

Plant attractants: integrating insights from pollination and seed dispersal ecology

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Abstract Reproduction in many angiosperms depends on attracting animals that provide pollination and seed dispersal services. Flowers and fleshy fruits present various features that can attract animal mutualists through visual, olfactory, acoustic, and tactile cues and signals, and some of these traits may result from selection exerted by pollinators and seed dispersers. Plant attractants can provide information regarding the presence, location, and quality of the reward. However, because of the different functional outcomes of pollination and seed dispersal, pollination systems are thought to be more highly specialized than seed dispersal systems. Despite these interesting parallels and contrasts, theoretical and empirical insights in the sensory ecology of pollination and seed dispersal are rarely considered together. Here, we review extant theory and data of sensory attractants from both pollination and seed dispersal systems. We discuss theoretical and empirical similarities and differences between pollination and seed dispersal and offer suggestions for ways in which insights from each field may benefit the other in future.

Keywords Animal–plant interactions · Communication · Coevolution · Foraging ecology · Mutualism · Sensory ecology

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Introduction

For many plant species, particularly angiosperms, reproduction requires animals as pollinators, seed dispersers, or both (Schaefer et al. 2007). Sessile plants that depend on animals for reproduction have evolved to offer rewards such as nectar or fleshy pulp. In addition, they present multiple attractants—signals and cues that are detectable to animal mutualists, which can result in increased foraging efficiency for animals, with a concomitant increase in plant fitness (Fægri and van der Pijl 1979; van der Pijl 1982). Numerous studies have demonstrated that plant signals and cues can strongly influence flower and fruit selection by animals (Jones and Reithel 2001; Schlumpberger et al. 2009; Linn et al. 2004; Korine and Kalko 2005; Hirsch 2010; Sobral et al. 2015). Signals refer to traits, such as color and odor, that are maintained by natural selection because they reliably convey information to other organisms (Schaefer and Braun 2009), whereas cues refer to traits that evolved in a context unrelated to signaling that may nonetheless convey reliable information to other organisms (Otte 1974). Because the distinction between signals and cues can be complex, but both can function to attract pollinators and dispersers, we hereafter use the term attractant for brevity.

The communication between a plant and its animal mutualist depends on three complex and highly variable factors: (1) plant attractant production and maintenance, which can comprise visual, chemical, tactile, and acoustic components (Fig. 1; Fægri and van der Pijl 1979; Lomáscolo et al. 2010), (2) the local environment (e.g., ambient light levels can span six orders of magnitude between a starlit night and midday sunlight (Warrant and Johnson 2013) altering the detectability of visual attractants), and (3) animal sensory phenotypes, which mediate the detectability of plant attractants [e.g., terrestrial vertebrate color vision ranges from monochromacy to tetrachromacy (Osorio and Vorobyev 2008)]. Early studies of plant attractants categorized them according to human capacities, and relied on subjective measurements. For example, color was categorized as red, blue, etc. (Fægri and van der Pijl 1979; Fischer and Chapman 1993) and odor was either classified categorically (e.g., “musky”) or in a binary fashion (e.g., odorous/odorless, Proctor et al. 1996; Tamboia et al. 1996). Only recently, with advances in spectroscopy and color modelling and the application of analytical chemistry, have researchers begun to quantify color and odor, and model it according to non-human sensory capacities (Knudsen et al. 1993, 2006; Hodgkison et al. 2007; Borges et al. 2008; Raguso 2008; Valenta et al. 2013; Nevo et al. 2016).

In general, plant attractants facilitating reproduction can be placed into two differing categories: (1) flower attractants that promote pollination, and (2) fruit attractants that promote seed dispersal (Wheelwright and Orians 1982). Pollination is usually mediated by invertebrates; however, some plants specialize on pollination by vertebrates, predominantly birds and bats (Fægri and van der Pijl 1979; Proctor et al. 1996). In contrast, seed dispersal is usually facilitated by vertebrates, predominantly birds and mammals (Howe 1986), but can involve insects (Midgley et al. 2015), fish (Galetti et al. 2008), reptiles (Liu et al. 2004), and invertebrates (Galetti et al. 2013). Flowers and fruits differ in two major factors (Wheelwright and Orians 1982). First, in pollination, plants require that the pollen is deposited on a conspecific flower and rewards this behaviour, while seed dispersal does not reward the animal for depositing the seed at specific locations. Thus, flowers are more likely to be under selection to attract a narrower range of visitors, whereas fruits benefit from interacting with a broad community of frugivores (Schaefer et al. 2004). As a result, plant-pollinator interaction networks are predicted to be more specialized than plant–seed

