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► To cite this version:

Pilar Fernandez-Conradi, Bastien Castagneyrol, Hervé Jactel, Sergio Rasmann. Combining phytochemicals and multitrophic interactions to control forest insect pests. *Current Opinion in Insect Science*, 2021, 44, pp.101-106. 10.1016/j.cois.2021.04.007 . hal-03252404

HAL Id: hal-03252404

<https://hal.science/hal-03252404>

Submitted on 7 Jun 2021

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Combining phytochemicals and multitrophic interactions to control forest insect pests

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Forest pests can cause massive ecological and economic damage worldwide. Ecologically sound solutions to diminish forest insect pest impacts include the use of their natural enemies, such as predators and parasitoids, as well as entomopathogenic fungi, bacteria or viruses. Phytochemical compounds mediate most interactions between these organisms, but knowledge of such chemically mediated multitrophic relationships is still at its infancy for forest systems, particularly when compared to agricultural systems. Here, we highlight the main gaps in how phytochemicals of forest trees facilitate or interfere with trophic interactions between trees, insect herbivores, and interacting organisms including predators, parasitoids and microbes. We propose future avenues of research on phytochemical-based biocontrol of forest pests taking into account the characteristics of trees and forests.

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Current Opinion in Insect Science 2021, **44**:101–106

This review comes from a themed issue on **Parasites/parasitoids/biological control**

Edited by **Feng Zhu**

<https://doi.org/10.1016/j.cois.2021.04.007>

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Introduction

Forests ecosystems cover about one third of the world land base and provide vital services to people, such as climate regulation, wood production or biodiversity reservoir [1]. But forests and their services are threatened by a diversity of forest pests responsible for important ecological and economic losses worldwide [2,3]. Climate change is expected to increase the frequency and distribution of native and invasive insect outbreaks [4],

increasing the need to develop more efficient and sustainable pest control strategies.

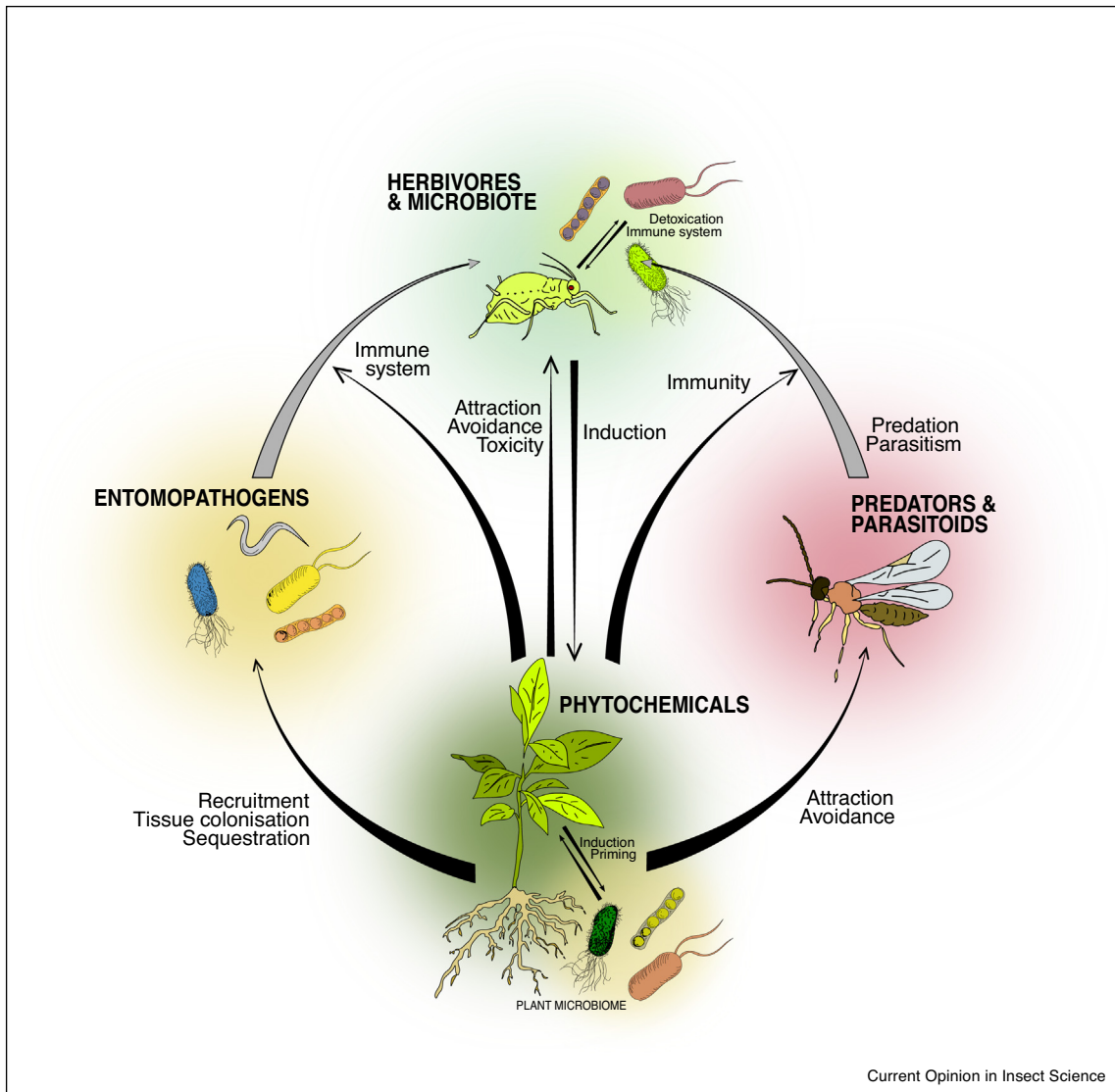
In nature, insect herbivory is ultimately controlled by bottom-up and top-down forces that are both influenced by plant phytochemicals [5]. Bottom-up forces include the production of toxic phytochemicals that inhibit, toxify or even kill the herbivore that has ingested the plant tissues [6]. On the other hand, top-down forces include the production of information-rich chemical cues that attract herbivore enemies, or that modifies insect susceptibility to their pathogens [7]. Therefore, a common pest control strategy in forest systems involves the release and acclimation of non-native natural enemies (classical biological control [8]) or the enhancement of local native enemies (conservation biological control [9]). However, current understanding of how such trophic interactions are mediated or influenced by host plant chemistry remains limited [10–12].

