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Floral Filters: Inviting Mutualists and Screening out Antagonists

Florale Filter: Attraktiv für Bestäuber und abschreckend für antagonistische Blütenbesucher

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Summary: Flowers interact with diverse organisms, some of them are beneficial and provide pollination service, others are detrimental to the plants' reproduction. The latter, antagonistic, flower visitors may act as nectar-thieves or robbers, feed on pollen and other floral tissues, aggressively defend floral resources against pollinators or even feed on them, or are microorganisms with potentially negative effects on pollination. Due to the presence of both, mutualistic and antagonistic flower visitors, flowers benefit from features that invite the former and screen out the latter functional group, i.e. traits that function as floral filters. In this review it is outlined how different flower traits affect the behaviour of flower visitors and how this relates to their potential as filters. Many flower morphologies such as deep and narrow nectar tubes effectively restrict the visitation to a small subset of the potential visitor spectrum. Likewise, other features such as trichomes covering sepals prevent crawling insects from reaching the nutritious rewards. The morphology, together with the colouration of flowers, strongly contributes to the optical display of the reproductive structures that may attract some flower-visitors. Colours are well known for their attractive function, either if animals have innate preferences for certain colours or after associative learning. On the other side, pigments stored in petals may serve as anti-feedants for florivorous animals, or the flowers may be inconspicuous for some flower visitors due to their colouration. The dual role of flower scents is indicated by studies that demonstrated that animals are attracted and/or repelled by certain scent bouquets or individual compounds. Similar to colours, the attractive function of scents may result from either innate preferences or from responses to learned cues associated with rewards. The floral resources by themselves may contain secondary metabolites that either have attractive or repellent properties. It becomes evident that the traits discussed here are multifunctional and thus facilitate efficient pollination, but also ward off unbidden flower visitors, and thereby maximise the plants' reproductive success. Furthermore, having acknowledged that flower traits function both ways, it is indicated that both mutualistic and antagonistic flower visitors select for floral phenotypes, representing a compromise between attraction and defence.

Keywords: colour, morphology, pollination, resources, scent.

Zusammenfassung: Pflanzen interagieren mit zahlreichen Organismen, die unterschiedliche Auswirkung auf deren Fortpflanzung haben. Besonders deutlich wird dies bei Blüten, die stark auf den Besuch von Tieren angewiesen sind, die den Pollen von einer Blüte zur nächsten transportieren und damit die Pflanzen bestäuben. Zu diesem Zwecke bieten die Blüten Ressourcen wie Nektar und Pollen an, die den Tieren als Belohnung zur Verfügung stehen. Jedoch gibt es auch zahlreiche Blütenbesucher, die zwar großes Interesse an dieser Nahrungsquelle haben, aber nicht zur Bestäubung beitragen oder die Blüten sogar zerstören. Daher benötigen Blüten einerseits Eigenschaften, um Bestäuber anzulocken, andererseits aber auch Eigenschaften, um Antagonisten vom Blütenbesuch abzuhalten. Beide Funktionen können durch sogenannte „Filter" ausgeübt werden, die attraktive und defensive Funktionen vereinigen. In diesem Artikel wird eine Übersicht über mehrere Blütenmerkmale gegeben, die das Verhalten von Blütenbesuchern beeinflussen, weiterhin wird erörtert, wie dies zu ihrer Rolle als florale Filter beiträgt. Morphologische Barrieren, wie zum Beispiel tiefe und enge

