REVIEWS

Journal of the Indian Institute of Science

A Multidisciplinary Reviews Journal

ISSN: 0970-4140 Coden-JIISAD

© Indian Institute of Science

# Fruit and Seed Volatiles: Multiple Stage Settings, Actors and Props in an Evolutionary Play

*Renee M. Borges*

**Abstract |** Plants emit volatile organic compounds (VOCs) from most parts of their anatomy. Conventionally, the volatiles of leaves, flowers, fruits and seeds have been investigated separately. This review presents an integrated perspective of volatiles produced by fruits and seeds in the context of selection on the whole plant. It suggests that fruit and seed volatiles may only be understood in the light of the chemistry of the whole plant. Fleshy fruit may be viewed as an ecological arena within which several evolutionary games are being played involving fruit VOCs. Fruit odour and colour may be correlated and interact via multimodal signalling in influencing visits by frugivores. The hypothesis of volatile crypsis in the evolution of hard seeds as protection against volatile diffusion and perception by seed predators is reviewed. Current views on the role of volatiles in ant dispersal of seeds or myrmecochory are summarised, especially the suggestion that ants are being manipulated by plants in the form of a sensory trap while providing this service. Plant VOC production is presented as an emergent phenotype that could result from multiple selection pressures acting on various plant parts; the "plant" phenotype and VOC profile may receive significant contributions from symbionts within the plant. Viewing the plant as a holobiont would benefit an understanding of the emergent plant phenotype.

**Keywords:** *fruit volatiles, holobiont, microbes, multimodal signalling, myrmecochory, niche construction, seed volatiles, sensory trap, yeasts*

## 1 Prelude

The purpose of this review is to place fruit and seed volatiles within a wider evolutionary context, and to identify questions that could be asked within such a wide canvas. Because of its large scope, this review is not meant to be exhaustive, but will refer to appropriate literature or existing reviews. It will focus on volatiles of fleshy fruit, hard seeds, and seeds that are dispersed by ants, since these three categories of plant diaspores present some special examples of evolutionary processes, conflicts between players, honesty of signals and the possibility of deceit.

In a seminal paper in 1974, Orians and Janzen[1] asked the question: Why are embryos so tasty? In this paper, they compared the embryos of animals with the propagules of plants, and suggested that since many animals invest in parental care, embryos of animals can afford to be non-toxic as they can be defended by their parents. In plants, investment in seeds and associated structures is itself the parental care strategy. Consequently, plants must package within the propagule and associated structures all the components that are needed for a) dispersal of the propagules, b) their survival and defence against biotic and abiotic factors, and c) germination and achievement of metabolic independence.[2] This is why, besides nutrition, plant propagules and associated structures are often laden with secondary metabolites, many of which are highly toxic.[3]

*Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560012, India.*

*renee@ces.iisc.ernet.in*

Several adaptive hypotheses have been proposed for the evolution and maintenance of secondary metabolites in fleshy fruit; these include defence against predators, effects on gut passage rate, and germination inhibitors[4,5] suggesting that there are many possible explanations for fruit chemistry.

Another fundamental difference between plants and animals is that plants are sessile and require *in situ* defence. This immobility can explain why plant parts in general are more toxic compared to animals. Correspondingly, toxicity in animals occurs in those taxa that are sessile, or less capable of escaping predators, and rarely occurs within higher trophic levels such as mobile top predators.[6] Consequently, selection on the chemistry of plant vegetative structures may influence the chemistry of plant reproductive structures, a view that is not often considered. Eriksson and Ehrlén[7] point out that secondary metabolites may occur in fruits as a by-product of their presence in leaves as a defence against leaf herbivory. They rightly suggest that evolutionary biologists must be able to define the trait that requires explanation, without which there is nothing to explain, e.g. correlated traits may be harder to define. As was pointed out several years ago by Primack,[8] selection on flowers or specific floral traits such as size and number of ovules may influence the structure of fruit and seeds. Furthermore, there can be trade-offs between reproductive traits in plants; for example, flower size and flower number in an inflorescence are negatively related across angiosperms.[9] The correlated evolution of plant traits needs greater examination. Moles and Westoby[10] concluded, for example, that seed size is likely impacted by a suite of life history traits such as plant size, longevity, juvenile survival and age at first reproduction. Herrera[11] found leaf and fruit size to be correlated in bird-dispersed plants. Burns *et al.*[12] suggested that fruit colour and thereby fruit chemistry is a result of correlated selection on leaf reflectance properties and, therefore, fruit colour may be constrained by the spectral properties of leaf backgrounds. There is, however, evidence for directed selection on the chemistry of fruits *per se*, a selection pressure independent of the chemistry of vegetative structures.[13,14] Since fruit and seed chemistry have direct bearing on fruit and seed volatiles, investigation of direct or indirect selection on fruit traits is vital to an understanding of volatile emission from plant propagules.

## 2 Act I: Volatiles in Fleshy Fruit

Angiosperms have a large diversity of fruit and seeds that range in size from the microscopic dust-like seeds of orchids to the giant fruit and

seeds of legumes and palms.[15,16] Mack[17] suggested that fruit pulp evolved as a response against seed predators rather than as an incentive for seed dispersers, suggesting that the defensive tissues surrounding the seeds were an exaptation (*sensu* Gould and Vrba[18]) to the evolution of rewarding tissues. Whatever the origin of fleshy fruit, in many extant angiosperms, ripe fruit pulp is attractive to frugivores, many of which perform fruit removal and seed dispersal services for the plant in return for nutrients in the pulp.[19,20] A large diversity of volatiles are emitted by fleshy fruit pulp.[21–23] However, unlike floral volatiles whose diversity has been examined even for many wild species,[24,25] documentation of fleshy fruit volatiles or fruit aroma volatiles has been restricted mainly to domesticated fruits,[26,27] with a few exceptions.[28–31] This paucity of data on the volatile profiles of wild fruit makes generalisations difficult. However, certain interesting patterns have emerged and could set the stage for further investigations.

### 2.1 Sex-limited fruit volatiles

Borges *et al.*[29] found a clear difference in the volatile profiles of female (seed) figs compared to male (gall) figs in a dioecious species of mammal-dispersed *Ficus*. Female figs contain seeds, while pollinating fig wasps only develop within figs on male trees. Female figs must be attractive to frugivores and potential seed dispersers; therefore, compared to male figs, female figs emitted higher total amounts of volatile organic compounds (VOCs) and higher concentrations of VOCs such as fatty-acid derivatives, especially amyl acetates and 2-heptanone, that are potentially attractive to mammalian dispersers. This makes adaptive sense since male figs should not be consumed by frugivores as they contain developing pollinating wasps. How might this differential consumption of seed figs over gall figs be achieved? Dumont *et al.*[32] and Weiblen *et al.*[33] have demonstrated that seed figs of bat-dispersed fig species are much richer in carbohydrates and lipids compared to gall figs; these seeds figs are therefore nutritionally more rewarding compared to gall figs. The chemical composition of seed figs would also allow for greater production, compared to gall figs, of fatty-acid derived VOCs that are highly attractive to paleotropical bats.[31] Borges *et al.*[29] also found that only gall figs of mammal- and bird-dispersed fig species emitted high concentrations of the repellent VOC methyl anthranilate. Methyl anthranilate is used in commercial formulations to repel birds and is also active against mammals.[34,35] It appears that gall figs in which pollinating fig wasps breed produce

**Exaptation:** a trait that performs a function for which it was not originally evolved.

**Dioecy:** a plant breeding system in which male and female reproductive structures are present in separate individual plants.

