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Plant-Insect Interactions

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Introduction

Plants and insects are highly diverse groups due to their ability to exploit a wide range of niches, from the desert to the arctic zone and also almost all the plant species growing on the planet. Plants and insects make up together approximately half of all known species of multicellular organisms. Each plant interacts with insects in a different manner; insects may act as protection, dispersers, or fertilizers for plants while plants may be a food/energy resource or nest location for insects. Starting with herbivory, plant-insect interactions date back to the Devonian period, about 420 million years ago, when plants first began their conquest of the land. But it was most probably in the Upper Carboniferous, about 320 million years ago, that these interactions became more intense, characterized also by the appearance of entomophily (i.e., insect pollination) about 252 million years ago, before the appearance of flowering plants (angiosperms).

General Overviews

Plant-insect interactions are classically viewed as mutualistic, antagonistic, or commensalistic. Mutualism is characterized by help between each partner, with both benefiting and neither harmed. Mutualisms include pollination (e.g., flowering plant/insect pollinator systems), plant guarding, or seed dispersal (e.g., plant/ant systems). In antagonistic relationships, one counterpart benefits and the other is harmed. This relationship includes phytophagy by insects (e.g., insect pests) but also insectivory by plants (e.g., carnivorous plants). In commensalism, one counterpart benefits but the other is not harmed (e.g., the commensal relationship of the Monarch butterfly larvae with certain species of milkweeds to store cardiac glycosides for defensive purposes). The founders of the field of plant-insect interactions include Jean-Henri Fabre, one of the pioneers of insect behavior and ecophysiology as well as the study of chemical communication in insects (Fabre 1879). Charles Darwin was the first to highlight the coevolution process between insect and plant communities (Darwin 1899). Andrew D. Hopkins's theory was the first to explain a mechanism of host plant fidelity in phytophagous insects (Hopkins 1916). Karl von Frisch was the first to describe sensorial perception in insects inside their environment, particularly in plants (von Frisch 1953). Several pioneering scientists pointed out the importance of plant chemistry to the establishment of such intimate relations (see Dethier 1941), and Snelling 1941 is the first work to define plants' defense mechanisms against herbivorous insects. In 1958, the late Jan de Wilde organized the first symposium on insect-plant interactions in Wageningen, The Netherlands. This timing of this symposium corresponded to the first issue of the well-known scientific journal *Entomologia Experimentalis et Applicata* (see Journals). At the same time, a pioneering paper, Fraenkel 1959, defined the role and importance of secondary plant metabolites in plant-insect interactions; and knowledge of the sensory physiology of the gustatory systems of insects took a big step forward with Schoonhoven and Dethier 1966, after incredibly sound research on insect olfaction by pioneering works such as Viallanes 1887, probably the first to study the antennal lobe structure in a hornet. The first major scholars of plant-insect interactions in the early 21st century include May R. Berenbaumand and Art R. Zangerl at the University of Illinois, pioneers in chemical ecology of insect-plant interactions/detoxification of plant defenses/coevolution. Elizabeth (Liz) Bernays at Arizona University was considered one of the most influential scientists working on plant-herbivore interactions in the 1980s. Dame Miriam Rothschild was a classical example of a grand-old lady in caterpillar-plant interactions. Fritz and Simms 1992 is the first synthesis of plant-insect interactions.

Darwin, Charles. 1899. *The various contrivances by which orchids are fertilized by insects*. 2d ed. London: John Murray.

Darwin was the first to show plant-insect interactions in many orchid flowers that had evolved elaborate structures by natural selection in order to facilitate cross-pollination. He suggested that orchids and their insect pollinators evolved by interacting with one another over many generations, a process referred to as coevolution.

Dethier, Vincent G. 1941. Chemical factors determining the choice of food plants by *Papilio* larvae. *American Naturalist* 75:61–73.

One of the first reviews on the importance of chemicals in the attraction between insects and plants (species of Papilio and Umbelliferae).

Fabre, Jean-Henri. 1879. *Etudes sur l'instinct et les moeurs des insectes*. Souvenirs Entomologiques. Paris: Librairie Charles Delagrave.

The author introduced ethology (i.e., ecological studies) for the first time, studying insects' behavior and linking it to their environment. The author also described female giant peacock moths' (*Saturnia pyri*) attraction of male counterparts by odorant emission, introducing for the first time chemical communication in insects.

Fraenkel, Gottfried S. 1959. The raison d'être of secondary plant substances. *Science* 129:1466–1470.

The founder of the notion of the influence/importance of secondary plant substances on insect's physiology and behavior.

Fritz, Robert S., and Ellen L. Simms. 1992. *Plant resistance to herbivores and pathogens*. Chicago: Univ. of Chicago Press.

The first synthesis book on plant-herbivore interactions mostly focused on plant resistance, emphasizing ecological and evolutionary bases of resistance.

Hopkins, Andrew D. 1916. Economic investigations of the scolytid bark and timber beetles of North America. In *US Department of Agriculture Program of Work for 2017*. Edited by US Department of Agriculture, 353. Washington, DC: US Department of Agriculture.

Hopkins was the first to observe that "a species which breeds in two or more hosts will prefer to continue to breed in the host to which it has become adapted" (p. 353). This concept was called HHSP (Hopkins' Host Selection Principle).

Schoonhoven, Louis M., and Vincent G. Dethier. 1966. Sensory aspects of host-plant discrimination by lepidopteraous larvae. *Archives Néerlandaises de Zoologie* 16:497–530.

Among the first studies on chemosensory systems in insects. The authors are among the pioneers of sensory systems analyses in phytophagous insects for host-plant discrimination.

Snelling, Ralph O. 1941. Resistance of plants to insect attack. *Botanical Review* 7:543–586.

This is the first paper to define plants' resistance to insects. In 1951, Painter categorized the mechanisms of plant resistance into three: tolerance, antibiosis, and non-preference (R. H. Painter, "Insect Resistance in Crop Plants," *Botanical Review* 7.10 [1951]: 543–586). Available online by subscription.

Viallanes, Henri. 1887. *Etudes histologiques et organologiques sur les centres nerveux et les organes des sens des animaux articulés*. Paris: Masson.

This book in French contains one of the first studies of the olfactory system of arthropods.

von Frisch, Karl. 1953. *The dancing bees: An account of the life and senses of the honey bee*. New York: Harcourt, Brack.

Centered on sensory perceptions of honeybees inside their environments, and particularly toward plants, including the first investigation into the meaning of the waggle dance. A translation of *Aus dem Leben der Bienen*, 5th revised edition (Berlin: Springer-Verlag, 1953).

Journals

Plant-insect interaction is a particularly rich subject that generates both basic and academic studies as well as applied studies on the management of ecosystems or crop protection. It is therefore natural that the study of interactions between insects and plants requires the application of several disciplines. For this reason, plant-insect interactions feature prominently in a wide range of peer-reviewed journals—perhaps more than 150—covering different fields. A relatively large proportion of such articles appear in high-ranking general journals such as *Science*, *Nature*, *PNAS*, *Nature Communication*, *Plos One*, *Proceedings of the Royal Society of London B*, *Current Biology*, and *Naturwissenschaften*. Moreover, high-ranking ecology journals, such as *Ecology Letters*, *Oecologia*, *Journal of Chemical Ecology*, *Molecular Ecology*, *Functional Ecology*, and *Oikos*, as well as high-ranking plant science journals, such as *Annual Plant Reviews*, *Plant Journal*, and *New Phytologist*, all dedicate a significant proportion of their available space to articles focusing on different aspects of plant-insect interactions. Because they are more specialized, a large number of entomological journals are excellent sources of information for studies on plant-insect interactions. However, there are some journals that are more specific to the field than others, namely the *Annual Review of Entomology*, *Arthropod-Plant Interactions* (a journal recently founded and dedicated in insect-plant interactions), and *Entomologia Experimentalis et Applicata*. On the basis of their profoundly important role in the management of ecosystems or crop protection, plant-insect interactions are also prominent in applied literature. This is the case for *Agriculture, Ecosystems & Environments*; *Crop Protection*; and *Journal of Pest Science*. In addition, different journals dealing also with climate/global change are more and more considering the field of plant-insect interactions, such as *Climatic Change* and *Global Change Biology*.

***Agriculture, Ecosystems & Environments*. 1983–.**

Publishes scientific articles dealing with the interface between agroecosystems and the natural environment, specifically how agriculture influences the environment and how changes in that environment impact agroecosystems.

***Annual Review of Entomology*. 1956–.**

Covers an enormous range of subjects related to the field of entomology. Different aspects of plant-insect interactions have figured prominently in various issues of the journal.

***Arthropod-Plant Interactions*. 2007–.**

Publishes papers and reviews with a broad fundamental or applied focus on ecological, biological, and evolutionary aspects of the interactions between insects and other arthropods with plants. Coverage extends to all aspects of such interactions including chemical, biochemical, genetic, and molecular analysis, as well reporting on multitrophic studies, ecophysiology, and mutualism. Available online by subscription.

***Climatic Change*. 1977–.**

Publishes papers dedicated to the totality of the problem of climatic variability and change, its descriptions, causes, implications, and interactions among these. The purpose of the journal is to provide a means of exchange among those working in different disciplines on problems related to climatic variations. Available online by subscription.

***Crop Protection*. 1982–.**

Publishes papers describing an interdisciplinary approach showing how different control strategies can be integrated into practical pest management programs, covering high and low input agricultural systems worldwide. It covers all practical aspects of pest, disease, and weed control.

***Entomologia Experimentalis et Applicata*. 1958–.**

Publishes many papers on both fundamental and applied aspects of plant-insect interactions, including development, physiology, ecology, and biological control. This journal is actually used to publish the proceedings of the regular symposium on insect-plant interactions (SIP) created in 1958. Available online by subscription.

***Global Change Biology*. 1995–.**

Exists to promote understanding of the interface between all aspects of current environmental change that affects a substantial part of the globe and biological systems. Available online by subscription.

***Journal of Pest Science*. 1927–.**

Publishes papers on all aspects of pest science in agriculture, horticulture (including viticulture), forestry, urban pests, and stored products research, including health and safety issues. Available online by subscription.

History of Plant-Insect Interactions

The complex relationships between plants and insects are the result of a long common evolution. The appearance and evolution of terrestrial plants have strongly influenced insects' evolution; similarly, pressures exerted by insects on plants took a large part in the diversification of plants. A recent synthesis, Schatz, et al. 2017, showed how fossil records, which contain different types of "signals," allow the reconstitution of the history of the relationships between plants and insects (e.g., morphological characteristics of buccal pieces of fossilized insects providing direct evidence of feeding habits as showed in Nel 1997, or traces of phytophagy on fossilized plants showed in Labandeira and Sepkoski 1993). Currano, et al. 2008 shows a positive correlation between damages on fossilized plants caused by insects and increasing mean temperature during the Paleocene-Eocene transition some fifty-five million years ago. Moreover, as stated in Schatz, et al. 2017, the phylogeny and molecular clock concepts provide robust assumptions on the age of the insect lines, or even on the relationship between insects and their host plants, when these data are tested with paleontological data (see Ronquist, et al. 2012 and Nel, et al. 2013). In this context, a good example of host fidelity over geologic time in the use of oaks by oak gall wasps is described in Leckey and Smith 2015. Schatz, et al. 2017 is a good synthesis of different steps and periods of the evolution of plant-insect interactions, reporting the main distinct phases of evolution of interactions between arthropods and plants (see also Labandeira 2006).