Nektarröhren, bieten einen sehr effektiven Schutz gegen unerwünschte Blütenbesucher, die durch diese Strukturen den Nektar nicht erreichen können. Andere Blüten schützen sich durch Trichome an den Kelchblättern vor krabbelnden Insekten. Andererseits hat die Morphologie, zusammen mit der Färbung, einen entscheidenden Einfluss auf das optische Erscheinungsbild von Blüten, das für viele Besucher attraktiv erscheint. Die Attraktivität von Blütenfarben resultiert zum einen aus angeborenen Präferenzen einiger Besucher, zum anderen dienen die Farben als Merkmale, die mit den Blütenressourcen assoziiert werden und den wiederholten Besuch fördern. Pigmente, die die Färbung von Blüten bewirken, dienen in einigen Fällen jedoch auch dem Schutz der Blütenblätter, die durch die Einlagerung der Pigmente für einige Insekten ungenießbar werden. Außerdem können einige Blütenfarben von gewissen potenziellen Besuchern schlecht wahrgenommen werden, was zu einer Reduzierung der Besuche führen kann. Die doppelte Funktion von Blütendüften erschließt sich aus Studien, die sowohl eine anlockende Wirkung der Düfte zeigen, und aus Studien, die belegen, dass viele Organismen von Blütendüften abgeschreckt werden. Ähnlich zu den Farben kann die Anlockung auf angeborenen Präferenzen basieren oder durch assoziatives Lernen hervorgerufen werden. Sekundärmetabolite, die in Pollen und Nektar vorkommen, können die Ressourcen mit attraktiven und / oder defensiven Funktionen ausstatten. Es soll deutlich werden, dass die aufgeführten Merkmale mehrere Funktionen gleichzeitig ausüben und dabei effiziente Bestäubung fördern und andererseits unerwünschte Organismen vom Blütenbesuch abhalten. Beide Eigenschaften tragen dazu bei, dass sich Pflanzen möglichst optimal fortpflanzen können. Diese zweifache Wirkung legt weiterhin nahe, dass sowohl mutualistische als auch antagonistische Blütenbesucher an der Selektion des Blütenphänotyps beteiligt sind. Das Erscheinungsbild der Blüten entspricht daher einem Kompromiss aus Anlockung und Abwehr.

Schlüsselwörter: Bestäubung, Duft, Farbe, Morphologie, Ressourcen.

1. Introduction

Over two hundred years ago, Christian Konrad Sprengel (1793) published his work „Das entdeckte Geheimnis der Natur im Bau und in der Befruchtung der Blumen“ and thereby founded modern pollination biology. Ever since, naturalists, including Darwin (1862), were fascinated by the diversity of interactions between flowers and their visitors and by the adaptations of both trophic levels that either facilitate sexual reproduction of the plants, or nutrient intake by the flower visitors. Accordingly, flower traits such as colour, morphology, scent, and rewards had been interpreted as advertisements for more or less specialised pollinators, which led to the concept of “pollination syndromes” that hypothesize suites of floral features that are evolved as adaptations to certain visitor groups (Knuth 1908; Vogel 1954; Faegri & Pijl 1979). According to these syndromes, pleasant and lightly scented, red to purple flowers with fair amounts of nectar in long tubes, for example, tend to be pollinated by butterflies, while beetle pollinated flowers are often heavy scented, dull coloured and produce large amounts of pollen (Faegri & Pijl 1979). However, the concept of pollination syndromes has been criticised (Waser et al. 1996) and recent studies demonstrated that the syndromes do not predict the dominant flower visitors (Ollerton et al. 2009) and that flowers sharing traits are not visited by the same visitor spectrum in different habitats (Lazaro et al. 2008). The lack of accuracy in the predictability of pollinators by flower features suggests that further selective agents shaped floral traits.

Almost one hundred years after Sprengel (1793) had described floral adaptations to pollinators, Anton Kerner von Marilaun (1879) published his work “Die Schutzmittel der Blüthen gegen unberufene Gäste” emphasising the existence of non-pollinating flower visitors that exploit floral resources and thereby may be detrimental for the plants' reproduction. Besides mutualists that disperse pollen in exchange to floral rewards, multiple organisms consume pollen, nectar, petals, anthers and stigmas without contributing to the pollination of flowers (KERNER 1879; IRWIN et al. 2004; MCCALL & IRWIN 2006). These antagonists often have detrimental effects on the plants' reproduction by either reducing the pollination service by mutualists (JUNKER et al. 2010a) or by destroying whole flowers (MCCALL & IRWIN 2006). Since flowers are reproductive structures, resource sinks, and represents a high investment for plants, their loss may be more costly than the loss of vegetative tissues (KESSLER & HALITSCHKE 2009). In KERNER's (1879) point of view, the morphology of flowers reflects the necessity to screen out these detrimental flower visitors. In fact, plants are exposed to various interacting organisms with highly variable net effects on the plants' performance and reproductive success. Therefore, the phenotype of a plant may be the result of adaptations to different organisms and functional groups. Individual traits may thus not be the product of a tight co-evolution between the plant and a specific (and mutual) interaction partner, but rather the outcome of conflicts between opposed selective pressures leading to trade-offs that optimise fitness-gain (STRAUSS & IRWIN 2004; KESSLER & HALITSCHKE 2009). The visitation of flowers by diverse functional groups with contrasting net effects on the plant's reproduction suggests that both SPRENGEL's (1793) and KERNER's (1879) concepts are realised in flowers. Here, I promote the notion that floral traits represent filters that are attractive for mutualists but at the same time defensive against antagonists.

