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## **From Plant Exploitation to Mutualism. Chapter 3**

François Lieutier, Kalina Bermudez-Torres, James Cook, Marion O. Harris, Luc Legal, Aurélien Sallé, Bertrand Schatz, David Giron

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RESEARCH**

INSECT-PLANT INTERACTIONS IN A CROP  
PROTECTION PERSPECTIVE



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DENIS THIÉRY

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# ADVANCES IN BOTANICAL RESEARCH

## Insect-Plant Interactions in a Crop Protection Perspective

Volume Editor

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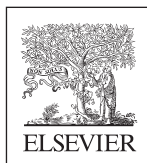
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# From Plant Exploitation to Mutualism

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## Abstract

Phytophagous insects have developed mechanisms of various complexity levels to utilize plants in spite of the barriers that plants have built to resist aggressions. Plant exploitation, the simplest level, is the use of plant defence chemicals for the benefit of insects. It is illustrated by the use of plant toxins for defence against predators. The energetic cost of that defence strategy is discussed according to the toxicity of the chemicals and the necessity of protecting the herbivore, and the modes of action on predators are presented. Furthermore, manipulation of the plant can reorient the plant metabolism to satisfy insect needs. Drastic remodelling of the host plant can occur, from ultrastructure to anatomy levels, with alteration of both its nutritional quality and secondary metabolism. The mechanisms involved are being investigated. Outcomes concern optimization of the nutritional value of the host plant and protection from adverse abiotic and biotic (natural enemies, competition) conditions. Cooperation with conspecifics or microorganisms often interferes. At the highest level of complexity, mutualism is the result of a compromise between insect and plant where each partner benefits from the association. Pollination is a typical example. Pollinators vary from generalists to specialists and belong to a community of insect linked to a community of plants. In the fig—fig wasp mutualism, the various mechanisms involved in situations of monoecy and dioecy are discussed, as well as the existence of coadaptations and cospeciations. The chapter ends with a presentation of research perspectives for improving crop productivity.



## 1. INTRODUCTION

Living plants are source of food for phytophagous insects furnishing them with most of the nutrients required for their development and

reproduction. However, plants may lack certain essential compound. Moreover, they possess a wide array of defensive strategies, including physical structures, a large diversity of secondary metabolites and proteins which can interfere with the colonization and development of phytophagous insects. Nevertheless, insects have evolved to cope with these physical and chemical barriers and have developed mechanisms/strategies to avoid and even to use them. The present chapter covers diverse situations of utilization of plant tissues and compounds by insects, representing various levels of relations between insects and their living host plant, including various ‘insect strategies’.

The simplest level is plant exploitation. It is more than simple plant utilization and can be defined as a misappropriation of plant defence chemicals for the benefit of insects. A more elaborated level is plant manipulation, where the plant natural mechanisms are reoriented so that the plant system becomes manipulated to serve the insect needs. This can be realized without or with modification of the plant genetic program. At the highest level of plant utilization, a compromise has been established between insects and their host plants, which benefits both partners in a mutual agreement called mutualism. A large array of insect feeding behaviours (from browsers to galling and wood-borers), as well as of plant categories (herbs, trees) can be concerned and are illustrated in the chapter. Finally, applied perspectives are tentatively presented.



## 2. DEFENCE AGAINST PREDATORS

Insect predation is a complex world involving multiple interactions. Among the phytophagous species, many examples illustrate extreme sophistication in the use of secondary metabolites for their *defence* (Agrawal et al., 2015; Mithöfer et al., 2012; Schuman & Baldwin, 2016), their adaptive processes of evolutionary history-dependent among insect families (Stam et al., 2014) and also in their relationship to host plants (Gols, 2014). Though the term *defence* implies broad protection against a threat, it can be split into active and passive defence.

While many Hymenoptera such as wasps, bees and ants are capable to defend themselves actively with poisonous stings or bites, most insects have developed antipredator behaviours/strategies (Clark & Faeth, 1997; Vulinec, 1990), which is to accumulate or transform active/toxic substances from host plants. However, in few cases, insects can produce *de novo* antipredatory substances (Pasteels, Duffey, & Rowell-Rahier, 1990). Some intermediate

cases are illustrated by some bugs or some beetles which project chemical substances on their predators (Krall, Bartelt, Lewis, & Whitman, 1999). In this part, we will only present the passive chemical antipredation strategies.

## 2.1 Sequestration or Metabolism?

There are two types of passive chemical antipredation. The first is represented by insects feeding on very poisonous plants (Euphorbiaceae, Asclepiadaceae, Solanaceae) but without accumulating these secondary compounds (Hundsdoerfer, Tshibangu, Wetterauer, & Wink, 2005). The flow of toxic compounds in the haemolymph or digestive tract is sufficient to make insects unpalatable to predators. In general, only a stage of the insect (mainly larvae) is protected. In the second, and more common type, the insect accumulates and often concentrates a toxic plant substance. This kind of antipredation strategy is known as *sequestration*, which includes, the selective uptake, transport, modification, storage and deployment of plant secondary metabolites for the insect's own defence (Heckel, 2014). Several studies indicate a relationship between sequestration and the degree of phytophagy specialization, showing that specialists sequester more efficiently than generalist insects (Dobler, 2001; Dyer, 1995; Lampert & Bowers, 2010; Lampert, Dyer, & Bowers, 2014). Mode and sites of accumulation are generally poorly known (Duffey, 1980; Petschenka & Anurag, 2016). Some authors assume the existence of cellular compartments comparable to plant vacuoles (Frick & Wink, 1995), while others hypothesize the existence of a balance between toxicity of chemical compounds and metabolic resistance of the insects. In addition, some insects are specialized in storing chemical compounds in glandular systems (Bowers, 1990). In this type of accumulation, there are three possible processes:

- The insect can sequester a plant substance that is toxic to predators without being affected by it, suggesting that the insect is resistant to the toxin (Scott, Liu, & Wen, 1998).
- More frequently, the insect can sequester a little or nontoxic precursor of a toxic substance. When attacked by a predator the precursor passes from an amorphous to a toxic state, often by air oxidation, similarly to action mode of some phytoalexins in plants (Nishida & Fukami, 1990).
- In few cases, the insect accumulates a chemical precursor from the host plant but performs one or more metabolic steps that transform this substance into a toxin against which it is resistant (Von Nickisch-Rosenegk & Wink, 1993; Wink & Legal, 2001; Wink, Legal, & von Nickisch-Rosenegk, 1998).

### 2.1.1 Example of Metabolism Excretion

The study by [Hundsdoerfer et al. \(2005\)](#) on the Spurge Hawk-moth, *Hyles euphorbiae* (Linnaeus, 1758) (Lepidoptera, Sphingidae), a common species in Europe, is a good illustration of such a situation. The sphingid moths are large nocturnal moths whose caterpillars often have bright colours and have the particularity to feed on very toxic plants such as Euphorbiaceae and Solanaceae ([Bernays & Janzen, 1988](#)). These bright colours associated with toxic compounds are called aposematism because they can inform the predators on the toxicity of potential prey. Certain chemical compounds found in Euphorbiaceae are phorbol esters which are among the most potent natural toxins known ([Goel, Makkar, Francis, & Becker, 2007](#)). Experiments were performed with caterpillars of *H. euphorbiae* to determine if phorbol ester compounds were sequestered and used as substances for defence against predators ([Hundsdoerfer et al., 2005](#)). Approximately 80% of the 12-tetradecanoyl-phorbol-13-acetate (TPA) was used for metabolism and the remaining 20% eliminated in the faeces. When TPA was directly injected into caterpillars, almost all of the TPA was found circulating into haemolymph and intestinal tracts. When attacked by a predator, caterpillars protect themselves by regurgitation of their food bowl filled with fragments of euphorbias and therefore still rich in TPA. Aposematic colour is well associated with a hazard for the predator, but it does not automatically mean a phenomenon of sequestration by prey, in the above case just a regular flux of toxin in the intestinal tract is sufficient to provide protection.

### 2.1.2 Example of Toxic Compounds Sequestration

Brassicaceae are rich in glucosinolates which are toxic compounds or at least antipalatable for many phytophagous. Larvae of the cabbage sawfly, *Athalia rosae* (Linnaeus, 1758) (Hymenoptera, Tenthredinidae), are rarely attacked by predators. It is not known if this species metabolizes (slow circulation strategy, see former case) or sequesters toxic compounds but the larvae, when attacked by a predator, produce small drops of haemolymph excreting it to the integument ([Müller et al., 2001](#)). This type of defence is called 'reflex bleeding'. It has been demonstrated that the larvae incorporate and concentrate glucosinolates produced by the host plant ([Müller et al., 2001](#)).

### 2.1.3 Example of Precursor Sequestration and De Novo Biosynthesis

This example is borrowed from the papers by [Laurent, Braekman, Daloz, and Pasteels \(2003\)](#) and [Laurent, Dooms, et al. \(2003\)](#). Among Chrysomelidae, there is a strong dependency on the chemistry of host plants. In many

cases, the compounds (pyrolizidic alkaloids, curcubitacines) come directly from the host plant with little or no changes. Some de novo synthesis have been described, and it is worth noting that the biosynthesis pathways of the various compounds produced by insects are very close or even identical to the pathways found in plants (Wink, 2016).

Some very recent advances suggest that horizontal gene transfer (HGT) may be at the origin of such similarities, with some complete genetic systems almost identical between bacteria/fungi/plants but also insects. These HGTs may be much more common than formerly suspected and represent a new and promising research theme (Wink, 2016).

Only few insects are able to perform for a same defence compound, both de novo biosynthesizes and sequestration from their food plant. The Burnet moth *Zygaena filipendulae* (Linnaeus, 1758) (Lepidoptera, Zygaenidae) is one of these rare examples. Its larvae alternate between de novo biosynthesis and sequestration of cyanide glucosides based on the ingested amount of plant-derived cyanide glycosides from the food-plant *Lotus corniculatus* L. (Fabaceae). Thereby, the de novo biosynthesis is associated with an apparent higher cost or reduced fitness compared to the sequestration from the food-plant (Fürstenberg-Hägg et al., 2014).

## 2.2 Energy Cost of Chemical Defence

The insect using plant toxics to defend itself against other insects faces a paradox. It is indeed itself basically susceptible to these substances since they act mostly on insect's basal metabolism. It must thus acquire at least a partial resistance to them. Various processes can be involved but all have an energy cost. A balance between the antipredation chemical and efficacy against predators is therefore subject to a negative trade-off. Several strategies aiming at minimizing the cost of this chemical defence are recognized.

- The energetically cheapest strategy is to accumulate products of low toxicity (Pasteels, Theuring, Witte, & Hartmann, 2003). A precursor of the plant toxin is generally drained by the Malpighian tubes of the digestive tract (Tsoupras, Luu, Hetru, Muller, & Hoffmann, 1983). Subsequently, in all known cases, the precursor can stay in the haemolymph or be accumulated in specialized glands. When staying in the haemolymph, the toxin will be produced by an open air oxidation of the precursor during an injury of the insect (Pasteels et al., 1990). A similar mechanism also exists in some cases when the precursor is stored in glands, but one (or a few) additive metabolic step can be necessary in

other cases to transform it into a toxin within the glandular tissues (Von Nickisch-Rosenegk & Wink, 1993).

- A more costly strategy is the direct sequestration of the plant toxin itself by the insect. Many hypotheses have been advanced for the storing of such substances. Organized granules are often visible in cells and some authors suspect the sequestration is stored in pseudovacuoles (Wink & Roberts, 1998). Thereby, the toxin is not directly in contact with the potential metabolic targets.
- Finally, some insects have an impressive armada of detoxification enzymes such as esterases and cytochrome P450, which allow a steady stream of toxins in the haemolymph without affecting the metabolism of the insect (Schuler, 1996). A continuous regulated enzyme activity must be balanced with the concentration of ingested toxins. In such cases, the insects are living on the most toxic plants and the host plant specificity is generally very high (Scott & Wen, 2001).

