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Invited Review for Current Biology: 3000-4000 words, at least 3 figures, at least 50 refs

Mutualisms and (a)symmetry in plant-pollinator interactions

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Summary

The majority of flowering plants relies on animal pollinators for sexual reproduction and many animal pollinators rely on floral resources. However, interests of plants and pollinators are often not the same, resulting in an asymmetric relationship that ranges from mutualistic to parasitic interactions. Our understanding of the processes that underlie this asymmetry remains fragmentary. In this review, we bring together evidence from evolutionary biology, plant chemistry, biomechanics, sensory ecology and behaviour to illustrate that the degree of symmetry often depends on the perspective taken. We also highlight variation in (a)symmetry within and between plant and pollinator species as well as between (geographic) locations. Through taking different perspectives from the plant and pollinator side we provide new ground for studies on the maintenance and evolution of animal pollination and on the (a)symmetry in plant-pollinator interactions.

Keywords: chemical ecology, biophysics, pollination, reproduction, evolution

Introduction

The fascinating interaction between plants and pollinators is sometimes referred to as a mutual partnership [e.g. 1], but the interaction is driven by the different and often conflicting interests of plants and pollinators. Plants need reliable pollen dispersal and receipt at minimal costs, whereas pollinators seek floral rewards that can be harvested as fast and efficient as possible. The resulting interaction is sometimes referred to as (balanced) mutual exploitation [sensu 2].

Plants and pollinators have evolved traits that influence the balance of this mutual exploitation to their advantage [3–5] (Figure 1). Plants essentially face two connected challenges: (1) How to optimise the (amount of) reward offered to actual pollinators? (2) How to prevent access to floral resources by flower visitors that collect rewards but do not pollinate? To paraphrase Danforth and colleagues [3]: pollinators are like overly demanding lovers: they are great to have around, but if left without boundaries, they will take over your life and ruin it. Many plant adaptations restrict access to floral rewards in a variety of ways, ranging from morphological to mechanical or chemical boundaries. Conversely, pollinators evolved strategies to increase exploitation of floral resources to their advantage, such as morphological, behavioural and/or physiological adaptations.

The suite of (co-evolved) adaptations mediates a tension between plants and pollinators, which results in different types of interactions. The (relative) benefit for plants versus pollinators ranges from solely beneficial for flower visitors (e.g. reward robbing) via more balanced interactions to solely beneficial for plants (e.g. pollination by deception; Figure 1). Understanding the different aspects of the tension between plants and pollinators calls for a cross-disciplinary view, because the traits involved span across different scientific domains.

In this review, we discuss classic and recent work on the chemical, mechanical and sensory aspects of plant-pollinator interactions, and how work from various disciplines can help understanding the transition from mutualism to antagonism. We also argue that the degree of symmetry in the interaction between plants and pollinators is more variable than often appreciated, and depends on the perspective taken, species and/or geographic location.

Plant reward chemistry and pollinator dietary preferences

Many pollinators, in particular bees, depend on pollen, nectar and/or floral oils as major or sole food sources. Except for pollen, which primary function is to fertilise ovules, the only function of other types of rewards is to reward pollinators. Their chemical/nutritional composition (mainly protein, lipids, sugars and micro-nutrients) could therefore be adjusted to the needs of a specific pollinator group and be under selective pressure by pollinators (Figure 2). However, with few exceptions (e.g. specialized oligolectic bees restricted to few plant species/genera), the nutritional composition of floral rewards often does not meet the specific dietary preferences of potential pollinators. For instance, bumblebees (*Bombus terrestris* and *B. impatiens*) were found to preferentially collect pollen with a protein to lipid (P:L) ratio of between 5:1 and 10:1 [6], but that ratio is found in only a minority of species, viz. 33 out of 86 (38%) plant species [7]. Similarly, the majority of the 82 plant species chemically analysed by Vaudo and colleagues [8] fell within P:L ratios lower than 3:1. By the same token, honeybee (*Apis mellifera*) workers prefer nectar with a protein to carbohydrate (P:C) ratio of 1:250 [9], which was found in only three out of 304 nectar samples (<1%) from overall 34 plant species (C Venjakob, AM Klein and SD Leonhardt, unpublished data). Recent evidence suggests that preferences for specific nutrient contents and ratios are linked to reproductive fitness (for *B. terrestris* see e.g. [10] and [11]). If (foraging) preferences generally mirror nutritional requirements and are linked to pollinator fitness still needs to be elucidated.