**Life history strategy:** a strategy that determines the reproduction of an organism during its lifetime; e.g. life history parameters such as body size, age at first reproduction, number of reproduction events, interval between reproduction events, and longevity, can influence an organism's reproductive or life history strategy.

repellents against frugivores, and with their lower concentrations of carbohydrates and lipids emit lower amounts of attractive VOCs while seed figs emit high concentrations of attractive VOCs and no repellent compounds. This appears to be a dual strategy of sex-limited attraction and repulsion mediated by fruit volatiles. It would be interesting to see if these patterns are replicated in other dioecious fig species.

## 2.2 Volatiles emitted during fruit development

While the emission of fruit volatiles during the ripening of cultivated fruit has been extensively researched,[36] there is scant investigation of changes in VOC profile with development in wild fruit. Fruit can vary in their patterns of ripening which may depend on ethylene production. In non-climacteric fruit, for example, ripening is gradual and there is no peak in VOC production, while in climacteric fruit, sharp rises in ethylene result in rapid ripening and a peak in VOC emission.[27,37] Based on its ripening profile, Borges *et al.*[30] suggested that wild *Ficus racemosa* has a climacteric fruit; in the ripe fruit of this species, there was an absence of day–night differences in VOC production. However, in wild *Ficus benghalensis*, which is believed to have non-climacteric fruit that are dispersed by birds in the day and by bats during the night, sesquiterpenes dominated the diurnal VOC profile of the fruit while fatty acid derivatives such as esters and benzaldehyde dominated the profile at night.[30] There does not appear to be any other study of VOC profiles in relation to ripening in wild fruit.

## 2.3 Microbes and fruit volatiles

Since ripe fleshy fruit contain nutrients that make them attractive to dispersal agents, these rich resources also make them attractive media for microbial development. This sets up an arena for conflict. Daniel Janzen[38] suggested that fruit and seeds are attacked by microbes resulting in spoilage because the microbes make the flesh unpalatable to fruit removal agents to avoid being consumed and killed by fruit dispersers. Rotting fruit attacked by fungi were indeed less attractive to birds.[39] Janzen's theory has recently received theoretical support,[40] but empirical tests are still awaited. Fleshy fruit pulp that is a rich nutrient source for fruit dispersers might also serve as an excellent growth medium for fermenting yeasts that produce alcohols attractive to dispersal agents. However, legitimate dispersers such as bats were deterred when the alcohol content in the fruit exceeded certain levels.[41,42]

Some yeasts that grow in fruit engage in constructing a suitable niche for themselves that attracts fruit flies.[43] Such flies may not be attracted by the volatiles of the particular fermenting fruit *per se* but by specific volatiles produced by the yeasts; this was confirmed when flies showed the same level of attraction to volatiles collected from the headspace of yeasts growing on synthetic minimal medium.[44] In yeasts, the aroma gene *ATF1* is responsible for producing several "fruit" aroma volatiles especially acetates via the enzyme alcohol acetyl transferase Atf1. Deletion of this gene in yeasts caused the antennal lobe response of drosophilids to mutant yeast-generated volatiles to change in comparison to the response exhibited to the volatilome of wild-type yeasts; there was greater response by *Drosophila* to the wild-type yeast volatilome.[45] The system governed by yeast VOCs produced on a fruit-based culture medium is likely a mutualism within an ecosystem engineered by the yeasts since attractive yeasts increase fruit fly larval survival and the adults flies serve as dispersal agents for these yeast propagules.[43,46] In natural yeast populations, *Saccharomyces* yeasts with strong fermentation abilities were more attractive than the less fermentative non-*Saccharomyces* species, pointing to the kind of yeasts that could manipulate *Drosophila* attraction to form mutualistic relationships with the flies[47] within a fruit niche.

## 2.4 Fruit volatiles as parasite attractants and repellents

*Drosophila melanogaster* as well as several Asian drosophilids use citrus fruit volatiles such as limonene and valencene as short-distance cues for oviposition.[48] A parasitoid wasp *Leptoplina boulardi* that is a specialist on *Drosophila* larvae was repelled by these volatiles although the olfactory neurons of the wasp were highly responsive to them.[48] Therefore, drosophilids may use yeast-generated volatiles as long-distance "fruit" aroma cues while intrinsic fruit volatiles such as limonene and valencene may be used as short-distance cues for fruit that are suitable for oviposition since such fruit also emit VOCs that repel parasitoids. Drosophilids are also sensitive to volatiles, such as geosmin, that are harmful to their developing larvae and avoid rotting fruit occupied by microbes producing such odours.[49] Similarly, grapevine moths, whose larvae infest grapes, avoided volatiles produced by grapes infected with a phytopathogenic fungus.[50] Horticulturists are attempting to find ripe fruit volatile attractants for fruit-damaging flies such as the invasive African fruit fly *Bactrocera invadens*,[51] the oriental fruit

**Headspace:** the space immediately around the organism within which volatiles emitted by the organism are present before their diffusion or removal by air currents.

**Volatilome:** the set of volatiles emitted by the organism.

**Climacteric fruit:** a fruit that ripens very quickly usually in response to a sharp rise in ethylene.

fly *Bactrocera dorsalis*,[52] the West Indian fruit fly *Anastrepha obliqua*,[53] and the tomato fruit fly *Neoceratitis cyanescens*.[54] Such attempts may result in designing better VOC traps for the flies resulting in greater fruit crop protection.

If the fruit is the ecological theatre in which these evolutionary plays are being enacted, there are several other fascinating scenes embedded within diverse ecological settings. The sex pheromone receptor of the codling moth *Cydia pomonella* responds strongly to an ester, (*E,Z*)-2,4-decadienoate, produced by the pear fruit into which it oviposits.[55] This correspondence between the receptor for the moth pheromone (codlemone) and a host fruit kairomone is an example of how the scents of host fruit and of sex converge. Similarly α-pinene which is a component of the sex pheromone blend of the olive fruit fly *Bactrocera oleae* is also a volatile found in unripe olive fruit and enhances fly mating success.[56] Differential attractiveness and sensitivity to the scent of host fruit is also the basis of the classic model system demonstrating host race formation and the possibility of sympatric speciation in wild insects, e.g. the case of the apple maggot fly *Rhagoletis pomonella*.[57–59] In this system, the fruit flies shifted from their native host, the hawthorn *Crataegus mollis*, to the introduced apple *Malus domestica*, with corresponding shifts in sensitivity to the volatiles of the host fruit on which male flies congregate; mating is followed by oviposition into the host fruit.[60] Recently, reproductive isolation has been discovered between flies on different species of hawthorn,[61] suggesting the involvement of fruit volatiles in this isolation. Host fruit VOCs can drive sensory specialisation as found recently for *Drosophila erecta*, a specialist on the fruit of the tropical screw pine *Pandanus*, that showed olfactory sensitivity towards 3-methyl-2-butenyl acetate, a characteristic *Pandanus* fruit volatile.[62] This volatile induces oviposition in *D. erecta* but not in *D. melanogaster* indicating ecological specialisation on a fruit volatile.[62]

## 2.5 Fruit volatiles and multimodal signalling

While fruit volatiles provide important cues to fruit parasites such as fruit flies,[63] host finding behaviour in these flies is augmented by visual cues such as fruit colour;[64–66] therefore, multimodal sensory effects operate in this fruit parasitism. Fruit colour is also correlated with fruit odour in bird- and bat-dispersed *Ficus* fruit[67] as with *Ficus* fruit size, fruit placement (axillary, cauliflorous or geocarpic), and life history traits such as plant size.[68,69] These findings suggest correlated

evolution or phenotypic integration between the traits of fruit odour, fruit colour and life history parameters. However, on a global scale, fruit colours exhibit only half the diversity of flower colours[70] suggesting constraints on fruit colour. Some of these constraints could involve abiotic factors such as high illumination coupled with low temperatures that may select for anthocyanins,[71] or may be due to the pleiotropic effects of ripe fruit colour alleles on other plant traits that influence the attack by insect seed predators on unripe fruit.[72]