## 2.3 Modes of Action of Secondary Metabolites on Predators

According to its mode of action, the chemical defence of insects from predators are divided into three broad categories:

- Toxicity: The chemicals can irritate, injure, poison or drug the predators.
- Antiappetence: The defence is based on antipalatable compounds for predators, mainly products that are bitter for the predator's palate.
- Adherence and immobilisation: Products that adhere to the predators and immobilize them are involved.

### 2.3.1 Toxicity

We can subdivide the actions of the various families of molecules into two broad categories:

- Selective actions of defence molecules that act specifically on a chemical target by changing its configuration and metabolic function.
- Nonselective molecules that cause generalized metabolic disorders in predators.

In the first category, the defence molecules can have multiple targets depending on whether they have an amino group. The positive charged nitrogen can interact with the negative charged groups from glutamic or aspartic acids of proteins. In this way, defence compounds modulate the three-dimensional structure of proteins, inducing a loss or reduction of their metabolic activity, thus modifying the predator metabolism. Within the nonpolar substances without nitrogen, for example, terpenes, an association

with lipophilic molecules interferes (Wink, 2016 for review and references therein). In the second category, toxic molecules act mostly by changes in the permeability of cell membranes. Biomembranes are amphipathic consisting of a double layer of phospholipids which is impervious to a variety of external molecules. Within this structure, several types of proteins allow a selective passage of some molecules such as ion channels, transporters and receptors. Several types of toxic molecules such as terpenes, alkaloids and steroids may interact with these proteins, thus modifying the membrane permeability.

An example is given by Eisner et al. (2000), Peschke and Eisner (1987), Palmeira and Wallace (1996), Guo, Reigan, Siegel, and Ross (2008) and Cosby et al. (1976). The bombardier beetle, *Metrius contractus* (Eschscholtz, 1829) (Coleoptera, Carabidae), is capable of projecting on the predators a mixture of products, among them 1, 4-benzoquinone. This product has the advantage of being less volatile and more stable than 2-methyl-1, 4-benzoquinone that is the most common compound produced in other species of bombardiers. These authors have showed that not only the quinone but also the mix of hydrocarbons plays a role in defence against predators. These products were tested and they were shown to be repellent against the ant *Monomorium pharaonis* (Linnaeus, 1758) (Hymenoptera, Formicidae) and irritating on the cockroach *Periplaneta americana* (Linnaeus, 1758) (Blattaria, Blattidae). Using the mitochondria of rat liver, the same authors have showed that several anthraquinones induce a formation of nonspecific pores in the (cell or mitochondria) membrane. In addition, these products inhibit the action of nicotinamide adenine dinucleotide (NADH)-ubiquinone oxidoreductase. Also, Cosby et al. (1976) have demonstrated that naphthoquinones inhibit cancer cell growth. These quinones induce the oxidation of NADH, and one of the results is the blocking of the conversion of thymine preventing DNA synthesis.

### 2.3.2 Antiappetence

Insects have developed another defence strategy which consists in producing 'unpleasant' compounds that are repellent to the predators' palate. These compounds interact on the predator's chemical receptors and more specifically on deterrence receptors, informing of the unpalatable characteristic of the prey. Such compounds are found in various types of molecules: terpenes, alkaloids and quinones. A review on the different ways for a predator to recognize antipalatable preys was done by Glendinning (2007).

Eisner, Goetz, Hil, Smedley, and Meinwald (1997), González, Hare, and Eisner (1999), and González, Schroeder, Meinwald, and Eisner (1999) have shown that species of the genus *Photuris* (Coleoptera, Lampyridae) (called ‘femmes fatales’) attract males of another species of glow worms (of the genus *Photinus*) to consume them. The mode of attraction is to mimic sex pheromones. *Photuris* females not only consume males of other species but also assimilate their prey defence compounds, which consist of steroids (lucibufagines) that the predatory *Photuris* cannot produce. The *Photuris* females that have fed off *Photinus* males are repulsive for spiders of the genus *Phidippus* (Salticidae). Moreover, lucibufagine together with betaine is transferred by *Photuris* females to their eggs, inducing their ‘protection’. This mixture is also antipalatable for larvae of the ladybird *Harmonia axyridis* (Pallas, 1773) (Coleoptera, Coccinellidae) and ants of the species *Leptothorax longispinosus* (Roger, 1863) (Hymenoptera, Formicidae), but less effective against the Common Earwig, *Forficula auricularia* (Linnaeus, 1758) (Dermaptera, Forficulidae).

### 2.3.3 Adherent Products

Adherent products act in a mechanical manner to immobilize temporarily or permanently the predator. A variant of this strategy is to ‘paste’ the predators’ mandible or (sensilla) receptors. In some cases, these products (typically proteins, terpene resins and mixtures of hydrocarbons or long-chain waxes) are mixed with low molecular weight molecules that have the function of antiappetence (Betz & Kölsch, 2004).

Chen, Henderson, and Laine (1999), Quintana et al. (2003), and Dettner, Scheuerlein, Fabian, Schulz, and Francke (1996) have shown that, when termite soldiers *Coptotermes formosanus* (Shiraki, 1909) (Isoptera, Rhinotermitidae) are attacked by predators, they release a mixture of sticky products through their mandibles. This glue is composed of n-alkanes, mucopolysaccharides and long-chain fatty acids, mainly lignoceric and hexacosanoic acids. Other species of termites among the genus *Reticulitermes* (Isoptera, Rhinotermitidae) produce a sticky mixture mainly composed of terpenes: monoterpenes such as  $\alpha$ -pinene,  $\beta$ -pinene and limonene and a wide variety of sesquiterpenes. In the case of the collembolan, *Tetrodontophora bielanensis* (Waga, 1842) (Entognatha, Collembola), a sticky mixture is produced which induces disorientation and cleaning behaviour in the beetle *Nebria brevicollis* (Fabricius, 1792) (Coleoptera, Carabidae), allowing enough time for the collembolan to jump away.

## 2.4 Diversity of Chemical Defence Types

### 2.4.1 Defence Against Insect Predators

Only a small proportion of insects is specialized in predation of other insects (Table 1) but it is found in the largest insect orders such as Odonata, Heteroptera, Coleoptera and Diptera (e.g., asilids). Few specialist predators exist in Hymenoptera; they are mostly specialized in parasitism. Finally, a few Lepidoptera caterpillars are also entomophagous.

**Table 1** Main Insects and Insect Predators

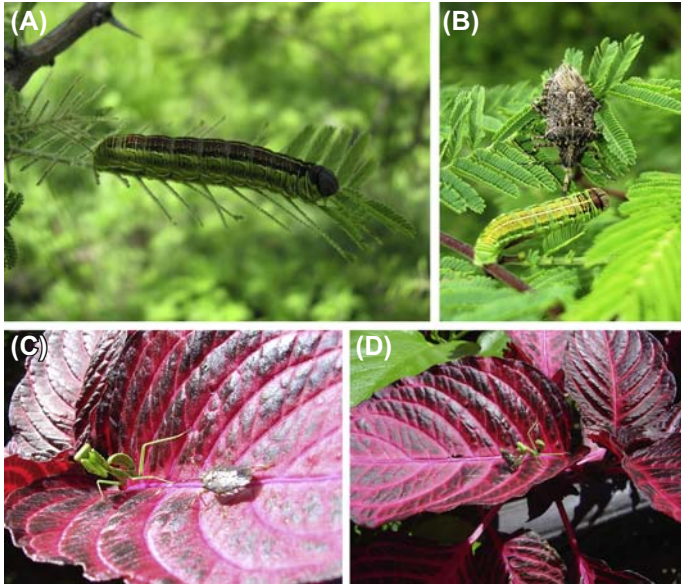
Order	Family	Name	Prey
Coleoptera	Cantharidae	Several genera	Small nectar-feeding
Coleoptera	Carabidae	<i>Pasimachus</i> sp.	Terrestrial insects
Coleoptera	Carabidae	<i>Cicindela</i> sp.	Terrestrial insects
Coleoptera	Coccinellidae	Several genera	Mites, aphids and mealy bugs
Coleoptera	Melyridae	Especially <i>Collops</i> sp.	Terrestrial insects
Diptera	Asiliidae	Several genera	Flying insects
Diptera	Cecidomyiidae	Especially <i>Aphidoletes</i> sp.	Especially aphids
Diptera	Dolichopodidae	Several kind	Small insects of wetlands
Diptera	Syrphidae	Several genera	Especially aphids
Dyctioptera	Mantidae	Several genera	Terrestrial insects
Heteroptera	Anthracoridae	Especially <i>Orius</i> sp.	Especially thrips
Heteroptera	Gerridae	Several genera	Aquatic insects
Heteroptera	Nabidae	Especially <i>Nabis</i> sp.	Phytophagous insects
Heteroptera	Pentatomidae	Several genera	Phytophagous insects
Heteroptera	Phymatidae	Especially <i>Phymata</i> sp.	Pollinators, bees
Heteroptera	Reduviidae	Several genera	Aquatic insects
Hymenoptera	Crabonidae	Especially <i>Eucercis</i> sp.	Flying insects
Lepidoptera	Lycaenidae	<i>Feniseca</i> , <i>Maculinea</i>	Aphids, ants
Neuroptera	Chrysopidae	<i>Chrysoperla</i> sp.	Phytophagous, aphids
Neuroptera	Corydalidae	Several genera	Aquatic and terrestrial insects
Neuroptera	Hemerobiidae	Several genera	Aphids
Neuroptera	Mantispidae	Several genera	Terrestrial insects
Neuroptera	Myrmeleotidae	Several genera	Especially ants
Neuroptera	Raphiidae	Especially <i>Raphidia</i> sp.	Mostly beetles
Odonata	All		Aquatic and terrestrial insects
Orthoptera	Tettigonidae	Several genera	Flying insects
Plecoptera	Mainly Perlodidae	Several genera	Aquatic insects

Most insect predators are generalists (Table 1). However, some are more specialized and feed off chemically protected insects. This is the case for beetles of the Coccinellidae family and the genus *Pasimachus* (Carabidae), and some Diptera such as the Syrphidae and the Cecidomyiidae. These predatory insects are part of a trophic network and in turn may become potential preys for top predators (mostly birds). A selective advantage of this specialization is the sequestration or, at least, the use of defence compounds of the preys, the toxic compounds of the plant passing to the predator via phytophagous feeding. An extreme case occurs when two predators are in competition. For example, the spotted ladybug beetle, *Coleomegilla maculata* (De Geer, 1775) (Coleoptera, Coccinellidae), and the chrysopid, *Chrysoperla rufilabris* (Burmeister, 1839) (Neuroptera, Chrysopidae) are predating on the same (chemically protected) aphid. When populations of the two predators are high, intraguild predation occurs between the two predators. Thereby first and second instars of the Coccinellidae are actively captured and consumed by chrysopid larvae (Lucas, Coderre, & Brodeur, 1997) (Fig. 1).