Moreover, the production of phytochemicals by the plants, and how they impact insect pests, is also influenced by the microbes that are intimately associated with the plants and the insects [13]. So far, most work on the chemically-mediated interactions between insect pests, their natural enemies and their associated microbes, and how this can be used for effective biological control, has predominantly focused on agricultural systems. Accordingly, comparatively fewer chemical-ecology studies have been targeted for reducing insect pest load in forest ecosystems, and this merits further attention. Below, we highlight recent research on the mediation of tri-trophic interactions between trees, insect herbivores and their enemies by plant phytochemicals, including the role of the tree and insect microbiomes (Figure 1). We further discuss how this research can be exploited for controlling forest pests in a more ecologically-sound manner.

Chemically mediated trophic interactions between plants, herbivores predators, parasitoids and entomopathogens Semiachemicals mediates insect herbivore host recognition by predators and parasitoids

A wealth of research has shown that when an insect herbivore damages a plant, lays its eggs or sometimes only lands on it, it triggers the production of volatile organic compounds (VOCs) by that plant [14,15]. Such

Figure 1



Current Opinion in Insect Science

Overview of how phytochemicals can mediate or interfere with multitrophic interactions between trees, insect herbivores and their enemies. Phytochemicals can influence herbivores directly, by modifying insect searching behavior (i.e. host plant attraction or avoidance) and the quality of their host plant (i.e. toxicity). Moreover, phytochemicals can also influence herbivores indirectly, by modifying their immune response to their natural enemies (entomopathogens, predators and parasitoids) and natural enemy's ability to recognise and/or colonise the tree. Additionally, phytochemical production and its effect on herbivores may depend on plant and insect microbiomes (i.e. some bacteria, fungi, virus, protist and nematodes), respectively. Plant microbiome can modify plant phytochemicals by inducing plant defense against herbivory or even priming the plant against future herbivore attacks. On the other hand, insect microbiome may detoxify or interfere with secondary compounds production by the plant and influence insect immune system. Black arrows represent direct interactions mediated by phytochemicals. Grey arrows represent indirect consequences of phytochemicals on trophic interactions between insect herbivores and their natural enemies.