If fruit colour has to be a reliable and honest signal of the "tastiness" of the propagules in order to invite fruit removal by legitimate seed dispersers, then colour must correlate with content; indeed content may affect colour and also aroma.[26] Valido *et al.*[73] found that visual properties of fruit were correlated with nutrient content in over 100 Mediterranean plant species. Fruit colour was associated with lipid content while fruit brightness was correlated with soluble carbohydrates; this pattern was stronger for bird-dispersed fruit than for those dispersed by mammals. Consequently, birds choosing less bright fruit selected for greater lipid content, a choice that might have considerable survival value.[74] In more than 100 species of vertebrate-dispersed fruit in a Brazilian Atlantic rainforest community, high fruit sugar content was correlated with dark colour and low colour saturation.[75] While there appears to be a biochemical correlation between fruit colour and fruit content, some caveats are necessary. Fruit colour (hue, saturation, brightness) is not an absolute measurement but depends on the colour receptor sensitivities of the organism viewing the fruit; often approximations need to be made based on generalised avian or vertebrate colour receptor sensitivity values. Much more work is required on both the measurement of fruit colour, and its evaluation as a reliable signal of fruit reward content which may be presented as a multimodal signal combining colour and odour, with odour components being derived from fruit pigments[26] and from other fruit constituents.

Fleshy fruits are different from flowers in the sense that the fruit itself often serves as the reward for the fruit dispersal agent while the flower petal is not the reward for the pollinator. Therefore, flowers have many more degrees of freedom in their colour (and associated floral chemistry) compared to fruit that must signal their content honestly. Flower morphology has also diverged much more than fruit morphology[76] suggesting more stringent constraints on fruit in general. The impact of these

**Pleiotropy:** a phenomenon in which the expression of a single gene affects more than one phenotypic trait.

**Kairomone:** a chemical emitted by one organism and that can be used by another organism to its advantage to detect the presence of the emitter; this is in the context of predators detecting prey, or parasites detecting hosts.

**Multimodal signalling:** the use of more than one sensory channel for communication, e.g. vision and odour.

constraints on fruit signalling by odour and/or colour is a profitable area of research.

## 3   Act II: Volatiles of Hard Seeds

Seeds develop from ovules, which are stalked nucelli (megasporangia); nucelli are enclosed by single (gymnosperms) or double (angiosperms) layers called integuments.[77] The integuments form the seed coat. In angiosperms, the seeds and ovules are enclosed within the ovary with fruit tissues developing from the ovary wall and other associated structures.[77] After their removal from the plant by biotic or abiotic dispersal mechanisms, seeds undergo a variable waiting period before germination, an interval referred to as dormancy. Several types of dormancy have been described.[78] Some seeds germinate immediately on being released from associated fruit structures, while other may require physiological changes before germination can begin.[79] Seeds are vulnerable to seed predators prior to their germination, after which seedlings become vulnerable to herbivores. Many seeds are protected from predation by being toxic, by landing in secure sites away from predation, or by having hard seed coats.[80–82] Since seeds house embryos and nutritious endosperm comprising mainly lipids and carbohydrates,[83,84] pre-germination basal metabolism occurring in seeds is bound to release volatiles that could attract seed predators.[85] Rodents are important seed predators and detect seeds by their odours.[86] However, these very seed predators could also be seed dispersers, especially when rodents deposit collected seeds in caches or larders and later either fail to retrieve them before they germinate, or are unable to consume all of the cached seeds especially when seed storage occurs during a masting year (i.e. when seed production is very high).[87,88] Therefore, some plants receive seed dispersal services from their seed predators and must evolve strategies to counter the complete consumption of seed crops.

Physical dormancy is a feature typical of hard seeds; in this type of dormancy, seeds are covered by a water impermeable hard coat.[78] Such hard coats do not allow the diffusion of seed volatiles outside the seed and protect seed volatiles from being detected by seed predators.[89,90] Experiments conducted with two hard-seeded species demonstrated that such seeds produced fourteen VOCs that were readily detected by hamsters when water was allowed to penetrate into the seeds releasing their volatiles. Paulsen et al.[89,90] suggest that the hardness of seeds and their impermeability to water could be an adaptation, especially in hot, dry conditions, to prevent untimely loss of water and possible germination during the wrong season, as well as to achieve crypsis from the acutely sensitive volatile detection systems of seed predators such as rodents. In an experiment conducted with seeds of wild and domesticated plant species such as sunflowers, Hollander et al.[91] found that cultivated seeds were detected much faster than wild seeds by rodents probably because the wild species have been under intense selection to reduce the emission of volatiles to avoid detection by seed predators.

Research on seed volatiles is still in its infancy, and this new hypothesis on crypsis of seed volatiles leading to the evolution of hard seededness is interesting and deserves further investigation.

## 4   Act III: Volatiles of Ant-Dispersed Seeds

Seed movement studies have been largely confined to vertebrates such as bats, primates, birds and rodents since they are regarded as the principal seed dispersal agents and seed predators. However, invertebrates such as slugs,[92] wasps[93] and ants also disperse plant seeds.[94,95] Ants have many important interactions with plants, many of which are mutualistic in terms of protecting plants from herbivores or providing plants with nitrogen in return for lipid or carbohydrate-rich food and shelter,[96–98] while others involve seed dispersal.[99] In ant-dispersed seeds, ants are rewarded with a nutrient-rich elaiosome, which is derived from many different seed-associated tissues to converge onto an ant-sized nutrient-rich seed appendage.[100,101] Ant dispersal of seeds is called myrmecochory and is believed to have evolved independently at least 100 times, occurring in 11,000 species within 77 angiosperm families.[101,102] Myrmecochory must therefore be an important process for both plants and ants.

### 4.1   Seed volatiles in ant-garden epiphytes

Volatiles associated with ant movement of seeds have been investigated in two ecological settings or contexts. The first context is that of the ant garden; this is an arboreal collection of epiphytes growing in clusters within which ants build their nests. Ants carry the epiphyte seeds into the upper portions of the trees where they germinate, thereby sowing the seeds for the garden. In this system, plants benefit from seed dispersal while ants engineer a nest ecosystem using the epiphytes. Not all epiphyte species within an ant garden have elaiosome-bearing seeds. In the first ever study of the phenomenon of chemically-mediated movement of neotropical ant-garden epiphyte

**Masting:** a plant reproductive phenomenon characterised by synchronous flowering and fruiting of plants within a population or within a geographical area.

seeds by ants, Seidel *et al.*[103] and Davidson *et al.*[104] demonstrated that methyl 6-methylsalicylate (6-MMS), a compound found in the femoral gland of the ant *Camponotus femoratus*, was a seed volatile that elicited the greatest seed-carrying response in bioassays conducted with *C. femoratus* using artificial seeds coated with pure compounds. Youngsteadt *et al.*[105–107] confirmed these observations, and also found that the seeds of ant-garden epiphyte species produced a special set of phenolic and terpenoid volatiles; such VOCs (e.g. 6-MMS, geranyl linalool, β-springene, geranyl geraniol and α-springene) appear to be unique to ant-garden epiphytes, being absent from non-ant garden congeners. Moreover, while these VOCs were unattractive to non-arboreal ants, some of them such as geranyl linalool were especially attractive to arboreal ant-garden forming species such as *C. femoratus*.[106] While 6-MMS has only been found in seeds of ant-garden epiphytes,[106] it is an important semiochemical in ants[108] and other Hymenoptera[109] suggesting that ant-garden plants have converged on a compound active in insect communication. Ant gardens also occur in Asian rainforests.[110,111] While solvent extracts of Asian ant-garden seeds also elicited seed-carrying behaviour in ants, the compounds responsible for this behaviour were not identified, and compounds that occured in common across ant-garden species were not detected as in the neotropical setting.[112] Clearly, Asian ant-gardens need much more investigation.