#### 2.4.2 Defence Against Noninsect Predators

Apart from insects, several organisms are insectivorous. Among them are arachnids, which are all predators of insects, many birds, reptiles, amphibians and some mammals. The case of bats will not be treated here, even though they are the main predators of nocturnal insects. Unlike predator insects, arachnids do not seem to sequester or synthesize defence substances. Arachnid venoms are mostly proteic and are not derived from chemical compounds of the host plants of their prey. Within arachnids, we can observe two broad strategies:

- The first is to build traps such as nets that are typically unselective. The main question is what to do with toxic preys which are caught in these traps. Our results and those described in the literature show that in model species such as *Nephila clavipes* (Leach, 1815) (Arachnida, Araneae), prey selection is done according to two main criteria: the size (compared to that of the spider) (Hénaut, Delmé, Legal, Williams, 2005) and the chemical defences (Lucas-Silva & Trigo, 2002). When some toxic preys are trapped [especially Lepidoptera Danainae, Ithomiinae, Heliconinae (all Nymphalidae)], they are placed by the spider in a sort of ‘trash can’ without consuming them. This ‘garbage’ is often the food supply of other spiders (referred to as kleptoparasites) such as *Argyrodes* (Hénaut et al., 2005), but also some lizards which, while feeding on this ‘trash’, can become prey of *N. clavipes*.



**Figure 1** How a praying *Mantis* can use a toxic nutrient source coming from a chemically protected insect? How to hunt a predator which detoxifies defence substances from an initial prey? *Baronia brevicornis* (Lepidoptera, Papilionidae) is the most 'primitive' species in the world. It is endemic to the Mexico. This butterfly lives on a highly toxic *Acacia cochliacantha*, Fabaceae) very rich in cyanogenic glucosinolates. This chemical defence (probably by sequestration) is ineffective against the predatory bugs (Heteroptera, Pentatomidae, *Brochymena* or *Parabrochymena* sp.). Although mantises are poisoned by this type of caterpillars, they are fond of their predators (which metabolize cyanogenic compounds). Indirectly, the praying *Mantis* can thus feed off not palatable preys. (A) Caterpillar, (B) Caterpillar eaten by a Pentatomide bug, (C) Mantis predate the same bug species, (D) Mantis eats the Pentatomide. Photos: L. Legal and J. Albre, Sierra de Huautla, Morelos, Center Mexico.

- Arachnids that hunt actively are more diverse. Some consume chemically protected insect species while others seem to avoid them. Most of time, diurnal species that using their vision appear to avoid toxic prey (Skow & Jakob, 2006), while the nocturnal species that locate their prey by vibration and/or chemical detection appears to be indifferent to the toxicity of the prey (Dor, Machkour-M'Rabet, Legal, Williams, & Hénaut, 2008).

Some birds specialize on one of the most toxic butterfly species, *Danaus plexippus* (Linnaeus, 1758) (Lepidoptera, Nymphalidae), also called the Monarch, an emblematic species in North and Central America. Every year, they migrate from Canada to Mexico (Brower, 1995; Zhu, H. et al., 2008). The mixture of cardiac glycosides and alkaloids from its host plants

(milkweed, *Asclepiadaceae*) makes this butterfly very toxic ([Malcolm & Brower, 1989](#); [Oyeyele & Zalucki, 2008](#)). Only traces of the toxins are accumulated in the wings at adult stage. Therefore, the continuous fluxes of toxins during the larval stage and from nectar of toxic plants eaten by adults are required to guarantee the defence. The toxins act on sodium channels which regulate the ouabaine levels ([Holzinger & Wink, 1996](#)). Two species of birds [*Icterus galbula* (Linnaeus, 1758) (Icterinae) and *Pheucticus melanocephalus* (Swainson, 1827) (Cardinalinae)] manage to pass the chemical barrier of defence of the butterflies. In the State of Michoacán/Mexico, it was estimated that 60% of predation of the monarch was carried out by these two species ([Fink & Brower, 1981](#)). The question is how these birds overpass the chemical defence of the monarch. Their learning behaviour through observation is exceptional. During migration, the rate of toxins in the insect body goes down when density of host plant availability decreases ([Fink & Brower, 1981](#)), and the birds learn to predate butterflies preferentially in places where the toxic plant is rare. In addition, the birds eat only the abdomen of the butterflies, where most defence substances have already been metabolized by the insect. Finally, the two bird species are partially resistant to cardiac glycosides and alkaloids of the insect. This case represents an extreme situation that combines coevolution and learning behaviour of the predators.



### 3. HOST PLANT MANIPULATION

Manipulation of plant development by insects results in improved nutritional value of plant tissues and/or nutrient access for insects. These changes have been interpreted as adaptations that address the mismatch between the nutrient status of unmodified host-plant tissues and the herbivore's requirements ([Giron, Huguet, Stone, & Body, 2016](#)).

#### 3.1 Insect-Induced Effects on Plants

##### 3.1.1 Remodelling From Ultrastructure to Anatomy

Gall-inducing insects are iconic examples of plant manipulation, with spectacular and complex tissue reorganization, sometimes resulting in new visually apparent plant organs within which the insect feeds and grows ([Mani, 1964](#); [Price, Waring, & Fernandes, 1986](#); [Shorthouse, Wool, & Raman, 2005](#)). In response to stimuli from the ovipositing mother and/or her offspring, host tissues usually dedifferentiate and gall development often involves a combination of cell division and growth ([Carneiro, Oliveira, &](#)

Isaias, 2014; Giron et al., 2016; Suzuki, Bedetti, & Isaias, 2015). Changes in cell ultrastructure also occur. For example, larval-induced nutritive cells in galls of the Hessian fly, *Mayetiola destructor* (Say, 1817) (Diptera, Cecidomyiidae), exhibit an increase in cytoplasmic staining and numbers of cellular organelles, along with development of numerous fragmented small vacuoles and endo-reduplicated or hypertrophied nuclei and nucleoli (Harris et al., 2006). Additionally, nutritive cells often have thin walls, presumably due to their developmental stage as well as insect-induced inhibition of cell-wall fortification and expansion. Thin walls facilitate the breakdown that releases cell contents to larvae of cynipid gall wasps (Hymenoptera) and cecidomyiid gall midges (Diptera) (Bronner, 1992; Harris et al., 2006; Rohfritsch, 1992). Most likely, however, harvest of the contents of nutritive cells by insects results from a combination of increased permeability of plant cell walls, enlarged plasmodesmata, high turgor pressure in the nutritive cells, mechanical action of larval mouthparts and possibly secretion and injection of proteases into cells by gall-inducing insects.

Modified plant tissues also are often supported by changes in vascular tissues which facilitate nutrient translocation towards the insect's feeding site (Rohfritsch, 1992; Stone, Schönrogge, Atkinson, Bellido, & Pujade-Villar, 2002; Wool, Aloni, Ben-Zvi, & Wollberg, 1999). Gall tissues act as a strong resource sink for photo-assimilates and can be associated with massive changes in plant growth, metabolism and investment (Giron et al., 2016; see Section 3.3.1).

### 3.1.2 Interaction With Primary Metabolism

Plants are often considered suboptimal food for phytophagous insects (Schoonhoven, Van Loon, & Dicke, 2005). Host manipulation offers the opportunity to alter the nutritional quality of the host plant by creating additional or novel feeding tissues, upregulating nutrient synthesis in situ or modifying source–sink relationships (Giron, Kaiser, Imbault, & Casas, 2007; Kaiser, Huguet, Casas, Commin, & Giron, 2010; Schwachtje & Baldwin, 2008; Stone & Schönrogge, 2003).

The ability to alter the physiological state of plant tissues, particularly of the cells adjacent to the feeding site, has been well described for a range of plant-manipulating arthropods (e.g., Abrahamson & Weis, 1987; Dardeau et al., 2015; Giron, Frago, Glevarec, Pieterse, & Dicke, 2013; Harris et al., 2006; Hartley, 1998; Larson & Whitham, 1991; Nability, Haus, Berenbaum, & DeLucia, 2013). Gall inducers, but also some leaf miners such as *Phyllonorycter blancardella* (Fabricius, 1781) (Lepidoptera,

Gracillariidae) are among the best examples of how plants can be manipulated to improve the nutrition they supply to insects (Giron et al., 2016). Induced nutritive tissues contain high levels of nutrients, including minerals, lipids, proteins, amino acids, sugars and/or starch (Bronner, 1992; Stuart, Chen, Shukle, & Harris, 2012). For example, some gall-inducing insects increase plant amino acid content through alteration of their synthesis and/or transport (Gündüz & Douglas, 2009; Zhu L. et al., 2008). Active transport of sugars towards the insect's feeding site is also frequently observed due, at least partially, to increased invertase activity, and glucose in excess can be transformed into lipids (Nabity et al., 2013; Rehill & Schultz, 2003).

### 3.1.3 Interaction With Secondary Metabolites

Besides offering imperfect nutrition, plants are suboptimal hosts because of a dazzling array of secondary metabolites, many of which harm insects (Schoonhoven et al., 2005). Insects have a number of strategies for dealing with these metabolites, including excretion, sequestration and degradation. As a fourth strategy, direct modulation of plant metabolism as a way to circumvent plant defences at source, has also been reported for several gall-inducing insect lineages, leaf miners and caterpillars that build leaf shelters (Lill & Marquis, 2007). Phenolic compounds, for example, are substantially lower in tissues close to the insect feeding site but accumulate at the periphery of host plant tissues infested by the woolly poplar aphid, *Phloeomyzus passerinii* (Signoret, 1875), some *Pontania* sawflies and of cynipid wasp galls (Dardeau, Deprost, et al., 2014; Ikai & Hijii, 2007; Nyman & Julkunen-Tiitto, 2000). Similarly, *M. destructor* and *P. blancardella* have also been shown to cope with plant defences by inhibiting phenylpropanoid pathways (Liu et al., 2007; Giron unpublished). A fifth strategy is to manipulate the plant, through mass attack, to overwhelm its production of secondary metabolites. This cooperative strategy is presented in Section 3.2.3.

Finally, phytophagous insects can also interfere with the plant's defence signalling pathways (reviewed in Guiguet et al., 2016). Interference of the corn earworm, *Helicoverpa zea* (Boddie, 1850) (Lepidoptera, Noctuidae) with early danger signalling by the plant suppresses glandular trichome production and inhibits expression of defensive genes regulated by jasmonic acid (JA) and ethylene (ET) pathways (Wu, Peiffer, Luthe, & Felton, 2012). Release of bacteria in the oral secretions of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say, 1824) (Coleoptera, Chrysomelidae), results in activation of a plant microbial defence response through induction of the salicylic acid (SA) pathway (Chung et al., 2013). This benefits the

caterpillar by leading, through negative cross talk, to downregulation of the JA-responsive antiherbivore response.

## 3.2 Mechanisms Involved in Plant Manipulation

### 3.2.1 Effectors

Oral secretions of insect herbivores are important recognition cues that can be used by plants as ‘elicitors’ of induced defences. Oral secretions also have important functions for herbivores as effector proteins having various functions, including, suppression of plant defence, alteration of plant development and manipulation of plant resources (Chung et al., 2013; Consales et al., 2012; Giron et al., 2016; Guiguet et al., 2016; Hogenhout & Bos, 2011). Information about the effectors used by herbivorous insects is just beginning to emerge (e.g., Giron et al., 2016; Zhao et al., 2016). In-depth functional molecular approaches are now required to determine the mechanisms that contribute to plant manipulation and to characterise a greater number of candidate effectors in a larger array of plant-manipulating species, possibly leading to identification of convergent mechanisms.