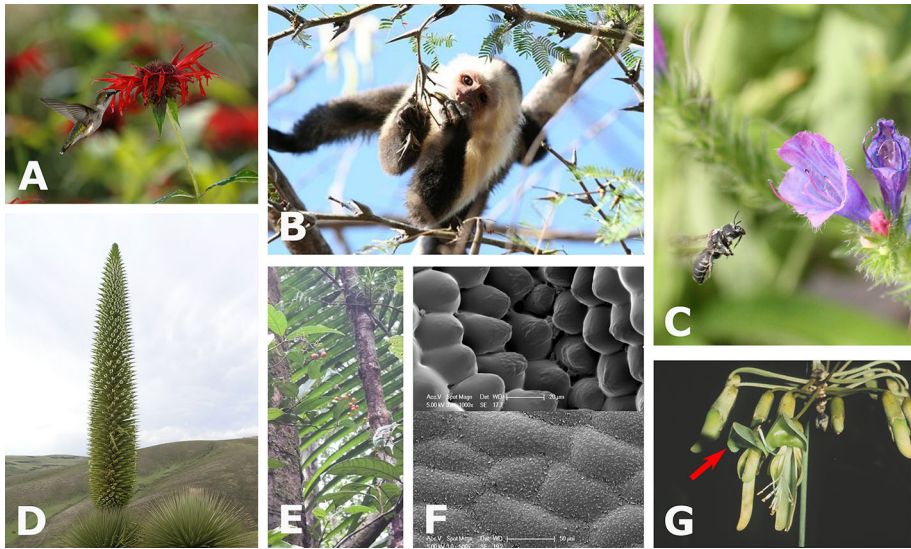


Fig. 1 The diversity of plant attractants. **a** A ruby-throated hummingbird feeding on nectar of *Monarda didyma* (Lamiaceae). Birds show a perceptual bias to red and many bird-pollinated flowers have evolved to exploit this bias (Schiestl and Johnson 2013). Photo: Joe Schneid. [CC BY-SA 3.0 (<http://creativecommons.org/licenses/by-sa/3.0>)], via Wikimedia Commons. **b** A capuchin monkey sniffing fruits of *Acacia* sp. (Fabaceae). Photo: Ed Luinstra. **c** An oligolectic *Hoplitis adunca* bee approaches flowers of *Echium plantagineum*. While the blue color of species of this genus acts as an attractant, host specific recognition by specialized oligolectic bees is based on floral scent, which differs between species (Burger et al. 2010). Photo: Hannah Burger. **d** *Puya raimondii*, “The queen of the Andes” is the largest species in the Bromeliaceae family. Its large inflorescence helps pollinating birds locate and identify the flowers (Salinas et al. 2007). Photo: Pepe Roque [CC BY-SA 3.0 (<http://creativecommons.org/licenses/by-sa/3.0>)], via Wikimedia Commons. **e** Fruits of bird-dispersed *Psychotria cincta* (Rubiaceae), north-eastern Peru. The color of many bird-dispersed fruits contrasts against the foliage background and allows them to be detected by tetrachromatic birds (Cazetta et al. 2007). Photo: O. Nevo. **f** Scanning electron microscopy of epoxy casts of conical and flat celled petals. Conical cells increase pollinator grip and thus foraging and pollination efficiency (Whitney et al. 2009a). Photo reproduced and adapted from Whitney et al. (2009a). Copyright 2009, with permission from Elsevier. **g** Flowers of bat-pollinated *Mucuna holtonii* at La Selva, Costa Rica. The raised vexillum (marked) mirrors bat sonar calls, allowing them to locate the flowers (von Helversen and von Helversen 1999). Photo: Marco Tschapka. (Color figure online)

disperser networks (Blüthgen et al. 2007) and therefore flower attractants are overall expected to evolve under more specific selective pressures. Second, fruits usually develop from a subset of the flower’s parts and are therefore subjected to more developmental constraints (Giovannoni 2004; Stournaras et al. 2013). Despite the great potential in contrasting these systems, they are rarely considered together in either theoretical or empirical treatments.

Here, we provide a comprehensive evaluation of how plants attractants mediate their mutualistic interaction with animal vectors during pollination and seed dispersal. For each mode of attractant we first consider how the attractant operates, then present examples for that attractant for both pollination and seed dispersal, addressing similarities and differences between pollination and seed dispersal systems. In a concluding section we discuss multimodal functionality of plant attractants, explore their evolutionary pathways, and offer future directions for a more integrative understanding of plant attractants.

Visual attractants

The selective reflectance of light which is perceived as color can be produced either chemically, with pigments, or physically (Whitney et al. 2009b; Glover and Whitney 2010; Miller et al. 2011; Vignolini et al. 2012), and both flowers and fruits often produce color changes associated with food rewards (Stournaras et al. 2013). Color change is perhaps the oldest body of literature on plant reproductive signals (Allen 1879), but it has traditionally been evaluated subjectively based on human sensory abilities (Willson et al. 1990). This ignores color variation that can be detected by insects and vertebrates that can discern colors not detected by humans, and how color is mediated by biotic (e.g., canopy density) and abiotic factors (e.g., natural illuminants). Recent advances in molecular biology and spectroscopy have facilitated the quantification of color-vision capabilities and color signals allowing an unprecedented view of the role of color production by plants, and its perception by animal mutualists (Briscoe and Chittka 2001; Osorio and Vorobyev 2008).

Plants have evolved a great diversity of colors and display strategies to draw pollinator and seed disperser attention, which is often critical to flower and fruit selection (Wright and Schiestl 2009; Weiss 1995; Nuttman and Willmer 2003; Valenta et al. 2013). With respect to flowers, petals and sepals are usually the colorful structures, though other floral parts, such as anthers, filaments, ovaries, floral bracts, and pollen, can also be visually attractive (Miller et al. 2011; Lunau 1995, 2000). Floral colors often change during development and as a function of pollination state, pollinator assemblages, and even time of the day (Weiss 1995; Farzad et al. 2002; Ida and Kudo 2003; Nuttman and Willmer 2003; Willmer et al. 2009; Sobral et al. 2015). With fruits, usually the exocarp or aril is the colorful structure, though other fruit parts, include elaisomes and fruit/seed contrasts may also act as visual attractants (van der Pijl 1982).