### 4.2 The scent of elaiosomes

The scent of elaiosomes is the second context in which ants and seed volatiles have been investigated. In elaiosome-bearing seeds, the releasers of seed-carrying behaviour in ants are thought to be fatty acids, in particular oleic acid and the diglyceride 1,2 diolein,[113–118] or linolenic acid in combination with oleic acid;[118] however, another study had a contrary finding.[119] Compounds such as oleic acid are known to elicit corpse-carrying or necrophoric behaviours in ants within their nests,[120] since such compounds are also produced during insect decomposition. Necrophoric behaviours triggered by volatiles that signal decomposition of dead adults, larvae or pupae are vital to nest hygiene. Despite their antennal responses to fatty acids, it has been debated whether ants use compounds such as oleic acid as relatively longer-distance olfactory cues or whether such compounds serve as contact gustatory cues[121] owing to their lower volatility. Recently, desert ants showed great sensitivity and heightened

behavioural response to linoleic acid, and were confirmed to use volatile plumes of this fatty acid, despite its low vapour pressure, to locate prey,[122] affirming that volatiles from elaiosomes could attract ants from a distance via an olfactory process. Hughes *et al.*[116] also suggested that the similarity in chemical composition between elaiosomes and insect prey has been instrumental in enticing carnivorous and omnivorous ants to perform seed dispersal functions. Cheater myrmechorous plants, even those without an elaoisome, elicit seed-carrying behaviour in ants by producing the releaser compounds oleic acid and linolenic acid.[118] Interestingly, granivorous ants are not attracted by elicitor compounds present in elaiosomes.[123] Whether granivorous ants use other VOCs to find seeds does not appear to have been investigated and is a field wide open for research.

### 4.3 Conditional mutualism in volatile-mediated myrmecochory

Several myrmechorous plants have converged on a strategy of making the elaiosome attractive but different nutritionally from the seed; elaiosome nutrient content is believed to be closer to the nutritional needs of ants, having much higher amino acid content compared to the seed.[124] Considering the large numbers of plants involved in myrmecochory, and that also bear elaiosomes,[102] it would then appear that this association between plants and ants is a straightforward case of mutualism; plants benefit from seed dispersal and ants benefit from the nutrition provided by the elaiosomes. Indeed elaiosomes enhanced the reproductive output of several ant species.[125–127] However, it is possible that this is a conditional mutualism (*sensu* Bronstein[128]) since the ant *Aphaenogaster* benefitted from elaiosomes only when insect prey were scarce.[129] Furthermore, in another study with *Aphaenogaster* using stable isotopes, ants were found to assimilate the elaiosome nutrients but could not effectively translate them into greater reproductive output.[130] In another example, the ant *Aphaenogaster* preferred to remove *Trillium grandiflorum* seeds, probably due to its high oleic acid content, even though ant colonies fed with *Trillium* elaiosomes had reduced reproductive output.[131] Turner and Frederickson[131] invoke the possibility of a sensory trap being used by plants to manipulate the behaviour of ants as is known to occur in other plant–animal interactions.[132,133] The contextual importance of elaiosomes and the convergence of seed-carrying elicitors between

**Semiochemical:** a chemical produced by one organism that can modify the behaviour of another organism that detects the chemical.

**Releaser:** a chemical that triggers a stereotyped behaviour in an organism, e.g. object-carrying behaviour in ants.

**Sensory trap:** a condition in which an organism, with a previous sensory bias for a particular stimulus, is compelled to perform a behavioural act even when this stimulus is proffered in an inappropriate context; e.g. ants are compelled to carry seeds if the releaser employed by plants is the same chemical that stimulates corpse-carrying or hygienic behaviour in ant nests.

myrmechorous species is worthy of much more research.

## 5 Coda

G. Evelyn Hutchinson famously wrote about the ecological theatre and the evolutionary play.[134] The evolutionary play is all about survival and reproduction, and is being enacted in numerous ecological theatres under varied ecological settings, by different guilds of actors. The fruit and the seed, or the diaspore, are units of plant reproduction, and their morphological and chemical properties are the props that contribute to the success of the play within a variety of ecological contexts. Since investment in fruit and seeds constitutes parental care in plants,[1,135] variation in these props can affect plant reproductive success, and thereby the success of the evolutionary play. Selection pressures acting on the whole plant or on different parts of the plant but which affect whole plant survival and reproduction must be taken into account when examining the different Acts of this Evolutionary Play. An integrated view ought to be taken of whole plant evolution and this view may inform our understanding of the individual parts and processes. For example, flower size and fruit size are correlated.[136] What implication does correlation between flower and fruit traits have for plant reproductive success when flowers and fruit interact independently with a multiplicity of players? It is quite clear that even when just fruit and seed volatiles are considered, we would need to understand the sensory abilities and nutrient requirements of legitimate interactants such as mutualists, as well as of predators and parasites to make sense of the adaptive significance, if any, of a trait. We still do not know whether all VOCs emitted by plants are produced by the plants independently or by commensalistic or parasitic fungal endophytes or bacteria.[137–139] Which players are responsible for the "plant" VOC phenotype?

All organisms, particularly those as complex as plants must therefore be viewed as entities whose emergent phenotype may incorporate the effects of multitudinous symbiotic organisms.[140] Recognising that plants are holobionts is fundamental to this view of life,[140,141] and is vital to our understanding of the real contributors to the success or failure of the plant phenotype.

## Acknowledgements

## References

1. Orians, G.H. & Janzen, D.H. Why are embryos so tasty? *The American Naturalist* **108**, 581–592 (1974).

2. Fenner, M. & Thompson, K. *The ecology of seeds*. Cambridge, Cambridge University Press, 260 pp. (2005).

3. Tewksbury, J.J. Fruits, frugivores and the evolutionary arms race. *New Phytologist* **156**, 137–139 (2002).

4. Cipollini, M.L. & Levey, D.J. Secondary metabolites of fleshy vertebrate-dispersed fruits: adaptive hypotheses and implications for seed dispersal. *The American Naturalist* **150**, 346–372 (1997).

5. Cipollini, M.L. Secondary metabolites of vertebrate-dispersed fruits: evidence for adaptive functions. *Revista Chilena de Historia Natural* **73**, 421–440 (2000).

6. Berenbaum, M.R. The chemistry of defense: theory and practice. *Proceedings of the National Academy of Sciences USA* **92**, 2–8 (1995).

7. Eriksson, O. & Ehrlén, J. Secondary metabolites in fleshy fruits: are adaptive explanations needed? *The American Naturalist* **152**, 905–907 (1998).

8. Primack, R.B. Relationships among flowers, fruits, and seeds. *Annual Review of Ecology and Systematics* **18**, 409–430 (1987).

9. Sargent, R.D., Goodwillie, C., Kalisz, S. & Ree, R.H. Phylogenetic evidence for a flower size and number trade-off. *American Journal of Botany* **94**, 2059–2062 (2007).

10. Moles, A.T. & Westoby, M. Seed size and plant strategy across the whole life cycle. *Oikos* **113**, 91–105 (2006).

11. Herrera, C.M. Correlated evolution of fruit and leaf size in bird dispersed plants: species level variance in fruit traits explained a bit further? *Oikos* **97**, 426–432 (2002).