2. Functional groups of flower visitors

Obligate out-crossing animal-pollinated plants are strongly dependent on their pollinating mutualists that are most often rewarded by nutritious nectar and pollen. Flower visitors that have physical contact to anthers and stigmas serve, in most cases, as pollinators with, however, varying efficiency (e.g. KANDORI 2002; SAHLI & CONNER 2007). All other visitors that display different behaviours while visiting flowers and thus do not contribute to pollination are exploiters of these rewards. Flower visitors are thus traditionally assigned to either mutualistic or antagonistic agents, emphasizing the net effect for the plant of a given interaction. This phytocentric point of view is helpful if the plant's reproduction is in focus and if the interaction between a specific species pair is under consideration. However, it is not possible to unequivocally attribute one of the categories to a flower visiting species in a context where several plant species are involved. Morphological (mis-)matches of insects and flowers or the insects' behaviour while collecting floral resources may determine whether the interaction is mutualistic or antagonistic. For example, bees are very efficient pollinators of many plants but are severe pollen thieves (HARGREAVES et al. 2009) or nectar robbers (MALOOF & INOUYE 2000) in the interaction with other species. For instance, the bumblebee *Bombus occidentalis* pollinates several plant species but is also a nectar robber of others (IRWIN & MALOOF 2002). Likewise, ants usually are nectar thieves but some plant species rely on ants as pollinators (GOMEZ & ZAMORA 1992; DE VEGA et al. 2009). Even an undescribed orthopteran species, an insect order that usually is not associated with pollination, was recently found to be the exclusive pollinator for an orchid in Mauritius and Reunion (MICHENEAU et al. 2010). Similarly to these examples, most flower-visiting taxa can be assigned to different functional groups, depending on the plant species visited (Tab. 1). Thus, the net effect of flower visitors on the reproduction of the visited plants depends also on the plant species visited. Furthermore, the behaviour and thus net effect of visitors on flowers of a

Tab. 1: Typical flower visiting insect orders and families and their assignment to multiple functional groups. Citations refer to studies discussing their role as flower visitors (functional group). Examples show that taxa regarded as mutualistic flower visitors can also have negative effects on plants' reproduction and *vice versa*.

Tab. 1: Insektenordnungen und -familien, die häufig auf Blüten anzutreffen sind, können unterschiedlichen funktionellen Gruppen angehören. So können Taxa, die als Bestäuber bekannt sind, ebenso Nektardiebe und Nektarräuber, Pollendiebe, Blütenfresser oder Parasiten sein oder sie verhalten sich als Aggressoren, die Bestäuber von den Blüten vertreiben. Andererseits, gibt es auch viele Beispiele in denen ansonsten antagonistische Blütenbesucher, effektive zur Bestäubung beitragen. Die Zitate verweisen auf Literatur, die sich mit der Rolle (funktionellen Gruppe) der Blütenbesucher beschäftigen.

Taxon	Functional group	Reference
Apidae	pollinators	Faegri & Pijl 1979
	nectar thieves	Inouye 1980
	nectar robbers	Irwin 2003
	pollen thieves	Hargreaves et al. 2009
	removal of petals	Rozen et al. 2010
Coleoptera	pollinators	Faegri & Pijl 1979
	pollen thieves	Hargreaves et al. 2009
	florivores	McCall & Irwin 2006
	emasculators	Hargreaves et al. 2009
Diptera	pollinators	Faegri & Pijl 1979
	nectar thieves	Hunter et al. 2000
	pollen thieves	Hargreaves et al. 2009
Formicidae	pollinators	Gomez & Zamora 1992
	nectar thieves	Junker et al. 2010a
	nectar robbers	Inouye 1980
	aggressors	Junker et al. 2007
Lepidoptera	pollinators	Faegri & Pijl 1979
	nectar thieves	Inouye 1980
	parasites	Dötterl et al. 2006
Orthoptera	pollinators	Micheneau et al. 2010
	florivores	McCall & Irwin 2006

single plant species may be variable over space and time (Irwin & Maloof 2002) and may depend on additional factors such as other flower visiting species or the resource (e.g. nectar or pollen) collected (Junker et al. 2010 a).