To date, the Hessian fly is the only gall-inducing insect with a sequenced genome as well as a researched salivary gland transcriptome and proteome (Chen et al., 2008; Zhao et al., 2015). It is also the only gall-inducing insect for which there are candidate genes having both elicitor and effector functions (Aggarwal et al., 2014; Zhao et al., 2015, 2016). Elicitor function, which benefits the plant, is better understood than effector function, which benefits the attacking larva. Hessian fly salivary proteins can function as elicitors because they can be detected by a plant surveillance system mediated by *resistance* (*R*) genes. Each *R* gene product detects the product of a particular Hessian fly *Avirulence* (*Avr*) gene in what is known as the ‘gene-for-gene’ interaction (Harris et al., 2003, 2015; Stuart et al., 2012). Detection triggers induced downstream defence responses, which kill the larva. These can be avoided if the larva has a mutation in its matching *Avirulence* gene (Aggarwal et al., 2014; Zhao et al., 2015, 2016). Presumably these mutations spread through populations under selection pressure from the *R* gene. Gene-for-gene interactions have also been documented for two other gall-inducing insects, the wheat midge, *Sitodiplosis mosellana* (Gehin, 1857) and the Asian rice gall midge, *Orseolia oryzae* (Wood-Mason, 1889) (Diptera, Cecidomyiidae), and also for several aphids that are not gall inducers (Harris et al., 2003, 2015). It is expected that plant parasites that exhibit gene-for-gene interactions (including microbes, insects and nematodes) produce effectors

to suppress the plant's basal immune systems and manipulate the plant to deliver better or more food (Jones & Dangl, 2006). It is not known how proteins encoded by the four Hessian fly candidate effector genes contribute to these two goals, although interference with downstream signalling and phytohormones seems likely (Aggarwal et al., 2014; Zhao et al., 2015, 2016). The Hessian fly's genome sequence points to the importance of effectors (Zhao et al., 2015). One-eighth of genes encode putative effectors. One of the effector gene families is the largest known arthropod gene family. Members have structural similarities with both bacterial effectors and the E3 ubiquitin ligases of plants. The authors proposed that Hessian fly effectors have proliferated as a result of an arms race with plant immune systems mediated by *Resistance* genes.

Emerging evidence suggests that plant-feeding insects use salivary effectors to interfere with 'early danger signals' of their hosts, deploying apyrases, calreticulins and peroxiredoxins in saliva (reviewed in Guiguet et al., 2016). Given links between these molecules and plant growth and defence, we propose that these effectors interfere with phytohormone signalling, and therefore have a special importance for plant-manipulating insects. More specifically, insect-derived apyrases act by degrading extracellular ATP released by the plant during wounding and insect feeding (Guiguet et al., 2016). Apyrases and/or an ATPase activity have been identified in the salivary secretions of several insect herbivores (reviewed in Guiguet et al., 2016).

### 3.2.2 Plant Growth Regulators

Experimental data support the role of phytohormones in plant manipulation (Bartlett & Connor, 2014; Giron et al., 2016; Tooker & Helms, 2014). Because auxins and cytokinins (CKs) lie at the very core of molecular mechanisms controlling the balance between the rate of cell division and differentiation, they have long been hypothesized to be involved in insect-induced plant manipulation. However, it is likely that plant defensive hormones such as jasmonic acid (JA), ethylene (ET), SA and abscisic acid (ABA) are also involved (Bartlett & Connor, 2014; Tooker & Helms, 2014; Zhang et al., 2016).

Insect salivary secretions and accessory oviposition gland substances applied to the plant can act directly on the plant's hormone biosynthesis, degradation, transport or signalling pathways to alter phytohormonal balance (Giron et al., 2016). Many organisms are also known to be able to synthesize these phytohormones *de novo* (especially auxins and CKs), and insect-associated symbionts may play a key role in

the production/delivery of phytohormones (Giron et al., 2013, 2016; Kaiser et al., 2010; Zhang et al., 2016).

In many plants, herbivory stimulates the production of JA and ET while other organisms stimulate the production of SA (Erb, Meldau, & Howe, 2012). Several lines of evidence suggest that plant-manipulating insects can counteract defences mediated by JA and SA. Hormones such as auxins and CKs can influence plant defensive responses (Erb et al., 2012; Giron et al., 2013). This hypothesis is consistent with data showing that several gall inducers and leaf miners induce increased levels of auxins or CKs in galls and mines, but fail to induce higher levels of JA or SA (Giron et al., 2016; Zhang et al. 2016).

### **3.2.3 Behaviour and Cooperation With Conspecifics**

Actual intraspecific cooperation (i.e., excluding dose-dependence effects) for the purpose of plant manipulation is only known in the particular case of bark beetles (Scolytinae). For most bark beetle species, establishment on a host tree requires mass attacks to overcome tree resistance, and there is a critical attack density threshold below which all attacks fail and above which they succeed (Berryman, 1976). The main mechanism of conifer defence against bark beetles is a hypersensitive reaction, which rapidly develops in the phloem and the outer sapwood adjacent to attack sites (e.g., Berryman, 1972; Reid, Whitney, & Watson, 1967). Tissues are invaded by terpenes and phenols, with this leading localized death, which renders tissues unsuitable for beetles. Because beetle attacks are generally completed in just a few days, the tree must rapidly synthesize large quantities of secondary compounds simultaneously at all attack points to achieve the concentrations needed to stop the aggressors. However, synthesis of such compounds is energy demanding. Each tree only has a limited quantity of energy. An important element of the beetle population strategy is thus to manipulate tree defensive activities by increasing the energy demand for syntheses through increasing the number of attacks (Berryman, 1972; Raffa & Berryman, 1983; Wood, 1982). Above a certain attack density, the tree becomes unable to build efficient defences at all aggression points, and the critical threshold is reached (Christiansen, Waring, & Berryman, 1987). This ‘exhausting tree defences’ or ‘intraspecific cooperative’ strategy (Lieutier, 2004) is typically enabled via aggregation pheromones emitted by pioneer beetles, allowing a rapid gathering of a large number of conspecifics (Wood, 1982). After its defences are exhausted, the tree, no longer able to stop beetle brood development or invasion by the various types of organisms introduced by the beetle, finally dies.

The energy that the tree is able to rapidly mobilize depends on its genotype and physiological status. The critical attack density threshold thus depends on tree genotype and physiological conditions, as well as beetle aggressiveness. Threshold values range from 50 to 850 attacks per m<sup>2</sup> of bark (Lieutier, Yart, & Sallé, 2009). Whether such intraspecific cooperation is at play in other plant-manipulating systems awaits further investigations. There are other species whose colonization is characterized by coordinated attacks by large numbers of individuals, e.g., the horse-chestnut leaf miner, *Cameraria ohridella* (Deschka & Dimic, 1986) (Lepidoptera, Gracillariidae) (Lees, Lopez-Vaamonde, & Augustin, 2011).

### 3.2.4 Cooperation With Other Organisms

Microorganisms have been shown to be important ‘hidden players’ in insect–plant interactions (e.g., Gutzwiller, Dedeine, Kaiser, Giron, & Lopez-Vaamonde, 2015; Sugio, Dubreuil, Giron, & Simon, 2015; see chapter: Influence of Microbial Symbionts on Plant–Insect Interactions by Giron et al., 2017 for details) and can affect many insect traits, including their ability to manipulate plant physiology for their own benefit (Kaiser et al. 2010; Sugio et al. 2015). Insect symbionts can directly or indirectly affect the plant by interfering with plant signal transduction pathways or by altering plant primary and secondary metabolism (Body, Kaiser, Dubreuil, Casas, & Giron, 2013; Giron et al. 2013; Sugio et al. 2015; Zhu, Poelman, Dicke, 2014).

In many conifer bark beetle species that attack live trees, the remarkable intraspecific cooperation that leads to attack success (see Section 3.2.3) is made even much more efficient through cooperation with fungi, which also elicit the tree’s defences (Lieutier et al., 2009). In fact, a complex community of organisms is present in the beetle galleries, including several species of fungi, yeasts, bacteria, mites and nematodes (Hofstetter, Dinkins-Bookwalter, Davis, & Klepzig, 2015). These organisms interact among each other as well as with beetles and the tree. The role of fungi in stimulating the tree’s defences during bark beetle attack seems now recognized in several bark beetle–fungi associations (Hofstetter et al., 2015; Lieutier et al., 2009). Information regarding other groups is, however, very limited.

#### 3.2.4.1 Fungal Contribution to Manipulating Tree Defences

Most bark beetle species are associated with and carry spores of Ophiostoma-toid fungal species mainly of the *Ophiostoma*, *Ceratocystis*, *Ceratocystiopsis* and *Grosmannia* genera and the related anamorph *Leptographium* (Kirisits, 2004;

Six, 2012). In addition to the contribution of fungi to exhausting tree defences, beetles can benefit from improved nutrition through mycophagy or modification of phloem substrate (e.g., Klepzig & Six, 2004). For fungi, the obvious benefit is the transportation that beetles provide. The added stimulation of the tree's defences provided by fungi can be measured by comparing, on a same tree, the development of the hypersensitive reaction around beetle galleries with or without fungi (Lieutier, Garcia, Yart, & Romary, 1995). The tree devotes more energy to defence when fungi are present. An immediate benefit for the beetle is a lowering of the critical attack density threshold. This can mean the difference between colonization success and failure, as is the case of the southern pine beetle, *Dendroctonus frontalis* (Zimmermann, 1868) (Coleoptera, Curculionidae) (Bridges, Nettleton, & Conner, 1985).

#### 3.2.4.2 Modulation of the Fungal Contribution to Manipulating Tree Defences

Efficiency of the beetle–fungus association to stimulate the tree's defences varies depending on fungal species, as well as isolates of the same species (Lieutier, Yart, Ye, Sauvard, & Gallois, 2004). For some bark beetle species, their fungal associates participate in the stimulation of tree defences but also can invade the phloem, making it unsuitable for larvae (Klepzig & Six, 2004; Paine, Raffa, & Harrington, 1997; Six & Paine, 1998; among others). Why these fungal species have not been selected against may be explained by a trade-off between the benefits the insect gains from the fungus helping to counter plant defence versus the losses the insect suffers because of the reduced availability of larval feeding sites (Lieutier et al., 2009). In the case of *D. frontalis*, complex interactions among fungal species can occur. For instance, an *Entomocorticium* sp. is able to stop the development of *Ophiostoma minus*, a species involved in host defence stimulation. Consequently, *O. minus* cannot reach the phloem used by larvae and do not compromise their survival (e.g., Klepzig & Six, 2004).

Experimental observations strongly suggest that bacteria may interfere, positively or negatively, in tree defence manipulation by ophiostomatoid fungi. A diverse set of bacteria inhabits beetle galleries. *In vitro* bioassays have showed that some are able to stimulate or inhibit fungal growth, alone or in combination with host tree compounds (Adams, Currie, Cardoza, Klepzig, & Raffa, 2009). For example, the mycelial growth of *Grosmannia clavigera*, a fungus associated with the mountain pine beetle, *Dendroctonus ponderosae* (Hopkins, 1902) (Coleoptera, Curculionidae), known to strongly

stimulate the hypersensitive reaction of pine, is favoured by a combination of *Pseudomonas* and racemic alpha-pinene, whereas the mycelial growth of *Ophiostoma ips*, an associate of several *Ips* species, appears less favoured. Fungal reproduction can also be stimulated by bacteria, especially in the case of beetles that are adapted to successfully attack living trees having vigorous defences (Adams et al., 2009). In the *D. frontalis* system, bacteria are able to produce selective antibiotics that strongly inhibit *O. minus* (Scott et al., 2008).

### 3.3 Outcomes of the Interaction

#### 3.3.1 Consequences for Plant Vigour and Survival

In most cases plant-manipulating insects are considered to be parasites, that is, they harm but do not kill their hosts (Stone & Schönrogge, 2003). However, in some systems, the host plant may reap benefits from the modifications of its tissues. For instance, eucalypts colonized by *Leptocybe invasa* (Fisher & La Salle, 2004) (Hymenoptera, Chalcidoidea) have an increased tolerance to cold (Rocha et al., 2013). The interaction can also secondarily evolve into a mutualistic relationship (see Section 4.2 for example).