As with flowers, changes in fruit color during development (ripening) can act as attractants to dispersers, and dispersers in turn may act as a selective force on fruit colors. Fruit color has experienced particularly strong selection for visual conspicuousness in bird-dispersed species (Duan et al. 2014). A study investigating 130 bird-dispersed species, found that 96% of bird-dispersed fruits were chromatically conspicuous against backgrounds when modelled in avian-specific color space (Schaefer et al. 2007; Fig. 1e). Additionally, color contrasts have been found to be more pronounced in bird-dispersed species than they are among fruits that rely primarily on mammalian dispersers (Lomáscolo and Schaefer 2010). Fruit color has been shown to reliably convey information regarding fat content to seed-dispersing birds (Schaefer et al. 2014), but not primates (Worman and Chapman 2005). Despite the reduced capacity for color discrimination of mammals relative to birds, models of mammalian color vision predict an advantage of mammalian trichromats over dichromats in finding fruits against foliage (Osorio and Vorobyev 1996), and some studies indicate that in trichromatic primates, photopigments are optimized for finding colored fruits (Sumner and Mollon 2000; Regan et al. 2001; Melin et al. 2014).

With both fruits and flowers, color contrast may be as important as color per se in attracting animal mutualists, though the locus of that contrast is different. In flowers, it is often the variation within a floral structure itself that offers colorful contrasts (e.g. the difference between petal and anther colors) (Miller et al. 2011). On the other hand, in fruits, meaningful color contrasts are often considered as the contrast between ripe and unripe fruit, or ripe fruit and background leaves (Schaefer et al. 2007). However, in some species, particularly arillate fruits, the contrast within the fruit structure itself may

represent the color contrast, as in the color difference between a seed coat and a partially exposed seed.

In both fruits and flowers, the perception of colors and color contrasts depends on the visual system of the receiver (Menzel and Backhaus 1991). Pollinating insects and birds generally perceive color between 300 and 700 nm (Briscoe and Chittka 2001; Bennett and Théry 2007), while mammals perceive color between 400 and 700 nm (Jacobs 2009). In nocturnal pollinated flowers the presence of color may not be important for pollinator attraction, although there is evidence showing that some nocturnal moths can discriminate flower colors under starlight illumination (Kelber et al. 2003). Many pollinators show innate preferences (Dobson and Bergström 2000; Gumbert 2000; Pohl et al. 2008; Blackiston et al. 2011) or perceptual bias (birds, Schiestl and Johnson 2013) to some colors (Fig. 1a) that can result in selective pressure on flowers (Renoult et al. 2013). While seed dispersers generally have reduced color discrimination capabilities relative to pollinators, nonetheless, fruits in some systems show a match between fruit colors and the ability of frugivores in those systems to discriminate them, indicating that as with flowers, fruit color may partly result from selection by seed dispersers (Irwin et al. 2003; Frey 2004; Rausher 2008; Schaefer and Ruxton 2011).

As with pollinators, there is high variation in the visual phenotypes of seed dispersers. Vertebrate color vision ranges from monochromacy, the presence of a single cone type and complete color blindness, to tetrachromacy, which is characterized by the presence of four cone types and often includes the ability to detect colors in the ultraviolet (UV; 300–400 nm) range (Mollon 1989; Tan et al. 2005; Bennett and Théry 2007). While tetrachromacy is common to many birds, the presence of four functional cone types in a single individual has not been discovered in mammals, of which most frugivores are dichromats, or red–green color blind, possessing only two cone types (Hunt et al. 2009). Primates represent an interesting exception to the general rule of mammalian dichromacy, as new world howler monkeys and all old world monkeys and apes are routinely trichromatic (Jacobs 2009). Additionally, some lemurs and most new world monkeys have an X-linked polymorphism that maintains both a medium- and long-wavelength (M/LWS) sensitive opsin gene, resulting in the presence of trichromacy in heterozygous females, and dichromacy in homozygous females and males (Jacobs 2009).

Differences in pollinator and disperser visual phenotypes likely contributes to innate preferences or biases to specific colors in pollinators and seed dispersers (Fig. 1a; Dobson and Bergström 2000; Gumbert 2000; Rausher 2008; Schaefer and Ruxton 2011; Schiestl and Johnson 2013; Valenta et al. 2013); however, preferences are not always consistent (Willson et al. 1990) and color contrasts against foliage background do not always result in greater foraging efficiency by animal mutualists (Valenta et al. 2015). Such inconsistencies may in part result from the fact that color perception can be strongly affected by variation in ambient light and disperser visual capacities. For example, dichromatic marmosets have a foraging advantage on fruits under shaded conditions, while trichromats of the same species are able to outperform dichromats when foraging in the sun (Caine et al. 2010). Inconsistencies may also be due to the fact that innate preferences can be modified by experience and animals can learn to associate color with the presence and quality of a reward (Gumbert 2000; Chittka et al. 2003; Giurfa 2004; Dyer et al. 2006). For instance, trained bumblebees can successfully identify rewarding artificial flowers among slightly different colored distractors (Chittka et al. 2003; Dyer et al. 2006).