In addition to nutrients, pollen and nectar often contain significant amounts of species-specific plant secondary metabolites (PSMs, [12]), including alkaloids, fatty acid derivatives, different glycosides, flavonoids and terpenoids). Many of these compounds are toxic if consumed at high doses [e.g. toxins in *Aconitum* nectar; 11] (Figure 2). PSMs decrease reward palatability [14,15] and often require specific physiological adaptations, such as specific enzymes (e.g. of the cytochrome family), for detoxification [e.g. 16]. The amount and composition of PSMs can differ between floral rewards, i.e. pollen and nectar, of the same plant [12]. These qualitative and quantitative differences can increase attractiveness of one resource while simultaneously decreasing attractiveness of the other. For example, in two *Dipsacus* species the PSM dipsacus saponin occurs in pollen but not nectar, which renders pollen unattractive to some bumblebee species, resulting in less grooming and thus increased pollen deposition on stigmas [17]. Moreover, PSMs can be toxic or repellent to some flower visitors (or herbivores) and attractive or beneficial to others [reviewed by 18]. PSMs in floral rewards can therefore be a filter mechanism and restrict the spectrum of flower visitors to actual pollinators, which generally increases pollination success and pollinator benefits [18,19]. The question why not all plants use PSMs to restrict visitor spectra to preferred pollinators remains to be answered.

Various physiological strategies help pollinators to deal with nutritionally imbalanced pollen and nectar diets and to mitigate negative effects of PSMs (Figure 3). For example, eusocial honeybees (*Apis mellifera*) and some species of stingless bees (Apidae: Meliponini) feed their offspring with glandular secretions rather than with pure pollen and nectar [reviewed by 20,21]. Such secretions match nutritional requirements and protect bee larvae from PSMs [22]. Some primitively eusocial bumblebees as well as some solitary bees also add nutritive salivary secretions to nectar and/or pollen prior to feeding larvae (as e.g. shown for *B. terrestris*, [23], and *Anthophora*, [24]). Other (solitary) species are able to digest toxic compounds with the help of specialised digestive systems or specific gut microbiota [25], which allows them to tolerate toxic PSMs. Interestingly, the evolution of tolerance for specific PSMs appears to independent of dietary specialization (i.e. oligolecty vs. polylecty) and shows no phylogenetic pattern [18].

Pollinators can also learn to avoid harmful reward compounds and adjust their foraging behaviour through complementary foraging (Figure 3). Diversified reward collection (i.e. allocating and mixing floral resources from different plant species) benefits pollinators through increasing overall resource quantity/quality, diluting toxic compounds or decrease costs associated with handling time (e.g. through mixing resources from morphologically similar flowers) [26–29]. Such mixed foraging likely requires cognitive flexibility and the ability to rapidly assess reward quality (e.g. through prioritized perception, [10]) in order to both readily switch to new floral sources and quickly learn to handle flowers and access rewards (Figure 3). Whether cognitive and behavioural flexibility is associated with an increased tendency of resource mixing has, however, not yet been investigated.