Currano, Ellen D., Peter Wilf, Scott L. Wing, Conrad C. Labandeira, Elizabeth C. Lovelock, and Dana L. Royer. 2008. Sharply increased insect herbivory during the Paleocene-Eocene thermal maximum. *Proceedings of the National Academy of Sciences of the United States of America* 105:1960–1964.

A paper showing a positive correlation between damages on fossilized plants caused by insects and increasing mean temperature during the Paleocene-Eocene transition some fifty-five million years ago. Suggests that increased insect herbivory is likely to be a net long-term effect of anthropogenic $p\mathrm{CO}_2$ increase and warming temperatures.

Labandeira, Conrad C. 2006. The four phases of plant-arthropod associations in deep time. *Geologica Acta* 4:409–438.

A reference paper describing the spatiotemporally distribution of vascular-plant hosts, their arthropod herbivores, and associated functional feeding groups into four major herbivore expansions during the past 420 million years.

Labandeira, Conrad C., and John J. Sepkoski Jr. 1993. Insect diversity in the fossil record. *Science* 261:310–315.

A paper illustrating the use of fossil "signals" such as traces of phytophagy on fossilized plants to provide direct evidence of diversity of feeding habits in ancestral insects.

Leckey, Erin H., and Dena M. Smith. 2015. Host fidelity over geologic time: Restricted use of oaks by oak gallwasps. *Journal of Paleontology* 89.2: 236–244.

In this paper the authors showed a high degree of host fidelity by oak gall wasps over their evolutionary history by studying twenty-five fossil floras from the Oligocene through Pliocene of the western United States. Available online by subscription.

Nel, André. 1997. The probabilistic inference of unknown data in phylogenetic analysis. *Mémoires du Muséum National d'Histoire Naturelle* 173:305–327.

An article illustrating the use of fossil "signals" such as morphological characteristics of buccal pieces of fossilized insects to provide direct evidence of feeding habits of the ancestral insects.

Nel, André, Patrick Roques, Patricia Nel, et al. 2013. The earliest-known holometabolous insects. *Nature* 503:257–261.

A good example of the use of fossil records and phylogeny to reveal a notable penecontemporaneous breadth of early eumetabolan insects.

Ronquist, Fredrik, Seraina Klopfstein, Lars Vihelmsen, Susanne Schulmeister, Debra L. Murray, and Alexandr P. Rasnitsyn. 2012. A total-evidence approach to dating with fossils, applied to the early radiation of the Hymenoptera. *Systematic Biology* 61:973–999.

In this paper, the authors used an approach that includes fossils along with the extant taxa in a Bayesian total-evidence analysis. They focus on the early radiation of the Hymenoptera.

Schatz, Bertrand, Nicolas Sauvion, Finn Kjellberg, and André Nel. 2017. Plant-insect interactions: A palaeontological and an evolutionary perspective. In *Insect-plant interactions in a crop protection perspective*. Edited by Nicolas Sauvion, Paul-André Calatayud, and Denis Thiéry, 1–24. Advances in Botanical Research 81. London: Academic Press.

This chapter provides the most recent updated synthesis on the paleontological and evolutionary perspective of plant-insect interactions. Available online by subscription.

Main Evolutionary Trends of Plant-Insect Interactions

Studying the evolution of plant-insect interactions needs multidisciplinary approaches within a historical (i.e., phylogenetic) framework. Since phytophagous insects represent nearly a quarter of all terrestrial macroscopic biodiversity, their high diversity is attributed to their generally specific association with angiosperms in Kergoat, et al. 2017. The main evolutionary trends of these insect-plant associations described in the literature include taxonomical conservatism with insect diversification behind the host plants (Dethier 1954), coevolution (Ehrlich and Raven 1964, supported by the important work Edger, et al. 2015), co-speciation or co-cladogenesis (Miller 1987), chemical specialization (Becerra 1997 and Kergoat, et al. 2005), ecological specialization (Rundle and Nosil 2005), and eco-geological colonization (Gómez-Zurita, et al. 2000). A recent synthesis, Kergoat, et al. 2017, mentioned, thanks to phylogenetic-based studies, that insects and their host plants have not co-speciated, and it validated the concept of phylogenetic conservatism of host-use with insect diversification, behind the host plants. It also shows that diet is highly labile, and that specialization is not a dead end. However, it highlights that there is still not a clear link between herbivory and increased speciation. In addition and thanks to the recent development of powerful phylogenetic methods in biogeography (see Ronquist and Sanmartín 2011), the relative contributions of biotic and abiotic factors to diversification, and their time scales, is discussed in Kergoat, et al. 2017.

Becerra, Judith X. 1997. Insects on plants: Macroevolutionary chemical trends in host use. *Science* 276:253–256.

A reference paper showing historical patterns of host plants strongly correspond to the patterns of host chemical similarity, indicating that plant chemistry has played a significant role in the evolution of host shifts by phytophagous insects.

Dethier, Vincent G. 1954. Evolution of feeding preferences in phytophagous insects. *Evolution* 8:33–54.

Shows for the first time the taxonomical conservatism between insects and plants on insect feeding.

Edger, Patrick P., Hanna M. Heidel-Fischer, Michaël Bekaert, et al. 2015. The butterfly plant arms-race escalated by gene and genome duplications. *Proceedings of the National Academy of Sciences of the United States of America* 112.27: 8362–8366.

By investigating the evolutionary histories of *Brassica* species and insects, the authors showed that increases in chemical defense complexity were followed by butterflies' evolving countertactics, allowing them to continue to feed on the plants.

Ehrlich, Paul R., and Peter H. Raven. 1964. Butterflies and plants: A study in coevolution. *Evolution* 18:586–608.

Brought the concept of coevolution to the scientific literature.

Gómez-Zurita, Jesús, Carlos Juan, and Eduard Petitpierre. 2000. The evolutionary history of the genus *Timarcha* (Coleoptera, Chrysomelidae) inferred from mitochondrial COII gene and partial 16S rDNA sequences. *Molecular Phylogenetics and Evolution* 14:304–317.

In phylogenetic analyses of thirty-one taxa of leaf beetles, this paper reveals an eco-geological colonization process of the evolutionary history of *Timarcha*, with host plants involving a widening of insect's trophic regime.

Kergoat, Gaël J., Alex Delobel, Gilles Fédière, Bruno le Ru, and Jean-François Silvain. 2005. Both host-plant phylogeny and chemistry have shaped the African seed-beetle radiation. *Molecular Phylogenetics and Evolution* 35:602–611.

A recent interesting paper that investigates taxonomic conservatism in host-plant fidelity by insects and host-plant chemistry. Demonstrates that the nature of the plant secondary compounds might be the major factor driving the diversification of a large clade of seed-beetle specializing on the subfamily Mimosoideae in which host-plant taxonomy is not consistent with chemical similarity.

Kergoat, Gaël J., Andrea Meseguer, and Emmanuelle Jousselin. 2017. Evolution of plant-insect interactions: Insights from macroevolutionary approaches in plants and herbivorous insects. In *Insect-plant interactions in a crop protection perspective*. Edited by Nicolas Sauvion, Paul-André Calatayud, and Denis Thiéry, 25–54. Advances in Botanical Research 81. London: Academic Press.

This chapter provides the most recent updated synthesis on the main evolutionary trends of plant-insect interactions. Available online by subscription.

Miller, James S. 1987. Host plant association in the Papilionidae: Parallel cladogenesis or colonization? *Cladistics* 3:105–120.

A literature review that concludes that no documented examples of parallel cladogenesis between insects and plants are known. This review supports the idea that insects have "colonized" their hosts subsequent to plant cladogenesis and suggests that host association patterns in the Papilionidae have resulted from repeated colonization of plants belonging to a relatively small number of families. The author highlighted the importance of plant secondary chemicals as barriers to insect colonization. Available online by subscription.

Ronquist, Fredrik, and Isabel Sanmartín. 2011. Phylogenetic methods in biogeography. *Annual Review of Ecology, Evolution, and Systematics* 42:441–464.

Proposes phylogenetic methods to address ecological interactions and climate change in biogeographic inference.

Rundle, Howard D., and Patrik Nosil. 2005. Ecological speciation. *Ecology Letters* 8:336–352.

A review of the ecological speciation, considering its constituent components: an ecological source of divergent selection, a form of reproductive isolation, and a genetic mechanism linking the two. Available online by subscription.

Pollination Syndromes: Major Evolutionary Innovations

The appearance of entomophilous pollination constitutes a major evolutionary innovation in plant-insect interactions, with important diversification in insects and plants related in Labandeira, et al. 2007 and Peñalver, et al. 2012. A parallel was established between pollinators' mouthparts and flower morphology, the result of coevolution between pollinating insect communities and plant communities, and defined as pollination syndromes in Faegri and van der Pijl 1979. An emblematic example, described in Darwin 1877, is the relationship between Orchidae and pollinators. In this mutualism between plants and pollinating insects, Crane, et al. 1995 highlights that diversification of flowers constitutes a feature that in turn may drive diversification of pollinating insects, allowing the radiation of angiosperms and of pollinating insects. More recent research on pollinators and coevolution are being carried out in Bill Hansson's lab in the Max Planck Institute for Chemical Ecology, Jena, Germany (see Haverkamp, et al. 2016).

Crane, Peter R., Marie E. Friis, and Kaj R. Pedersen. 1995. The origin and early diversification of the angiosperms. *Nature* 374:27–33.

In this paper the authors determined how new paleobotanical discoveries, combined with recent phylogenetic analyses of morphological and molecular data, can clarify the initial phases of the angiosperm radiation.

Darwin, Charles. 1877. *The various contrivances by which orchids are fertilised by insects*. 2d ed. London: John Murray.

The first reference book on the fertilization of Orchideae by insects.

Faegri, Knut, and Leendert van der Pijl. 1979. *The principles of pollination ecology*. 3d ed. Oxford: Pergamon Press.

This reference textbook defines pollination syndromes.

Haverkamp, Alexander, Julia Bing, Elisa Badeke, Bill S. Hansson, and Markus Knaden. 2016. Innate olfactory preferences for flowers matching proboscis length ensure optimal energy gain in a hawkmoth. *Nature Communications* 7:11644.

In this paper, the authors showed that the hawk moth *Manduca sexta* exhibits an innate preference for volatiles of *Nicotiana* flowers, which match the length of the moth's proboscis, supporting Darwin's initial hypothesis on the coevolution of flower length and moth proboscis.

Labandeira, Conrad C., Jiri Kvacek, and Mikhail B. Mostovski. 2007. Pollination drops, pollen, and insect pollination of Mesozoic gymnosperms. *Taxon* 56:663–695.

Among the papers showing the implication of pollination as a major evolutionary innovation in plant-insect interactions with an important diversification in insects and plants.

Peñalver, Enrique, Conrad C. Labandeira, Eduardo Barrón, et al. 2012. Thrips pollination of Mesozoic gymnosperms. *Proceedings of the National Academy of Science of the United States of America* 109:8623–8628.

This paper provides direct evidence of specialized collection and transportation of pollen grains by thrips and likely gymnosperm pollination by 110–105 million years ago, possibly considerably earlier.

