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The chemical ecology of plant-pollinator interactions: recent advances and future directions

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Floral chemistry mediates plant–pollinator interactions through floral scents and reward components. Although improved techniques have increased interest in studying floral volatiles and nectar chemistry, these two foci have generally been studied in isolation. The ecological functions of floral chemistry have been relatively well studied and focused on pollinator behaviour. While studies comparing chemistry between plant parts and across phylogenies are increasing, work on the evolution of floral chemistry and the importance of community context in mediating pollinator responses is lacking. Future research should concentrate on more holistic studies that include both signal and reward chemistry to understand the relative contribution of these complex and dynamic floral traits to the ecology and evolution of plants and their pollinators.

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Introduction

Animal-pollinated plants generally attract pollinators by advertising their floral rewards with visual and olfactory signals. While the role of plant chemistry in mediating plant–pollinator interactions has long been recognized, technical advances have made floral chemical analyses more feasible, accurate and accessible to ecologists and evolutionary biologists. Although measuring floral chemistry remains challenging (Box 1), the field is flourishing. Studies on floral volatiles have dominated the literature, while nectar chemistry has lagged behind until very recently, likely due to additional difficulties in analyzing trace compounds in small volumes of nectar. Beyond technical differences in examining floral volatiles and nectar chemistry, these two chemical aspects of floral biology have remained somewhat distinct fields. Our review focuses on the most recent work addressing how floral chemistry contributes to the ecology and evolution of plant–pollinator interactions (Figure 1). Specifically, we highlight the theoretical and empirical links between floral volatiles and nectar chemistry and summarize pollinator responses to plant chemistry with the aim to create an integrated view of floral chemical ecology.

Floral chemistry functions

Floral volatiles act as long distance attractants and provide unique chemical signatures to flowers, thereby influencing pollinator preference and constancy, while nectar chemical composition can affect initial foraging decisions, time pollinators spend foraging and the likelihood of visiting a conspecific flower. Current advances in understanding functional differences of floral scent often compare variation in systems with different pollen vectors [1]. In *Mimulus*, bumblebee preference is driven by its antennal sensitivity, which may subsequently contribute to reproductive isolation between plant species [2•]; similar preference patterns are detected in pollinating beetles of *Protea* [3]. However, increased attention to repellent/defensive aspects of floral volatiles [4,5] suggests that limiting our view to pollinator attraction severely reduces our understanding of floral chemical trait function.

Historically, nectar sugars were assumed to drive preferences, however the prevalence of nectar secondary metabolites led to a reassessment in light of these putatively noxious compounds. While nectar compounds can deter pollinators and alter their behaviour on flowers, experiments often find these negative effects only with concentrations significantly higher than occur naturally in nectar [6,7]. At low concentrations, nectar secondary metabolites may be neutral or even attractive and their functions may go beyond simple attraction/deterrence. Caffeine-enriched nectar improved honeybees' ability to retain associations between floral scent and reward due to caffeine's effect on adenosine receptors in the insect brain [8••]. Furthermore, plants may seek to manipulate pollinators into consuming less nectar, especially if this leads to higher outcrossing rates [9]. Bumblebees and birds consume less nicotine-enriched nectar [7,10] and honeybee nectar storage declines with increased nectar nicotine concentrations [11]. However, sugar can

Box 1 Studying dynamic and complex traits

Floral nectar and scent, composed of multiple chemical constituents mixed together in precise ratios, are both complex and highly variable. The chemical composition of nectar and scent is often dominated by attractive components but can also contain deterrent or even toxic secondary metabolites. Furthermore, floral chemistry can change in response to abiotic and biotic factors, with changes occurring immediately or over the flowering period. Floral scent and nectar also often exhibit temporal cycles in production reflecting strategies to optimize pollinator attraction and/or antagonist deterrence. A major challenge to studying the chemical ecology of pollination therefore lies in the fact that chemical traits are often in flux, making it difficult to measure, modify and effectively gauge pollinator responses. For example, do single snapshots of chemical profiles (either scent or reward) tell us anything about the true phenotype of the plant? And if so, does this represent conditions that floral visitors encounter in the field? Ultimately, finding general patterns in or responses to floral chemistry may require substantially more replication and more sophisticated statistical techniques than studies focused on less dynamic or complex floral traits. However, overcoming these challenges offers an unparalleled opportunity to understand the ecology and evolution of plant behaviour.