Pollinators can also adjust their way of feeding to nectar sugar concentrations in various ways, as shown by fluid dynamic models combined with pollinator experiments. For example, bees, which consume nectar via dipping their tongue, typically feed on nectar with 50-60% sugar concentration, whereas butterflies and birds, which feed via suction, typically feed on nectar with 35% sugar concentration, likely because nectar viscosity quickly decreases uptake via suction [30]. Intriguingly, honeybees can switch between suction and lapping, depending on the sugar content and viscosity, which increases their foraging efficiency [31]. Eusocial pollinators like honeybees and bumblebees store collected nectar in nests, which requires foragers to regurgitate nectar from crops. Recent work suggests that offloading complicates maximum energy transfer rates [32], because the offloading process also has implications for efficiency and energy-transfer-rate.

Morphological gate keeping of floral rewards, and how to access them

Natural selection favours plant traits that (1) increase the pollen transfer efficiency of pollinators, and (2) exclude antagonists such as herbivores and floral robbers (Figure 2). However, total pollen export to multiple recipient stigmas does not increase linearly with the amount of pollen placed on the bee's body, but rather follows a pattern of diminishing return [33]. Thus, gradual placing of pollen on the right pollinator and body part is often key to outcrossing success [33,34] and decreases the influence of stochastic effects (e.g. death of pollinators before pollen transfer).

Plants evolved a range of specialised biomechanical adaptations to regulate access to rewards and optimise pollen transfer (Figure 2), including keel flowers [35], lever-mechanism flowers [36,37], trigger flowers [38,39], explosive pollen release [40,41], heteranthery [42], and buzz-pollinated flowers [43]. For example, keel flowers present in many Fabaceae and Polygalaceae require floral visitors to exert a significant amount of force to access nectar and pollen rewards [37,44]. As the bee pushes its body to access nectar, the keel is pushed downwards, exposing pollen that is deposited on the bee's body. Keel morphology acts effectively as a pollinator filter, because it excludes floral visitors that do not have the physical attributes (e.g., butterflies) or strength (small bees, flies) to push open these flowers [44]. The keel morphology may also contribute to regulating pollen dispensing [45] and pollen placement on the visitor's body [46]. These three roles (pollinator filtering, pollen dispensing, and improved pollen placement) are not mutually exclusive and probably jointly explain the evolution of the keel and other specialised floral morphologies.

The anther-lever mechanisms, such as are present in most of *Salvia* (Lamiaceae) species, provide another example of how flower biomechanics filter pollinators by requiring a specific amount of strength to access rewards (Figure 2). The stamens form a physical barrier to the nectar, and the floral visitor (e.g. bees, moths or hummingbirds) needs to push through, bringing the anthers into contact with the dorsal side of the floral visitor [47]. Medium and large-sized bees can exert forces of 20-100 mN when visiting *Salvia,* which is enough to trigger the lever mechanism [36,44]. Biomechanical adaptations aimed at excluding some visitors thus seem most effective against insects other than bees, such as flies, butterflies and moths.

Buzz pollination further illustrates how floral visitors have driven the evolution of the biomechanical properties of flowers. Buzz-pollinated flowers often display anthers that open through small gaps or pores (poricidal anthers) instead or laterally dehiscing as most flowers do. During buzz pollination, bees produce vibrations to remove pollen from flowers, which are also usually nectarless [48]. Poricidal anthers thus act as filters excluding or discouraging visits by some animals (*e.g.*, flies, butterflies, non-buzzing bees) (Figure 2). In addition, poricidal anthers may also improve pollination efficiency by acting as pollen dispensers in which pollen release by individual buzzing bees is physically restricted [49]. Gradual pollen dispensing allows distributing pollen loads across more floral visitors, which can increase reproductive success when visitation rates are high and pollen delivery uncertain [33,50]. In turn, pollinators have evolved different behavioural characteristics that enable them to most efficiently exploit floral resources (Figure 3). For example, more than 50% of bee species, including bumblebees, carpenter bees and euglossine bees, are able to use their (flight) muscles to produce vibrations on flowers, i.e. buzz flowers, and so collect pollen from buzz-pollinated flowers [51]. The evolution of buzz pollination involves the co-option of a pre-existing behaviour by bees (buzzing) [52] to increase the rate of pollen removal from flowers, and the co-evolution of increasingly restrictive floral morphologies, such as poricidal anthers, that restrict and regulate pollen removal [53]. The vibrations produced vary widely in frequency, amplitude and duration, properties which determine the amount of pollen released from buzz-pollinated flowers [43,53,54]. They presumably are a function of the bees' morphological, physiological and neurological characteristics, but little is known about what exact characteristics determine the vibrations bees produce and how this varies between species [55].