Strategies of Plant Exploitation

The history of insects' diversification is inseparable from that of plants. During the evolution of these organisms, the gradual diversification of plants led insects to develop different adaptations at various complexity levels to utilize the plants in spite of the barriers they built to resist to their aggressions. These include behavioral (cf. host/resource selection, Thompson and Pellmyr 1991), morphological (Bernays, et al. 1991), and physiological strategies (cf. synchronization of reproductive cycle between insects and plants, Seger and Brockmann 1987). Initially, insect strategies for plant exploitation certainly focused on ensuring insect reproduction and development (van Veen, et al. 2006). Insects developed cooperation with other organisms, in particular conspecifics and microorganisms, using the same plant resource for the benefit of both users (Paine, et al. 1997). Different strategies have been developed by insects to optimize the nutritional value of their host plants and to ensure their protection from adverse abiotic and biotic conditions (natural enemies, competition). Among these strategies, the most described are manipulation of plants to reorient their metabolisms to insect's needs (e.g., effectors in Hogenhout and Bos 2011 and plant growth regulators or phytohormones in Zhang, et al. 2016); remodeling the host plant, from ultrastructure to anatomy levels, alternating both its nutritional quality and secondary metabolism (Lieutier, et al. 2017); and plant exploitation by the use of plant toxins for defense against predators (Reichstein, et al. 1968 and Duffey 1980). The energetic cost of that last strategy depends on the toxicity of the chemicals, the necessity of protecting the herbivore, and the modes of action on predators (see Lieutier, et al. 2017).

Bernays, Elisabeth A., Edmund A. Jarzembowski, and Stephen B. Malcolm. 1991. Evolution of insect morphology in relation to plants. *Philosophical Transactions of the Royal Society B: Biological Science* 333:257–264.

Relates some of the major physical problems faced by phytophagous insects and some of the morphological adaptations that have to be adopted. The review mainly focuses on the nature of the plant surface (cf. size of the insects) and the difficulty of dealing with hard or tough plant tissues (cf. mandibles adaptations).

Duffey, Sean S. 1980. Sequestration of plant natural products by insects. *Annual Review of Entomology* 25:447–477.

A review of insect sequestration strategy and its different impacts (cf. adaptations for defense).

Hogenhout, Saiska A., and Jorunn I. Bos. 2011. Effector proteins that modulate plant-insect interactions. *Current Opinion in Plant Biology* 14:422–428.

A paper on tools for high-throughput effector identification and functional characterization to study the effectors that suppress plant defenses in the saliva of piercing-sucking hemipteran insects.

Lieutier, François, Kalina Bermudez-Torres, James Cook, et al. 2017. From plant exploitation to mutualism. In *Insect-plant interactions in a crop protection perspective*. Edited by Nicolas Sauvion, Paul-André Calatayud, and Denis Thiéry, 55–109. Advances in Botanical Research 81. London: Academic Press.

This chapter gives the most recent synthesis on different strategies for plant exploitation. Available online by subscription.

Paine, Timothy D., Kenneth R. Raffa, and Thomas C. Harrington. 1997. Interactions among scolytid bark beetles, their associated fungi, and live host conifers. *Annual Review of Entomology* 42:179–206.

In this review, the authors, using an emblematic example, show how the scolytid bark beetles that colonize living conifers have developed cooperations with specific fungi to colonize the host trees with a mutual benefit to the fitness of both beetles and fungi.

Reichstein, Tadeau, Joseph von Euw, John A. Parsons, and Miriam Rothschild. 1968. Heart poisons in the monarch butterfly. *Science* 161:861–866.

The first paper that shows that cardenolide-rich monarch butterflies become distasteful and toxic to predators.

Seger, Jon, and Jane H. Brockmann. 1987. What is bet-hedging? In *Oxford surveys in evolutionary biology*. Vol. 4. Edited by Paul H. Harvey and Linda Partridge, 182–211. Oxford: Oxford Univ. Press.

The authors used seed-dormancy and insect-diapause models as good bet-hedging models to show how synchronization of reproductive cycles between insects and plants can be important strategies to spread these two components.

Thompson, John N., and Olle Pellmyr. 1991. Evolution of oviposition behavior and host preference in Lepidoptera. *Annual Review of Entomology* 36:65–89.

A synthesis showing how oviposition behaviors developed by Lepidoptera contribute to the evolution of plant preference and specificity.

van Veen, Franck F. J., Rebecca J. Morris, and Charles J. Godfray. 2006. Apparent competition, quantitative food webs, and the structure of phytophagous insect communities. *Annual Review of Entomology* 51:187–208.

The authors review the experimental evidence for both short-term and long-term apparent competition in phytophagous insect communities and discuss the possible interactions between apparent competition and intraguild predation or shared mutualists.

Zhang, Hui, D. Thomas de Bernonville, Mélanie Body, et al. 2016. Leaf-mining by *Phyllonorycter blancardella* reprograms the host-leaf transcriptome to modulate phytohormones associated with nutrient mobilization and plant defense. *Journal of Insect Physiology* 84:114–127.

A recent study that provides an extensive characterization of how the leaf miner *Phyllonorycter blancardella* modulates the major phytohormones and the transcriptional activity of plant cells in leaves of *Malus domestica*. This paper consolidates previous hypotheses on insect’s production of cytokinins to the plant as a strategy to manipulate the physiology of the leaf to create a favorable nutritional environment.

Mutualism

Beyond plant exploitation, mutualism (the highest level of association) is a good compromise between insects and plants where each part benefits from the association. Pollination (and particularly for obligatory pollination by insects on fig, some palm trees, and cactus) is the emblematic example that varies from generalists to specialists and belongs to a community of insects linked to a plant community (see Dressler 1982; Buchmann 1987; Grant 1994; Neal, et al. 1998; Pellmyr and Krenn 2002; and Raguso 2008; see also Pollination Syndromes: Major Evolutionary Innovations). The fig–fig wasp mutualism is a good illustration, consisting of various mechanisms involving monoecism and dioecism situations, as well as coadaptations and co-speciations (see Lieutier, et al. 2017).

Buchmann, Stephen L. 1987. The ecology of oil flowers and their bees. *Annual Review of Ecology and Systematics* 18:343–369.

Among the first reviews stating a morphological parallel between floral characteristics and associated bees.

Dressler, Robert L. 1982. Biology of the orchid bees (Euglossini). *Annual Review of Ecology and Systematics* 13:373–394.

A review on the biology of bees associated to orchid pollination.

Grant, Verne. 1994. Modes and origins of mechanical and ethological isolation in angiosperms. *Proceedings of the National Academy of Sciences of the United States of America* 91:3–10.

A good paper showing how mechanical and ethological isolation between species is widespread in angiosperms with specialized animal-pollinated flowers.

Lieutier, François, Kalina Bermudez-Torres, James Cook, et al. 2017. From plant exploitation to mutualism. In *Insect-plant interactions in a crop protection perspective*. Edited by Nicolas Sauvion, Paul-André Calatayud, and Denis Thiéry, 55–109. Advances in Botanical Research 81. London: Academic Press.

This chapter gives the most recent synthesis on the different aspects of mutualism. Available online by subscription.

Neal, Paul R., Amots Dafni, and Martin Giurfa. 1998. Floral symmetry and its role in plant-pollinator systems, terminology, distribution, and hypotheses. *Annual Review of Ecology, Evolution, and Systematics* 29:345–373.

A review on the role of floral symmetry in plant-pollinator interactions, elaborating a classification scheme for floral symmetry; a short review of the distribution of floral forms in angiosperm families; and provides hypotheses supporting evidence for the causes of the evolution of floral symmetry.

Pellmyr, Olle, and Harald W. Krenn. 2002. Origin of a complex key innovation in an obligate insect-plant mutualism. *Proceedings of the National Academy of Sciences of the United States of America* 99:5498–5502.

A paper on the obligate mutualism between yuccas and yucca moths by using anatomical data from phylogenetically pivotal moth species indicating that this complex key morphological trait (tentacles and adjacent mouthparts in pollinators) for the mutualism has a surprisingly simple origin, apparition of tentacles.

Raguso, Robert A. 2008. Wake up and smell the roses: The ecology and evolution of floral scent. *Annual Review of Ecology, Evolution, and Systematics* 39:549–569.

A review that shows the importance of floral volatile compounds and on the floral scent to promote specialization in plant-pollinator relationships.

Food Webs Associated with Plants

As a central resource, plants are the centers of many food webs, and these food webs are key to ecosystem stability. Relationships between plants and insects are currently placed in many trophic or even non-trophic interactions that influence plant herbivory by insects. In a more recent synthesis, Corcket, et al. 2017 describes the biological interactions of plants and insects within food webs. It describes the trophic cascades including non-trophic interactions (insect predation, insect parasitism), intraguild competition, interference, abiotic resources, microclimate, and changes in animal behavior as drivers, which may influence plants and insects, and thus their trophic relationships. Among the insects' ecological roles in the plant world, the vectored phytopathogenic agents are important because of their negative effects on plant physiology. Moreover, this vectoring process raises important research questions on complexes between three biological partners (plant, insect, and virus or bacteria) at both the cellular and molecular levels within the ecosystem (see Nault 1997; Harper, et al. 2002; Gray and Gildow 2003; Belliure, et al. 2005; Rojas, et al. 2005; Hogenhout, et al. 2008; and Ammar, et al. 2009). Analysis of food webs is booming, with recent progress in molecular markers and metagenomic approaches (e.g., Clare 2014 and Roslin and Majaneva 2016).

Ammar, El-Desouky, Chi-Wei Tsai, Anna E. Whitfield, Margaret G. Redinbaugh, and Saskia A. Hogenhout. 2009. Cellular and molecular aspects of rhabdovirus interactions with insect and plant hosts. *Annual Review of Entomology* 54:447–468.

The authors provide an overview of plant rhabdovirus interactions with their insect hosts. They focus on cellular and molecular aspects of vector/host specificity, transmission barriers, and virus receptors in the vectors; and they discuss recent advances in understanding rhabdovirus-plant interactions.

Belliure, Belén, Arne Janssen, Paul C. Maris, Dick Peters, and Maurice W. Sabelis. 2005. Herbivore arthropods benefit from vectoring plant viruses. *Ecology Letters* 8:70–79.

In this original paper, the authors show that potential vectors benefit from viral attacks on plants because virus-infected plants are of higher quality for the vector's offspring. They propose that plant pathogens in general have evolved mechanisms to overcome plant defenses against their vectors, thus promoting pathogen spread. Available online by subscription.

Clare, Elizabeth L. 2014. Molecular detection of trophic interactions: Emerging trends, distinct advantages, significant considerations and conservation applications. *Evolutionary Applications* 7:1144–1157.

This paper illustrates nicely how the use of high-throughput sequencing, coupled with taxonomically broad sequence repositories, gives the capacity to rapidly identify thousands of species-level interactions.

Corcket, Emmanuel, Brice Giffard, and René F. H. Sforza. 2017. Food webs and multiple biotic interactions in plant-herbivore models. In *Insect-plant interactions in a crop protection perspective*. Edited by Nicolas Sauvion, Paul-André Calatayud, and Denis Thiéry, 111–137. Advances in Botanical Research 81. London: Academic Press.

This chapter gives the most recent updated synthesis on the different aspects on food webs and multiple biotic interactions in plant-herbivore models. Available online by subscription.

Gray, Stewart, and Frederick E. Gildow. 2003. Luteovirus-aphid interactions. *Annual Review of Phytopathology* 41:539–566.

This review focuses on the genetic, cellular, and molecular mechanisms regulating the complex and specific virus-aphid interactions.

Harper, Glyn, Roger Hull, Ben Lockhart, and Neil Olszewski. 2002. Viral sequences integrated into plant genomes. *Annual Review of Phytopathology* 40:119–136.

This paper focuses on the integration of various DNA plant viruses into the host genome and highlights the fact that integration of viral sequences is widespread in the plant kingdom and has been occurring for a long period of time.

Hogenhout, Saskia A., El-Desouky Ammar, Anna E. Whitfield, and Margaret G. Redinbaugh. 2008. Insect vector interactions with persistently transmitted viruses. *Annual Review of Phytopathology* 46:327–359.