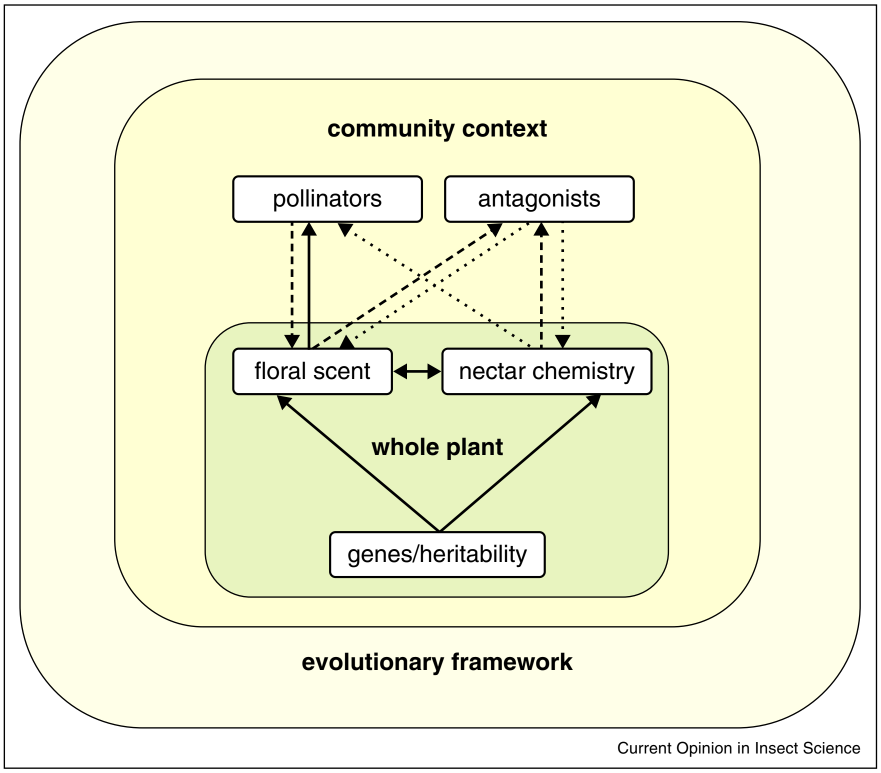
modulate responses; birds and honeybees tolerate higher nicotine concentrations with increased sugar levels [10,11]. Thus nectar chemistry may reflect a complex interplay of pollinator behaviours and tolerances in addition to alternate functions such as protection from antagonists. Similar processes may drive function and evolution of pollen chemistry, however this is a poorly understood aspect of floral chemistry (Box 2).

Comprehensive studies of floral advertisements and rewards (including pollen) are required to understand whether chemistry has additive or emergent functions in plant–pollinator interactions. Furthermore, pollinator foraging constancy can be enhanced for multimodal signals such as colour and odour combined; in *Ipomopsis*, the volatile indole is sufficient to attract hawkmoth pollinators but does not elicit nectar probing behaviour without the appropriate petal colour [12]. Thus inroads into understanding functions of floral chemistry must include the broader context of floral traits.

Whole plant chemistry

Early studies on floral chemistry focused on analysing floral headspace or nectar in isolation but more recently,

Figure 1



A schematic of a research framework for floral chemistry. Double-headed arrows represent correlations, single headed arrows are effects; solid = positive (e.g. attraction), dashed = negative (e.g. repellence/defence, reduction), dotted = range of effects from negative to neutral to positive. Floral chemistry (nectar and scent) is embedded within the whole plant and interacts within a broader community context. Nectar and floral tissue microbes are a potentially important player in the community context, however we do not include them here because their effects are complex and only just being explored (see Box 3). Additionally, both conspecific and heterospecific plants can contribute to community context. The evolutionary framework aims to explain chemical variation at phenotypic and genotypic levels and how biotic (e.g. pollinators and antagonists) and abiotic selective agents drive evolution of chemical traits.