While both flower and fruit color may respond to selective pressure from animal mutualists, selective pressure on flower color diversification may be stronger to ensure visitation by specialist pollinators (Gumbert et al. 1999), while fruits may benefit from

convergence upon similar colors to attract multiple dispersers (Burns 2005; Valenta et al. 2015). Specialized color attractants will increase the likelihood of pollinator constancy by ensuring pollinators visit one conspecific after another, resulting in successful pollination. On the other hand, fruit colors that restrict seed dispersers—those that are not conspicuous to a wide range of seed dispersers—will likely be selected against. This is because seed dispersal by a small number of specialists can result in clumped seed distribution patterns with subsequent intra-specific competition and density-dependent mortality effects (Schaefer et al. 2004). Reduced fruit color diversity may be further buttressed by the stronger developmental constraints on fruits relative to flowers (Giovannoni 2004).

Thus while color and color contrast are important attractants of both flowers and fruits, the degree of color specificity represents a critical difference between flowers and fruits. While flowers are expected to diversify color to facilitate pollinator specificity, fruits are expected to converge upon similar colors that are visually detectable to a wide range of animals (Valenta et al. 2015). Furthermore, the greater variation in the visual phenotypes of pollinators relative to seed dispersers should result in greater flower color diversity, while the narrower range of seed disperser visual phenotypes should result in lower fruit color diversity. Indeed, a comparison of fruit and flower colors across temperate and tropical systems has found that flower colors are twice as diverse as fruit colors, and that flower colors occupy a much greater range of color space than do fruits (Stournaras et al. 2013).

Olfactory attractants

Odorants are almost always a blend of several volatile organic compounds (VOCs) that may be composed of over 100 different compounds (Raguso 2008). VOC emission can change quantitatively (overall emission rate) and qualitatively (ratio between odorants) across the diel cycle in both flowers and fruits (Raguso et al. 2003; Huber et al. 2005; Borges et al. 2013). Thus, in both flowers and fruits, odor is comprised of different partly-independent elements that may be subjected to conflicting selective pressures and constraints (Schaefer et al. 2004; Schiestl 2015).

In both flowers and fruits, odor production may be particularly important in plant species that do not have clear visual attractants (Hiramatsu et al. 2009; Melin et al. 2009; Lomáscolo et al. 2010; Corlett 2011) and in species that rely on nocturnal pollinators or seed dispersers (Korine and Kalko 2005). The scent of flowers and fruits can attract animals at both long and short ranges (Dominy et al. 2001; Huber et al. 2005; Corlett 2011; Nevo and Heymann 2015). Long-distance attraction is common in flowers that rely on nocturnal pollinators (Huber et al. 2005) and in environments where visual attractants are obscured (Pettersson et al. 2004; Muchhala and Serrano 2015). Additionally, long-distance attraction is common in highly-specialized interactions in which pollinators search for patchily-distributed floral resources (Ackerman 1986; Gottsberger and Silberbauer-Gottsberger 1991). Similarly, nocturnal bats and elephants that often feed of at night and who have very poor eyesight, can detect fruits based on odor over several kilometers (Chapman et al. 1992; von Helversen et al. 2000).

For both odors of flowers and fruits, the detectability of VOCs in an odor plume is strongly affected by external factors, such as background odors and wind (Schaefer and Ruxton 2011; Riffell et al. 2013, 2014; Beyaert and Hilker 2014; Farré-Armengol et al. 2016). Therefore, while odorants can be used by animals to detect the location of flowers

and fruits, discerning reward amount or quality based on odorants may be more challenging. This may partly explain why nocturnal foragers behave similarly when presented with odorants varying tremendously in concentration (Riffell et al. 2009; Schaefer and Ruxton 2011; but see Riffell et al. 2014).

While odorants may represent important long-distance attractants, there is evidence to suggest that they can also be a useful indicator of flower and fruit rewards at close range. Some evidence suggests that floral scent can provide nuanced information regarding the reward's quality at close-range (Hartlieb and Anderson 1999). Studies of primate seed disperser behaviour have also found that at close range some species deliberately smell fruit (Valenta et al. 2015; Fig. 1b), can identify ripe vs unripe fruit based on odor (Siemers et al. 2007) and make distinctions between stages of ripeness based on odorants alone (Nevo et al. 2015). Additionally, some fruits have been found to alter their VOC profiles on ripening, which may serve as a useful close-range attractant (Nevo et al. 2015, 2016; Valenta et al. 2016).

Despite the many similarities in flower and fruit odorants, there are also striking differences, most notably, the existence of highly specialized flower-pollinator mutualisms, and the higher diversity of odorants in flowers compared to fruits. Flowers of many species rely on very few, or even a single functional pollinator group (Fenster et al. 2004) and floral scent has been found to play a crucial role in host recognition (Schiestl 2015). In some specialized systems flowers use completely different odorants such as sulfur-containing compounds for bat pollination (Pettersson et al. 2004; Dobson 2006), spiroacetals for attraction of oligolectic bees in *Campanula* spp. (Campanulaceae) (Milet-Pinheiro et al. 2013) or lilac aldehydes and alcohols for moth attraction (Dötterl and Jürgens 2005). While the role of chemical attractants in seed dispersal is in its infancy, clear differences with flowers emerge, principally with respect to animal mutualist specificity and the diversity of odorants. Unlike highly specialized flower-pollinator systems, fruit odorants tend to resemble more generic odor profiles. Specialized seed-dispersal interactions mediated by specialized chemistry appears to be much rarer than flower-pollinator specialization, with few exceptions (Midgley et al. 2015). As well, flower odorant diversity is much higher in flowers than in fruits, with over 1700 odorants identified in the headspace of flowers, and far fewer in that of fruits (Knudsen et al. 2006). Increased specialization and odorant diversity of flowers versus fruits may partly result from the paucity of extant data on fruit odorant attractants. However, it may also reflect the general trend towards increased pollinator-flower specialization relative to disperser-fruit specialization.