Non-pollinating, antagonistic flower visitors may be assigned to one (or more) of the following groups (compare to Tab. 1): (a) Nectar thieves are animals that consume nectar without pollinating. Prominent examples are ants (Junker et al. 2011 b). (b) Nectar robbers consume nectar that is reached via self-bitten holes in the corolla (nectar thieves, in contrast, do not damage flowers). Short tongued bees are often observed to illegitimately exploit nectar (Irwin et al. 2010). (c) Pollen thieves are animals that consume pollen but do not transfer it between flowers and / or have no contact to stigmas. Bees that serve as pollinators in some plant-species are common pollen thieves in other species, beetles often consume entire stamina (Hargreaves et al. 2009; Junker et al. 2010 a). (d) Florivores consume flower tissues such as petals and thereby destroy the flowers, e.g. orthopterans (McCall & Irwin 2006). (e) Predators of pollinators such as crab spiders exploit floral signals that attract pollinators and lead them to the predators

(Dukas & Morse 2003). (f) Besides animal antagonists, pathogenic microorganisms that cause diseases such as fire blight are a major threat for flowers (Buban et al. 2003). Additionally, non-pathogenic microorganisms may negatively interfere with pollination. For instance, yeast dwelling in flower nectar has been shown to alter the sugar composition of nectar in a way that it becomes less preferable for pollinators (Herrera et al. 2008).

The diversity of functional groups of antagonistic flower visitors suggests that defence, next to attraction, is a very important function of floral traits, and that flowers need to perform both of the contrasting tasks simultaneously. Thus, pollinators and exploiters of floral rewards may be selective agents affecting flower traits that either facilitate visits by mutualists or prevent visits by antagonists (Junker et al. 2011 b; Schiestl et al. 2011). Often, the direction of the selection may be the same: long nectar tubes exclude short tongued insects but invite insects with long mouth parts and promise a more exclusive resource for them (Heinrich 1976). In other cases mutualists and antagonists exert contrasting selective pressures, e.g. if pollinators prefer floral traits that offer no effective protection against antagonists (e.g. Galen & Cuba 2001).

3. Adaptations of flowers to diverse functional groups

Flowers are challenged by the simultaneous presence of mutualists and antagonists and thus by the demand to attract and defend. **Therefore, floral filters are required, which are traits that select visitors from the potential and available spectrum in order to maximize pollination success and thus increase plant fitness.** Flowers usually stand out from the surrounding vegetation by their conspicuous appearance, their complex morphology, the multiple types of resources offered to visitors and by displaying olfactory and visual stimuli. All of these traits are known to facilitate the visitation of pollinators due to their attractive function, but they also have the potential to ward off antagonists and thus are potent floral filters.

It has been demonstrated that some flower visitors primarily use visual cues to find their host plants (Omura & Honda 2005), others primarily rely on scent (Primante & Dötterl 2010). Other studies, however, suggest that both colour and scent are needed to evoke behavioural responses (Raguso & Willis 2005). Additionally, going into more detail, only a fraction of the volatiles that are emitted by flowers may be used by pollinators to locate them (Riffell et al. 2009). Similarly, only one or few volatiles of a floral scent bouquet may be needed to repel antagonistic flower visitors (Junker et al. 2011 c). These examples raise the question why flowers display multimodal signals and why floral scent bouquets often are composed of dozens of different volatiles. The seemingly behavioural inactive components were often considered as "noise" that are functionless biosynthetic by-products of the behavioural active components (Raguso 2003). However, signal components that may have no function in the interaction between a flower and one visitor, may still be important for the interaction with another visitor. Furthermore, components that have no function if presented individually may have synergistic effects with another scent compound or if it is presented with a visual stimulus. This has been investigated in the context of associative learning where combined signals (colour **and** scent) were faster and more reliably associated with rewards than signals consisting of only one stimulus only (colour **or** scent) (Leonard et al. 2011). Thus, the synergistic or additive effects of scent and colour in pollinator attraction may explain part of the complexity of flower signals (Leonard et al. 2011; Hebets & Papaj 2005). However, studies demonstrating that only one stimulus or even only part of an stimulus are required for pollinator attraction (e.g. OMURA & HONDA 2005; RIFFELL et al. 2009) imply that several functions (e.g. attraction and defence) contribute to the high complexity of cues and morphologies found in flowers. Here, I will discuss the multiple functions of some flower traits, which may help to explain the complexity of floral phenotypes encountered in nature. One obvious mechanism to promote visits from mutualists and avoid visits from antagonists is to adapt the flowering phenology to the activity pattern of the visitors, i.e. to advertise the flowers when the pollinators are active but to be inconspicuous when antagonists reach their peak activity (STONE et al. 1996; KESSLER et al. 2010). For instance, *Arabidopsis halleri* subsp. *gemmifera* plants growing in areas with a high abundance of the florivorous beetle *Phaedon brassicae* flower much earlier than plants that experience no florivory, in order to escape from these antagonistic flower visitors (KAWAGOE & KUDOH 2010). This and other examples suggest that floral phenology is selected by pollinators and antagonistic flower visitors and represents an effective mechanism to avoid conflicts with the latter. However, in the following I will focus on floral traits that have the potential to act as floral filters, i.e. have a dual function in the interaction with potential partners.