Box 2 Pollen chemistry

For many plant species, pollen is simply the vehicle for gamete transportation, however insects often exploit pollen as a resource. Pollen can therefore play a dual role in many systems, having both sexual and reward functions and its chemical composition may influence how insects interact with flowering plants. Like nectar, pollen contains both nutritional and non-nutritional components, with recent studies finding compounds such as alkaloids [47] and non-protein amino acids [48]. These compounds may have negative [48] or neutral [49] post-consumption effects and may prompt pollen-collecting insects to seek multiple pollen sources in order to reduce costs associated with pollen toxins [50]. Despite the importance of pollen protein for many social and solitary bees, studies on pollen chemical ecology are sparse. This area of research is rich in questions, poor on data and deserves significantly more attention.

researchers have taken a comparative whole plant approach to assess patterns of production, expression and allocation of compounds and test functional hypotheses. Similar secondary metabolite profiles across tissues suggest that nectar chemistry reflects shared biosynthetic pathways or pleiotropy [13••]. Whole plant studies show many nectar secondary metabolites are found throughout plants and concentrations are positively correlated across plant parts in many species, although secondary metabolite concentrations are often orders of magnitude smaller in nectar relative to flowers, leaves [6,13••,14] and phloem [15]. However, flowers often possess distinct chemical components or ratios/concentrations (especially in floral scents), which may either signal or shape functional and adaptive differences between flowers and other plant parts. The leaves and flowers of *Brassica rapa* emit nearly identical volatile profiles but compound concentrations were not correlated [16]. In milkweeds (*Asclepias* species), composition and concentrations of individual cardenolides varied across plant parts and two species had a unique nectar compound [6]. Further, leaf and floral volatiles may differ but act synergistically to attract visitors, suggesting that volatiles need to be understood in a whole plant context [17]. Differences in floral chemistry of leaves and flowers are not unexpected, as plants are under selection to attract pollinators to flowers but deter herbivores from leaves. Given that the overall chemical composition of nectar differs significantly from phloem, indicating modification of nectar precursors via metabolism or selective secretion [15], there is mounting evidence to refute that secondary metabolites simply leak into nectar.

Community context

Although plant–insect interactions are often studied in a pair-wise fashion, plants and their visitors are embedded in communities of interacting organisms. Community context can influence pollinator choices that may alter evolutionary trajectories for species. For example, although nectar alkaloids are often deterrent, pollinators can prefer alkaloid-enriched nectar when paired with higher sucrose concentrations than alkaloid-free counterparts [18]. Within communities environmental factors may impede searching and animal visitors must learn to detect floral signals amongst complex backgrounds. *Manduca sexta* can maintain its innate preference for certain volatiles while learning to associate new odours with rewards, but background plays a large role in their ability to detect odours [19,20••]. Similar general patterns are seen for bumblebees where foraging behaviour is enhanced when colour and odour are more conspicuous relative to background stimuli [21]. While gains in understanding pollinator behaviour are being made in lab settings, much less is known about how these interactions play out in nature. In a Mediterranean shrubland, floral signalling, rewards and visitation for the entire community varies seasonally [22••] suggesting whole communities may adjust the intensity of signalling and reward production to pollinator abundance, investing more in recruiting during lean times. However, floral scents and rewards as well as subsequent interactions with mutualists, may be modified by herbivory [23,24]. Further, recent studies have honed in on the community ecology of nectar itself, addressing interactions of nectar microbes and their influence on nectar chemistry (see Box 3), highlighting that community context acts on several scales.

The community perspective raises fundamental questions about signal and reward ecology and evolution that remain unexplored. For example, does the intensity of selection on floral scent vary with community background? What is the role of facilitation and competition between species on the types and intensity of floral scents? How do rewards of co-flowering species affect evolution of nectar chemistry? Can plants adjust signals/rewards depending on the community context? And how do interacting networks of mutualists and antagonists shape floral signals and rewards?