herbivore-induced VOCs can then be perceived by the natural enemies of the herbivorous insect as semiochemical cues informing on the presence or even the identity of their host or prey [16]. The resulting reduction in herbivory is called induced indirect resistance [17] and indirect defense when it ultimately increases plant fitness [18]. Tritrophic interactions mediated by VOCs are

widespread in the plant kingdom, including tree-based systems; such as in pine [19,20], birch [21], beech [22], hornbeam [23], oak [23], linden [23], willow [24,25], elm [11], wild apple [26], eucalyptus [27] and fig [24]. However, for obvious methodological reasons related to sampling in the tree canopy of mature forests, and sampling in outdoor variable conditions, most studies on VOCs

emitted by trees have been carried out on excised branches or potted saplings. The few experiments conducted in more realistic conditions have thus resolved to use young and small trees [11,22–24; but see Ref. 28]. These issues raise the question about the effectiveness of VOCs in dense forests of tall trees. First, VOCs emitted by the leaves of trees must be perceived by herbivores' natural enemies against a background of abundant and complex odours emitted by the entire canopy [22], which, added to the fact VOCs can degrade quickly by interacting with atmospheric gases [29], may dilute their effectiveness. Second, tree-to-tree signalling or eavesdropping [25,29] can lead to the emission of info-chemicals from neighbouring trees, reinforcing, or, on the contrary, disturbing the perception of attractive signals by natural enemies. Third, forests are characterized by a great diversity of herbivorous species, which can combine their attacks on the same tree, and inevitably induce a larger and more diverse production of VOCs. Finally, VOCs can be perceived by a more or less specialized guild of natural enemies [22]. Thus, the release of VOCs, upon herbivore damage, can influence more complex trophic interactions than predation, such as apparent competition [18] or hyper-parasitism [30]. It would therefore be interesting to combine multiple chemical induction experiments on adult trees with exhaustive arthropod community sampling, and including parasitoid rearing protocols, not only to better understand their ecological and evolutionary relevance [17], but also the application perspectives for forest protection.

Phytochemicals influence insect herbivore susceptibility to natural enemies

Secondary compounds may have direct effects on the predators, parasitoids and pathogens of insect herbivores, thus affecting biocontrol efficacy. For example, Sandre *et al.* [31], found that larvae of the Tussock moth (*Orgyia antiqua*) was more sensitive to the entomopathogenic fungus *Metarhizium anisopliae* when growing on less chemically-defended willows (*Salix* spp.), probably because of the negative effect of plant glycosides on the pathogen. Moreover, phytochemicals can also affect herbivore enemies, indirectly, because they modify the insect immune system [32,33], or because they can be sequestered by some insect species for their own protection [34,35]. For example, woolly bear caterpillars (*Grammia incorrupta*) are able to ingest plant toxins called pyrrolizine alkaloids, improving their survival against tachinid flies endoparasites [36]. Therefore, a better understanding of the phytochemical compounds implicated in insect-enemies interactions could improve biocontrol efficacy against forest pests [7,32], by either increasing or decreasing the natural enemies' efficacy and/or disabling the immune system of the insect. To achieve this aim, future studies will have to perform biological control experiments on various trees species or genotypes, exploring more thoroughly

the role of phytochemicals on these interactions by using chemical ecology approaches such as metabolomic profiling.

The microbiomes of trees and insects influence plant–herbivore interactions

Trees are holobionts. They are associated with a wide variety of microorganisms — the microbiome — that inhabits every tree organ (leaves: phyllosphere; roots: rhizosphere; internal plant tissues: endophytes) and with which they interact in numerous and complex ways [37,38^{*}]. Observational and experimental studies have revealed correlations between the taxonomic and functional characteristics of the plant microbiome and insect herbivory [39–41, but see Ref. 42]. Tree-associated microbes can act as either entomopathogenic agents or as mutualists, boosting tree defenses and producing metabolites which are deterrent or toxic to insects [43,44^{*}]. For example, Miller *et al.* [45] showed that a rugulosin-producing endophyte diminished defoliation by eastern spruce budworm. In addition, later research showed that seedling inoculation by such endophytic fungus can persist and produce rugulosin for a least ten years in the tree [46]. Based on these findings, the manipulation of tree microbial communities may be of great significance for the improved tolerance of forest ecosystems to pests. Moreover, plant microbiomes can induce and/or prime chemical defenses [38^{*},47], and modify the constitutive and induced production of VOCs [37,47], but how these molecules influence tritrophic interactions in forests is yet unknown. In this sense, a major task would be to identify and manipulate plant microbes with a special interest for pest control, taking into account the chemical interactions between the microbe and its host, as well as the indirect consequences on herbivore enemies. The increasing development of sequencing and metabolomic approaches have promising avenues to this end. However, it is primordial to understand how phytochemical compounds mediate plant-insect-enemies' interactions in order to predict ecosystem level consequences of microbiome manipulation.