While manipulation is typically expected to have a limited impact on the vigour or survival of the plant, there are clearly interactions where the plant's survival and fitness is drastically affected. The strategy of defence exhaustion of bark beetles is an extreme situation, which generally results in host plant death inasmuch as the plant is no longer able to control herbivores and pathogens (see Section 3.2.3). Gall induction can also have drastic effects on plant survival (e.g., Dardeau, Deprost, et al., 2014; Harris et al., 2015). When attacked by Hessian fly larvae, seedling plants could die, presumably because the creation of the larval-induced nutritive tissue 'starves' younger leaves of resources needed for cell growth (Anderson & Harris, 2006; Harris et al., 2006). A similar process probably impedes bud break of poplars previously infested by *P. passerinii* (Dardeau et al., 2015; Sallé unpublished). The differentiation of novel organs, or misshaping of preexisting ones, can dramatically alter the metabolism and anatomy of host plant tissues and compromise their initial function. For instance, galls induced in root systems and/or stems can interfere with uptake of nutrients and conduction of water or sap, resulting in partial or total plant stunting (Brown, Glenn, & Wisniewski, 1991; Granett, Walker, Kocsis, & Omer, 2001). Likewise, host-plant fitness can be sharply reduced by galls affecting the differentiation of reproductive organs and

preventing seed production (e.g., Harris et al., 2003; Post, Kleinjan, Hoffmann, & Impson, 2010). Modification of within-plant allocation of carbohydrates and nutrients can lead to similar outcomes. Plant-manipulating insects often turn their feeding sites into physiological sinks, drawing nutrients and photo-assimilates from surrounding tissues (see Section 3.1). The manipulated tissues therefore compete with natural plant sinks, like buds or catkins (Larson & Whitham, 1991, 1997). This can delay flowering and reduce seed viability, affect growth patterns or survival of plant modules and even modify the architecture of the host-plant (e.g., Kurzfeld-Zexer, Wool, & Inbar, 2010; Marini-Filho & Fernandes, 2012).

### 3.3.2 Costs and Benefits for the Insects

Plant manipulation can result in optimization of the nutritional value of host-plant tissues (Hartley & Lawton, 1992; Price, Fernandes, & Waring, 1987): this is the *nutrition hypothesis*. Such benefits have been described for gall inducers (Giron et al., 2016) and other plant-manipulating insects, such as aphids inducing chlorotic lesions (Sandström, Telang, & Moran, 2000), caterpillars that build leaf shelters (Lill & Marquis, 2007) and leaf miners (Kaiser et al., 2010). This is generally achieved through an optimization in nutrients and/or secondary metabolites (see Section 3.1) and enhances larval development, fecundity and survival (e.g., Dardeau, Pointeau, et al., 2014; Kaiser et al., 2010; Lill & Marquis, 2007). For the leaf miner *P. blancardella*, manipulation also maintains nutrient-rich green tissues and creates an enhanced nutritional microenvironment in leaves which are otherwise senescing (Body et al., 2013; Giron et al., 2007). Behavioural benefits may also be reaped from plant manipulation, and higher acceptance rates, and optimized probing and feeding behaviours have been reported from insects feeding on manipulated tissues (Dardeau, Pointeau, et al., 2014; Kaiser et al., 2010). These benefits, together with an increased development rate, could shorten the exposure of plant-manipulating insects to adverse biotic and abiotic factors (Dardeau, Pointeau, et al., 2014).

Plant manipulation could also shelter insects from adverse abiotic conditions, particularly desiccation (Price et al., 1987; Stone & Schönrogge, 2003): this is the *microenvironment hypothesis*, which is relevant for partially or totally enclosing galls, leaf mines, and leaf shelters (Lill & Marquis, 2007; Pincebourde & Casas, 2006; Stone & Schönrogge, 2003). Abiotic conditions within plant ‘shelters’ can differ sharply from ambient conditions in terms of temperature, relative humidity, solar radiation and wind exposure (Lill &

Marquis, 2007; Price et al., 1987; Stone & Schönrogge, 2003). Insects develop in moister conditions than they would in ambient air and are therefore protected from drought. Leaf temperature modulation by leaf miners, through a manipulation of leaf absorbance and stomatal conductance, can also increase the development of caterpillars and shorten their exposure to parasitoids (Pincebourde & Casas, 2006).

Manipulation may also protect plant-manipulating insects from natural enemies, decreasing detection by predators, preventing attacks and/or recruiting protecting allies (Lill & Marquis, 2007; Price et al., 1987; Stone & Schönrogge, 2003): this is the *enemy hypothesis*. Intraspecific variation in some gall traits such as increased hardness and thickness of gall tissues, external coatings with hairs and recruitment of ant guards with nectar secretions can be associated with increased survival of gall inducers (Stone & Schönrogge, 2003).

Finally, plant manipulation can also offer an opportunity to *escape from intraguild competition* and/or *limit exploitation of the same host plant* by other herbivores and pathogens (Giron et al., 2016). For example, host defence exhaustion through intraspecific cooperation and association with Ophiostomatoid fungi allows the establishment of insects in vigorous trees, while most bark beetle species are only able to colonize dead or decaying trees. However, mass attacks, especially those that occur on vigorous trees for which the critical threshold of attack density is high, may result in intense intraspecific larval competition impacting the productivity and the quality of offspring (Sallé & Raffa, 2007). In addition, cooperation with microorganisms can also result in interspecific competition between offspring and particular inoculated fungi (see Section 3.2.4.2).

### **3.3.3 Modulation of Plant Manipulation**

#### **3.3.3.1 Host-Related Factors Including Host Resistance**

The physiological status of the host plant can have different outcomes on plant–insect interactions, depending on the manipulation strategy considered. In the bark beetle strategy of host defence exhaustion, the critical threshold of attack density depends on the amount of energy that can be mobilized by the host tree. Consequently, this threshold, and therefore the host resistance level, positively correlates with host vigour (Lieutier et al., 2009; Raffa & Berryman, 1983). On the contrary, the abundance and performance of gall-inducing insects often correlates with the size of the manipulated plant module, or more generally with host vigour (Koricheva, Larsson, & Haukioja, 1998; Quiring, Flaherty,

Johns, & Morrison, 2006). In this regard, gall inducers fit the predictions of the plant vigour hypothesis (Price, 1991; Quiring et al., 2006). There are several exceptions to this general pattern though, and negative, parabolic or nonsignificant relationships between plant module size and the abundance and performance of gall-inducing insects have also been observed (Quiring et al., 2006). An alternative hypothesis, the *optimal module size hypothesis*, predicts that gall-inducer performance will be enhanced on intermediate-sized plant modules (Björkman, 1998; McKinnon, Quiring, & Bauce, 1999). Fast-growing and large plant modules may alter the performance of gall inducers because of higher competition among plant and insect-induced sinks. In addition, in such plant modules the induction stimulus could be excessively diluted, which would compromise the success of manipulation (Björkman, 1998; McKinnon et al., 1999).

Host-manipulating insects also maintain complex interactions with the endophytic fungi inhabiting the tissues of their host plants. The profile of fungal endophyte communities is modified within manipulated tissues because of their anatomical, biochemical and physiological remodelling (Lawson, Christian, & Abbot, 2014). Depending on the systems investigated, the endophytic fungi may have positive, negligible or antagonistic effects on the development and survival of leaf miners or gall inducers and may also alter the spatial and temporal distribution of the insects on their host plant (Raman et al., 2012).

### 3.3.3.2 Site-Related Factors

Environmental factors affecting host growth and vigour can modulate the ability of an insect to manipulate its host. When manipulation requires a reconfiguration of host metabolism or anatomy, host-manipulating insects are predicted to be adversely affected by environmental constraints affecting plant growth, such as water deficit, which could impair the initiation and growth of manipulated tissues (e.g., Koricheva et al., 1998). Nonetheless, environmental constraints could also enhance the manipulation success in resistant host plants, in situations where the constraints interfere with resistance mechanisms, while still allowing a reconfiguration of primary metabolism by the insect (e.g., Björkman, 1998). This emphasizes that both constraint intensity and host genotype can affect the outcome of an environmental constraint on plant manipulation. Similarly, depending on the study system, environmental conditions promoting plant growth and nitrogen content in plant tissues can have very different effects on the success

of plant manipulation, which might be further modulated by interactions with the host plant genotype (e.g., Dardeau et al., 2015; McKinnon et al., 1999). When manipulation is favoured by reduced host vigour, as for host defence exhaustion, environmental constraints are generally predicted to promote the establishment and development of insects (e.g., Koricheva et al., 1998). However, in agreement with the growth differentiation balance hypothesis (Herms & Mattson, 1992), constraint intensity might modulate these predictions since a mild water shortage can enhance host resistance (Sallé, Ye, Yart, & Lieutier, 2008).



## **4. MUTUALISM: A RESULT OF COEVOLUTION? GENETIC AND FUNCTIONAL ASPECTS**

### **4.1 Pollination Mutualisms**

While insect–plant interactions often involve antagonism, because the insects eat the plants, there are also important cases of mutualism, in which both insect and plant benefit from the interaction, e.g., in seed dispersion or leaf/bud protection by ants. However, a much wider category of mutualism, of considerable ecological and evolutionary significance, involves insect pollination of plants. Perhaps 90% of angiosperms are pollinated by animals, with insects playing the largest role. Insects typically benefit from the interaction by gaining food from either pollen itself and/or nectar. The plants benefit because insects vector their pollen to conspecifics and bring the pollen of conspecifics to their ovaries. Another form of interaction that might be regarded as indirect mutualism involves emission of volatile organic compounds by plants under attack by herbivores, leading to recruitment of parasitoids that attack the herbivores.

#### **4.1.1 From Generalists to Specialists**

Insect pollination has evolved many times and takes many different forms, involving more than 20,000 species of bees, wasps, flies, beetles, moths and butterflies and thrips. The best-known pollinators are probably honey bees, *Apis mellifera* (Linnaeus, 1758) (Hymenoptera, Apidae), whose activities are crucial to human agriculture. Both wild and managed pollinators have a globally significant role in crop pollination, although their relative contributions differ according to crop and location (IPBES, 2016). In addition, beekeepers manage hives to provide pollination services to commercial growers, e.g., the massive almond crop in California. Honeybees are highly generalist (polylectic) pollinators and may visit a wide variety

of plant species, although a particular hive at a given time and place may be far more specialized. Wild bees in general, with perhaps 10,000 species globally, are a hugely important group of pollinators. Many species are polylectic, such as the honeybee, but other oligolectic species visit only a restricted range of plants.

Finally, some pollinators may be strongly or strictly associated with a single plant species. One system involves the *Ophrys* orchids in the Mediterranean region that mimic female bees, using both chemical and visual cues, deceiving male bees into acting as pollen vectors (Schatz, Hossaert-McKey, & Kjellberg, 2013). This pollinator attraction without nectar is a clear case of manipulation and useful to keep in mind when considering other cases of mutualism, because it emphasizes that the evolutionary interests of insect and plant are separate and may not be well aligned. Floral morphologies can also select for pollinator specialization. Deep corollas and long spurs of flowers oblige insect visitors to be equipped respectively by a long tongue or by a trunk (only in Lepidoptera) to locate nectar and then become pollinators.

We have established that insect pollinators vary from host plant generalists to specialists. An active research field in the last decade has involved the study of pollination networks, i.e., networks linking a community of plants to a community of insect pollinators at a particular site. This can help reveal many interesting aspects, including the number of different insect species visiting a given plant species and the number of plants visited by a given pollinator species. Such networks can also be summarized statistically in terms of aspects such as linkage and connectance, as has been done extensively for trophic food webs. As a result, they allow to identify species acting as ‘hubs’ by being central in the organization of such pollination networks while other species are more peripheral (Bascompte & Jordano, 2007).