4. Morphology

A key invention of angiosperms was the unification of male reproductive structures in an outer whorl and female structures in an inner whorl on a single shoot (GLOVER 2007). The reproductive structures are surrounded by sterile parts, the perianth, usually divided in green sepals and coloured petals (LEINS 2000). Although the first flowers may have lacked the perianth (SUN et al. 1998), most recent flowers possess it. The perianth forms the complex and diverse morphological structures found across the angiosperm phylogeny. The diversification of floral form came along with an increasing importance of animal pollination, which replaced the less effective pollen dispersal by wind (GLOVER 2007). MÜLLER (1881) proposed a classification system for the diversity of flower types, which was, however, strongly related to the main visitors that are commonly observed at flowers displaying these morphologies. Therefore, his classification may be a circular argument when flower types are used to predict the effect on the visitor spectrum of a flower. KUGLER (1970) proposed another classification system, which was solely based on the morphology of flowers and makes no assumptions on the dominant visitor. Both classifications systems for floral morphology are still widely used to communicate a first impression on the morphology of a flower (KLOTZ et al. 2002). Although the diversity of floral structures is indicated by these categorical classifications, they may still underestimate the variety encountered even within each category, especially if the accessibility of resources to, and the preferences and aversions of diverse potential flower visitors are under consideration. To evaluate the match or mismatch between flowers and their potential visitors, metrics with a continuous scale are preferable, i.e. the nectar of a given flower is reachable for a flower visitor only, if the morphology of the flower does not prevent the access. For instance, nectar consumption by insects is possible only from flowers that offer nectar in tubes that are as wide or wider than the insects' head capsule. This relationship between the flower's and the insect's morphology explained part of the presence or absence of ant-flower interactions (JUNKER et al. 2011 b). Likewise, insects with a long proboscis are able to reach deeply hidden nectar in corollas that is inaccessible for insects with a short proboscis. The importance of such morphological barriers has been demonstrated in a diverse flower-visitor community where the corolla-depth of the flowers precisely predicted the minimum size of their visitors' proboscis (Stang et al. 2006). Thus, morphological barriers are very potent floral filters that strongly influence the visitor spectrum of flowers by granting access only to those visitors that match their morphology. Besides barriers imposed by long and narrow corolla tubes, other flower structures such as hairs, spines and sticky surfaces are also well suited to reduce or prevent the visitation of detrimental agents (Kerner 1879). Furthermore, the architecture of flowers also facilitates the precision and thus efficiency of pollen transfer by pollinators that are forced to behave in a way as dictated by the flower's morphology during flower visits (Armbruster et al. 2004).

The morphology of flowers is not only a physical barrier or a guide for pollinators, it also strongly contributes to the optical display of the flowers that invites or discourages visitors to interact with the flowers. For example, many flower visitors prefer large (Glaettli & Barrett 2008) and more symmetrical (Moller & Eriksson 1995) flowers over smaller and unsymmetrical ones. Both, size and symmetry, are floral characteristics formed by the perianth and thus are strongly affected by the floral morphology.

5. Colour

Flowers reflect certain wavelengths of visible and UV light and absorb others, resulting in a characteristic colouration of petals and other floral structures. The wavelength-specific reflection and absorption properties are achieved by pigments that are synthesized and stored in cells of flowers (Davies 2004; Tanaka et al. 2008). The major classes of floral pigments are flavonoids (anthocyanins), carotenoids and betalains, the latter being restricted to the plant order Caryophyllales (Grotewold 2006). Carotenoids appear mostly yellow to red in terms of human vision, while flavonoids are responsible for more diverse colours covering the full range of human colour vision except for green that is caused by chlorophyll (Davies 2004). The specific coloration of flowers (reflection spectrum) results from the presence of one or more pigments or are the effect of interactions between pigments and co-pigments, which modify the absorption spectrum of flavonoids (Glover 2007). A large number of different pigments are identified including over 600 carotenoids and over 7000 flavonoids (Davies 2004). Hydrophilic flavonoids are usually found in vacuoles while the lipophilic carotenoids are associated with plastids of epidermal or sub-epidermal cells of petals (Davies 2004).