On the other side, insect herbivores are also tightly associated with a large diversity of microorganisms on their body surface, in their gut or in specialized organs, which, in turn, can interact with phytochemicals in several ways [48^{**},49]. Well-known examples for how insect microbiomes are essential for forest insects is the microbial provision of cellulolytic and lignolytic enzymes, as well as essential nutrients, that the insects, in particular bark beetles, wood borers and to some extent sap-feeders, cannot directly obtain from their woody diet [39,50,51]. Moreover, the insect microbiome interacts with phytochemicals through the detoxification of plant chemical defenses [48^{**},52–54], or the regulation of plant signalling pathways triggered by herbivory [55–57]. For instance, Mason *et al.* [54] demonstrated that the bacteria

extracted from gypsy moth larvae midgut can detoxify phenolic glycosides and condensed tannins produced by trembling aspen (*Populus tremuloides*), although this results in only a slight increase of insect performance. Although our understanding of the ecological role of insect microbiomes is still very limited, recent research is highlighting their potential applications for forest pest control [58,59,60]. For example, the VOCs produced by conifer bark beetles-associated fungi can act as attractants or repellents for their insect hosts, but also their predators and parasitoids [58,60]. Exploiting these compounds could provide new means for efficient forest pest control. Additionally, the effects of phytochemicals on insect pathogens may also be mediated by the insect microbiome. In this sense, Gasmi *et al.* [61] showed, in an agricultural system, that artificial VOCs sprayed on *Spodoptera exigua* larvae increased their susceptibility to *Bacillus thuringiensis* and multiple nucleopolyhedroviruses, probably because of induced changes in the insect microbiome. Further research along these lines could help to identify new strategies for the biocontrol of pests. However, to our knowledge, this field of research is currently still very scant of examples for forested systems. Manipulations of insect microbiome may largely modify how insect pests exploit their host and improve top-down control by their natural enemies [49]. One of the forthcoming challenges for future studies will be to connect forest insect microbiome manipulations with their effects on higher trophic level organisms.

Conclusions and perspectives for future research

While the chemical ecology and phytochemical-mediated mechanisms of plant-insect-microbe interactions are intensively being addressed in model plants and crop systems, we are confronted with an enormous gap for similar research in forested systems. During the last two decades, phytochemicals have been progressively included as the focus of research for novel pest control strategies in forests. Phytochemicals may be used for developing more efficient biopesticides, repellents for insect pests, volatile based attractants for natural enemies, plant defenses elicitor sprays, as well for developing novel plant selection strategies based on phytochemical traits [14,16,30]. Nonetheless, current agroecological system-based knowledge cannot easily be transposed to forest systems. For example, the use of tree varieties that emit specific HIPVs, or the use of dispensers with natural enemies' attractants are hardly approachable for large forest systems (selection time too long [8] and/or too expensive [62]). Instead, a promising approach would be the 'attract-and-reward' strategy as conservation biological control method [63], which would combine, in a context of mixed-species forests, tree species of economic interest for production, companion species sensitive to herbivores and emitting VOCs and other tree or shrub species providing nesting (e.g. tree-related microhabitats) or food resources (e.g. pollen, honeydew) for the natural enemies. Similarly

challenging for forests' applications, compared to its agricultural counterpart, is the use of inducers of defenses in plants (e.g. by injecting or spraying jasmonic acid, salicylic acid, methyl jasmonate or methyl salicylate [16]), since the magnitude of other confounding factors seems to be much greater than within a crop field. However, recent research is showing that trees' defense induction can indeed be manipulated by exogenous phytohormonal applications [28,64,65,66], and in turn potentially exploitable for forest protection against economically important pests. Furthermore, a major task would be to identify the extent of tree defense inducers, from an individual scale to a forest community perspective, as well as the temporal scale of effectivity of such induction events. In this sense, we call for future studies combining experimental manipulations of tree defenses and diachronic surveys of tri-trophic interactions at different spatial scales in forest systems.