In cases where there is low plant–pollinator partner specificity, the associations may be diffuse and involve potentially complex mixtures of costs and benefits. For example, it is beneficial to plants for insects to carry pollen to or from another conspecific plant. However, if the insect carries pollen to or from a heterospecific plant, this wastes pollen/ovules or produces hybrid offspring (Neiland & Wilcock, 1999). In addition, pollinators can also vector plant sexual diseases such as fungi or various pathogens. Variations in the quality and quantity of resource provided by plants, and in the activity and capacity of insects to transport pollen, lead to a great diversity of pollination situations, linked to various costs/benefits and partner specificities.

In cases with high partner specificity, a given insect species always interacts with a given plant species, which provides the opportunity for strong plant–insect coevolution with species-specific costs/benefits and mechanisms. In cases such as the sexually deceptive orchid, there may be strong evolutionary forces but the interaction is not a mutualism, since the plant exploits the insect without reward. However, a major class of plant–pollinator interactions with high partner specificity is characterized by mutualism; these are obligate pollination mutualisms (OPMs) involving insects whose larvae are seed predators.

#### **4.1.2 Overview of Obligate Pollination Mutualisms**

OPMs are highly specialized species interactions in which both the plant and the pollinator depend upon the partner species for successful reproduction and, for the insects, offspring survival. The most famous case involves fig trees (*Ficus*) and fig wasps (see below). However, another well-known example involves yucca plants and moths, and a dramatic recent discovery in 2003 was the existence of OPMs involving hundreds of plants in the family Phyllanthaceae (especially the genus *Glochidion*) and small moths in the genus *Epicephala*. Table 2 lists known cases of OPMs but it is likely that the novel systems remain to be discovered, even in other plant families.

In general the insect pollinators involved in OPM's transport pollen between male and female flowers of a single plant species. This high specificity is obviously beneficial to the host plant in reducing the production of hybrid offspring and wastage of pollen or ovules through crosses with gametes from other plant species. In some OPMs (e.g., the *Yucca* and *Glochidion* systems) the insects have evolved specialized behaviours to affect active pollination. This is in stark contrast to most insect pollination, which occurs passively as a by-product of insect foraging. OPM pollinators typically lay eggs within at least some of the ovules that they fertilize and pollinator offspring develop by feeding on one or more of the plant seeds, leading to the term 'nursery pollination systems'.

The pollinator offspring develops only in the host plant seeds and the pollen is transported only by adults of the same insect species. Consequently, there is obligate reproductive interdependence of the partners. However, as in other mutualisms, their evolutionary interests are not perfectly aligned and partnership brings both costs and benefits; some plants, as in *Yucca* and *Glochidion*, may selectively abort flowers or inflorescences when too many pollinator eggs are laid in them. An obvious avenue for conflict is the number of seeds that pollinator offspring eat and a considerable amount

**Table 2** Obligate Pollination Mutualisms Involving Insects and Plants, With an Indication of the Approximate Number of Plant Species

Plants (Family, Genus)	No. of Species	Pollinators (Family, Order)	References
Agavaceae: <i>Yucca</i> , <i>Senita</i>	Ca. 50	<i>Yucca</i> moths (Lepidoptera: Proxodidae)	Pellmyr and Huth (1994), Svensson et al. (2005), and Svensson, Pellmyr, and Raguso (2006)
Araceae: <i>Peltandra</i>	Ca. 50	<i>Elachipetra</i> (Diptera: Chloropidae)	Patt et al. (1992)
Arecaceae: <i>Chamaerops</i>	Ca. 200	<i>Derelomus</i> (Coleoptera: Curculionidae)	Dufay, Hossaert-McKey, and Anstett (2003, 2004)
Caryophyllaceae: <i>Silene</i> , <i>Dianthus</i> and <i>Saponaria</i>	Ca. 50	<i>Hadena</i> (Lepidoptera: Noctuidae)	Jürgens, Witt, and Gottsberger (2002, 2003), Dötterl, Burkhardt, Jürgens, and Mosandl (2007), Dötterl et al. (2006), and Gimenez-Benavides, Dötterl, Jürgens, Escudero, and Iriondo (2007)
Eupomatiaceae: <i>Eupomatia</i>	1	<i>Elleschodas</i> (Coleoptera: Curculionidae)	Bergström et al. (1991)
Moraceae: <i>Ficus</i>	>750	Fig wasps (Hymenoptera: Agaonidae)	Chen and Song (2008), Proffitt et al. (2009), and Hossaert-McKey et al. (2010)
Phyllanthaceae: <i>Breynia</i> , <i>Glochidion</i> and <i>Phyllanthus</i>	Ca. 500	<i>Epicephala</i> (Lepidoptera: Gracillariidae)	Kato, Takimura, and Kawakita (2003) and Okamoto, Kawakita, and Kato (2007)
Ranunculaceae: <i>Trollius</i>	1	<i>Chiastochaeta</i> flies (Diptera: Anthomyiidae)	Ibanez et al. (2010) and Lemke and Porembski (2013)
Zamiaceae: <i>Zamia</i> and <i>Macrozamia</i>	Ca. 10	<i>Cycadothrips</i> (Thysanoptera: Aeolothripidae), <i>Tranes</i> (Coleoptera: Curculionidae)	Terry et al. (2004) and Terry, Walter, Moore, Roemer, and Hull (2007)

of research has been carried out in OPM systems towards understanding this fundamental problem (Dufaÿ & Anstett, 2003; Jaeger, Till-Bottraud, & Després, 2000).

In these OPMs, the chemical message emitted by the host plant plays a role in maintaining species specificity with the pollinator, thanks to quantitative and qualitative differences in relative proportions of both major and minor volatile organic compounds emitted by host plants (Raguso, 2008). Moreover, scents also provide information on developmental stage, particularly on whether the plant is receptive and ready to be pollinated (Hossaert-McKey, Soler, Schatz, & Proffitt, 2010). The host plant scent signal must be specific to attract its specific and obligate partner and permit the required tight coordination and synchronization of their phenologies. Scent also supports various forms of intraspecific variation (dioecy, phenological stages, postpollination) and may be also used by the third actors to exploit these mutualisms. In the system with most data available on floral scent (figs and fig wasps), the message responsible for pollinator attraction is usually constituted by a species-specific blend of compounds, generally dominated by one or a few common terpenoids, the identity of which differs among sympatric species (Chen et al. 2009; Proffitt et al. 2009).

## 4.2 The Fig/Pollinator Mutualism

Figs and fig wasps comprise the most famous OPM; indeed, knowledge of the life cycle of the fig–wasp interaction is essential for the traditional cultural practice of caprification with the common edible fig *Ficus carica* L. This involves removing small branches from trees with fruits emitting wasps and securing them to branches of other trees bearing receptive figs awaiting pollinators. Cultivation of *F. carica* in the Mediterranean region represents one of the earliest forms of agriculture, dating back perhaps 4000 years, but different species of figs (*F. pumila*) have also long been cultivated in China.

### 4.2.1 Origin, Diversity, Biogeography

Recent research has led to independent dated molecular phylogenies for fig trees and their associated pollinating wasps (family Agaonidae), suggesting a single origin of the mutualism approximately 75 million years ago (Cruaud et al., 2012), followed by radiation to produce more than 750 fig species, with a somewhat larger number of pollinator species. Globally, figs and fig wasps are found throughout the tropics and some other warmer parts of the world. The genus *Ficus* is of considerable importance in rainforests throughout the tropics and one of few genera of plants to be of high

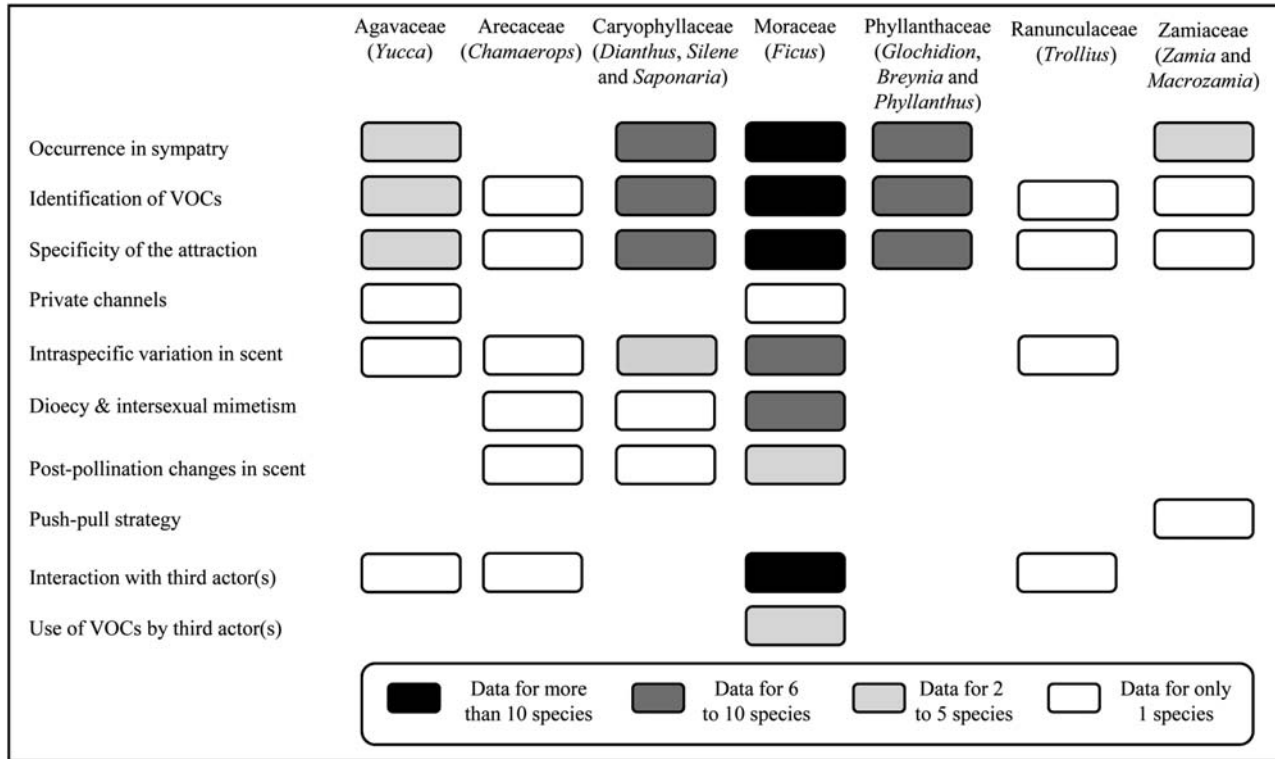
ecological and evolutionary significance on all tropical landmasses (Harrison, 2005). Rainforest figs have a number of different growth forms, including hemi-epiphytes or ‘stranglers’, but also free-standing trees, banyans, creepers and understory shrubs. Figs are also important in many savannah habitats, where two important life strategies are rock splitters (lithophytes) typically growing on boulders on rocky outcrops, and free-standing trees that grow along the banks of seasonal watercourses.

Figs are classified in one large genus *Ficus* (subdivided into 6 subgenera and about 20 sections), whereas their pollinators have family status as the Agaonidae with about 20 genera. To a first approximation, pollinator genera match with *Ficus* sections. For example, section *Americana* is pollinated by wasps in the genus *Pegoscapus* and section *Malvanthera* by *Pleistodontes* wasps, which reflects their underlying history of cospeciation. Nevertheless, taxonomic and phylogenetic analyses also provide evidence for some recent and even ancient host shifts by wasps to different fig taxa. In addition, some fig lineages in Africa, support two or more pollinator that each seem to be coradiating with the figs (McLeish & van Noort, 2012).