In this review the authors highlight the progress made in research on vector interactions of the more than two hundred plant viruses transmitted by hemipteroid insects beginning a few hours or days after acquisition, up to the life of the insect, that is, in a persistentcirculative or persistent-propagative mode.

Nault, Lowell R. 1997. Arthropod transmission of plant viruses: A new synthesis. *Annals of the Entomological Society of America* 90:522–541.

An important review that describes the biology and the mechanisms of the transmission mode of the more important arthropod vectors of plant viruses.

Rojas, Maria R., Charles Hagen, William J. Lucas, and Robert L. Gilbertson. 2005. Exploiting chinks in the plant's armor: Evolution and emergence of geminiviruses. *Annual Review of Phytopathology* 43:361–394.

This reviews show the geminiviruses acquired and evolved mechanisms to manipulate the plant cell cycle machinery for DNA replication, and to optimize the number of cells available for infection, explaining why they are one of the most successful viral pathogens, causing severe economic losses to agricultural production worldwide.

Roslin, Tomas, and Sanna Majaneva. 2016. The use of DNA barcodes in food web construction—terrestrial and aquatic ecologists unite! *Genome* 59:603–628.

Another good illustration on how DNA-based techniques, and DNA barcodes in particular, have recently been used to construct food web structure in both terrestrial and aquatic systems.

Plant-Insect-Symbiont Interactions

Paradoxically, from the point of view of insects, the host plants can often be considered poor and deficient nutrient media (see Schoonhoven, et al. 2005). To compensate for these deficiencies, one of the insect strategies established during their long evolutionary history was to associate with one or more symbiotic partners by providing insects with key nutrients, as described in Douglas 2013 and Sugio, et al. 2015. But insect-microbial associations are not limited to this type of interaction. Microorganisms hosted by insects may also have other types of direct or indirect influences on plant-insect interactions. As in many animals, symbionts play a role in several life history traits of their hosts, and several examples illustrate changes in physiology and behavior, striking examples being provided by aphids, in which the range of exploited plants is affected by such symbionts. For example, microbes may interfere with plants to modulate food provisioning to insect and plant defenses (Sugio, et al. 2015). Insect symbionts can also alter insect reproduction (Engelstädter and Hurst 2009) or insect immunity, with consequences on plant exploitation (Dubreuil, et al. 2014), and they can modulate insect interactions with natural enemies or plant-associated organisms such as other herbivores, plant symbionts, or plant pathogens as described in Biere and Bennett 2013; Chuche, et al. 2017; Frago, et al. 2012; and Sugio, et al. 2015. The literature on insect-associated bacterial diversity is prolific in recent years (see Giron, et al. 2017) in particular due to technical advances in molecular analysis (see Moran 2016). Mechanisms underlying plant-insect-microbe interactions are increasingly apprehended (Sugio, et al. 2015). Even if there is still much to discover, the literature already shows the extraordinary complexity of these multitrophic interactions, and their importance for both an applied and a fundamental point of view.

Biere, Arjen, and Alison E. Bennett. 2013. Three-way interactions between plants, microbes and insects. In *Special issue: Plant-microbe-insect interactions*. Edited by Arjen Biere and Alison E. Bennett. *Functional Ecology* 27:567–573.

An editorial of a special issue on thematic “plant-microbe-insect interactions.” It highlights the ecological importance of the three-way “plant-microbe-insect” (PMI) interactions: microbial mediation of plant-insect interactions, insect mediation of plant-microbe interactions, and plant mediation of insect-microbe interactions.

Chuche, Julien, Nathalie Auricau-Bouvery, Jean-Luc Danet, and Denis Thiéry. 2017. Use the insiders: Could insect facultative symbionts control vector-borne plant diseases? *Journal of Pest Science* 90:51–68.

This article reviews the literature on insect vectors of crop diseases and their symbiotic microorganisms, suggesting future integrated management techniques based on current research on insect-vectored human diseases. Potential candidates are discussed, taking into account advantages and limitations of the development of such techniques in agriculture. Available online by subscription.

Douglas, Angela E. 2013. Microbial brokers of insect-plant interactions revisited. *Journal of Chemical Ecology* 39:952–961.

Angela Douglas is a long-term researcher on bacteriocyte symbioses in plant sap feeding insects. Her group applies metabolic models and experimental approaches, informed by genomic, transcriptomic, and proteomic data, to establish how essential amino acid overproduction by the symbiotic bacteria is sustained and scaled to host demand. Available online by subscription.

Dubreuil, Géraldine, Emeline Deleury, Didier Crochard, Jean-Cristophe Simon, and Christine Coustau. 2014. Diversification of MIF immune regulators in aphids: Link with agonistic and antagonistic interactions. *BMC Genomics* 15:762.

In this article, the authors aim to understand immune-related genes implicated in the maintenance of the mutualistic association between the pea aphid and its symbionts. This work provides evidence that while aphid’s antibacterial arsenal is reduced, other immune genes widely absent from insect genomes are present, diversified, and differentially regulated during antagonistic or agonistic interactions.

Engelstädter, Jan, and Gregory D. D. Hurst. 2009. The ecology and evolution of microbes that manipulate host reproduction. *Annual Review of Ecology, Evolution, and Systematics* 40:127–149.

Manipulation of host reproduction inherited microbes is a common feature in insect biology. Here, the authors review the natural history and evolutionary ecology of inherited reproductive parasites (feminization, parthogenesis induction, early male killing, late male killing, cytoplasmic incompatibility) before examining their impact on host ecology and evolution.

Frago, Enric, Marcel Dicke, and Charles H. Godfray. 2012. Insect symbionts as hidden players in insect plant interactions. *Trends in Ecology & Evolution* 27:705–711.

In this review, the authors introduce the term “hidden players” to highlight the importance of microbial mutualistic symbioses in insect-plant interactions. The terms, concepts, and different types of interactions are clearly and elegantly described in this highly referenced article.

Giron, David, Franck Dedeine, Géraldine Dubreuil, et al. 2017. Influence of microbial symbionts on plant-insect interactions. In *Insect-plant interactions in a crop protection perspective*. Edited by Nicolas Sauvion, Paul-André Calatayud, and Denis Thiéry, 225–258. Advances in Botanical Research 81. London: Academic Press.

Gives the most recent updated synthesis on the influence of the microbial symbionts on the plant-insect interactions. Available online by subscription.

Moran, Nancy A. 2016. When obligate partners melt down. *mBio* 7.6: e01904–e01916.

Nancy Moran is one of the most influential and prolific researchers on the biology of symbiosis, particularly that between multicellular hosts and microbes. Among many other themes, she has contributed to major advances on genomics of bacterial symbionts of plant sap-feeding insects, genomic evolution of *Buchnera*, and molecular phylogenetics of Sternorrhyncha.

Schoonhoven, Louis M., Joop J. A. van Loon, and Marcel Dicke. 2005. *Insect plant biology*. 2d ed. Oxford: Oxford Univ. Press.

There are many books on plant-insect interactions, for example those of Elizabeth Bernays, but her words in the preface justify the inclusion of the second edition of this seminal book: “For anyone with an interest in any aspect of plant and insect interactions, this text will be a firm and reliable resource” (p. vii).

Sugio, Akiko, Géraldine Dubreuil, David Giron, and Jean-Christophe Simon. 2015. Plant-insect interactions under bacterial influence: Ecological implications and underlying mechanisms. *Journal of Experimental Botany* 66:467–478.

Recent developments in sequencing technologies and molecular tools have dramatically enhanced opportunities to characterize the microbial diversity associated with plants and insects. The authors focus on this diversity and the ecological consequences of bacterial communities associated with plants and herbivorous insects. They also highlight the known mechanisms by which these microbes interfere with plant-insect interactions.

Plant-Insect-Pathogen Interactions

Plants and insects interact with phytopathogens through very intimate and sophisticated associations that can be described by at least three ways: plant-vector interactions (i.e., specific organism that transmits a pathogen), pathogen-vector interactions, and plant-pathogen interactions. The majority of plant pathogens are transmitted by insects of the Hemipteroid assemblage, including hemipterans (aphids, whiteflies, psyllids, coccids, leafhoppers, plant hoppers, Heteroptera) and thrips (see the important Brown 2016). The predominant feature of these insects as vectors is that they have needle-like stylet structures (i.e., specialized piercing-sucking mouthparts) that can puncture cells at the surface of a leaf or in plant tissues (parenchyma, phloem, xylem). For over a century, plant-vector interactions have been predominantly focused on hemipteran-virus associations because of the economical importance of the plant virus (see Roossinck 2015). But in more recent years, because vector-borne bacteria have caused some of the most devastating plant diseases in perennial and annual crops, intensive research has been conducted on their interactions with the hemipteran insect and plants (see Perilla-Henao and Casteel 2016). Important questions include: What are the pathogen routes within the vector (Whitfield, et al. 2015)? Which viral/bacterial ligands determine interaction with the vector (Ng and Zhou 2015)? How do pathogens affect vector physiology or behavior (Fereres and Moreno 2009)? And, how do viruses/bacteria affect host plant physiology, and in turn impact vector behavior and/or fitness (Orlovskis, et al. 2015)? Recently, fascinating questions have been studied despite technical difficulties: for example, identification of specific receptors of phytopathogen within vector (Uzest, et al. 2010) and intimate mechanisms of acquisition/inoculation (Martin, et al. 1997 and Backus 2016).

Backus, Elaine A. 2016. Sharpshooter feeding behavior in relation to transmission of *Xylella fastidiosa*: A model for foregut-borne transmission mechanisms. In *Vector-mediated transmission of plant pathogen*. Edited by Judith K. Brown, 173–195. Saint Paul, MN: American Phytopathological Society Press.

The purpose of this review is to answer the “essential question”: What (specific) probing behaviors are associated with *X. fastidiosa* inoculation in plants? The author summarizes all work in the last twelve years to identify and define the probing behaviors of the vectors (sharpshooters), describing a conceptual model for xylem vessel acceptance, and presents the “salivation-egestion” hypothesis for the probing behaviors likely to control *X. fastidiosa* inoculation.

Brown, Judith K. 2016. *Vector-mediated transmission of plant pathogens*. Saint Paul, MN: American Phytopathological Society Press.

Comprehensive monograph explains the complex range of factors and interactions related to the vector-mediated transmission of plant pathogens. Each chapter offers detailed examples of particular pathogen-vector interaction modes, tying together many years of research to advance understanding of pathogen-vector biology and interactions at biochemical, cellular-tissue-organ, and functional genomic levels.

Fereres, Alberto, and Aranzanzu Moreno. 2009. Behavioural aspects influencing plant virus transmission by homopteran insects. *Virus Research* 141:158–168.

This review considers how the probing and feeding behaviors of piercing-sucking insects (essentially aphids, whiteflies, leafhoppers) influence the transmission and spread of plant viruses depending on the type of virus-vector relationship. The review also focuses on which are the most likely retention sites within the insect's body of cuticula-borne viruses.

Martin, Begonia, Jose Luis Collar, Freddy W. Tjallingii, and Alberto Fereres. 1997. Intracellular ingestion and salivation by aphids may cause the acquisition and inoculation of non-persistently transmitted plant viruses. *Journal of General Virology* 78:2701–2705.

This elegant article demonstrates the behavioral events associated with uptake (acquisition) and release (inoculation) of two non-persistently aphid-transmitted viruses by using the electrical penetration graph (EPG) technique. A widely accepted hypothesis postulates that virus acquisition occurs during ingestion of plant cell contents, and inoculation during egestion or regurgitation of previously ingested sap. Here, the authors propose the "ingestion-salivation" hypothesis as an alternative. Available online by subscription.

