sensory properties to understand behavioral patterns is very challenging, as highlighted by Garcia et al.. The authors applied a modeling function that takes into account psychophysics data to model how birds use color information in (visually) complex environments to make meaningful choices. The ability to process and learn olfactory stimuli in complex environments appears to be essential for pollinators not only to detect flowers and make appropriate choices, but also to navigate in foraging habitats, as demonstrated by Evans et al. for *B. terrestris*. Together, these contributions highlight the importance of evolving appropriate sensory modalities for foraging pollinators and the complex interplay between floral stimuli, pollinator sensory modalities and foraging behavior. These works further suggest that we should be cautious with usage of pesticides that targets insect sensory systems, such as neonicotinoids. In this context, Straub et al. showed that treating bees with a field-realistic dose of the neonicotinoid clothianidin decreased the antennal sensitivity to a common floral odor compound (2-phenylethanol) in the mason bee *Osmia bicornis* and in *B. terrestris*. Clothianidin also negatively affected the foraging behavior of *O. bicornis*.

Use of traits for deception by plants and pollinators

Pollinators are deceived by plants *via* mimicry, where a mimic resembles a model, and/or the exploitation of perceptual biases. In the latter case, the pollinator has a sensory or cognitive

bias for a trait, such as a certain odor or color pattern, and that bias is co-opted by the plant to achieve pollination without offering any reward. Traits involved can address different sensory modalities, like vision, olfaction, taste or touch, and can target different pollinator needs, like food, mating partners or breeding sites. In their field study, Rupp et al. investigated deceptive pollination in *Aristolochia microstoma*, which belongs to a genus that is known for its fly-deceptive pollination strategy. The authors recorded a wide diversity of arthropod flower visitors, but only dipterans of the family Phoridae were found to carry pollen during the female phase of the flowers, indicating that they are the exclusive pollinator of *A. microstoma*. The authors also found that floral scent was strongly dominated by oligosulphides, which are widespread among plants pollinated by carrion-flies and bats. Taking both findings together, the authors hypothesized that *A. microstoma* is a fly-deceptive plant that mimics brood-sites of invertebrate carrion.

In flowering plants, pollen contains the male gametes and its transfer thus is essential for outcrossing, but pollen may also function as a reward for pollinators. To reduce consumption of pollen, plants have evolved multiple strategies. For example, in some monoecious plants, the unrewarding female flowers mimic the pollen-rewarding male flowers. Russell et al. set out to investigate whether pollinators can learn to discriminate between rewarding and unrewarding flowers to maximize their foraging efficiency. They investigated whether flower size variation in the monoecious *Begonia odorata*, where unrewarding female flowers are on average 30% larger than male flowers, affects the discrimination ability of *B. impatiens*. The authors found that the bees quickly learned to avoid unrewarding female flowers and then choose the rewarding male flowers, independent of size variation.

Nectar is produced by flowers to attract potential pollinators, but nectar-robbing bees bypass the reproductive organs by entering the flower from a different direction, e.g., through biting a hole in the corolla. Whereas the impact of nectar robbing on plant fitness is well-studied, less is known about the behavioral and cognitive processes underlying robbing. Richman et al. reviewed the literature about the sensory and cognitive processes involved in nectar robbing and highlight open questions, such as differences in the degree of an innate preference for nectar robbing (i.e., the underlying motor patterns) between flower visiting species or the role of previous experiences, e.g., encounters of open vs. (still) closed flowers during the initial foraging flight.

Variation in floral traits and perception as basis for the evolution of new interactions?

Many studies, including several in this Research Topic, have demonstrated the high degree of inter- and intraspecific variation in flower traits or behavior of pollinators (Füssel et al., 2007; Palmer-Young et al., 2019; Sapir et al., 2021; van der Kooi et al., 2021). Such variation is pivotal for the local adaptation of both interaction partners as well as for their resilience against environmental change (Bolnick et al., 2011). It likely also provides the basis for the evolution of novel interactions, provided that pollinators show sufficient flexibility in their sensory systems. For example, Burger et al. showed that naïve *Chelostoma rapunculi* bees were equally attracted by olfactory cues of two non-host plant species (*Malva moschata* and *Geranium sanguineum*. This attractiveness may be explained by shared olfactory and visual stimuli. However, each plant species still has its individual scent profile, indicating that in particular naïve *C. rapunculi* bees show relatively large sensory flexibility or a high degree of generalization, which may eventually enable its plant host expansion or switch. Conversely, if pollinators show an innate preference for specific signals, e.g., color, and thus rather low sensory flexibility, plants may only exploit them as pollinators if they adapt their trait phenotypes to the pollinators' sensory range. A neat experiment by Byers and Bradshaw investigated flower color preferences of *Mimulus* monkeyflowers. The authors manipulated two flower color loci and tested the attractiveness of the resulting four color phenotypes (red, yellow, pink, and white) to hawkmoths. They demonstrated that hawkmoths strongly preferred derived (yellow, pink, and white) over ancestral (red) colors. Owing the simple flower color genetics, the authors could follow an elegant prospective approach to understand plant diversification.

In summary, the mesmerizing diversity of flowers is in large part driven by the sensory ecology of pollinators. This Research Topic covered a very small part of the enormous body of work on this most fascinating topic, and included some important aspects such as perception and learning by pollinators, deception by plants, and inter- and intraspecific trait variation. No doubt the future will bring much more illuminating research that will stimulate the senses and thinking of (sensory) ecologists.

Author contributions

CK and SL drafted the editorial, with specific input from JS. All authors agree to the final version.

Conflict of interest

Publisher's note

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