12. Burns, K.C., Cazetta, E., Galetti, M., Valido, A. & Schaefer, H.M. Geographic patterns in fruit colour diversity: do leaves constrain the colour of fleshy fruits? *Oecologia* **159**, 337–343 (2009).

13. Whitehead, S.R. & Bowers, M.D. Evidence for the adaptive significance of secondary compounds in vertebrate-dispersed fruits. *The American Naturalist* **182**, 563–577 (2013).

14. Whitehead, S.R., Jeffrey, C.S., Leonard, M.D., Dodson, C.D., Dyer, L.A. & Bowers, M.D. Patterns of secondary metabolite allocation to fruits and seeds in *Piper reticulatum*. *Journal of Chemical Ecology* **39**, 1373–1384 (2013).

15. Coombe, B.G. The development of fleshy fruits. *Annual Review of Plant Physiology* **27**, 207–228 (1976).

16. Spjut, R.W. *A systematic treatment of fruit types*. Memoirs of the New York Botanical Garden, Volume 70, 182 pp. (1994).

**Holobiont:** an "individual" that is represented by its own body and all the symbionts that it normally harbours; e.g. humans are holobionts when all their gut microbes are considered.

17. Mack, A.L. Did fleshy fruit pulp evolve as a defence against seed loss rather than as a dispersal mechanism? *Journal of Biosciences* **25**, 93–97 (2000).

18. Gould, S.J. & Vrba, E.S. Exaptation—a missing term in the science of form. *Paleobiology* **8**, 4–15 (1982).

19. Fleming, T.H. & Kress, W.J. A brief history of fruits and frugivores. *Acta Oecologica* **37**, 521–530 (2011).

20. Fleming, T.H. & Kress, W.J. *The ornaments of life: coevolution and conservation in the tropics*. Chicago, University of Chicago Press, 616 pp. (2013).

21. Dudareva, N., Negre, F., Nagegowda, D.A. & Orlova, I. Plant volatiles: recent advances and future perspectives. *Critical Reviews in Plant Sciences* **25**, 417–440 (2006).

22. Dudareva, N., Klempien A., Muhlemann, J.K. & Kaplan, I. Biosynthesis, function and metabolic engineering of plant volatile organic compounds. New Phytologist **198**, 16–32 (2013).

23. Rodríguez, A., Alquézar, B. & Pena, L. Fruit aromas in mature fleshy fruits as signals of readiness for predation and seed dispersal. *New Phytologist* **197**, 36–48 (2013).

24. Knudsen, J.T., Tollsten, L. & Bergström, L.G. Floral scents—a checklist of volatile compounds isolated by head-space techniques. *Phytochemistry* **33**, 253–280 (1993).

25. Knudsen, J.T., Eriksson, R., Gershenzon, J. & Ståhl, B. Diversity and distribution of floral scent. *The Botanical Review* **72**, 1–120 (2006).

26. Lewinsohn, E., Sitrit, Y., Bar, E., Azulay, Y., Ibdah, M., Meir, A., Yosef, Y., Zamir, D. & Tadmor, Y. Not just colors—carotenoid degradation as a link between pigmentation and aroma in tomato and watermelon fruit. *Trends in Food Science & Technology* **16**, 407–415 (2005).

27. Klee, H.J. & Giovannoni, J.J. Genetics and control of tomato fruit ripening and quality attributes. *Annual Review of Genetics* **45**, 41–59 (2011).

28. Schlumpberger, B.O., Clery, R.A. & Barthlott, W. A unique cactus with scented and possibly bat dispersed fruits: *Rhipsalis juengeri*. *Plant Biology* **8**, 265–270 (2006).

29. Borges, R.M., Bessière, J-M. & Hossaert-McKey, M. The chemical ecology of seed dispersal in monoecious and dioecious figs. *Functional Ecology* **22**, 484–493 (2008).

30. Borges, R.M., Ranganathan, Y., Krishnan, A., Ghara, M. & Pramanik, G. (2011). When should fig fruit produce volatiles? Pattern in a ripening process. *Acta Oecologica* **37**, 611–618 (2011).

31. Hodgkison, R., Ayasse, M., Häberlein, C., Schulz, S., Zubaid, A., Mustapha, W.A.W., Kunz, T.H. & Kalko, E.K.V. Fruit bats and bat fruits: the evolution of fruit scent in relation to the foraging behaviour of bats in the New and Old World tropics. *Functional Ecology* **27**, 1075–1084 (2013).

32. Dumont, E.R., Weiblen, G.D. & Winkelmann, J.R. Preferences of fig wasps and fruit bats for figs of functionally dioecious *Ficus pungens*. *Journal of Tropical Ecology* **20**, 233–238 (2004).

33. Weiblen, G.D., Lomascolo, S.B., Oono, R. & Dumont, E.R. Nutritional dimorphism in New Guinea dioecious figs. *Biotropica* **42**, 656–663 (2010).

34. Mason, J.R., Adams, M.A. & Clark, L. Anthranilate repellency to starlings: chemical correlates and sensory perception. *Journal of Wildlife Management* **53**, 55–64 (1989).

35. Nolte, D.L., Mason, J.R. & Clark, L. Avoidance of bird repellents by mice (*Mus musculus*). *Journal of Chemical Ecology* **19**, 427–432 (1993).

36. Defilippi, B.G., Manriquez, D., Luengwilai, K. & González-Agüero, M. Aroma volatiles: biosynthesis and mechanisms of modulation during fruit ripening. *Advances in Botanical Research* **50**, 1–37 (2009).

37. Pech, J.C., Purgatto, E., Bouzayen, M. & Latché, A. Ethylene and fruit ripening. *Annual Plant Reviews* **44**, 275–304 (2012).

38. Janzen, D.H. Why fruits rot, seeds mold, and meat spoils. *The American Naturalist* **111**, 691–713 (1977).

39. Cipollini, M.L. & Stiles, E.W. Fruit rot, antifungal defense, and palatability of fleshy fruits for frugivorous birds. *Ecology* **74**, 751–762 (1993).

40. Ruxton, G.D., Wilkinson, D.W., Schaefer, H.M. & Sherratt, T.N. Why fruit rots: theoretical support for Janzen's theory of microbe–macrobe competition. *Proceedings of the Royal Society Series B: Biological Sciences* **281**, 20133320. doi:10.1098/rspb.2013.3320 (2014).

41. Sánchez, F., Korine, C., Pinshow, B. & Dudley, R. The possible roles of ethanol in the relationship between plants and frugivores: First experiments with Egyptian fruit bats. *Integrative and Comparative Biology* **44**, 290–294 (2004).

42. Orbach, D.N., Veselka, N., Dzal, Y., Lazure, L. & Fenton, M.B. Drinking and flying: does alcohol consumption affect the flight and echolocation performance of phyllostomid bats? *PLOS ONE* **5**, e8993 (2010).

43. Goddard, M.R. Quantifying the complexities of *Saccharomyces cerevisiae*'s ecosystem engineering via fermentation. *Ecology* **89**, 2077–2082 (2008).

44. Becher, P.G., Flick, G., Rozpędowska, E., Schmidt, A., Hagman, A., Lebreton, S., Larsson, M.C., Hansson, B.S., Piškur, J., Witzgall, P. *et al.* Yeast, not fruit volatiles mediate *Drosophila melanogaster* attraction, oviposition and development. *Functional Ecology* **26**, 822–828 (2012).

45. Christiaens, J.F., Franco, L.M., Cools, T.L., De Meester, L., Michiels, J., Wenseleers, T., Hassan, B.A., Yaksi, E. & Verstrepen K.J. The fungal aroma gene *ATF1* promotes dispersal of yeast cells through insect vectors. *Cell Reports* **9**, 425–432 (2014).