Pollinator body size also plays an important role in several other interaction contexts. For example, bees with larger bodies can save energy owing to a higher surface to volume ratio, and so fly longer distances [56]. Large bees can thus cover large foraging areas, which may support floral resource mixing through collecting rewards from a greater diversity of flowers. Larger bodies or mandibles may further facilitate robbing in bees, allowing species to circumvent morphological features of plants (i.e. elongated tubes, poricidal anthers, keel flowers, anther-lever) aimed at restricting access to specific pollinators. Conversely, small bees may bypass physical barriers and so rob nectar while failing to trigger the lever mechanism thus removing the reward without pollination (Figure 3). Notably, robbing is a facultative behaviour, as most robbers also forage regularly on flowers [57] thereby providing the actual pollination service. It hence seems unlikely that pollinators evolved specific traits to facilitate robbing, but rather use pre-existing ones, such as large/strong maxillae or small elongated bodies.

Sensory interplay between plants and pollinators

Flowers create signals via colour, odour and/or shape, and pollinators perceive these signals via visual, olfactory and/or tactile mechanisms, which involve various biophysical processes. To be detected by pollinators, flowers have to stand out from the environment; for example, by producing colours that contrast with the background [58] and/or via emitting attractive scents [59]. Further, to promote repeated visitation, flowers should be memorably rewarding, which can be achieved by generating a stimulus that the pollinator will associate with a reward.

To attract pollinators – ideally while simultaneously being cryptic to antagonists – plants often combine different types of signals. Sensory signals can thus be used to selectively inform pollinators that perceive specific signals, while excluding antagonists (Figure 2). For example, most pollinating insects have very poor visual sensitivity in the red part of the light, which creates a “private niche” in colour space for birds, which do see red colours [60]. However, colour can only work as pollinator-selective signal when pollinators and non-pollinators have different visual systems. In the case of bees, of which there are both pollinators and robbers, colour vision is highly similar among species [61,62], thus preventing colour as sole filter. In these cases, scent, shape or patterning can aid deterring or at least reducing conspicuousness to antagonists. The morphologically similar flowers of two related *Gomphocarpus* species (Apocynaceae), for example, attract pollinators (bees versus specid wasps) mostly by emitting different scents [63]. Floral scent also seems to be the principal mechanism that determines pollinator specificity in orchids pollinated by euglossine male bees, who collect the chemical compounds and mix them to produce perfumes that attract females [64]. Moreover, a meta-analysis that compared the attractiveness of floral scents to pollinators and antagonists suggested that scents can serve the dual function of both attracting pollinators and deterring antagonists [65].

Some plant species alter floral signals, for example after pollination to deter pollinators (and florivores) from already pollinated flowers (Figure 2). Flowers that lose colour are less attractive to pollinators, but still enhance long-distance attraction of the inflorescence as a whole [66], because the unpigmented, pale flowers generate a bright signal that will be visible from long-distances [58]. Flower visibility can also be reduced temporarily by closing inflorescences after pollination, which reduces conspicuousness to antagonists [67], due to changes in inflorescence display size/shape and a less colourful lower side of the florets [68,69]. Scent emission is more plastic than colour, and (diel) patterns in scent emission frequently match anthesis and nectar availability, particularly for nocturnal pollinated flowers [70,71]. In *Silene latifolia*, scent emission decreases more rapidly in pollinated than unpollinated flowers [72], likely resulting in decreased visitation by pollinators and anatagonists.