Fig sections and their associated wasp genera provide a useful taxonomic level for considering the biodiversity and biogeography of the mutualism. For example, only two fig sections occur naturally in the New World—the large *Americana* with >100 species and smaller *Pharmacosycea* with about 40 species. The former has active pollinators and a diversity of plant species, while the latter is a small radiation of free-standing trees associated with passive pollinators. Diversity is higher in the Palaeotropics and especially in Australasia with >500 species. Most *Ficus* sections have restricted geographic distributions, often in only one continent, but a few like *Urostigma* are distributed widely in the Old World.

#### 4.2.2 Monoecy, Dioecy and How to Protect Seeds

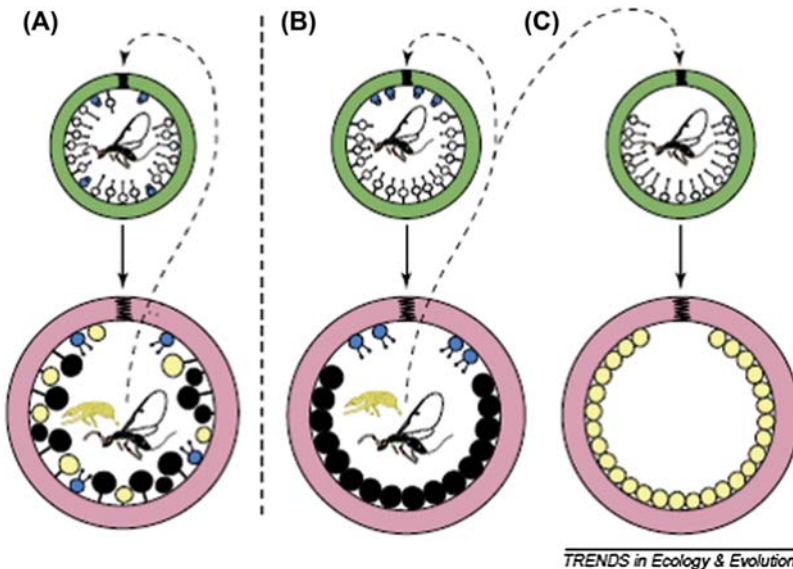
An important aspect of fig diversity is the distinction between monoecious and functionally dioecious species (Fig. 3). In monoecious species all trees produce the same kind of figs, but dioecious species have two kinds of tree (functionally female or male) that specialize in producing either seeds, or pollen and wasps. In dioecious figs, when female wasps enter the fruits of male trees they are able to lay eggs in the flowers by pushing their ovipositors down the short styles of the individualized female flowers and placing the egg in the plant ovule. The wasp larva hatches and feeds on the plant tissue produced by the single fig ovule, completing its whole development inside one flower. Typically only a few female wasps enter each fig to lay



**Figure 2** Diagram summarizing knowledge of nursery pollination interactions in which chemical mediation has been described. *Updated from Hossaert-McKey, M., Soler, C., Schatz, B., & Proffitt, M. (2010). Floral scents: their role in nursery pollination mutualism. Chemoecology, 20, 75–88. <http://dx.doi.org/10.1007/s00049-010-0043-5>.*

eggs but tens to hundreds of wasp offspring (dependent on species) develop in each fig. When they reach maturity they hatch and mate inside the fig before the females disperse to find new receptive figs to enter. At the time when the wasps are hatching individualized male flowers are also maturing inside the fig. Some fig wasp species are active pollinators—the females deliberately use brushes (coxal combs) on their legs to collect pollen into thoracic pollen pockets. In others, whose host figs liberate pollen inside the fig, there is no such behaviour and pollen is carried passively on the body, as in other insects.

After mating and collecting pollen, adult female wasps disperse through holes in the fig wall chewed by the wingless male wasps, which die soon afterwards. Female wasps now search for and enter receptive figs. If they enter a fig on a male tree, the life cycle repeats as described above. However, if they enter a fig on a female tree, the wasps are able to pollinate the flowers but unable to reproduce themselves, because the flowers have much longer styles, preventing them from laying eggs in the necessary place for successful offspring development. Facing the underlying conflict over the reproductive



**Figure 3** Figs develop from small receptive forms (green) to larger ripe ones (pink). In monoecious species (A) all figs are essentially the same and produce both wasps (black) and seeds (yellow). In dioecious species, male figs (B) give rise only to wasps, whereas female figs (C) nurture only seeds and contain no male flowers (blue) (Cook & Rasplus, 2003).

fate of fig flowers, the plants are selected to produce both seeds and wasps (to carry their pollen). However, short-term natural selection will favour wasps that maximize offspring production without setting aside some flowers for seed production. This conflict must be stabilized for long-term persistence of the mutualism. In the case of dioecious figs, the plants appear to be in control because they lure female wasps into female figs, where they cannot lay eggs. Intersexual mimicry through fig chemical cues contributes to this plant control of the conflict situation (Soler, Proffitt, Bessiere, Hossaert-McKey, & Schatz, 2012). In *F. carica*, a particular form of seasonality also ensures that many adult female wasps are emerging at a time when the vast majority of available receptive figs are female.

However, over half of all fig species are monoecious, and every fig tends to produce both seeds and wasp offspring. In some respects this makes things simpler: searching female wasps can enter any receptive fig of the right species to lay eggs. However, it makes it harder to understand how the tree limits seed predation and stabilizes the mutualism in the longer term. In contrast to the situation in dioecious trees, the distribution of style lengths is continuous. Moreover, in many species the wasps appear to have ovipositors long enough to lay eggs in most or all of the flowers that they encounter. Current evidence suggests that multiple mechanisms may have a role. In some species, figs may penalize wasps that do not pollinate actively by aborting fruits (Jandér, Herre, & Simms, 2012). In others, plant control of the closing of the ostiole (the only way into the fig) limits the number of female wasps that can lay egg inside and there are ‘not enough eggs’ to prevent seed production (Nefdt & Compton, 1996). Finally, different flowers may offer different fitness outcomes for wasp offspring, so that ‘optimal foraging’ for oviposition sites by female wasps may cause a slowing of the rate of seed destruction (Dunn, Segar, et al., 2008; Dunn, Yu, Ridley, & Cook, 2008; Yu et al., 2004). This is an exciting but complex topic (Cook & Rasplus, 2003; Herre, 1989) and an active area of debate and research (Herre, Jandér, & Machado, 2008).

#### **4.2.3 Coadaptation and Cospeciation**

The conflict over the fate of seeds is a key coevolutionary issue, but other impressive examples of coadaptation (i.e., mutual adaptation) can be found in the fig–pollinator mutualism. Kjellberg et al. (2001) showed that fig species with active pollinators invest far less in pollen production than those with passive pollinators. In fact, those with active pollinators have only about 10% male flowers while those with passive pollinators have about 30%.

Moreover, there is also a key difference in pollen liberation—passively pollinated species tend to burst their pollen sacs so that the pollen grains cover wasps, while this is not necessary in actively pollinated figs because the wasps deliberately collect the pollen. Importantly, there have been several changes between active and passive pollination in the evolutionary history of the mutualism but all cases investigated fit the coadaptive pattern of active wasps/low pollen or passive wasps/high pollen (Cook, Bean, Power, & Dixon, 2004; Kjellberg et al., 2001).

Another example of coadaptation is provided by correlated changes in wasp ovipositor length and fig breeding system (monoecy/dioecy) (Weiblen, 2004). In dioecious figs, wasps are faced with two highly divergent types of flowers, those with very short (in male figs) and those with very long (in female figs) styles. The long styles are too long for any wasps to lay eggs as far down as the fig ovule while the short styles require only a short ovipositor, so wasps from dioecious figs have short ovipositors. In contrast, wasps from monoecious figs face a continuous distribution of styles, lengths and a longer ovipositor makes more of these available for egg-laying. In fact, there is another, intriguing, twist to this story. Wasps that enter female dioecious figs are faced by flowers with long styles; however, they are so long that the wasps fail to reproduce. Consequently, all wasps in dioecious figs stem from ancestors that always reproduced in male figs, faced by short styles, so there is no successful natural selection for longer ovipositors. *In Ficus veritas!*

It is clear that figs and pollinators have coevolved extensively, leading to strong patterns of coadaptation of key traits. Consequently, it has long been suspected that figs and fig wasps have cospeciated, but is this the case? Strict cospeciation from a single origin of the mutualism should lead to 1:1 mapping of extant species associations and perfect phylogenetic correspondence. Such patterns are seen in some mutualisms (e.g., insects and obligate bacterial endosymbionts), where the symbiont spends its whole life cycle inside the host, but this is not the case for figs and wasps. Each adult female wasp chooses a new host individual, which is unlikely to be the same one she was born in (so not strict vertical transmission) and could even be a different species (host shift). Despite this, evidence from paired sampling of about 200 fig species and their pollinators support a long-term evolutionary history dominated by cospeciation (Cruaud et al., 2012), although with evidence of some host shifts and duplication of wasp lineages on a single host plant.

The other pattern to consider is present day fig—wasp associations. It was long thought that most fig species had a single (and unshared) pollinator

species. However, it has become increasingly obvious that many fig species have more than one pollinator species (Cook & Segar, 2010; Cook & Rasplus, 2003; Machado, Robbins, Gilbert, & Herre, 2005), though the number of pollinator species involved with a given fig is still small (2–5) (Cook & Segar, 2010; Darwell, al-Beidh, & Cook, 2014). Nevertheless, most of these pollinator species are specific to a single fig species, although there are exceptions to this, particularly from studies of the *Ficus* section *Americana* in Panama (Machado et al., 2005). Where one fig species is associated with multiple pollinator species, these may essentially replace each other geographically over a large host plant range (Silvieus, Clement, & Weiblen, 2007), or in other cases co-occur extensively at the same sites (Haine, Martin, & Cook, 2006; Machado et al., 2005). Yang et al. (2015) revealed that the former may be more common in dioecious figs and the latter in monoecious species (Fig. 3).

So, the long-term pattern of fig–pollinator diversification is dominated by cospeciation (Cruaud et al. 2012), but examination of current partner fidelity shows that many figs have multiple pollinator species and a few figs share pollinator species (Cook & Segar, 2010; Machado et al., 2005). These patterns are not necessarily incompatible, but may reflect processes over different timescales (Cook & Segar, 2010). Figs that currently have multiple pollinator species may have sister species of wasps that speciated recently without the host fig speciating, or they have acquired a new wasp species by host shift. These cases may generally be transient so that over longer time span only one wasp lineage persists, usually contributing to the long-term cospeciation signal, but occasionally to a host shift. In the medium term two wasp lineages may occasionally coexist for several millennia, as seen in some groups of African *Galoglychia* figs (McLeish & van Noort, 2012), but this is probably rare. One of the biggest unanswered questions is why the wasps apparently speciate frequently without fig speciation. This might be driven by factors largely unconnected to the mutualism with figs.

### 4.3 Obligate Pollination Mutualisms Interacting With Other Trophic Levels

Emitting an olfactory signal is a good way to signal to pollinators; however, a signal linked to a resource is also subject to exploitation by other kinds of insects. Nursery pollination mutualisms do not interact in isolation, but are integrated into ecosystems. Indeed, the scent emitted by host plants is also perceived by other insects that use this signal to locate and exploit resources

exchanged by mutualists. In nursery pollination mutualisms, both parasites (Cook & Rasplus, 2003; Jaeger et al., 2000) and predators (Bronstein, 1988; Schatz & Hossaert-McKey, 2003; Hossaert-McKey et al., 2010) have been reported to exploit plant seeds or ovaries, pollinators and/or associated insects. Hossaert-McKey et al. (2010) identified that interactions with third actors are known only in four types of nursery pollination mutualisms, but have been mainly investigated in the fig–fig wasp mutualism (Fig. 2). The role of these third actors certainly remains underestimated given that most of these mutualism occur in the tropics where biodiversity and interactions are often high. They are increasingly investigated with approaches from community ecology and network interactions (Schatz, Proffitt, Kjellberg, & Hossaert-McKey, 2013; Wang, Geng, Ma, Cook, & Wang, 2014). However, investigations in other nursery pollination mutualisms would be relevant for both fundamental knowledge and comparative analyses.