46. Buser, C.C., Newcomb, R.D., Gaskett, A.C. & Goddard, M.R. Niche construction initiates the evolution of mutualistic interactions. *Ecology Letters* **17**, 1257–1264 (2014).

47. Palanca, L., Gaskett, A.C., Günther, C.S., Newcomb, R.D. & Goddard, M.R. Quantifying variation in the ability of yeasts to attract *Drosophila melanogaster*. *PLOS ONE* **8**, e75332 (2013).

48. Dweck, H.K.M., Ebrahim, S.A.M., Kromann, S., Brown, D., Hillbur, Y., Sachse. S., Hansson, B.S. & Stensmyr, M.C. Odorant receptor Or19a mediates oviposition substrate preference in Drosophila. *Current Biology* **23**, 2472–2480 (2013).

49. Stensmyr, M.C., Dweck, H.K., Farhan, A., Ibba, I., Strutz, A., Mukunda, L., Linz, J., Grabe, V., Steck, K., Lavista-Lanos, S. *et al.* A conserved dedicated olfactory circuit for detecting harmful microbes in *Drosophila. Cell* **151**, 1345–1357 (2012).

50. Tasin, M., Knudsen, G.K. & Pertot, I. Smelling a diseased host: grapevine moth responses to healthy and fungus-infected grapes. *Animal Behaviour* **83**, 555–562 (2012).

51. Biasazin, T.D., Karlsson, M.F., Hillbur, Y., Seyoum, E. & Dekker, T. Identification of host blends that attract the African invasive fruit fly, *Bactrocera invadens. Journal of Chemical Ecology* **40**, 966–976 (2014).

52. Jayanthi, P.D.K., Kempraj, V., Aurade, R.M., Venkataramanappa, R.K., Nandagopal, B., Verghese, A. & Bruce, T.J. Specific volatile compounds from mango elicit oviposition in gravid *Bactrocera dorsalis* females. *Journal of Chemical Ecology* **40**, 259–266 (2014).

53. Cruz-López, L., Malo, E.A., Toledo, J., Virgen, A., Del Mazo, A. & Rojas, J.C. A new potential attractant for *Anastrepha obliqua* from *Spondias mombin* fruits. *Journal of Chemical Ecology* **32**, 351–365 (2006).

54. Brevault, T. & Quilici, S. Flower and fruit volatiles assist host-plant location in the tomato fruit fly *Neoceratitis cyanescens. Physiological Entomology* **35**, 9–18 (2010).

55. Bengtsson, J.M., Gonzalez, F., Cattaneo, A.M., Montagné, N., Walker, W.B., Bengtsson, B., Anfora, G., Ignell, R., Jacquin-Joly, E. & Witzgall, P. A predicted sex pheromone receptor of codling moth *Cydia pomonella* detects the plant volatile pear ester. *Frontiers in Ecology and Evolution* **2**, 33 (2014).

56. Gerofotis, C.D., Ioannou, C.S. & Papadopoulos, N.T. Aromatized to find mates: α-pinene aroma boosts the mating success of adult olive fruit flies. *PLOS ONE* **8**, e81336 (2013).

57. Cha, D.H., Powell, T.H., Feder, J.L. & Linn Jr, C.E. Identification of fruit volatiles from green hawthorn (*Crataegus viridis*) and blueberry hawthorn (*Crataegus brachyacantha*) host plants attractive to different phenotypes of *Rhagoletis pomonella* flies in the Southern United States. *Journal of Chemical Ecology* **37**, 974–983 (2011).

58. Cha, D.H., Powell, T.H., Feder, J.L. & Linn Jr, C.E. Identification of host fruit volatiles from three mayhaw species (*Crataegus* series *Aestivales*) attractive to mayhaw-origin *Rhagoletis pomonella* flies in the Southern United States. *Journal of Chemical Ecology* **37**, 961–973 (2011).

59. Cha, D.H., Yee, W.L., Goughnour, R.B., Sim, S.B., Powell, T.H., Feder, J.L. & Linn Jr, C.E. Identification of host fruit volatiles from domestic apple (*Malus domestica*), native black hawthorn (*Crataegus douglasii*) and introduced ornamental hawthorn (*C. monogyna*) attractive to *Rhagoletis pomonella* flies from the Western United States. *Journal of Chemical Ecology* **38**, 319–329 (2012).

60. Frey, J.E., Feder, J.L., Palma, J. & Bush, G.L. Differences in the electroantennal responses of apple- and hawthorn-infesting races of *Rhagoletis pomonella* to host fruit volatile compounds. *Chemoecology* **8**, 175–186 (1998).

61. Powell, T.H., Forbes, A.A., Hood, G.R. & Feder, J.L. Ecological adaptation and reproductive isolation in sympatry: genetic and phenotypic evidence for native host races of *Rhagoletis pomonella. Molecular Ecology* **23**, 688–704 (2014).

62. Linz, J., Baschwitz, A., Strutz, A., Dweck, H.K.M., Sachse, S., Hansson, B.S. & Stensmyr M.C. Host plant-driven sensory specialization in *Drosophila erecta. Proceedings of the Royal Society Series B: Biological Sciences* **280**, 20130626 (2013).

63. Aluja, M. & Prokopy, R.J. Host search behaviour by *Rhagoletis pomonella* flies: inter-tree movement patterns in response to wind borne fruit volatiles under field conditions. *Physiological Entomology* **17**, 1–8 (1992).

64. Aluja, M. & Prokopy, R.J. Host odor and visual stimulus interaction during intratree host finding behavior of *Rhagoletis pomonella* flies. *Journal of Chemical Ecology* **19**, 2671–2696 (1993).

65. Green, T., Prokopy, R.J. & Hosmer, D.W. Distance of response to host tree models by female apple maggot flies, *Rhagoletis pomonella* (Walsh)(Diptera: Tephritidae): interaction of visual and olfactory stimuli. *Journal of Chemical Ecology* **20**, 2393–2413 (1994).

66. Brévault, T. & Quilici, S. Interaction between visual and olfactory cues during host finding in the tomato fruit fly *Neoceratitis cyanescens. Journal of Chemical Ecology* **36**, 249–259 (2010).

67. Lomáscolo, S.B., Levey, D.J., Kimball, R.T., Bolker, B.M. & Alborn, H.T. Dispersers shape fruit diversity in *Ficus* (Moraceae). *Proceedings of the National Academy of Sciences USA* **107**, 14668–14672 (2010).

68. Lomáscolo, S.B., Speranza, P. & Kimball, R.T. Correlated evolution of fig size and color supports the dispersal syndromes hypothesis. *Oecologia* **156**, 783–796 (2008).

69. Harrison, R.D., Rønsted, N., Xu, L., Rasplus, J-Y. & Cruaud, A. (2012). Evolution of fruit traits in *Ficus* subgenus *Sycomorus* (Moraceae): To what extent do frugivores determine seed dispersal mode? *PLOS ONE* **7**, e38432 (2012).

70. Stournaras, K.E., Lo, E., Böhning-Gaese, K., Cazetta, E., Dehling, D.M., Schleuning, M., Stoddard, M.C., Donoghue, M.J., Prum, R.O. & Schaefer, H.M. How colorful are fruits? Limited color diversity in fleshy fruits on local and global scales. *New Phytologist* **198**, 617–629 (2013).

71. Schaefer, H.M. Why fruits go to the dark side. *Acta Oceologica* **37**, 604–610 (2011).

72. Whitney, K.D. & Stanton, M.L. Insect seed predators as novel agents of selection on fruit color. *Ecology* **85**, 2153–2160 (2004).