Plant-associated and insect-associated microbiomes are also promising, but yet largely underexplored, targets of research for the improvement of pest management control. For example, VOCs-producing microbes could be applied to trees in order to disrupt tree cues for insect herbivores food source location [14,67]. Moreover, the temporal stability of tritrophic interactions mediated by VOCs remains to be investigated in forests, especially for determining whether it is a sustainable option for managing herbivore damage over the long term of forestry cycles. The sustained release of VOCs can be a selection filter modifying the composition of herbivore communities (e.g. the ratio of specialists to generalists) and natural enemy communities [68]. The response of trees (e.g. induction of defense compounds or changes in leaf traits) depends on the phenotypic plasticity of plants but also on epigenetic processes that can change over time. The microbial communities involved may also be subject to selection pressure leading to micro-evolutionary processes. The combined result of these dynamics is difficult to predict, but working on perennial species such as trees, with a large number of herbivores cohabiting on the same individual, may provide a suitable field of study for such long-term studies.

Conflict of interest statement

Nothing declared.

Acknowledgements

This project was financed by a Swiss National Science Foundation grant (31003A_179481) to SR. We thank Thomas Boivin and anonymous reviewer for comments on previous versions of the manuscript.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest

1. Secretariat: *Global Assessment Report on Biodiversity and Ecosystem Services*. IPBES; 2019.
2. Wingfield MJ, Brockerhoff EG, Wingfield BD, Slippers B: **Planted forest health: the need for a global strategy**. *Science* 2015, **349**:832-836.
3. Diagne C, Leroy B, Vaissière A-C, Gozlan RE, Roiz D, Jarić I, Salles J-M, Bradshaw CJA, Courchamp F: **High and rising economic costs of biological invasions worldwide**. *Nature* 2021, **592**:571-576 <http://dx.doi.org/10.1038/s41586-021-03405-6>.
4. Jactel H, Koricheva J, Castagneyrol B: **Responses of forest insect pests to climate change: not so simple**. *Curr Opin Insect Sci* 2019, **35**:103-108.
5. Vidal MC, Murphy SM: **Bottom-up vs. top-down effects on terrestrial insect herbivores: a meta-analysis**. *Ecol Lett* 2018, **21**:138-150.
6. Schoonhoven LM, Loon BV, van Loon JJA, Dicke M: *Insect-Plant Biology*. OUP Oxford; 2005.
7. Cory JS, Hoover K: **Plant-mediated effects in insect-pathogen interactions**. *Trends Ecol Evol* 2006, **21**:278-286.
8. Kenis M, Hurley BP, Hajek AE, Cock MJW: **Classical biological control of insect pests of trees: facts and figures**. *Biol Invasions* 2017, **19**:3401-3417.
9. Jactel H, Moreira X, Castagneyrol B: **Tree diversity and forest resistance to insect pests: patterns, mechanisms, and prospects**. *Ann Rev Entomol* 2021, **66**:277-296.
10. Havill NP, Raffa KF: **Compound effects of induced plant responses on insect herbivores and parasitoids: implications for tritrophic interactions**. *Ecol Entomol* 2000, **25**:171-179.
11. Büchel K, Austel N, Mayer M, Gershenson J, Fenning TM, Meiners T: **Smelling the tree and the forest: elm background odours affect egg parasitoid orientation to herbivore induced terpenoids**. *BioControl* 2014, **59**:29-43.
12. Fischbein D, Villacide JM, López B, Corley JC, Martínez AS: **Host-related volatile cues used by a parasitoid wasp during foraging for its woodboring host**. *Entomol Exp Appl* 2018, **166**:907-913.
13. Wielkopolan B, Obre?palska-Ste?płowska A: **Three-way interaction among plants, bacteria, and coleopteran insects**. *Planta* 2016, **244**:313-332.
14. Bouwmeester H, Schuurink RC, Bleeker PM, Schiestl F: **The role of volatiles in plant communication**. *Plant J* 2019, **100**:892-907
Review on volatile communication between plants and other organisms, and its potential applications for agriculture.
15. Lämke JörnS, Unsicker SB: **Phytochemical variation in treetops: causes and consequences for tree-insect herbivore interactions**. *Oecologia* 2018, **187**:377-388.