#### **4.3.1 A Community of Parasites on the Fig–Fig Wasp Mutualism**

Several nonpollinating fig wasps (NPFWs) are known to exploit the OPM between figs and their pollinators (e.g., Kerdelhué, Rossi, & Rasplus, 2000; Segar, Dunn, Darwell, & Cook, 2014). Three main feeding strategies of NPFWs have been distinguished: gall makers, which transform fig ovaries into galls (their larvae feeding on these galled ovaries); inquilines, which feed on the gall tissue induced by pollinator larvae or by nonpollinating gall makers; and parasitoids, whose larvae feed on the larvae of other wasps (pollinators or NPFWs). Most NPFWs are assumed to be associated with a single *Ficus* species, but sometimes a single NPFW species exploits multiple fig species (McLeish, van Noort, & Tolley, 2010; Silvieus et al., 2007). A fig species can host up to 30 NPFW species (Cook & Rasplus, 2003), which raises the question of niche partitioning (Kerdelhué et al., 2000; Segar et al., 2014).

NPFWs must detect the exact time window when a particular resource is present at the right developmental stage in order to exploit it efficiently (Kerdelhué et al., 2000; Marr, Brock, & Pellmyr, 2001; Schatz & Hossaert-McKey, 2010) (Fig. 4). Such synchronization is achieved thanks to chemical mediation and NPFWs detect and use the progressive change of scent emitted by figs along the developmental stages (Proffitt, Schatz, Borges, & Hossaert-McKey, 2007; Proffitt et al., 2009). Extraction of volatile compounds during fig development and olfactometer experiments have been combined to demonstrate that NPFWs are attracted only by the specific scent of their own fig host and not those emitted by other sympatric



**Figure 4** Nonpollinating fig wasps laying their eggs, thanks to their extraordinary long ovipositor, from the outside surface of figs. Left: *Sycoscapter australis* on *Ficus macrophylla*; right: *Phylotripes caricae* on *Ficus carica*. (Left) photo: J. Cook; (Right) photo: B. Schatz.

fig species (Proffitt et al., 2009). Moreover, each NPFW species is able to detect the appropriate phase of fig development it uses for oviposition (Proffitt et al., 2007).

Interestingly, it has also been suggested that NPFWs may help to stabilize the conflict between monoecious figs and pollinators over the fate of fig ovules (Dunn, Segar, et al., 2008). The logic here is that outer fig ovules, close to the fig wall, are more accessible than inner fig ovules to female NPFWs laying eggs through the fig wall (Al Beidh, Dunn, Power, & Cook, 2012). Consequently, pollinator larvae face a higher risk of parasitism in the more numerous outer ovules than the smaller number of inner ovules (Dunn, Segar, et al., 2008). This should result in selection for female pollinators, when laying eggs inside the fig, to focus strongly on finding inner ovules in which to lay eggs, thus reducing the overall rate of seed predation.

The diversity of parasites remains poorly documented in other OPMs, with limited information on only a few other cases, e.g., *Yucca filamentosa* L. and *Trollius europaeus* L. In the latter case, several species of *Chiastochaeta* flies (Diptera, Anthomyiidae) visit the flowers successively. The earliest-arriving fly species acts as the pollinator, while later-arriving species are seed parasites only (Jaeger et al., 2000). However, the proximate mechanism explaining the succession of species is still to be discovered in this system. For *Yucca filamentosa*, two species of nonpollinating yucca moths co-occur but we lack knowledge about the signals used by these parasites to find their host. The moths appear to have evolved from a mutualist species, representing a reversion from mutualism to parasitism (Marr et al., 2001).

### 4.3.2 A Community of Predators on the Fig—Fig Wasp Mutualism

Insect predators act directly and indirectly in populations of herbivores and parasites involved in various plant—insect interactions. Among the different OPMs, ants are well known to be major and opportunistic predators in the fig—fig wasp mutualism (Bronstein, 1988; Rodriguez-Girones, Gonzalez, Llandres, Corlett, & Santamaria, 2013; Schatz, Proffitt, Rakhi, Borges, & Hossaert-McKey, 2006; Schatz, Kjellberg, Nyawa, & Hossaert-McKey, 2008). OPMs are generally associated with the presence near flowers of both pollinators and other insect visitors, which constitute a potential source of prey. As a result, the presence during the emergence phase of numerous fig wasps on fig surfaces often attracts various arthropod predators such as mantids, spiders and predatory beetles (Bronstein, 1988; Schatz & Hossaert-McKey, 2003; Zachariades, 1994; Zachariades, Compton, & Schatz, 2009). A large number of ant species are often present on figs (exploiting sugar from open fruits, other prey, attending aphids, etc.), but the main effect on the fig mutualism is often from ants specialized in arboreal predation such as *Oecophylla* and *Crematogaster* species (Hymenoptera, Formicidae). Bain, Harrison, and Schatz (2014) recently reviewed the known diversity of ‘how to be an ant on figs’.

In fig—wasp systems, ants are the dominant predators of fig wasps (both pollinators and NPFWs) (Bain et al., 2014; Bronstein, 1988; Schatz et al., 2008). Ants associated with *F. carica* prey mostly on pollinators (Schatz & Hossaert-McKey, 2003), while in other cases they also prey on pollinators and NPFWs on tropical fig species (Bain et al., 2014; Schatz et al., 2006; Wang et al., 2014). Unsuccessful predation attempts during fig patrolling greatly disturb the oviposition behaviour of NPFWs on the outer surface of figs. Both predation and disturbance can reduce the negative effects of NPFW and benefit the mutualists. Ants are particularly efficient in the capture of fig wasps, detecting the scent they emit and exhibiting olfactory learning (Ranganathan & Borges, 2009; Schatz, Anstett, Out, & Hossaert-McKey, 2003; Schatz & Hossaert-McKey, 2010). Moreover, as fig scent change with time (Proffitt et al., 2008), some ants are also able to learn the specific scent associated with developmental phases when the probability of the presence of fig wasps is higher, and to modulate their presence and their aggressiveness using these olfactory cues (Schatz & Hossaert-McKey, 2010). Such abilities explain why ants may be observed to anticipate the exit of fig wasps and how they exert a strong predation pressure on fig wasps (pollinators and NPFWs) (Bain et al., 2014; Schatz & Hossaert-McKey,

2010) and then be more abundant to male trees where fig wasps are more occurrent (Schatz et al., 2008).

Among other nursery pollination mutualisms, ants may also play a role as indirect mutualistic partners in yucca–yucca moth mutualisms. Indeed, Perry, Mondor, and Addicott (2004) showed that *Formica* species on *Yucca glauca* Nutt. deter oviposition of the nonpollinating moth *Tegeticula corruptrix* (Pellmyr, 1999) but not that of the pollinating moth *Tegeticula yuccasella* (Riley, 1872) (Lepidoptera, Prodoxidae). Unfortunately, no studies have investigated the possible role of chemical mediation in this system.

### 4.3.3 Towards a Network of Interactions

The OPM between figs and fig wasps is associated with numerous resources (galls, larvae, various insects used as prey, carbohydrates, etc.), which are exploited by many insect species, building a complex network of interactions (Fig. 4) (Bain et al., 2014; Bronstein, 1988; Schatz et al., 2006, 2008; Schatz, Proffit, et al., 2013; Wang et al., 2014; Zachariades, 1994). The majority of insects flying above the tropical forest canopy are linked to figs, and notably fig wasps (Harrison, 1996). Hitherto, NPFWs and ants on figs are the sole species acting as third actors in which the exploitation of the chemical mediation linked to nursery pollination mutualism has been demonstrated (Schatz & Hossaert-McKey, 2010). In this network, interactions exist among third actors; experimental exclusion of ants conducted on three fig species led to higher abundance of NPFWs, showing that ant presence can confer substantial protection upon pollinator larvae (Schatz et al., 2006). Wang et al. (2014) even demonstrated that predation by weaver ant *Oecophylla smaragdina* (Fabricius, 1775) (Hymenoptera, Formicidae) limits the success of the NPFWs *Platyneura mayri* Rasplus (Hymenoptera, Agaonidae) in *F. racemosa* and therefore indirectly benefits the mutualism by increasing the reproductive success of both the pollinator and the plant. Maschwitz, Fiala, Saw, Norma-Rashid, and Azarae (1994) and Bain et al. (2012) discovered two fig species *Ficus obscura* Blume var. *borneensis* (Miq.) and *F. subpisocarpa* Gagnep that have hollow internodes of young branches that ants may inhabit, suggesting that figs are sometimes involved in a plant–ant mutualism.

Taken together, the complexity of interactions and the diversity of involved species suggest that figs represent a keystone genus in numerous tropical habitats, since their presence permits that of numerous species of insects, particularly Hymenoptera (Borges, Bessière, & Hossaert-McKey, 2008; Lambert, & Marshall, 1991). In an era of global change, which tends

to simplify interspecific interactions, figs constitute fascinating models to investigate the impact of third actors on mutualisms and make comparative analyses (Bain et al., 2014; Schatz et al., 2008; Wang et al., 2014).



## 5. CONCLUSION

The diversity of plant utilization strategies by insects offers an array of possible human actions aiming at protecting crops and improving their productivity. The target of these actions must necessarily be the mechanisms that mediate insect–plant interactions. The various ways that phytophagous insects exploit host plant chemicals to defend themselves against their predators create a number of possibilities. Among others, ways to disturb the metabolism by which the herbivore resists toxins produced by host plants merit investigation. A complementary approach would be to modify or combine plant toxins to prevent the adaption of the herbivore. The various mechanisms underlying plant manipulation by insects also could be exploited to improve the nutritional value of crops by mimicking the nutrient sinks induced by plant-manipulating insects. Alternatively, a better understanding of the ecology of plant-manipulating insects and their interactions with their host plant could ultimately result in the selection of resistant plant genotypes and in designing cultural practices which might, through a modulation of the physiological status of the host plant, limit plant manipulation. Finally, the microorganisms that assist herbivores in their manipulation of plants also could be targets of human actions. In the field of plant–insect mutualisms, new possible actions may be considered to improve the efficacy of pollination services, including manipulation of the plant’s chemical signals to facilitate its discovery by pollinators.

From a pure scientific aspect, utilization of plants by phytophagous insects represents a fascinating interaction. Phytophagous insects indeed face a very particular challenge. They feed on plants that both are not nutritionally adequate for them and possess efficient defence mechanisms. Under the strong selection pressure resulting from such a situation, insects have adapted to the constraints imposed by the plants through much diversified strategies, which can fit in three levels of complexity. (1) They have exploited and misappropriated the plant secondary metabolites at their own advantage, for protection or communication purposes; (2) they have modified plant tissues and adapted them to their needs using various more or less sophisticated ways, ranging from simple physical to complex molecular interactions;

(3) they have even sometimes developed elaborated mutualism coevolutions resulting in benefits for both the plant and the insect. All these strategies are essential subjects of intense research activities in the field of plant–insect interactions. A particularly interesting aspect which deserves to be clarified is how antagonistic relations have evolved to mutualistic situations.

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Cover Image: The Hazel Leaf-roller Weevil, *Apoderus coryli* (Linnaeus, 1758) (Coleoptera: Curculionidae: Attelabinae), a primitive weevil that can reach a length of 6–8 millimetres (0.24–0.31 in).

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