Ng, James C. K., and Jaclyn S. Zhou. 2015. Insect vector–plant virus interactions associated with non-circulative, semi-persistent transmission: Current perspectives and future challenges. *Current Opinion in Virology* 15:48–55.

In 2006, Ng and Falk examined the complex and specific interactions between the hemipteran vector and the plant viruses, and in particular, those that are transmitted in nonpersistent and semi-persistent manners (*Annual Review of Phytopathology* 44 [2006]: 183–212). Here, in this very comprehensive and well-illustrated review, Ng and Zhou detail the established paradigms on the biology and the mechanisms of the non-circulative, semi-persistent transmission.

Orlovskis, Zigmunds, Maria C. Canale, Vera Thole, Pascal Pecher, Joao R. S. Lopes, and Saskia A. Hogenhout. 2015. Insect-borne plant pathogenic bacteria: Getting a ride goes beyond physical contact. *Current Opinion in Insect Science* 9:16–23.

The relationships between plant viruses and their respective vectors have been the subject of many recent reviews (e.g., Blanc, et al., "Current Opinion in Microbiology," 14 [2011]: 483–491). Here, this very well documented review focuses on the contribution of insects to the transmission of bacterial pathogens. Available online by subscription.

Perilla-Henao, Laura M., and Clare L. Casteel. 2016. Vector-borne bacterial plant pathogens: Interactions with hemipteran insects and plants. *Frontiers in Plant Science* 7.

The authors review current knowledge on economically important vector-borne bacterial pathogens and highlight recent approaches used in the involved studies. They discuss the application of this knowledge for control and future directions that will need to be addressed in the field of vector-plant-bacteria interactions.

Roossinck, Marilin J. 2015. Plants, viruses and the environment: Ecology and mutualism. *Virology* 479:271–277.

A very interesting review that looks at pathogen virus with a different regard from that of the "classical" phytopathologists. Indeed, in this review, the authors use the framework of symbiotic relationships to put the true nature of viruses into perspective. They discuss the diversity of plant viruses, from what we know about crop diseases to what is being discovered through metagenomic studies of wild plants, the complex role of insects in the plant-virus relationship, and the impacts of plant viruses on the evolution and ecology of their hosts.

Uzest, Marilyne, Daniel Gargani, Aviv Dombrovsky, Chantal Cazevieille, Didier Cot, and Stéphane Blanc. 2010. The "acrostyle": A newly described anatomical structure in aphid stylets. *Arthropod Structure & Development* 39:221–229.

In 2007, in a fascinating study by Uzest, et al. (*Proceedings of the National Academy of Sciences* 104.46 [2007]: 17959–17964) proved the existence, precise location, and chemical nature of the first receptor for a non-circulative virus in its insect vector, opening a major black box that might lead to new strategies to combat viral spread. In this very elegant article, the same authors described a highly conserved anatomical structure in aphid stylets that allow the virus to interact with their vectors to ensure plant-to-plant transmission. Available online by subscription.

Whitfield, Anna E., Bryce W. Falk, and Dorith Rotenberg. 2015. Insect vector-mediated transmission of plant viruses. *Virology* 479:278–289.

In this very well documented, illustrated, and comprehensive review, the authors focus on very economically important insect vector-transmitted viruses in the following genera: *Caulimovirus*, *Crinivirus*, *Luteovirus*, *Geminiviridae*, *Reovirus*, *Tospovirus*, and *Tenuivirus*. Not only do they discuss the current state of knowledge but also recent exciting translational applications of fundamental viral knowledge: insect-vector-interactions that have opened up new perspectives for plant virus and insect vector control.

Host Plant Selection

Preference-Performance Hypothesis (PPH) and Insect Experience

Most phytophagous arthropods have a relatively short lifespan. They must efficiently search for and select their trophic resource or that of their offspring while adapting these searching behaviors to the environment in which they evolve (Bernays and Chapman 1994). The choice of a host plant affects the fitness and resultant adult size of the offspring (Scriber and Slansky 1981, Fox and Czesak 2000, and Awmack and Leather 2002) and also the sex pheromone behavior of insects (Landolt and Phillips 1997), with a recent demonstration of interactions between plant's volatile organic compounds (VOCs) and sex pheromone composition made in Leppik and Frérot 2012. However, the link between host plants preference and insect growth, survival, and reproduction has been a central problem in insect-plant interactions. This notion of Preference-Performance Hypothesis (PPH), also known as the "naïve adaptionist hypothesis" or the "mother-knows-best hypothesis," was first proposed in Jaenike 1978 and states that maternal insects will generally prefer host plants that optimize the survival and performance of their offspring. A recent meta-analysis of the literature, Gripenberg, et al. 2010, supports the PPH. Host plant choice is also conditioned by individual experience (prenatal, natal, or postnatal) of the insect. Hopkins 1916 was the first work to study the influence of natal host plants on host-plant preference modulation. A recent literature analysis in Petit, et al. 2017 shows that host plant selection is largely conditioned by insect experience.

Awmack, Caroline S., and Simon R. Leather. 2002. Host plant quality and fecundity in herbivorous insects. *Annual Review of Entomology* 47:817–844.

Shows that host plant quality is a determinant factor of insect's fecundity and of insect's reproductive strategies: egg size and quality, the allocation of resources to eggs, and the choice of oviposition sites. Host plant quality affects insect's fecundity at both the individual and the population scale.

Bernays, Elisabeth A., and Reg F. Chapman. 1994. *Host-plant selection by phytophagous insects*. New York: Chapman & Hall.

A comprehensive textbook on host-plant selection processes by phytophagous insects dealing with patterns of host-plant use, chemicals in plants, sensory systems, impact of ecology and physiology, effects of experience, genetic variation in host selection, and evolution of host range. Available online by subscription.

Fox, Charles W., and Mary Ellen Czesak. 2000. Evolutionary ecology of progeny size in arthropods. *Annual Review of Entomology* 45:341–369.

Argues that much of the variation in progeny size among species, and among populations within species, is likely due to variation in natural selection and that much of the variation in progeny size among females within populations, and among progeny produced by a single female, is probably nonadaptative.

Gripenberg, Sofia, Peter J. Mayhew, Mark Parnell, and Tomas Roslin. 2010. A meta-analysis of preference-performance relationships in phytophagous insects. *Ecology Letters* 13:383–393.

In this extensive literature analysis, the authors assess the balance of evidence for and against the preference-performance hypothesis. Available online by subscription.

Hopkins, Andrew D. 1916. Economic investigations of the scolytid bark and timber beetles of North America. In *US Department of Agriculture Program of Work for 2017*. Edited by US Department of Agriculture, 353. Washington, DC: US Department of Agriculture.

Developed for the first time the concept of HHSP (Hopkins' Host Selection Principle).

Jaenike, John. 1978. On optimal oviposition behavior in phytophagous insects. *Theoretical Population Biology* 14:350–356.

In this paper, the author developed a model that predicts when an insect should choose a host plant for a suitable larval development.

Landolt, Peter J., and Thomas W. Phillips. 1997. Host plant influences on sex pheromone behavior of phytophagous insects. *Annual Review of Entomology* 42:371–391.

In this review, the authors show that chemicals from host plants often synergize or otherwise enhance insect responses to sex pheromones. By these means, host plants are used by insects to regulate or mediate sexual communication.

Leppik, Ene, and Brigitte Frérot. 2012. Volatile organic compounds and host-plant specialization in European corn borer E and Z pheromone races. *Chemoecology* 22:119–129.

In this paper, the authors demonstrate that the host plants shared a certain number of ubiquitous volatiles present in various ratios that likely constitute a species-specific cue to host-seeking corn borer moths. Their observations suggest that moth host fidelity with specific pheromone composition is steered by plant volatiles that are present in species-specific ratios of ubiquitous volatile organic compounds. Available online by subscription.

Petit, Christophe, Stéphane Dupas, Denis Thiéry, et al. 2017. Do the mechanisms modulating host preference in holometabolous phytophagous insects depend on their host plant specialization? A quantitative literature analysis. *Journal of Pest Science* 90:797–805.

This review shows that host plant selection is largely conditioned by insect's experience and that the positive influence of experience in the modulation of host plant preference occurred equally in polyphagous, oligophagous, and monophagous species. Available online by subscription.

Scriber, J. Marc, and Frank Slansky Jr. 1981. The nutritional ecology of immature insects. *Annual Review of Entomology* 26:183–211.

The authors assessed the importance of food quality relative to other environmental factors and organism adaptations that influence post-ingestive food utilization and growth performance of immature arthropods.

Host Plant Localization and Acceptance

The description of the different steps of an insect in search of its host plant was given initially in Bell 1990. Generally, according to a number of authors, there are two main steps in plant selection by insects: localization and plant acceptance. Localization of host habitats and plants involves smell and sight, chemical signals from plants, and plant volatile organic compounds (VOCs) and have been extensively studied. These studies allowed the development of a new discipline in ecology in 1960, chemical ecology (see Hartmann 2008). Initially these chemical signals were considered waste products from the plant's metabolism—then, secondary metabolites—and now as specific olfactory signatures of habitats and plants (cf. the odorscape notion; see Frérot, et al. 2017). The insects rely on plant VOCs to locate the host plant (Visser 1986; Pickett, et al. 1992; Renwick and Chew 1994); see the section Constitutive and Inductive VOCs in Host Plant Selection by Phytophagous Insects for additional details. Insect responses to host plants and their odors vary with the physiological status of both actors, plant and the insect (Frérot, et al. 2017, in which the authors cite the most relevant papers showing how chemical signals released by plants vary with plant physiology, diel periodicity, climatic factors, and pollution, and how these signals can be species- or even variety-specific). In addition to volatiles, when insects are getting closer to the plant, they also rely on visual characteristics of host plants such as color, size, and shape (see Prokopy and Owens 1983), which together with plant volatiles can allow a better host plant recognition and selection (Kulachi, et al. 2008). On the plant, insects use sight, touch, smell, and taste, as well as physical factors (e.g., color, hairiness) and chemical stimuli (olfactive and gustative) to definitively accept the plant as host. This ability has been demonstrated not only for oviposition (Renwick and Chew 1994) but also for food choice: in caterpillars and chewing insects, see Schoonhoven and van Loon 2002 and Chapman 2003; in hemipterans, see Powell, et al. 2006.

Bell, William J. 1990. Searching behavior patterns in insects. *Annual Review of Entomology* 35:447–467.

In this review the author presents the different steps of searching for a host plant by insects.

Chapman, Reg F. 2003. Contact chemoreception in feeding by phytophagous insects. *Annual Review of Entomology* 48:455–484.

Host plant selection in chewing insects and caterpillars depends on a balance of phagostimulatory and deterrent inputs, and, in some oligophagous and monophagous species, a host-related chemical.

Frérot, Brigitte, Ene Leppik, Astrid T. Groot, Mélanie Unbehend, and Jarmo K. Holopainen. 2017. Chemical signatures in plant-insect interactions. In *Insect-plant interactions in a crop protection perspective*. Edited by Nicolas Sauvion, Paul-André Calatayud, and Denis Thiéry, 139–177. Advances in Botanical Research 81. London: Academic Press.

The authors focused on the plasticity of pheromone emission, a recent discovery in the field of pheromones and the specific odorscape produced by the cultivated plants that is now shown to be related to plant physiological state, health, and the variability of chemical signals released by plants. Available online by subscription.

Hartmann, Thomas. 2008. The lost origin of chemical ecology in the late 19th century. *Proceedings of the National Academy of Sciences of the United States of America* 105.12: 4541–4546.

A good history and statement of the chemical ecology concept. Available online by subscription.