In fruits, the reward to the seed disperser of locating the fruit is typically obtaining nutrients, and the reward for the plant is seed dispersal (Janson and Chapman 2000). For flowers the situation is more complex. Indeed, pollinator rewards can themselves be diverse, including pollen (Dobson and Bergström 2000), nectar (Raguso 2004b), and oil (Dötterl and Schächler 2007; Schächler et al. 2015). Additionally, flower VOCs can represent non-nutritional rewards, a phenomenon as yet unknown in fruits. Some plants specialize on pollination by male orchid bees (tribe Euglossini), which collect and use these VOCs as pheromone analogs (Eltz et al. 2007). Additionally, carbon dioxide has been suggested to be a reliable indicator of nectar level (Guerenstein et al. 2004), and an olfactory long-distance attractant to moths (Goyret et al. 2008), as well as potentially signaling heat in flowers that itself may be a reward to pollinators (Seymour et al. 2003). In contrast to floral chemical profiles, published profiles of wild fleshy fruits are few, but indicate that fruits tend to emit rather generic odor mixtures, dominated by terpenoids, aromatic compounds, and fatty acid derivatives (Borges et al. 2008; Hodgkison et al. 2013;

Nevo et al. 2016). As with fruit color, fruits may converge on general odorants to attract as many seed dispersers as possible.

Another difference between flower and fruit odorants is that many flowers attract pollinators using odorants associated with nutrients, without offering a nutrient reward (Jersáková et al. 2009; Wright and Schiestl 2009). This phenomenon is as yet unknown for fruits, though mimetic fruits are known to exist (Galetti 2002), and identifying their odor profiles will be an exciting vein of future inquiry. Generalized food-deceptive flowers tend not to mimic a specific model, but display generic visual and olfactory traits (Schiestl 2005; Jersáková et al. 2009). Their fragrance also tends to be generic and contain mainly terpenoids and aromatic compounds (Salzmann et al. 2007; Jersáková et al. 2009, 2012). Mimicry of a particular flower model has been documented less, and involves visual rather than olfactory attractants, but flowers which employ olfactory mimicry are often weakly scented or scentless, because many pollinators may learn to discriminate and avoid cheaters based on olfactory cues (Jersáková et al. 2009; Wright and Schiestl 2009). The fact that these mimics have evolved to minimize their odor signatures is a strong indication for the importance of floral scent (Schaefer and Ruxton 2011).

Another phenomenon that is well known in flowers but little known in fruits is the generation of non-food odorant attractants, including brood site-specific odorants, and pheromones to attract pollinators (Schiestl and Johnson 2013). For example, sapromyophilous flowers emit odors rich in sulfur and nitrogen-containing compounds to mimic the odors of feces or carrion, which are feeding or oviposition sites of many flies and beetles that act as pollinators for these species (Jürgens et al. 2006, 2013). Another deceptive floral chemical strategy involves mimicking aggregation or alarm pheromones of pollinators or their pollinators' prey. For instance, *Dendrobium sinense* (Orchidaceae) flowers emit the major alarm pheromone compound of honey bees to attract hornets (Brodmann et al. 2009) and *Specklinia* (Orchidaceae) species produce a combination of aggregation pheromones of their fly pollinators (Karremans et al. 2015). Perhaps the most striking example of floral odor mimicry is that of sexually deceptive orchids that have evolved to mimic the sex pheromones of their respective pollinators' females. These are highly specialized systems in which usually pollinators of a single species is lured to trigger pseudocopulation with the flower (Dafni 1984; Schiestl 2005; Jersáková et al. 2006; Schiestl et al. 1999, 2003). Floral scent often mimics female chemical profiles with great accuracy and can be more attractive to males than genuine females (Schiestl 2004).

While understudied relative to mimetic flowers, some fruits have been found to produce chemical attractants that facilitate seed dispersal without offering a reward. Some species of ant-dispersed plants have been found to produce oleic acid, a chemical triggering dispersal behaviour in ants, without offering food rewards (Pfeiffer et al. 2010; Turner and Frederickson 2013). One species of dung-beetle-dispersed seed has been found to produce VOC emissions that are similar in composition to that of the dung of mammalian herbivores that beetles rely on for oviposition and feeding (Midgley et al. 2015). Beetles in this system were found to disperse and bury seeds of this species, with no reward for the beetle, indicating a truly deceptive interaction.