Innate preferences to flower colours have been described for several flower visitor taxa (Lunau & Maier 1995), which often overlap across visitor taxa, if based on human colour vision. For instance, honeybees and syrphid flies both have an innate preference for human-yellow flowers (the former also for human-blue) (Lunau & Maier 1995). The consideration of ultraviolet light may help to further elucidate specific preferences for certain colours (Lunau et al. 2011). Furthermore, innate preferences to certain wavelengths were indicated: the hawkmoth *Macroglossum stellatarum* exhibited preferences for 440nm and 540 nm (Kelber 1997). Evolutionary changes in flower colour associated with a change of the main pollinator are realized by mutations affecting genes that control the presence or absence of certain pigments (Bradshaw & Schemske 2003). Accordingly, the presence of certain pigments were attributed to the pollination systems of these flowers: Delphinidin was found to be common in bee-pollinated flowers, flowers predominantly visited by lepidopterans often contain cyanidin (Saito & Harborne 1992), the presence of carotenoid pigments increases the attraction of bumblebees (Bradshaw & Schemske 2003).

Besides their role in innate attraction, flower colours also commonly serve as recognition cues for flower visitors that associate optical cues with rewards (GIURFA 2004; CHITTKA & RAINE 2006), which may, however, be inaccurate as colours often are generalized by the flower visitors, i.e. colours similar to the reinforced colour are also preferred over colours that are less similar to the reinforced colour (GUMBERT 2000).

Three potential mechanisms how pigments and resulting colours may prevent or at least reduce the visitation of antagonistic taxa are conceivable but did not receive much attention so far. (a) Pigments may have anti-feedant properties. For instance, floral anthocyanins responsible for the blue coloration of parts of *Petunia hybrida* petals strongly decreased the performance and increased the mortality of moth larvae (JOHNSON et al. 2008). (b) The display of certain colours may sensorially exclude unwanted flower visitors. For instance, bees are not able to perceive UV-absorbing red and thus are less likely to visit flowers with that coloration (LUNAU et al. 2011). (c) Non-green plant parts apart from flowers often have been viewed as aposematic signals indicating toxic secondary metabolites to herbivorous animals (LEV-YADUN 2009). It may be possible that flowers indicate a high concentration of defensive secondary metabolites by vivid colours (SCHAEFER & ROLSHAUSEN 2006) and thus are avoided by herbivores due to an aposematic colouration (LEV-YADUN 2009). This potential mechanism, however, has not been thoroughly investigated in relation to floral ecology.

6. Scent

Floral scents are one of the most diverse and complex signals in plant-animal interactions and consist of products of the secondary metabolism. Floral scents are either produced in epidermis cells of floral tissues or in osmophores, glandular trichomes and hairs that are specialised organs for scent production and emission, the latter ones being restricted to few (highly evolved) taxa (EFFMERT et al. 2006). Volatiles emitted by flowers are blends of few up to more than one hundred different substances mostly with a molecular mass less than 300 facilitating the volatility (KNUDSEN & GERSHENZON 2006). The molecules derive from several different biosynthetic pathways, the most common chemical classes are mono- and sesquiterpenoids, benzenoids and fatty acid derivatives, less common are diterpenes, irregular terpenes, nitrogen or sulfur containing compounds and miscellaneous cyclic compounds (KNUDSEN et al. 2006). All of these substance classes may comprise oxygenated substances, i.e. hydrocarbons with functional groups. The most common functional groups are alcohols, aldehydes, esthers, ethers and ketones (KNUDSEN et al. 2006). Some individual compounds are emitted by a high percentage of flowering plant species, e.g. some monoterpenes occur in more than 70% of all floral scent bouquets analysed so far (KNUDSEN et al. 2006). Nonetheless, the interspecific variability of the composition of floral scent compounds is enormous due to the numerous combinatorial possibilities of frequently emitted substances and the presence of compounds unique to one or few plant species (RAGUSO 2008).