At the extreme, floral signals can also be used to deceive pollinators (Figure 2). Deception of pollinators, where flowers mimic food, mating or oviposition sites, has evolved in at least 7500 species (6%) across 32 animal-pollinated angiosperm families [73]. Intriguingly, deception of pollinators occurs almost exclusively in insect-pollinated plants, but whether this is due to insects being more easily cheated upon or because the vast majority of animal pollinators are insects is unknown. Deception often occurs because flowers generate signals that capitalise on innate behavioural responses of pollinators [74], which can have evolved outside the context of plant-pollinator interactions [75]. Innate colour preferences, for example, occur in many groups of flower-visiting insects, including flies, butterflies and bees [58,76,77], and have been thought to be important as a deceptive cue in, for example, orchids [78]. Combinations of fine-tuned visual, chemical and tactile signals can yield floral phenotypes that are deceptive to the point that pollinators choose the deceptive flower over the genuine object the flower mimics. For example, sexually deceptive *Ophrys* flowers are preferred by male wasps over a female conspecific [79]. In addition to colour and scent, some plant species evolved flower thermogenesis (heat production), e.g. they mimic a suitable egg-laying substrate, such as dung or carrion, and so co-opt innate cues used by insects to find oviposition sites [75]. However, visiting a warm, albeit rewardless, flower need not always be bad, because heat in itself can be a reward to insect pollinators, particularly when ambient temperatures are low [80].

In response to deception, pollinators can learn to avoid deceptive flowers after one or a few visits [81], which impedes future outcrossing (Figure 3). Indeed, aversive learning of inflorescence hue [82], colour patterns [83] and odour [84] occurs across insects that pollinate sexually deceptive flowers, and this is expected to lead to negative frequency-dependent selection of flower morphs. The situation becomes trickier when only some flowers on a plant are deceptive, because these few flowers may result in the entire individual suffering from reduced pollination. For example, pollinating bumblebees rapidly learn to detect and avoid rewardless (female) *Begonia odorata* flowers, which comes at the expense of visiting real (male) flowers that are highly similar in terms of visual signals [85]. Overall, bumblebees nevertheless benefit from their learning ability, because the time saved by avoiding rewardless flowers outweighs the effect of missing out on genuine flowers [85]. There are situations, however, where avoiding deceptive flowers becomes detrimental for the pollinators' own fitness. For example, male wasps learn to avoid areas with sexually deceptive *Chiloglottis trapeziformis* flowers [86]. As a consequence, they also avoid female wasps occurring in the same areas as the plants, which reduces mating events [86].

In the absence of extreme cases such as (sexual) deception, pollinators can also learn to use particular floral cues as indicators for reward quantity and/or quality (Figure 3). For example, bumblebees learn to associate floral scent compounds with the amount of reward in *Brassica rapa* and *Penstemon digitalis* [87,88]. In this case, distinct chemical cues are good candidates to honestly signal reward quantity [89]; however, flowers typically provide a plethora of (chemical) signals. To make sense of this signal complexity, pollinators may either simultaneously process multimodal information [90] or prioritise perception of those cues that are linked to compounds that are most influential (e.g. affect reproductive fitness), such as specific nutrients or toxic compounds, while ignoring others [10]. Taken together, the sensory interplay between plants and pollinators represents an impressive array of partly highly species-specific fine-tuning that involves a variety of biochemical and neuronal adaptations.

Variation in time and space, and phenotypic mosaics

Spatial or temporal variation in plant or pollinator phenotype, abundance or community can create mosaic-like patterns in the degree of mutualism [91]. In addition to interspecific variation, phenotypic variation can occur between populations, individuals and even within an individual, as is the case for plants bearing multiple flowers at a given moment. A neat example of geographic variation in the degree of plant-pollinator mutualism is that of *Lithophragma parviflorum* and its pollinator, *Greya pollitella* moths [4,92]. *Greya pollitella* are effective pollinators, though their larvae consume a small number of developing seeds. When *Greya* moths are the sole pollinators, their pollination service outweighs the antagonistic effects caused by the larvae. However, in populations with many bombyliid flies, which are equally efficient pollinators but do not parasitise developing seed, the interaction with *Greya* moths becomes antagonistic [4].