73. Valido, A., Schaefer, H.M. & Jordano, P. Colour, design and reward: phenotypic integration of fleshy fruit displays. *Journal of Evolutionary Biology* **24**, 751–760 (2011).

74. Schaefer, H.M., Valido, A. & Jordano, P. Birds see the true colours of fruits to live off the fat of the land. *Proceedings of the Royal Society Series B: Biological Sciences* **281**, 20132516 (2014).

75. Cazetta, E., Galetti, M., Rezende, E.L. & Schaefer, H.M. On the reliability of visual communication in vertebrate-dispersed fruits. *Journal of Ecology* **100**, 277–286 (2012).

76. Whitney, K.D. Comparative evolution of flower and fruit morphology. *Proceedings of the Royal Society Series B: Biological Sciences* **276**, 2941–2947 (2009).

77. Linkies, A., Graeber, K., Knight, C. & Leubner-Metzger, G. The evolution of seeds. *New Phytologist* **186**, 817–831 (2010).

78. Baskin, C.C. & Baskin, J.M. Seeds. *Ecology, biogeography, and evolution of dormancy and germination.* San Diego, CA, USA, Academic Press, 666 pp. (1998).

79. Baskin, C.C., Baskin, J.M. & Li, X. Taxonomy, anatomy and evolution of physical dormancy in seeds. *Plant Species Biology* **15**, 139–152 (2000).

80. Howe, H.F. & Smallwood, J. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* **3**, 201–228 (1982).

81. Willson, M.F. & Traveset, A. The ecology of seed dispersal. In *Seeds: the ecology of regeneration in plant communities*, Second edition (ed. M. Fenner), pp. 85–110. Wallingford, UK, CAB International (2000).

82. Traveset, A., Heleno, R., Nogales, M. & Gallagher, R.S. The ecology of seed dispersal. In *Seeds: the ecology of regeneration in plant communities*, Third edition (ed. R.S. Gallagher), pp. 62–93. Wallingford, UK, CAB International (2014).

83. Lopes, M.A. & Larkins, B.A. Endosperm origin, development, and function. *Plant Cell* **5**, 1383–1399 (1993).

84. Friedman, W.E. Organismal duplication, inclusive fitness theory, and altruism: understanding the evolution of endosperm and the angiosperm reproductive syndrome. *Proceedings of the National Academy of Sciences USA* **92**, 3913–3917 (1995).

85. Colville, L., Bradley, E.L., Lloyd, A.S., Pritchard, H.W., Castle, L. & Kranner, I. Volatile fingerprints of seeds of four species indicate the involvement of alcoholic fermentation, lipid peroxidation, and Maillard reaction in seed deterioration during ageing and desiccation stress. *Journal of Experimental Botany* **63**, 6519–6530 (2012).

86. Vander Wall, S.B. How rodents smell buried seeds: a model based on the behavior of pesticides in soil. *Journal of Mammalogy* **84**, 1089–1099 (2003).

87. Vander Wall, S.B. The evolutionary ecology of nut dispersal. *The Botanical Review* **67**, 74–117 (2001).

88. Vander Wall, S.B. How plants manipulate the scatter-hoarding behaviour of seed-dispersing animals. *Philosophical Transactions of the Royal Society Series B: Biological Sciences* **365**, 989–997 (2010).

89. Paulsen, T.R., Colville, L., Kranner, I., Daws, M.I., Högstedt, G., Vandvik, V. & Thompson, K. Physical dormancy in seeds: a game of hide and seek? *New Phytologist* **198**, 496–503 (2013).

90. Paulsen, T.R., Högstedt, G., Thompson, K., Vandvik, V. & Eliassen, S. Conditions favouring hard seededness as a dispersal and predator escape strategy. *Journal of Ecology* **102**, 1475–1484 (2014).

91. Hollander, J.L., Vander Wall, S.B. & Longland, W.S. Olfactory detection of caches containing wildland versus cultivated seeds by granivorous rodents. *Western North American Naturalist* **72**, 339–347 (2012).

92. Türke, M., Heinze, E., Andreas, K., Svendsen, S.M., Gossner, M.M. & Weisser, W.W. Seed consumption and dispersal of ant-dispersed plants by slugs. *Oecologia* **163**, 681–693 (2010).

93. Manohara, T.N. Wasp-mediated seed dispersal in agarwood plant (*Aquilaria malaccensis*), a critically endangered and overexploited species of North East India. *Current Science* **105**, 298–299 (2013).

94. Beattie, A.J. *The evolutionary ecology of ant–plant mutualisms*. Cambridge, Cambridge University Press, 182 pp. (1985).

95. Rico-Gray, V. & Oliveira, P.S. *The ecology and evolution of ant-plant interactions*. Chicago, University of Chicago Press, 320 pp. (2007).

96. Heil, M. & McKey, D. Protective ant-plant interactions as model systems in ecological and evolutionary research. *Annual Review of Ecology, Evolution, and Systematics* **34**, 425–453 (2003).

97. Mayer, V.E., Frederickson, M.E., McKey, D. & Blatrix, R. (2014). Current issues in the evolutionary ecology of ant–plant symbioses. *New Phytologist* **202**, 749–764 (2014).

98. Chanam, J., Sheshshayee, M.S., Kasinathan, S., Jagdeesh, A., Joshi, K.A. & Borges, R.M. Nutritional benefits from domatia inhabitants in an ant–plant interaction: interlopers do pay the rent. *Functional Ecology* **28**, 1107–1116 (2014).

99. Gómez, C. & Espadaler, X. An update of the world survey of myrmecochorous dispersal distances. *Ecography* **36**, 1193–1201 (2013).

100. Gorb, E. & Gorb, S. *Seed dispersal by ants in a deciduous forest ecosystem. Mechanisms, strategies, adaptations.* Dordrecht, Kluwer Academic Publishers, 226 pp. (2003).

101. Lengyel, S., Gove, A.D., Latimer, A.M., Majer, J.D. & Dunn, R.R. Ants sow the seeds of global diversification in flowering plants. *PLOS ONE* **4**, e5480 (2009).

102. Lengyel, S., Gove, A.D., Latimer, A.M., Majer, J.D. & Dunn, R.R. Convergent evolution of seed dispersal by ants, and phylogeny and biogeography in flowering plants: a global survey. *Perspectives in Plant Ecology, Evolution and Systematics* **12**, 43–55 (2010).

103. Seidel, J.L., Epstein, W.W. & Davidson, D.W. Neotropical ant gardens. I. Chemical constituents. *Journal of Chemical Ecology* **16**, 1791–1816 (1990).

104. Davidson, D.W., Seidel, J.L. & Epstein, W.W. Neotropical ant gardens II. Bioassays of seed compounds. *Journal of Chemical Ecology* **16**, 2993–3013 (1990).

105. Youngsteadt, E., Nojima, S., Häberlein, C., Schulz, S. & Schal, C. Seed odor mediates an obligate ant–plant mutualism in Amazonian rainforests. *Proceedings of the National Academy of Sciences USA* **105**, 4571–4575 (2008).

106. Youngsteadt, E., Baca, J.A., Osborne, J. & Schal, C. Species-specific seed dispersal in an obligate ant-plant mutualism. *PLOS ONE* **4**, e4335 (2009).

107. Youngsteadt, E., Bustios, P.G. & Schal, C. Divergent chemical cues elicit seed collecting by ants in an obligate multi-species mutualism in lowland Amazonia. *PLOS ONE* **5**, e15822 (2010).

108. Greenberg, L., Tröger, A.G., Francke, W., McElfresh, J.S., Topoff, H., Aliabadi, A. & Millar, J.G. (2007). Queen sex pheromone of the slave-making ant, *Polyergus breviceps*. *Journal of Chemical Ecology* **33**, 935–945 (2007).