Kulachi, Ipek G., Anna Dornhaus, and Daniel R. Papaj. 2008. Multimodal signals enhance decision making in foraging bumble bees. *Proceedings of the Royal Society of London B: Biological Science* 275:797–802.

This paper shows, for bumblebees, that the insects make more effective decisions when visual and olfactory signals act together rather than separately.

Pickett, John A., Lester J. Wadhams, Christine M. Woodcock, and Jim Hardie. 1992. The chemical ecology of aphids. *Annual Review of Entomology* 37:67–90.

The authors demonstrated that olfaction plays a more extensive role in the chemical ecology of aphids than previously thought.

Powell, Glen, Colin R. Tosh, and Jim Hardie. 2006. Host plant selection by aphids: Behavioural, evolutionary, and applied perspectives. *Annual Review of Entomology* 51:309–330.

In this review, the authors show that aphids are able to select their host plant by probing and suggest that the dominant cues controlling plant preference and initiation of reproduction are detected early during their stylet penetration process, well before the nutrient supply (phloem) is contacted.

Prokopy, Ronald J., and Elizabeth D. Owens. 1983. Visual detection of plants by herbivorous insects. *Annual Review of Entomology* 28:337–364.

Examines the visual properties of natural illuminants and plants, and properties of insects’ vision; the visual plant selection process of insects, emphasizing visual detection of plants or plant structures from a distance, from nearby, and from within a plant canopy. Intraspecific visual variation in plants and insects are also considered, as well as a comparison between generalist versus specialist insects.

Renwick, J. Alan A., and Frances S. Chew. 1994. Oviposition behavior in Lepidoptera. *Annual Review of Entomology* 39:377–400.

An important review in the elucidation of chemical factors that affect oviposition by Lepidoptera. Both this behavior and this family haven been extensively studied in insect-plant interactions. Available online by subscription.

Schoonhoven, Louis M., and Joop J. A. van Loon. 2002. An inventory of taste in caterpillars: Each species its own key. *Acta Zoologica Academiae Scientiarum Hungaricae* 48.Suppl. 1: 215–263.

A review paper summarizing clearly that plant recognition occurred in Lepidoptera larvae for selecting their food by their taste systems.

Visser, Hans J. 1986. Host odor perception in phytophagous insects. *Annual Review of Entomology* 31:121–144.

An extensive review on odor perception in phytophagous insects (including aphids, whiteflies, and plant hoppers) from the literature of the late 20th century.

Constitutive and Inductive VOCs in Host Plant Selection by Phytophagous Insects

Particular attention has been given on the influence of constitutive and inductive plant VOCs in host plant selection by phytophagous insects for food or oviposition by mediating their behaviour (Karban and Myers 1989; Dicke and van Loon 2000; Bruce, et al. 2005; Giunti, et al. 2018). Oviposition behaviour in host plant selection has been well/mostly studied since it is generally admitted that this particular behaviour is a form of resource utilization by insects on host plants and is crucial in the establishment of the relationship between insects and host plants: the choice of host plants by a female determines generally the fitness of its offspring (Thompson and Pellmyr 1991, Bernays and Chapman 1994, Renwick and Frances 1994). The oviposition preferences of gravid females utilizing the same host plant in a community can be influenced by the interactions among species (Shiojiri, et al. 2002). Thus, competition for, or facilitation in the use of the same resource can influence the final choice by the female for oviposition. The infochemicals from infesting stages (eggs or larvae) from other con- or hetero-specifics have been shown to influence gravid female oviposition choice, which serves to adjust population sizes to available resources with, in general, a preference for uninfested plants (Bernays and Chapman 1994; de Moraes, et al. 2001; Fatouros, et al. 2012). However, in some species, prior feeding of larvae by con- and/or hetero-specifics on a plant attracts females for oviposition on that plant (Sokame, et al. 2019).

Bernays, Elisabeth A., and Reg F. Chapman. 1994. *Host-plant selection by phytophagous insects*. New York: Chapman & Hall.

A comprehensive textbook on host-plant selection processes by phytophagous insects dealing with patterns of host-plant use, chemicals in plants, sensory systems, impact of ecology and physiology, effects of experience, genetic variation in host selection, and evolution of host range. Available online by subscription.

Bruce, Toby J. A., Lester J. Wadhams, and Christine M. Woodcock. 2005. Insect host location: A volatile situation. *Trends in Plant Science* 10:269–274.

An important review in the elucidation of plant volatiles that influence feeding and oviposition by phytophagous (herbivorous). In their review, the authors highlighted strong evidence that plant discrimination is due to central processing of olfactory signals by the insect, rather than their initial detection.

de Moraes, Consuelo M., Mark C. Mescher, and James H. Tumlinson. 2001. Caterpillar-induced nocturnal plant volatiles repel conspecific females. *Nature* 410:577–579.

Important paper showing that plants release temporally different volatile blends and that lepidopteran herbivores use induced plant signals released during the dark phase to choose sites for oviposition (cf. repelling conspecific females).

Dicke, Marcel, and Joop J. A. van Loon. 2000. Multitrophic effects of herbivore-induced plant volatiles in an evolutionary context. *Entomologia Experimentalis et Applicata* 97:237–249.

Beautiful review, in a journal not obviously devoted to reviews, on the developments done on the induction mechanism as well as the ecological consequences in a multitrophic and evolutionary context. The authors also addressed mechanistic aspects, such as the identification of the minimally effective blend of volatiles that explains the attraction of carnivores to herbivore-infested plants, and evolutionary aspects such as the fitness consequences of induced volatiles.

Fatouros, Nina E., Dani Lucas-Barbosa, Berhane T. Weldegergis, et al. 2012. Plant volatiles induced by herbivore egg deposition affect insects of different trophic levels. *PLoS One* 7:e43607.

In this paper, the authors explored the specificity and role of plant volatiles induced during the early phase of attack, that is, egg deposition by herbivorous insects, and their consequences on insects of different trophic levels. They showed for example that gravid specialist butterflies were repelled by volatiles from plants induced by cabbage white butterfly eggs, probably as a means of avoiding competition; and that volatiles from plants induced by eggs of the generalist moth did neither repel nor attract any of the tested community members.

Giunti, Giulia, Vincenzo Palmeri, Giuseppe Massimo Algeri, and Orlando Campolo. 2018. VOC emissions influence intra- and interspecific interactions among stored-product Coleoptera in paddy rice. *Scientific Reports* 8:1–9.

An example of a paper on Coleoptera showing the influence of VOC emissions on intra- and interspecific competition of pest of stored cereals.

Karban, Richard, and Judith H. Myers. 1989. Induced plant responses to herbivory. *Annual Review of Ecology and Systematics* 20:331–348.

An extensive review of the induced plant responses to herbivores as a plant defense without increasing herbivore preference or performance, or as a defensive reaction toward herbivores.

Renwick, J. Alan A., and S. Chew Frances. 1994. Oviposition behavior in Lepidoptera. *Annual Review of Entomology* 39:377–400.

An important review in the elucidation of chemical factors that affect oviposition by Lepidoptera. Both this behavior and this family have been extensively studied in insect-plant interactions.

Shiojiri, Kaori, Junji Takabayashi, Sshuichi Yano, and Aakio Takafuji. 2002. Oviposition preferences of herbivores are affected by tritrophic interaction webs. *Ecology Letters* 5:186–192.

The authors studied a tritrophic system: one consisting of a cabbage plant (*Brassica oleracea*), diamondback moth larvae (*Plutella xylostella*) and their parasitic wasp (*Cotesia plutellae*); another one consisting of a cabbage plant, cabbage butterfly (*Pieris rapae*) larvae and their parasitic wasp (*Cotesia glomerata*). They showed that adult *Pl. xylostella* oviposited preferentially on plants infested with *Pi. rapae*, whereas adult *Pi. rapae* revealed no significant preferences between uninfested plants or plants infested with *Pl. xylostella*.

Sokame, Bonoukpoè Mawuko, Eric Siaw Ntiri, Peter Ahuya, et al. 2019. Caterpillar-induced plant volatiles attract conspecific and heterospecific adults for oviposition within a community of lepidopteran stemborers on maize plant. *Chemoecology* 29:89–101.

A good example of a study showing for three moth species, namely *Busseola fusca*, *Sesamia calamistis*, and *Chilo partellus*, that gravid female moths significantly preferred VOCs emitted by plants infested by conspecific or heterospecific larvae over those from uninfested plants, and female moths did not systematically prefer VOCs emitted by plants infested by conspecifics.

Thompson, John N., and Olle Pellmyr. 1991. Evolution of oviposition behavior and host preference in Lepidoptera. *Annual Review of Entomology* 36:65–89.

A synthesis showing how oviposition behaviors developed by Lepidoptera contribute to the evolution of plant preference and specificity.

Mechanisms of Chemosensory Signal Detection in Insects

As in mammals, chemosensory signal detection in insects involves peripheral and central nervous structures (Touhara and Vosshall 2009). At the periphery, signals are detected by chemosensory receptor neurons housed in cuticular structure called sensilla (Altner and Prillinger 1980). Such sensilla are found on antennae, mouth parts, legs, ovipositor. . . . At the central nervous system level, olfactory receptor neurons connect to the antennal lobe where the signals are encoded (Haverkamp, et al. 2018) and taste neurons usually connect to the suboesophageal ganglion. At the periphery, chemosensory signals are first solubilized by soluble odorant-binding proteins (OBPs) and chemosensory proteins (CSPs) (Leal 2013; Pelosi, et al. 2018) to reach the membrane of sensory neurons within chemosensory sensilla. Signals then interact with different families of receptors (Montagné, et al. 2015; Robertson 2019), including odorant receptors (ORs), gustatory receptors (GRs) and ionotropic receptors (IRs), these last being involved in both olfaction and taste. Enzymes are proposed to participate in signal termination by degrading the odorants after interaction with the receptors (Leal 2013; Steiner, et al. 2019). Most functional studies of ORs have been conducted on the model insect *Drosophila melanogaster* (Hallem, et al. 2004; Hallem and Carlson 2006) as well as mosquitoes (Carey, et al. 2010) because of their impact on human health, but recent progress has been made on ORs from phytophagous species such as Lepidoptera (de Fouchier, et al. 2017). Less is known on GR functioning, but there are accumulative evidences of expansions of GR gene number in polyphagous Lepidoptera genomes compared to oligo/monophagous species, suggesting an important role in host plant selection (Gouin, et al. 2017). IRs have been discovered after ORs and GRs, but appeared to have a more ancient origin than ORs and GRs (Croset, et al. 2010).

Altner, Helmut, and Linde Prillinger. 1980. Ultrastructure of invertebrate chemo-, thermo-, and hygroreceptors and its functional significance. *International Review of Cytology* 67:69–139.

Membrane of sensory neurons are exposed to stimuli, but they also need to be protected from mechanical damage or desiccation. There is a variety of specialized structures called sensilla that serve such function, and their different morphological types and ultrastructure are described in this article.

Carey, Allison F., Guirong Wang, Chih-Yig Su, Laurence J. Zwiebel, and John R. Carlson. 2010. Odorant reception in the malaria mosquito *Anopheles gambiae*. *Nature* 464:66–71.

This paper presents the first systematic functional analyses of *Anopheles gambiae* odorant receptors using complementary functional assays. The authors used the *Drosophila* empty neuron system coupled to single sensillum recording (see Hallem, et al. 2004). The study revealed that *Anopheles* ORs exhibit a large diversity of odor-response profile and tuning breadth, some ORs being responsive to a single or small number of odorants and some other being broadly tuned receptors.

Croset, Vincent, Raphael Rytz, Scott F. Cummins, et al. 2010. Ancient protostome origin of chemosensory ionotropic glutamate receptors and the evolution of insect taste and olfaction. *PLoS Genetics* 6.8: e1001064.