Floral reward quantity and quality, as well as pollination service are often dynamic in both time and space. For plants, such variation in reward quality and availability occurs at various levels [88,93,94]. Predictable within-plant variation in reward availability can modify the degree of geitonogamy and thereby increase plant reproductive success. In vertical inflorescences, for example, a decreasing amount of nectar from lower to upper flowers, can encourage pollinators to leave a plant and go to another individual when facing a decreasing amount of reward per flower [95]. At the community level, variation in reward availability may result in increased pollen dispersal, because pollinators tend to fly longer distances after encountering rewardless flowers [96].

Regional and temporal differences in pollinator community can in turn impose varying selective pressures on floral traits. Geographic covariation of floral and pollinator traits has been reported for numerous traits, such as flower morphology and nectar properties versus bird beak morphology [97], optical properties and colour vision [98,99] and scent and pollinator community [100]. All else being equal, spatially heterogenous selection on any trait results in a non-homogeneous trait landscape. For example, in the spring ephemeral *Claytonia virginica*, populations of plants that are pollinated by pollen-collecting bees produced more pollen per flower and showed more staggered pollen release than populations pollinated by nectar-foraging bee-flies [101]. Such examples highlight local adaptation of individual plants to the present pollinator fauna, resulting in variable degrees of (a)symmetry even within the same plant species.

Studies on variation in floral rewards mostly focused on nectar properties, and how observed variation relates to diel patterns, pollinator activity, abiotic effects and/or flower age [95]. We lack knowledge on rewards other than nectar, how they vary in quantity (e.g. amount of heat as a reward) and quality (e.g. pollen chemical profile), and to what degree their value to pollinators is context-dependent.

Conclusions

The interaction between plants and pollinators is characterised by a tension arising from conflicting interests of both parties. Evolutionary adaptations in plants and pollinators can lead either to a balance between partners resulting in a symmetric relationship, or to an imbalanced, asymmetric relationship. How symmetric or asymmetric interactions between plants and pollinators really are is hard to determine, as information on pollination efficacy and/or actual nutritional requirements and tolerance of pollinators is lacking.

Relative benefits of plants and pollinators may or may not be balanced in the long term, but the frequently observed asymmetries suggest an evolutionary arms race. Understanding the sequence of evolutionary events will be useful to understand that putative arms race. For example, the colours and scents of flowers probably evolved long after the pollinator sensory systems that perceive them, and not vice versa [102,103], but how does this apply to other traits, such as reward quality versus pollinator dietary requirements, or restricted floral morphologies and the way pollinators circumvent these? In specialised interactions where plants and pollinators strongly depend on each other, pollinator and plant adaptations probably evolved synchronously [e.g. bees' ability to sonicate and poricidal anthers; 100]. Other taxa that were not originally part of the interaction may have evolved similar traits at a later stage, however. Capitalising on (repeated) switches between pollination systems [34,104,105], pollinator behaviour (e.g. buzz pollination; [52]) or floral phenotypes, is a powerful way to explore the evolutionary trajectory of adaptations and how they may have led to the extant interaction.

The degree of asymmetry often varies in time and space, which complicates matters further. Determining the factors that underlie inter- and intraspecific variation in the type, quantity, quality and accessibility of rewards across time and space, and how pollinators respond to such variation is central to understanding the degree of (a)symmetry in different plant-pollinator interactions. This is particular true for rewards that are dynamic and context-dependent (e.g. heat or mating opportunities).