Visitors are attracted to flowers either due to innate preferences to certain scent molecules or after conditional learning if floral rewards are associated with volatiles. In highly specialized systems “private channels” are often utilized to exploit the pollinators’ innate preferences for certain scents. For instance, deceptive orchids often emit sex-pheromones of female insects that attract mating partners (AYASSE et al. 2003). Key attractants in specialised flower-pollinator interactions that are not mediated by the insects’ sex pheromones may be uncommon or unique substances exclusively emitted by these plant-species, or common substances that may be quantitatively dominant in the bouquet (Dötterl et al. 2006). It was attempted to attribute certain volatile compounds or chemical classes of scents to flowers that are usually pollinated by specific insect orders or vertebrate classes (Dobson 2006), in order to add products of the secondary metabolism (not only paraphrases of scents such as “sweet” or “fruity”) to the suit of traits that describe the classical “pollination syndromes” (see Faegri & Pijl 1979). This extension of the pollination syndromes assumes that insect-orders or vertebrate classes have specific innate preferences to certain compounds or compound classes, which seems to be best realized in systems were vertebrates are involved as pollinators: bird pollinated flowers often lack any scent (Knudsen et al. 2004) and bat pollinated flowers mostly contain sulphur compounds in their odours (Bestmann et al. 1997). In systems involving insects as pollinators such patterns are hard to detect since many individual substances were attributed to several “syndromes” (Dobson 2006). For example, butterfly (Andersson et al. 2002), moth (Raguso & Pichersky 1995), wasp (Shuttleworth & Johnson 2010), bee (Dobson 2006) and fly pollinated flowers (Shuttleworth & Johnson 2010) emit linalool (monoterpene alcohol) in considerable amounts.

Besides innate preferences of flower scents, associative learning is a key-mechanisms for flower fidelity, and thus for mutual interactions, between generalized pollinators and plants. Natural floral scent bouquets are highly attractive to flower visitors that have an immediate positive experience to these bouquets, while con-specifics that previously experienced other bouquets in association with rewards respond neutral to negative to the same odours (Junker et al. 2010 c). Individual-based, short-term specificity of insects is often mediated via common scent compounds (Wright & Schiestl 2009), which emphasises the flexible cognition abilities of the animals. Moths, for example, have the ability to learn various substances as cue to locate nectar bearing flowers (Cunningham et al. 2004). Thus, the insects use scents to efficiently find and consume floral resources of plants to which they do not have co-evolved links. While naïve responses to odour blends are often stronger than responses to individual compounds (Stringer et al. 2008), learned responses mainly base on “key odorants” within bouquets that are required to recognize a reinforced multi-component signal (Laloi et al. 2000; Dötterl et al. 2006; Riffell et al. 2009).

In other contexts than flower ecology, many volatile substances that are also commonly emitted by flowers have been shown to have repellent, deterrent, toxic or antimicrobial properties (Gershenzon & Dudareva 2007; Unsicker et al. 2009). In the last years, several studies reported on the defensive properties of floral secondary metabolites that negatively affected antagonistic flower visitors. Negative responses to flower scents of taxa regarded as floral antagonists such as bush crickets (Junker et al. 2010 b) and other florivores (Theis et al. 2007) had been evaluated. Maybe the best studied group of floral antagonists regarding their responses to floral scents are ants and their aversion against floral scents has been repeatedly investigated (Junker & Blüthgen 2008; Willmer et al. 2009) and the ecological importance of ant-repelling floral scents has been demonstrated (Galen et al. 2011; Junker et al. 2011 b). However, also taxa usually regarded as mutualists are repelled by floral scents including butterflies (Omura et al. 2000), bees (Junker et al. 2010 c) and thrips (Koschier 2008). The defensive properties of flower scents are not restricted to the protection against antagonistic insects, flowers also avoid contacts with spiders (Junker et al. 2011 a) and bacteria (Huang et al. 2011; Junker et al. 2011 d) by means of scents.

The repellent effects had been attributed to the floral scent bouquet of several plant

Fig. 1: Examples of mutualistic, commensalistic and antagonistic flower visiting organisms. **a** Flower of *Metrosideros polymorpha* with (from left to right) *Hylaeus* sp., *Vespula* sp. and *Apis melifera*. **b** Flower of *M. polymorpha* with *Linepithema humile* ants. **c** Colony forming units of bacteria isolated from flowers of *Lotus corniculatus*. **d** *Misumena vatia* with prey on *Trifolium repens*. **e** *Formica rufibarbis* visiting a flower of *Daucus carota*. **f** *Meconema* thalassinum sitting on flower of *Brugmansia* sp. **g** *Echinacea* sp. flower visitied by *Inachis io* and *Apis mellifera*. **h** *Ipomoea indica* flower visited by Diptera.