Ionotropic receptors (IRs) constitute a variant subfamily of ionotropic Glutamate receptors and have been identified as a new class of olfactory receptors first in the fruit fly, *Drosophila melanogaster*. In marked contrast to the insect-specific odorant Receptor family, the authors show that IRs are present in olfactory organs across Protostomia, revealing that they represent an ancestral protostome chemosensory receptor family.

de Fouchier, Arthur, William B. Walker, Nicolas Montagné, et al. 2017. Functional evolution of Lepidoptera olfactory receptors revealed by deorphanization of a moth repertoire. *Nature Communication* 8:15709.

This work took advantage of the “empty neuron” system (see Hallem, et al. 2004) to functionally characterize the first large set of ORs from an herbivorous species. ORs detecting many VOCs have been identified and their phylogenetic analyses revealed some functional conservations within OR subfamilies.

Gouin, Anaïs, Anthony Bretaudeau, Kiwoong Nam, et al. 2017. Two genomes of highly polyphagous lepidopteran pests (*Spodoptera frugiperda*, Noctuidae) with different host-plant ranges. *Scientific Reports* 7:11816.

This paper reports genome sequencing and analyses of different *Spodoptera* noctuid pests and proposes hypotheses on adaptation to polyphagy and pesticide resistance. According to polyphagy, the study revealed extraordinary genomic expansions of GR genes in these genomes, with more than 230 GR genes annotated. This is much higher than what has been described in specialist Lepidoptera species, which contain only 60–70 GR genes in their genomes. GR expansions mainly occurred in the so-called bitter GR subfamily, suggesting they play an important role in diverse host plant detection and selection.

Hallem, Elissa A., and John R. Carlson. 2006. Coding of odors by a receptor repertoire. *Cell* 125:143–160.

This work is the first ever published on the functional study of a large set of ORs. Twenty-four *Drosophila melanogaster* ORs were expressed in the “empty neuron” system (see Hallem, et al. 2004) and challenged with one hundred odorants. This led to demonstrate that OR response spectra present a continuum from narrowly tuned to broadly tuned.

Hallem, Elissa A., Michael G. Ho, and John R. Carlson. 2004. The molecular basis of odor coding in the drosophila antenna. *Cell* 117:965–979.

This is a precursor article describing an *in vivo* system to identify insect OR function (determination of their ligands). The authors developed a mutant olfactory receptor neuron in *Drosophila* to be used as a “decoder”: the so-called empty neuron system. In this system, exogenous ORs are expressed in the empty neuron via genetic tools and the transformed neuron responses to a panel of odorants are registered *in vivo* by single sensillum recording. This approach allows determining the response spectrum of individual exogenous OR.

Haverkamp, Alexander, Bill S. Hansson, and Markus Knaden. 2018. Combinatorial codes and labeled lines: How insects use olfactory cues to find and judge food, mates, and oviposition sites in complex environments. *Frontiers in Physiology* 9:49.

This paper reviews how the insect olfactory system employs strategies of combinatorial coding to process general odors as well as labeled lines for specific compounds.

Leal, Walter S. 2013. Odorant reception in insects: Roles of receptors, binding proteins, and degrading enzymes. *Annual Review of Entomology* 58:373–391.

This article overviews the early processing events in odorant detection in insects, which are the uptake, binding, transport, and inactivation of odorants, as well as receptor activation and signal transduction. Most of the protein families involved are described, such as OBPs, ORs, IRs, ODEs, and sensory neuron membrane proteins (SNMPs), as well as their putative function, sometimes controversial.

Montagné, Nicolas, Arthur de Fouchier, Richard D. Newcomb, and Emmanuelle Jacquin-Joly. 2015. Advances in the identification and characterization of olfactory receptors in insects. *Progress in Molecular Biology and Transitional Science* 130:55–80.

This chapter reviews how the genomic era has led to an impressive gain of knowledge on chemosensory receptors in insects. Impressively, these gene families are some of the largest multigene families known in the animal kingdom. The authors also described the methods developed for functional studies of ORs, including *in vitro* heterologous expression in *Xenopus* oocytes or cultured cell and *in vivo* expression in *Drosophila* antenna used as a toll box (see Hallem, et al. 2004).

Pelosi, Paolo, Immacolata Iovinella, Jiao Zhu, Guirong Wang, and Francesca R. Dani. 2018. Beyond chemoreception: Diverse tasks of soluble olfactory proteins in insects. *Biological Reviews* 93:184–200.

A recent synthesis on OBP and CSP function as carriers of odorants and pheromones in insect chemoreception but also as general carriers involved in various non-sensory tasks.

Robertson, Hugh M. 2019. Molecular evolution of the major arthropod chemoreceptor gene families. *Annual Review of Entomology* 64:227–242.

This review depicts the evolutionary origins of the three major families of insect chemosensory receptors (ORs, GRs, IRs). The GR family originates at the base of animals, whereas the IR family originates at the base of protostomes, and the OR family at the base of insects. A major feature is that these chemoreceptor families are usually present in large clades of recently duplicated genes in insect genomes. Gene loss and gain have led to an extraordinary range of sizes of chemosensory receptor families in insects, from four to up to nine hundred genes, correlating with the complexity of the chemical ecology of each species.

Steiner, Claudia, Thomas Chertemps, and Martine Maïbèche. 2019. Diversity of biotransformation enzymes in insect antennae: Possible roles in odorant inactivation and xenobiotic processing. In *Olfactory concepts of insect control—alternative to insecticides*. Vol. 2. Edited by Jean-François Picimbon, 115–145. Cham, Switzerland: Springer.

The step of signal termination in insect antennae is poorly documented, although it plays an important role in the response kinetics. Some enzymes families present in olfactory sensilla are proposed to be involved in this step. This book chapter presents their diversity in insect olfactory organs and discusses their potential role in odorant processing but also in detoxification processes within the olfactory organ.

Touhara, Kazushige, and Leslie Vosshall. 2009. Sensing odorants and pheromones with chemosensory receptors. *Annual Review of Physiology* 71:307–332.

This review compares odorant and pheromone receptor structure, function, neuronal circuitry, and brain olfactory structures in mammals and insects.

Plant Defenses against Phytophagous Insects

Plant defenses against phytophagous insects are both direct and indirect. Among several pioneers in direct- and indirect-induced defenses against herbivores, Karban and Baldwin 1997 constitutes the first comprehensive synthesis. Direct plant defenses can be constitutive, involving secondary compounds and plant toxins, expressed even in the absence of the pest (Hanover 1975; Swain 1977; Pickett, et al. 1992; Herms and Mattson 1992), and also inducible, expressed as a result of an attack (Reid, et al. 1967; Howe and Jander 2008). Indirect plant defenses are mediated by the release of a blend of volatiles that specifically attract natural enemies of the herbivores and/or by providing food (e.g., extra floral nectar) and housing (e.g., domatia) to enhance the effectiveness of the natural enemies. This notion of indirect plant defenses was first introduced in Dicke and Sabelis 1987, and thereafter the notion of "cry for help" by the emblematic paper Turlings, et al. 1995.

Dicke, Marcel, and Maurice W. Sabelis. 1987. How plants obtain predatory mites as bodyguards. *Netherlands Journal of Zoology* 38:148–165.

Shows how plants, by providing pollen (i.e., food source) for predatory mites, promote not only their survival but also their development and egg production, ensuring the presence of bodyguards even before any damage by phytophagous mites. Plants under attack by spider mites also release a blend of volatiles that help the predatory mites localize their prey. Available online by subscription.

Hanover, James W. 1975. Physiology of tree resistance to insects. *Annual Review of Entomology* 20:75–95.

The author critically examines the concept of tree resistance to insects and reviewed the physiological mechanisms involved in resistance. Available online by subscription.

Herms, Daniel A., and William J. Mattson. 1992. The dilemma of plants: To grow or defend. *Quarterly Review of Biology* 67:283–335.

The authors review the evolutionary theories of plant defense. They show among others that a trade-off between plant growth and defense exists in the secondary metabolism. Available online by subscription.

Howe, Gregg A., and Georg Jander. 2008. Plant immunity to insect herbivore. *Annual Review of Plant Biology* 59:41–66.

Excellent review updating knowledge on plants' responses to herbivory by production of toxins and defensive proteins that target physiological processes in the insect. Shows how herbivore-challenged plants emit volatiles that attract insect predators and bolster resistance to future threats. Available online by subscription.

Karban, Richard, and Ian T. Baldwin. 1997. *Induced responses to herbivory*. Chicago: Univ. of Chicago Press.

First comprehensive evaluation and synthesis of this field of plant defense to insects by actively altering their chemistry and physiology in response to damage.

Pickett, John A., Lester J. Wadhams, Christine M. Woodcock, and Jim Hardie. 1992. The chemical ecology of aphids. *Annual Review of Entomology* 37:67–90.

The authors show the involvement of secondary compounds in plant defenses against aphids. Available online by subscription.

Reid, Robert W., Howard S. Whitney, and Jolanta A. Watson. 1967. Reactions of lodgepole pine to attack by *Dendroctonus ponderosae* Hopkins and blue stain fungi. *Canadian Journal of Botany* 45:1115–1126.

The authors demonstrate for the first time the hypersensible reaction of conifers toward the attacks of scolytids and their associated fungi. Available online by subscription.

Swain, Tony. 1977. Secondary compounds as protective agents. *Annual Review of Plant Physiology* 28:479–501.

The author reviews the nature of secondary compounds, their implication on plant diseases, allelopathy, insect’s deterrence, and protective agents against herbivores. Available online by subscription.

Turlings, Ted C. J., John H. Loughrin, Philip J. McCall, Ursula S. R. Röse, W. Joe Lewis, and James H. Tumlinson. 1995. How caterpillar-damaged plants protect themselves by attracting parasitic wasps. *Proceedings of the National Academy of Sciences of the United States of America* 92:4169–4174.

This emblematic paper showed for the first time that volatiles emitted by a plant attacked by herbivores are unique and specific enough to guide natural enemies toward their herbivore hosts. Available online by subscription.

Plant-Insect Interactions and Global Change

Several publications note that climate change is resetting the spatial and ecological equilibrium of complex coevolutionary relationships between plants and their insect herbivores. Climate change includes not only the impact of increased temperature and atmospheric CO_2 concentrations but also land use or landscape modifications by humans and their pollution. Sgrò, et al. 2016 reviews the different plastic insect responses and whether they contribute to adaptation to climate change. Bale, et al. 2002 reviews the impact of increased temperature on insect herbivores; Polce, et al. 2014 in pollinators; and Hance, et al. 2007 on parasitoids. Hunter 2001 reviews the impact of increased atmospheric CO_2 concentrations in insect herbivores and Zavala, et al. 2013 in plant-herbivores interactions. Leckey, et al. 2014 and Rasmann, et al. 2014 show the importance of using altitudinal gradients as surrogate natural laboratories to study the influence of the variation of environmental parameters (temperature, humidity, and rainfall variations) on insect-plant interactions. Concerning human actions, Tscharntke and Brandl 2004 and Chen, et al. 2015 review landscape modification and crop domestication in insect-plant interactions, while Butler and Trumble 2008 reviews the impact of pollutants.

Bale, Jeffery S., Gregory J. Masters, Ian D. Hodkinson, et al. 2002. Herbivory in global climate change research: Direct effects of rising temperature on insect herbivores. *Global Change Biology* 8:1–16.

This paper examines the direct effects of climate change on insect herbivores. Available online by subscription.