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Figure 1. Varying symmetry and relative benefits for flower visitors and plants. The horizontal bar depicts the relative benefit for pollinator (left) and plant (right). The figure shows exemplary cases. The position on the continuum strongly depends on the context, and is determined by the pollinator’s relative efficacy (pollen transferred versus reward removed), and the amount of reward obtained over energy invested.

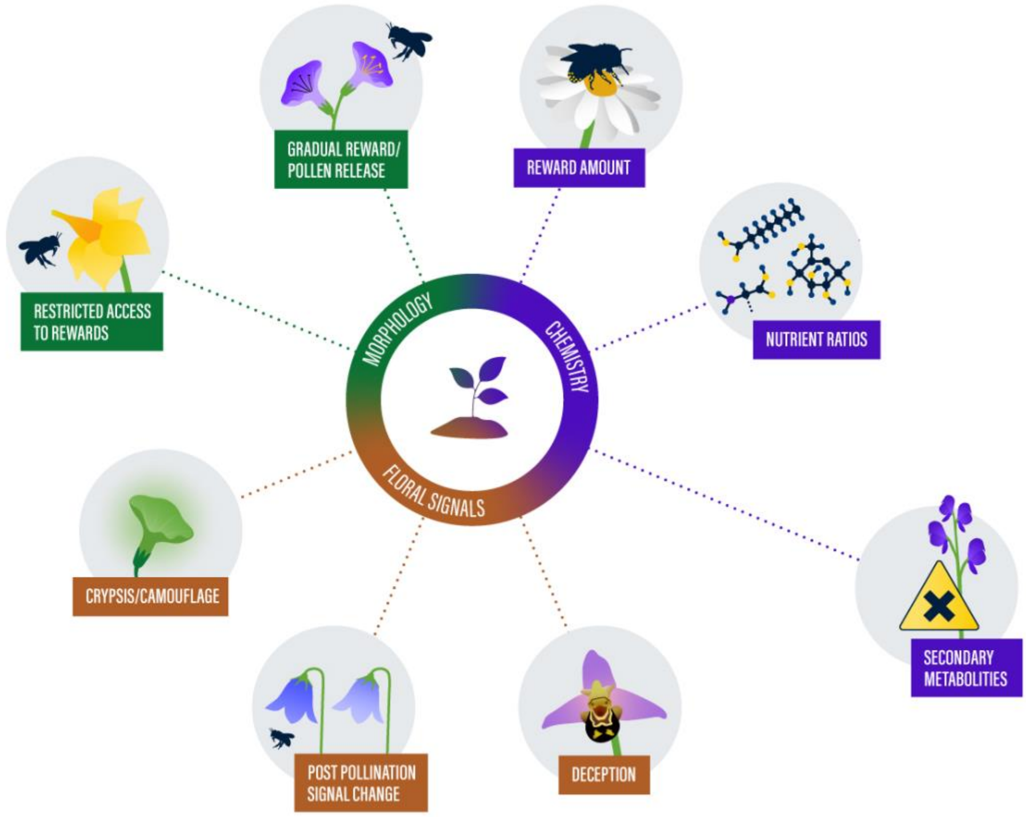

Figure 2. Exemplary plant adaptations to increase advantage from interaction with pollinators. Characteristics of the reward chemistry can render the reward quantity or quality suboptimal, and thereby deter certain flower visitors or incentivise a return visit. Signals acting on pollinator senses can increase or decrease floral attraction to pollinators and other flower visitors. Flower morphology and biomechanics determine the handling time and accessibility of rewards.

Figure 3. Exemplary pollinator adaptations and behavioural responses to increase exploitations of flowers. Pollinator senses and foraging behaviour determine how easily a pollinator can (learn to) detect or avoid flowers and associate signals with a reward. Morphological adaptations, such as body size, determine whether a pollinator can reach and enter the flower and access rewards. Physiological adaptations allow pollinators to efficiently exploit the rewards and to cope with reward toxicity.