For both pollinators and frugivores, a major challenge in the study of odorant attractants is the difficulty of identifying olfactory phenotypes of pollinator and dispersers (Hasin-Brumshtein et al. 2009). While color vision phenotypes can be determined relatively easily and non-invasively (Yokoyama 2002), matching olfactory genotypes and phenotypes can be quite complex, and involve labor-intensive conditioning experiments (Rizvanovic et al. 2013). The challenges in identifying olfactory phenotypes confound predictions about the

degree of odorant diversification in both fruits and flowers, and the relative importance of specific compounds and concentrations.

In summary, both flowers and fruits produce odorants to attract animal mutualists that can be detected over long and short distances, and that can be strongly mediated by ambient conditions, including background odors. Unlike visual attractants which can provide mutualists nuanced information at close range, odorants may be more important in long-distance communication with mutualists. However, as with visual attractants, flowers can be expected to display more highly specialized odors, to ensure greater pollinator specificity and the likelihood of pollinator visitation to multiple flowers of the same species. Fruit odorants, while understudied relative to flower odorants, may experience selective pressure to converge on generic odor profiles, to attract as many disperser species as possible. This may partly explain the lower diversity of fruit odorants discovered relative to flower odorants (Knudsen et al. 2006), though this may also be an artefact of the relatively few studies conducted on fruit odorants. Finally, seed dispersal usually merely requires that a fruit be consumed, and as such fruit odorants, at least for endozoochorous fruits, may be restricted to food-relevant attractants. Conversely, successful pollination may require that visiting mutualists behave in specific ways such as pseudocopulation, which result in the production of non-food floral odorants. This in turn can lead to greater diversity in floral odorants, and complex and highly specialized flower-pollinator mutualisms, such as the production of odorants that not only attracts a pollinator, but instigates a behavior that facilitates pollen transfer.

Shape and size

The size and shape of both flowers and fruits can partly reflect selection imposed by animal mutualists, in addition to physiological and phylogenetic constraints (Ollerton and Lack 1998). Fruits, while highly variable in size, overwhelmingly tend to be globular, which has been attributed to the observation that water is more efficiently stored in spherical structures (Schaefer and Ruxton 2011). Flower shapes, on the other hand are highly diverse (Fægri and van der Pijl 1979; Dafni and Kevan 1997). Floral shape may enhance pollinator attraction and facilitate flower handling, pollen deposition, and degree of pollinator specialization, and can affect the electrostatic properties of pollen deposition (Vaknin et al. 2001). For example, increased style length facilitates pollen detachment from pollinators, as well as its deposition on the stigma which may expedite pollen transfer between the oppositely-charged flower and pollinator (Vaknin et al. 2001). Floral form is also important in deceptive systems (Jersáková et al. 2006), especially in those in which olfactory attractants are weak or absent, although a closer resemblance is not always translated to more attractiveness and imperfect mimicry may be favored (Benitez-Vieyra et al. 2009).

For both fruits and flowers, size plays an important role in determining reward accessibility to animals. In both flowers and fruits, size varies tremendously, ranging from less than a millimeter in diameter, to inflorescences that can reach several meters in length (Davis et al. 2008; Salinas et al. 2007; Fig. 1d). The diversity of fruit and flower size likely results at least partly from the diversity of pollinator and dispersal vector sizes (Cariveau et al. 2004). Small flowers do not allow access to big pollination vectors, whereas big flowers can be difficult to be handle for small pollinators (Fenster et al. 2004). Flower size has been shown to be important in floral discrimination for hawkmoths (Kaczorowski et al. 2012), and increased floral size has been shown to increase foraging efficiency by

decreasing bee foraging time (Chittka and Raine 2006). Similarly, the size of fruits and seeds can be an important trait determining whether animals are effective dispersers—simply, small animals cannot ingest large fruits or seeds (Wheelwright 1993; Chapman et al. 1992; Chapman 1995; Galetti et al. 2013). Indeed, fruit size is one of the most important variables constraining fruit consumption amongst frugivores, and plants which produce seeds or fruits that are too big for the local frugivore community may be selected against (Galetti et al. 2013). Despite a tendency towards fruits that are able to be dispersed by animals of many different sizes, some fruit-frugivore relationships are highly specialized and clearly reflected in fruit sizes, e.g. *Wilsonia balanites*, which is so large, that it is only dispersed intact by elephants (Chapman et al. 1992). In addition to inter-specific differences in fruit sizes, studies have shown that within a species changes in fruit size can reliably indicate fruit ripeness (Coombe 1976), and fruit size was found to be a consistent predictor of fruit ripeness in a Malagasy forest (Valenta et al. 2016) as well as the only significant predictor of fruit foraging efficiency for common brown lemurs (*Eulemur fulvus*) (Valenta et al. 2015).

In summary, as with visual and chemical traits, variation in the size and shape of flowers tends to be greater than that of fruits, probably owing to the greater physiological constraints of fruits, and the fact that fruits do not clearly benefit from being available to only a small portion of the frugivore community (Schaefer et al. 2004; Schaefer and Ruxton 2011). Despite this, fruit size and shape can be important determinants of which animals successfully disperse seeds, and may partition the pollinator (Fenster et al. 2004) and seed disperser (Janson 1983; Balcomb and Chapman 2003) guilds. Large flowers and fruits may be preferred because they are more easily detected and typically contain more nutrients, though size can also constrain the capacity of pollinators or seed dispersers to pollinate or disperse them (Schaefer and Ruxton 2011).