109. Stökl, J., Dandekar, A.T. & Ruther, J. High chemical diversity in a wasp pheromone: a blend of methyl 6-methylsalicylate, fatty alcohol acetates and cuticular hydrocarbons releases courtship behavior in the *Drosophila* parasitoid *Asobara tabida*. *Journal of Chemical Ecology* **40**, 159–168 (2014).

110. Kaufmann, E., Weissflog, A., Hashim, R. & Maschwitz, U. Ant-gardens on the giant bamboo *Gigantochloa scortechinii* (Poaceae) in West-Malaysia. *Insectes Sociaux* **48**, 125–133 (2001).

111. Kaufmann, E. & Maschwitz, U. Ant-gardens of tropical Asian rainforests. *Naturwissenschaften* **93**, 216–227 (2006).

112. Kaufmann. E. 2002 *Southeast Asian ant-gardens: Diversity, ecology, ecosystematic significance, and evolution of mutualistic ant-epiphytic association*. PhD thesis, Frankfurt Am Main, Johann Wolfgang Goethe University, 203 pp. (2002).

113. Marshall, D.L., Beattie, A.J. & Bollenbacher, W.E. Evidence for diglycerides as attractants in an ant-seed interaction. *Journal of Chemical Ecology* **5**, 335–344 (1979).

114. Skidmore, B.A. & Heithaus, E.R. Lipid cues for seed-carrying by ants in *Hepatica americana*. *Journal of Chemical Ecology* **14**, 2185–2196 (1988).

115. Brew, C.R, O'Dowd, D.J. & Rae, I.D. Seed dispersal by ants: behaviour-releasing compounds in elaiosomes. *Oecologia* **80**, 490–497 (1989).

116. Hughes, L., Westoby, M.T. & Jurado, E. Convergence of elaiosomes and insect prey: evidence from ant foraging behaviour and fatty acid composition. *Functional Ecology* **8**, 358–365 (1994).

117. Boulay, R., Coll-Toledano, J. & Cerdá, X. Geographic variations in *Helleborus foetidus* elaiosome lipid composition: implications for dispersal by ants. *Chemoecology* **16**, 1–7 (2006).

118. Pfeiffer, M., Huttenlocher, H., & Ayasse, M. Myrmecochorous plants use chemical mimicry to cheat seed dispersing ants. *Functional Ecology* **24**, 545–555 (2010).

119. Reifenrath, K., Becker, C. & Poethke, H.J. Diaspore trait preferences of dispersing ants. *Journal of Chemical Ecology* **38**, 1093–1104 (2012).

120. Wilson, E.O., Durlach, N.I. & Roth, L.M. Chemical releasers of necrophoric behavior in ants. *Psyche* **65**, 108–114 (1958).

121. Sheridan, S.L., Iversen, K.A. & Itagaki, H. The role of chemical senses in seed-carrying behavior by ants: A behavioral, physiological, and morphological study. *Journal of Insect Physiology* **42**, 149–159 (1996).

122. Buehlmann, C., Graham, P., Hansson, B.S. & Knaden, M. Desert ants locate food by combining high sensitivity to food odors with extensive crosswind runs. *Current Biology* **24**, 960–964 (2014).

123. Gammans, N., Bullock, J.M., Gibbons, H. & Schönrogge, K. Reaction of mutualistic and granivorous ants to *Ulex* elaiosome chemicals. *Journal of Chemical Ecology* **32**, 1935–1947 (2006).

124. Fischer, R.C., Richter, A., Hadacek, F. & Mayer, V. Chemical differences between seeds and elaiosomes indicate an adaptation to nutritional needs of ants. *Oecologia* **155**, 539–547 (2008).

125. Morales, M.A. & Heithaus, E.R. Food from seed-dispersal mutualism shifts sex ratios in colonies of the ant *Aphaenogaster rudis*. *Ecology* **79**, 734–739 (1998).

126. Bono, J.M. & Heithaus, E.R. Sex ratios and the distribution of elaiosomes in colonies of the ant, *Aphaenogaster rudis*. *Insectes Sociaux* **49**, 320–325 (2002).

127. Gammans, N., Bullock, J.M. & Schönrogge, K. Ant benefits in a seed dispersal mutualism. *Oecologia* **146**, 43–49 (2005).

128. Bronstein, J.L. Conditional outcomes in mutualistic interactions. *Trends in Ecology & Evolution* **9**, 214–217 (1994).

129. Clark, R.E. & King, J.R. The ant, *Aphaenogaster picea*, benefits from plant elaiosomes when insect prey is scarce. *Environmental Entomology* **41**, 1405–1408 (2012).

130. Caut, S., Jowers, M.J., Cerda, X. & Boulay, R.R. Questioning the mutual benefits of myrmecochory: a stable isotope based experimental approach. *Ecological Entomology* **38**, 390–399 (2013).

131. Turner, K.M. & Frederickson, M.E. Signals can trump rewards in attracting seed-dispersing ants. *PLOS ONE* **8**, e71871 (2013).

132. Edwards, D.P. & Douglas, W.Y. The roles of sensory traps in the origin, maintenance, and breakdown of mutualism. *Behavioral Ecology and Sociobiology* **61**, 1321–1327 (2007).

133. Schaefer, H.M. & Ruxton, G.D. Deception in plants: mimicry or perceptual exploitation? *Trends in Ecology & Evolution* **24**, 676–685 (2009).

134. Hutchinson, G.E. *The ecological theater and the evolutionary play*. New Haven, Yale University Press, 139 pp. (1965).

135. Lloyd, D.G. Parental strategies of angiosperms. *New Zealand Journal of Botany* **17**, 595–606 (1979).

136. Whitney, K.D. & Rudgers, J.A. Constraints on plant signals and rewards to multiple mutualists? *Plant Signaling & Behavior* **4**, 1–4 (2009).

137. Schulz, S. & Dickschat, J.S. Bacterial volatiles: the smell of small organisms. *Natural Product Reports* **24**, 814–842 (2007).

138. Davis, T.S., Crippen, T.L., Hofstetter, R.W. & Tomberlin, J.K. Microbial volatile emissions as insect semiochemicals. *Journal of Chemical Ecology* **39**, 840–859 (2013).

139. Truyens, S., Weyens, N., Cuypers, A. & Vangronsveld, J. Bacterial seed endophytes: genera, vertical transmission and interaction with plants. *Environmental Microbiology Reports* doi: 10.1111/1758–2229.12181(2014).

140. Gilbert, S.F., Sapp, J. & Tauber, A.I. A symbiotic view of life: We have never been individuals. *The Quarterly Review of Biology* **87**, 325–341 (2012).

141. Gilbert, S.F. Symbiosis as the way of eukaryotic life: The dependent co-origination of the body. *Journal of Biosciences* **39**, 201–209 (2014).

**Renee M. Borges** is a Professor at the Centre for Ecological Sciences, Indian Institute of Science, Bangalore, where she is also currently the Centre's Chairperson. She has been trained in animal physiology and behavioural ecology, and studied the role of plant secondary metabolites and nutrients in the foraging ecology of the Indian giant squirrel for her doctoral work at the University of Miami, Florida. She is currently investigating the sensory ecology of mutualistic and parasitic interactions in a number of specialised systems such as the fig–fig wasp brood-site pollination system, trophic and protection mutualisms between ants and plants, and fungus farming by termites. She is also exploring visual and olfactory signals in a pollination network of seasonal cloud forest plants in the Western Ghats of India. She is researching the extended phenotype of termite mounds, and is attempting to understand how termites build structures to house their colonies and their fungus farms.