Box 3 Nectar microbes and floral chemistry

Microbes in nectar and their effects on pollination are an expanding field of research. Nectar yeasts have been characterized in a number of systems but only a few studies have also examined nectar bacteria, which can also be very common [51]. Flower visitors can transport nectar microbes, which alter nectar sugar composition [52] and nectar pH [53]. However, microbe identity may be important for these effects; nectar bacteria but not yeast weakened mutualistic interactions between *Mimulus aurantiacus* and its hummingbird pollinators [53] and honeybees discriminate between nectars containing bacteria or yeast and avoid those with bacteria [54]. Yeasts in nectar may even benefit plant fitness, as seen in *Delphinium nuttallianum* [55•]. Nectar secondary compounds have been hypothesized to play a role in flower microbe interactions, although data in this area are lacking. However, some floral scents can act as defence against bacteria pathogens [56], supporting the hypothesis that floral chemistry has antimicrobial functions.

Evolution of floral chemistry

Floral chemistry is hypothesized to be the product of natural selection yet research is only just considering the micro-evolution of these traits [25]. Selection on volatiles can be detected [26] and can be stronger than selection on other advertisements such as flower size or colour [27]. Indirect evidence for the potential for selection on nectar chemistry comes from fitness effects of pollinator responses. For example, nectar alkaloids reduced pollen receipt and subsequent *Gelsemium sempervirens* fruit set [28], however nectar alkaloid enrichment in *Delphinium barbeyi* had no plant fitness effects [29]. Because floral signals and rewards may be linked, especially if signals are honest [30], correlational selection may drive their evolution. Nectars themselves can be scented [31] suggesting a strong possibility for correlated evolution. Rapid evolution of floral scent is suggested by examples of reduced selfing in *Abronia umbellate* populations, where attractive scents are presumably no longer needed [32•,29], and variation among horticultural varieties of *Phlox* [33]. Further, selection on the eugenol synthesis gene in *Gymnadenia* suggests changes to single genes can increase floral scent complexity [34]. Although some biochemical pathways and genes associated with the production of alkaloids and/or floral volatiles have been characterized, heritability of their variation is largely unknown. Recent advances in understanding the genetic basis of chemistry include mapping the floral scent QTLs of cowpea [35] and correlating floral scent and AFLP data in *Sorbus* [36]. Use of hybrids has also shown the genetic bases of scent production can be complex, as hybrid scent can differ from parental scent or hybrids can express the parental mean depending on compounds [37,38]. There is a striking lack of data on the heritability of nectar chemistry and uncovering the genetic basis of these traits should be a research priority.

Evidence for floral chemical trait evolution comes from local adaptation and phylogentic studies, often suggesting that pollinators likely play a role. For example, in the rewarding *Gymnadenia odoratissima* and sexually deceptive *Ophrys sphegodes*, scent likely contributes to local adaptation of pollinator communities [39,40•]. In *Lithophragma*, where *Greya politella* moths act as both pollinators and seed parasites, closely related *Lithophragma* species exhibit extreme variation in floral scent [41•] that seems to drive moth preference for their local host species [42]. Broad phylogenetic sampling shows nicotine concentrations in *Nicotiana* nectar are lower in pollinator-dependent species [13••], suggesting that pollinators could drive chemical composition of nectar. Pollinator-mediated selection also likely drives floral scent evolution, as suggested by two meta-analyses of oviposition site mimics [43••] and beetle-pollinated plants [44]. Research incorporating the heritability of chemical traits, pollinator responses to trait variation, and pollinator-mediated phenotypic selection will greatly advance our understanding of the evolution of nectar and volatile chemistry.

Future directions

Studies that bridge spatial and temporal scales to address how floral chemistry affects multispecies interactions, feedback within communities and the co-evolution of plants and their pollinators will push forward the boundaries of our field. Recently, research considering floral chemistry in a changing climate has found that increases in temperature could have species-specific effects on volatile emissions [45] and, coupled with increases in carbon dioxide and nitrogen, can also affect nectar composition [46]. However, without a more comprehensive understanding of floral chemistry in shaping relationships between plants and pollinators, it becomes difficult to predict how shifts in chemical composition might affect the stability and sustainability of key mutualisms. The chemical ecology of plant–pollinator interactions is an emerging field ripe for exploration and will no doubt provide incredible insight into the ecology and evolution of species interactions.

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