Acoustic attractants

While rarely studied, variation in fruit and flower shape and size can result in acoustically mediated plant–animal interactions. Micro-chiropterans and Egyptian fruit bats (*Rousettus aegyptiacus*) use sonar to navigate through their environments (Jones and Teeling 2006), and some plants have adaptations that alter the reflectance of bat ultrasonic emissions. In *Mucuna holtonii* (Fabaceae) flowers possess a raised vexillum which reflects bat calls (von Helversen and von Helversen 1999; Fig. 1g). In *Marcgravia evenia* (Marcgraviaceae) a concave leaf situated above the inflorescence provides consistent acoustic reflectance in the cluttered environment of the canopy and the pitchers of this carnivorous plant act as ultrasound mirrors (Simon et al. 2011; Schöner et al. 2015). Fleshy animal-dispersed fruits tend to be globular (Schaefer and Ruxton 2011), thus, echolocation is inefficient for identification of most ripe fruits. Nonetheless, some fruits show a pendular morphology which allows bats to echolocate them (Kalko and Condon 1998). In both fruits and flowers, acoustic communication between plants and animals requires the evolution of specialized structures. The fact that fruits tend to present the same morphology in both ripe and unripe phases renders acoustic communication more difficult to achieve in attraction of seed dispersers than in the attraction of pollinators. Acoustic attractants generally are either quite rare, or understudied.

Tactile signals and cues

Tactile features of both flowers and fruits surfaces may act as close-range attractants to animal mutualists, though the locus of tactile indicators in fruits and flowers is different. Descriptions of tactile signals in flowers have focused on micro-morphological traits on specific floral parts (Whitney et al. 2009a, 2011), whereas fruit descriptions have focused on the hardness of entire fruits (Dominy 2004; Lambert et al. 2004). Using the mechano-receptive sensilla of the antennae or feet, some insects can identify micro-morphological variation in floral structures to discriminate between flowers with different rewards. For example, bumblebees have been shown to prefer petals which include conical cells that increase their grip (Whitney et al. 2009a, 2011; Fig. 1f) and mutant flowers of *Antirrhinum majus* (Plantaginaceae), which contain conical cells, experience increased pollination (Glover and Martin 1998). Variation in fruit tactile attractants and haptic perception amongst frugivores is also important in many fruit-frugivore interactions (Jacobson 1978). Many birds swallow fruits whole (Levey 1987) and therefore have little opportunity for tactile assessment of fruits. In contrast, primates possess high manual capabilities (Torigoe 1985), and evaluate fruits with digits, teeth, and/or the mouth (van Roosmalen 1985; Dominy et al. 2001). Fruit hardness acts as a physical defense of unripe fruits (Lucas and Corlett 1998; Lambert et al. 2004) and fruit softening (Paliyath et al. 2008) may reliably indicate the presences of increased rewards. Fruit softening has been shown to progress at different rates from visual signals, which suggests that it may not be a trait only under selection to be a tactile signal (Brady 1987). However, seed dispersers have been seen to palpate fruits during selection and manually opening fruits a few days before natural dehiscence occurs (Dominy et al. 2001), as well as orally assessing fruit texture (van Roosmalen 1985; Corlett 2011). One study found that among all traits characterizing ripe fruits, only changes in fruit hardness were salient across all species in a frugivore community in Madagascar (Valenta et al. 2016), with ripe fruits significantly softer than unripe fruits; thus the role of tactile signals/cues may be an underappreciated sense in the fruit literature.

In general, owing to the difficulty of assessing haptic sensitivity in pollinators and seed dispersers, the role of tactile signals and cues is an understudied, yet potentially important, aspect of plant–animal mutualisms. Given the size differences between pollinators, which are often insects, and seed dispersers, which are typically vertebrates, it is not surprising that tactile plant traits are at the microscopic level for pollinators and macroscopic for seed dispersers. In flowers, the presence of natural variance in floral microstructures and clear preferences by pollinators (Whitney et al. 2009a, 2011) indicates that selection is likely taking place. In contrast, fruit hardness may be a byproduct of maturation making it merely a useful cue.

Discussion

Plant attractants include multiple traits that can be used by animals to infer the presence, location, or quality of flowers or fruits and can act complementarily when attracting pollinators and seed dispersers (Raguso 2004a). Some traits can be used to locate flowers or fruits from a long distance, while others operate over shorter ranges to provide more detailed information regarding exact location and quality of the reward. As a result, animals are likely use multimodal stimuli which may generate selection pressures on plants to

retain attractants that communicate via different channels (Leonard and Masek 2014; Junker and Parachnowitsch 2015). For example, some pollinating insects and bats may be more attracted to a combination of two stimuli, both visual and olfactory (Burger et al. 2010; Milet-Pinheiro et al. 2012; Dötterl et al. 2014; Fig. 1c) or acoustic and olfactory (Gonzalez-Terrazas et al. 2016) than to any single stimulus. Multimodal signaling can also ensure perception by mutualists when environmental conditions affect some communication channels, but not others: For example, an olfactory cue may be redundant in some situations, but crucial when poor light conditions render visual cues useless, while visual cues may compensate for loss of olfactory cues due to wind (Kaczorowski et al. 2012; Junker and Parachnowitsch 2015). Similarly, attractants which are partly redundant may be maintained because each one alone does not provide all the needed information (Hebets and Papaj 2005). Partially-redundant attractants may be maintained when a plant relies on pollination or seed dispersal from a diverse group of mutualists having different sensory capacities (Junker and Parachnowitsch 2015). For example, generalist honeybees are more attracted to olfactory versus visual stimuli of *Salix caprea* (Salicaceae) flowers (Dötterl et al. 2014), while *Hoplitis* spp. and *Chelostoma* spp. bees prefer visual to olfactory attractants of *Echium* (Boraginaceae) and *Campanula* (Campanulaceae) flowers (Burger et al. 2010; Milet-Pinheiro et al. 2012). Further, research suggests that the multi-modality of plant attractants themselves may facilitate attraction and memory of animal mutualists (Leonard et al. 2011).