Abb. 1: Beispiele von mutualistischen, kommensalistischen und antagonistischen Blütenbesuchern. **a** Blüten des Baumes *Metrosideros polymorpha* mit (von links nach rechts) *Hylaeus* sp., *Vespula* sp. und *Apis melifera*. **b** Blüten von *M. polymorpha* mit *Linepithema humile* Ameisen. **c** Kolonie bildende Einheiten von Bakterien, die zuvor von den Blüten von *Lotus corniculatus* isoliert wurden. **d** *Misumena vatia* mit Beute auf *Trifolium repens*. **e** *Formica rufibarbis* besucht eine Blüte von *Daucus carota*. **f** *Meconema* thalassinum sitzt auf einer Blüte von *Brugmansia* sp. **g** *Echinacea* sp. Blüte, die von *Inachis io* und *Apis mellifera* besucht wird. **h** *Ipomoea indica* Blüte, die von Diptera besucht wird.

Photo credit: **a, b, e, g, h** Robert R. Junker, **c** Christina Loewel, **d** Michael Werner, **f** Manja Wendt.

species (Junker & Blüthgen 2008; Willmer et al. 2009; Junker et al. 2010 c; Junker et al. 2011 b) or to individual substances commonly found in floral scent bouquets (Kessler & Baldwin 2006; Junker & Blüthgen 2008, 2010; Junker et al. 2011 a). Furthermore, behavioural responses may be concentration-dependent where the same substances that are attractive in low concentrations, have a repellent effect at high concentration on the same flower visitors (Galen et al. 2011; Terry et al. 2007).

7. Resources

Nectar is basically composed of water and the primary metabolites sugar and – to a lesser extent – amino acids (Baker et al. 1978). Secondary metabolites are also solved in this liquid including alkaloids, phenolics, iridoid glycosides and terpenoids and may add a defensive character to the otherwise attractive nectar (Adler 2000; Kessler & Baldwin 2006; Gegear et al. 2007; Hansen et al. 2007). Johnson et al. (2006), for example, explored the function of phenolic compounds in the floral nectar of *Aloe vryheidensis* and documented both the deterrent effect on detrimental flower visitors and the attractive effect on beneficial ones. It has also been proposed that secondary metabolites solved in flower nectar may make this watery solution unpalatable for ants and thus provide a general explanation for the absence of ants from many flowers (Janzen 1977). Although some examples of ant-deterrent nectars are known, it seems not to be the main reason why ants avoid flowers in many cases (Junker & Blüthgen 2008; Junker et al. 2011 b).

Pollen also emit various volatile secondary metabolites (Bertoli et al. 2011). Pollen synthesize and emit scents that are also emitted by petals of the same flowers, but some volatiles may be exclusively produced by pollen (Dobson et al. 1996). It has been proposed that these volatiles also have attractive and repellent functions (Dobson & Bergström 2000), but this has not been tested in greater detail so far.

8. Conclusion

The examples summarized in the previous paragraphs indicate that floral traits – including morphology, colour, scent and features of nectar and pollen – can have dual functions in interactions with potential flower visitors. They both, facilitate interactions with flower visitors that match the flower's morphology and / or have innate or learned preferences for the visual or olfactory cues displayed by the flowers, and they reduce or prevent interactions with flower visitors that either are not able to reach or digest floral resources or have aversions against floral cues. Often, the attracted flower visitors are pollinating mutualists and the excluded ones are antagonists, which renders these traits as floral filters that maximize the plants' reproductive success. Therefore, both Sprengel's (1793) and Kerner's (1879) notions – viewing floral traits as attractants or defences, respectively (see introduction) – need to be considered for a full understanding of floral traits and for a comprehensive interpretation of floral evolution. The fact that many floral traits act as filters suggests furthermore that both mutualists and antagonists are selective agents shaping floral phenotypes.

Future studies should further investigate how floral traits shape the visitor spectrum and how mutualistic **and** antagonistic visitors shape floral traits. Often, the attractive and defensive function of floral traits had been investigated in isolation from each other; future studies should address both functions within a single system to gather full information on the adaptive value of flower traits.

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