Butler, Casey D., and John T. Trumble. 2008. Effects of pollutants on bottom-up and top-down processes in insect-plant interactions. *Environmental Pollution* 156:1–10.

Provides a synthesis of available data by pollution type and herbivore guild as well as how bottom-up (host plant quality) and top-down (natural enemies) changes by pollutants both influence the fitness and population dynamics of herbivores. Available online by subscription.

Chen, Yolanda H., Rieta Gols, and Betty Benrey. 2015. Crop domestication and its impact on naturally selected trophic interactions. *Annual Review of Entomology* 60:35–58.

Showed how crop domestication, which is a process of artificially selecting plants to increase their suitability to human requirements (taste, yield, storage, and cultivation practices), can profoundly alter interactions among plants, herbivores, and their natural enemies. Available online by subscription.

Hance, Thiery, Joan van Baaren, Philippe Vernon, and Guy Boivin. 2007. Impact of extreme temperatures on parasitoids in a climate change perspective. *Annual Review of Entomology* 52:107–126.

Analyzed the effects of global warming and extreme temperatures on the life-history traits of parasitoids and interactions with their hosts. Available online by subscription.

Hunter, Mark D. 2001. Effects of elevated atmospheric carbon dioxide on insect-plant interactions. *Agricultural and Forest Entomology* 3:153–159.

Focused on what is known about changes in plant quality under elevated CO_2 and how such changing food quality might interact with other ecological variables to alter the performance and abundance of insects on plants. Available online by subscription.

Leckey, Erin H., Dena M. Smith, César R. Nufio, and Katherine F. Fornash. 2014. Oak-insect herbivore interactions along a temperature and precipitation gradient. *Acta Oecologica* 61:1–8.

A good example of using an elevation gradient from coastal northern California to the upper montane woodlands of Sierra Nevada, to examine the relationship between climatic factors (temperature and precipitation) and oak herbivory levels at multiple scales, across all oak species pooled, between evergreen and deciduous species and within species. Available online by subscription.

Polce, Chiara, Michael P. Garratt, Mette Termansen, et al. 2014. Climate-driven spatial mismatches between British orchards and their pollinators: Increased risks of pollination deficits. *Global Change Biology* 20:2815–2828.

Examined the distribution of orchard species (apples, pears, plums, and other top fruits) and their pollinators in Great Britain for present and future climatic conditions projected for 2050 under the SRES A1B Emissions Scenario (a report of N. Nakićenović, J. Alcamo, G. Davis, et al., 2000 IPCC Special Report on Emissions Scenarios [SRES] [Cambridge, UK: Cambridge University Press, 2000]). Available online by subscription.

Rasmann, Sergio, Loïc Pellissier, Emmanuel Defossez, Hervé Jactel, and Georges Kunstler. 2014. Climate-driven change in plant-insect interactions along elevation gradients. *Functional Ecology* 28:46–54.

Documents variations in herbivory and plant defenses along altitudinal gradients that act as “natural experiments.” The authors use an empirical model to predict how specialist herbivore abundance may shift with respect to elevation in the near future. Available online by subscription.

Sgrò, Carla M., John S. Terblanche, and Ary A. Hoffmann. 2016. What can plasticity contribute to insect responses to climate change? *Annual Review of Entomology* 61:433–451.

Since plastic responses figure prominently in research on insect adaptation to climate change, this paper reviews the different types of insect’s plastic responses and whether they contribute much to adaptation. Available online by subscription.

Tscharntke, Teja, and Roland Brandl. 2004. Plant-insect interactions in fragmented landscapes. *Annual Review of Entomology* 49:405–430.

Important review of the effects of habitat loss and habitat fragmentation on plant-herbivore, herbivore-enemy, and plant-pollinator interactions. Available online by subscription.

Zavala, Jorge A., Paul D. Nabity, and Evan H. deLucia. 2013. An emerging understanding of mechanisms governing insect herbivory under elevated CO_2. *Annual Review of Entomology* 58:79–97.

Focused on emerging mechanisms by which increasing CO_2 alters the defense chemistry (by changing the chemical composition of foliage) and signaling of plants and, in parallel, the responses of folivorous insects to these changes, which are, however, highly variable. Available online by subscription.

Insect Declines Caused to Global Changes

There is no doubt that insects constitute, by their abundance, diversity, and adaptability, a crucial component of life on earth. They enable the maintenance and dynamic equilibrium of ecosystems through the services they provide, such as pollination (Öckinger and Smith 2007; Ollerton, et al. 2011); herbivory and detritivory (Mattson and Addy 1975, Yang and Gratton 2014); nutrient cycling (Yang and Gratton 2014); pest control; and food source provision for birds, mammals, and amphibians. A good overview published in *UN-Environment Foresight Brief* (Gordon, et al. 2019) highlights how insects' decline is "accelerating," mostly attributed to global changes (climate change and human being activities). This paper explores insect services, threats, and solutions to sustain insect populations.

Mattson, William J., and Norton D. Addy. 1975. Phytophagous insects as regulators of forest primary production. *Science* 190.4214: 515–522.

This paper examines, for the first time, evidence for the hypothesis that insects can act as regulators of primary production and nutrient cycling and thus perform a vital function in ecosystem dynamics.

Gordon, Ian, Paul-André Calatayud, Philippe le Gall, and Lionel Garnery. 2019. We are losing the "Little things that run the world." *UN Environment Foresight Brief* 11:1–9.

A good overview on how insect decline is "accelerating," mostly attributed to global changes (climate change and human being activities). This paper explores also insect services, threats, and solutions to sustain insect populations.

Öckinger, Erick, and Henrik G. Smith. 2007. Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology* 44.1: 50–59.

An extensive survey of butterflies and bumble bees indicating that habitat fragmentation and intensified agricultural practices are considered to be a threat against services provided by pollinators.

Ollerton, Jeff, Rachael Winfree, and Sam Tarrant. 2011. How many flowering plants are pollinated by animals? *Oikos* 120.3: 321–326.

This paper estimated the number and proportion of flowering plants that are pollinated by animals using published and unpublished community-level surveys of plant pollination systems that recorded whether each species present was pollinated by animals or wind. The authors estimated that the global number and proportion of animal-pollinated angiosperms as 308,006, which is 87.5 percent of the estimated species-level diversity of flowering plants.

Yang, Louie H., and Claudio Gratton. 2014. Insects as drivers of ecosystem processes. *Current Opinion in Insect Science* 2:26–32.

This paper highlighted that insects constitute large direct inputs of biomass of detrital pool. They transform biomass and alter decomposition rates.

Protecting Plants from Pest Damages

Most of the major crop pests have been introduced more or less recently, and their geographical area has been altered by growth in agricultural activity and commercial trade. The main means of protection are using natural plants' resistant genes, habitat management, using natural enemies, managing the behavior of phytophagous insects by semiochemicals, and action on the insect's physiology. Naturally resistant genes have been largely used in classical breeding programs (see de Morais and Pinheiro 2012). Since the first description of genetically modified (GM) plants resistant to crop pests in 1987, insect-resistant biotech crops have been well developed (see Gatehouse, et al. 2011, which gives an updated statement on their impacts on beneficial arthropods, or natural enemies). Another notion integrating supporting and regulating ecosystem functions has been proposed as a promising way to decrease agrochemical inputs and negative environmental impacts while maximizing crop productivity. The term “agroecology” appeared in the 1930s, and the concept underwent a significant development during the 1980s (Rusch, et al. 2017, which shows the importance of using both habitat management and biological control to maximize crop production). Semiochemicals, such as insect pheromones and plant kairomones that divert crop pests from their targets, have also been studied (Hokkanen 1991). New control tools for the identification and possible use of natural antagonists or analogues of plant molecules (biopesticides) have also been developed. The plant world is a particularly interesting source of such biopesticides. It is thus possible to control or at least limit the attacks of insect pests by acting on their physiology by using either hormone-acting molecules or plant toxins (Darrouzet and Desneux 2013).

Darrouzet, Eric, and Nicolas Desneux. 2013. Action sur la physiologie des insectes. In *Interactions insectes-plantes*. Edited by Nicolas Sauvion, Paul-André Calatayud, Denis Thiéry, and Frédéric Marion-Poll, 709–719. Versailles, France: Éditions Quae.

An overview on the use of natural antagonists or analogues of plant molecules (either hormone-acting molecules or plant toxins) that act on the physiology of crop pests.

de Morais, Alexndre Augusto, and José Baldin Pinheiro. 2012. Breeding for resistance to insect pests. In *Plant breeding for biotic stress resistance*. Edited by Roberto Fritsche-Neto and Aluizio Borem, 103–125. Berlin and Heidelberg, Germany: Springer-Verlag.

Relates the history and the contribution of the conventional breeding of plant resistance to insect pests as well as the biotechnology (cf. genetic engineering techniques allowing isolated genes to be introduced in cultivars). Available online by subscription.

Gatehouse, Angharad M. R., Natalie Ferry, Martin G. Edwards, and Howard A. Bell. 2011. Insect-resistant biotech crops and their impacts on beneficial arthropods. *Philosophical Transactions of the Royal Society B: Biological Sciences* 366:1438–1452.

The paper discusses the findings to date with respect to both commercial and experimental GM crops expressing anti-insect genes, with particular emphasis on insect predators and parasitoids.

Hokkanen, Heikki M. T. 1991. Trap cropping in pest management. *Annual Review of Entomology* 36:119–138.

A good review on the different strategies that enhance the attractiveness of trap systems to divert the crop pests to their targets. Available online by subscription.

Rusch, Adrien, Riccardo Bommarco, and Barbara Ekbom. 2017. Conservation biological control in agricultural landscapes. In *Insect-plant interactions in a crop protection perspective*. Edited by Nicolas Sauvion, Paul-André Calatayud, and Denis Thiéry, 333–355. Advances in Botanical Research 81. London: Academic Press.

Gives a clear, updated synthesis on habitat management and biological control in order to protect crops from pests and maximize crop production. Available online by subscription.

Predicting Insect Pests Phenology for a Better Plants Protection

While biodiversity is at risk at the global scale, pests are responsible for potential crop losses from 50 percent to 80 percent on major crops, so that crop protection plays a central role in safeguarding crop productivity (Oerke 2006). Among pests, crops are especially threatened by insects, principally because of herbivory and transmission of viruses. It is thus critical to develop models that accurately predict insect pest phenology to adjust control practices and interventions at the right time. Insects sensitivity to temperature is well known, but their potential responses together with the response of their associated natural enemies to the ongoing climate change remain unclear. So in recent years, the need to understand and predict future ecological effects of climate change has renewed interest in studying the relationship between temperature and organisms’ performance metrics such as development rate for both herbivores and their associated natural enemies (Rebaudo and Rabhi 2018). Development rate is a central feature of an ectotherm’s life history (Taylor 1981) and the building block of most population dynamics models (Hilbert and Logan 1983). Temperature-dependent development rate allows for the estimation of species’ emergence time through the seasons (phenology), number of generations (voltinism), or potential distribution (Moore and Remais 2014), with practical applications for agriculture and epidemiology (Roy, et al. 2002).

Hilbert, David W., and Jesse Logan. 1983. Empirical model of nymphal development for the migratory grasshopper, *Melanoplus sanguinipes* (Orthoptera: Acrididae). *Environmental Entomology* 12.1: 1–5.

Among the more than thirty equations available to date, this paper presents an example of a mathematical equation to characterize the nonlinear relationship between temperature and development rate in insects, as an alternative to the traditional degree-day model.

Moore, Julia L., and Justin V. Remais. 2014. Developmental models for estimating ecological responses to environmental variability: Structural, parametric, and experimental issues. *Acta Biotheoretica* 62.1: 69–90.

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back to top