The multivariate nature of plant attractants poses difficulties in discerning whether individual traits are signals—traits that have evolved for the purpose of attracting animals to a nutrient reward—or cues, traits that have evolved for reasons unrelated to animal signaling that nonetheless convey reliable information. Signaling theory predicts that honest signals (i.e., those which reliably provide information regarding the reward) will be costly to produce (Olson and Owens 1998). While the question of the costliness of signals has been broached for animal communication systems (Smith and Harper 1995), little is known about the costs of plant investment (Schaefer et al. 2004).

Some plant attractants, such as ripe fruit texture (Paliyath et al. 2008), are byproducts of other processes, thus while they are likely useful cues, they cannot be attributed to frugivore selection. Other attractants, like flower micromorphology, in which a single mutation determines whether petal surface is characterized by conical or flat cells (Whitney et al. 2009a), is likely to be under selective pressure from animal mutualists. Given that animal color vision preceded the radiation of many plant species, it is likely that floral, and possibly fruit coloration, are evolved signals (Chittka 1996). However, for many attractants it is difficult to determine to what degree animal behavior contributed to their evolution.

A further complication in delineating plant–animal mutualisms is that animals have the capacity to learn and associate honest signals with the presence and quality of a reward. Honest signals in flowers and fruits may evolve even without genetic associations between signal and reward (Raguso 2008; Wright and Schiestl 2009; Schiestl 2015; but see Schäffler et al. 2015), as animals can “punish” cheaters by switching to other plants. For example, in *Brassica rapa* (Brassicaceae), emission of phenylacetaldehydes is reliably associated with nectar and pollen amount (Knauer and Schiestl 2015) and bumblebees develop preferences for these signals (see also the association of fruit color and lipid content with preferences by birds; Schaefer et al. 2014). Possibly combining this associative learning process with avoidance of cheaters could lead to a fixation of reliable signals.

The evolution of pollination and seed dispersal mutualisms between fruiting plants and animals involves complex interactions with many co-varying traits. In both pollination and

seed dispersal, plants offer rewards and generate attractants to facilitate reproduction. While color, odor, acoustic, size and tactile traits can act as attractants to both seed dispersers and pollinators, fruit traits tend to converge upon generalist attractants, while flower traits tend towards pollinator-specific attractants (Wheelwright and Orrians 1982). This may be one reason why literature on pollination and seed dispersal systems rarely intersects. Despite differences in the functional outcomes of pollination and seed dispersal, and the degree of plant trait and animal mutualist specificity, integrating insights across fields has great potential to expand understanding of plant–animal mutualisms. We offer the following suggestions for potential avenues of future research that we hope will promote this field of study.

1. While many studies of plant–animal mutualisms focus on the existence of plant traits that act as attractants, further research should further emphasize the role of agonists (e.g. predators, parasites and pathogens) in the evolution and maintenance of plant traits. Multidirectional selection pressures, including those exerted by agonists, have received more focus in the study of flowers (Gronquist et al. 2001; Kessler and Halitschke 2009; Schiestl 2015). In fruits, while preliminary work shows that fruit exocarp hardness (a mechanical defense against seed predation) is used as a cue of fruit ripeness to seed dispersers (Valenta et al. 2015, 2016), less is known on how and to what extent agonists shape other fruit traits like odor and color.
2. Increasingly the effect of the multimodality of plant signals are being noted (Leonard et al. 2014), though this is as yet limited to preliminary empirical work on flowers. Quantifying multiple fruit signals and relating these to how animal mutualists interact with plants is an understudied and potentially critical vein of future research.
3. To understand the evolution of pollination and seed dispersal mutualisms a clear identification of the fitness consequences of this variation may help to resolve the locus of selective pressure. For example, when studying the evolution of traits related to seed dispersal, it is clear that simply quantifying the removal of seeds from the parent is insufficient, and an understanding of the fate of dispersed seeds in terms of seed fate, establishment, and growth is needed (Schupp 1993; Balcomb and Chapman 2003). Similarly, increased understanding of not just pollen removal, but also pollen deposition on suitable conspecifics will allow for a greater understanding of the fitness consequences of animal–plant mutualisms, and the role of attractants in mediating it.
4. The study of plant mimicry is well advanced in the floral literature, but there is little work on mimetic fruits, or “cheaters”—fruits that receive dispersal services without providing nutrient rewards. Because of the increased tendency of fruits to attract a wide variety of dispersers, mimetic fruits may be more common than has been traditionally supposed (Schaefer and Ruxton 2009). Identifying nutrient rewards in fruits, and linking these to plant attractants may provide increased insight into both the link between fruit nutrients and attractants, as well as the prevalence of deceptive fruits.

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