16. Turlings TCJ, Erb M: **Tritrophic interactions mediated by herbivore-induced plant volatiles: mechanisms, ecological relevance, and application potential**. *Ann Rev Entomol* 2018, **63**:433-452.
17. Karban R: **The ecology and evolution of induced responses to herbivory and how plants perceive risk**. *Ecol Entomol* 2020, **45**:1-9.
18. Pearse IS, LoPresti E, Schaeffer RN, Wetzel WC, Mooney KA, Ali JG, Ode PJ, Eubanks MD, Bronstein JL, Weber MG: **Generalising indirect defence and resistance of plants**. *Ecol Lett* 2020, **23**:1137-1152.
19. Mäntylä E, Kipper S, Hilker M: **Insectivorous birds can see and smell systemically herbivore-induced pines**. *Ecol Evol* 2020, **10**:9358-9370
Nice example on how herbivore induced changes on plant volatiles and leaf light reflectance affects tree attraction by predatory birds.
20. Hilker M, Kobs C, Varama M, Schrank K: **Insect egg deposition induces *Pinus sylvestris* to attract egg parasitoids**. *J Exp Biol* 2002, **205**:455-461.
21. Klemola T, Ammунet T, Andersson T, Klemola N, Ruohomäki K: **Larval parasitism rate increases in herbivore-damaged trees: a field experiment with cyclic birch feeding moths**. *Oikos* 2012, **121**:1525-1531.
22. Gossner MM, Weisser WW, Gershenson J, Unsicker SB: **Insect attraction to herbivore-induced beech volatiles under different forest management regimes**. *Oecologia* 2014, **176**:569-580.
23. Volf M, Weinhold A, Seifert CL, Holicová T, Uthe H, Alander E, Richter R, Salminen J-P, Wirth C, van Dam NM: **Branch-localized induction promotes efficacy of volatile defences and herbivore predation in trees**. *J Chem Ecol* 2021, **47**:99-111.
24. Mrazova A, Sam K: **Application of methyl jasmonate to grey willow (*Salix cinerea*) attracts insectivorous birds in nature**. *Arthropod Plant Interact* 2018, **12**:1-8.
25. Yoneya K, Takabayashi J: **Plant-plant communication mediated by airborne signals: ecological and plant physiological perspectives**. *Plant Biotechnol* 2014, **31**:409-416.
26. Amo L, Jansen JJ, van Dam NM, Dicke M, Visser ME: **Birds exploit herbivore-induced plant volatiles to locate herbivorous prey**. *Ecol Lett* 2013, **16**:1348-1355.
27. Low PA, McARTHUR C, Fisher K, Hochuli DF: **Elevated volatile concentrations in high-nutrient plants: do insect herbivores pay a high price for good food?** *Ecol Entomol* 2014, **39**:480-491.
28. Mageroy MH, Christiansen E, Långström B, Borg-Karlson A-K, Solheim H, Björklund N, Zhao T, Schmidt A, Fossdal CG, Krokene P: **Priming of inducible defenses protects Norway spruce against tree-killing bark beetles**. *Plant Cell Environ* 2020, **43**:420-430.
29. Holopainen JK, Blande JD: **Where do herbivore-induced plant volatiles go?** *Front Plant Sci* 2013, **4**.
30. Cusumano A, Harvey JA, Bourne ME, Poelman EH, G de Boer J: **Exploiting chemical ecology to manage hyperparasitoids in biological control of arthropod pests**. *Pest Manag Sci* 2020, **76**:432-443.
31. Sandre S-L, Tammaru T, Hokkanen H: **Pathogen resistance in the moth *Orygia antiqua*: direct influence of host plant dominates over the effects of individual condition**. *Bull Entomol Res* 2011, **101**:107-114.
32. Shikano I: **Evolutionary ecology of multitrophic interactions between plants, insect herbivores and entomopathogens**. *J Chem Ecol* 2017, **43**:586-598.
33. Yoon SA, Harrison JG, Philbin CS, Dodson CD, Jones DM, Wallace IS, Forister ML, Smilanich AM: **Host plant-dependent effects of microbes and phytochemistry on the insect immune response**. *Oecologia* 2019, **191**:141-152.
34. War AR, Buhroo AA, Hussain B, Ahmad T, Nair RM, Sharma HC: **Plant defense and insect adaptation with reference to secondary metabolites**. In *Co-Evolution of Secondary Metabolites*. Edited by Mérillon J-M, Ramawat KG. Springer International Publishing; 2020:795-822.
35. Kaiser L, Ode P, van Nouhuys S, Calatayud P-A, Colazza S, Cortesero A-M, Thiel A, van Baaren J: **Chapter six - the plant as a habitat for entomophagous insects**. In *Advances in Botanical Research*. Edited by Sauvion N, Thiéry D, Calatayud P-A. Academic Press; 2017:179-223.
36. Singer MS, Mace KC, Bernays EA: **Self-medication as adaptive plasticity: increased ingestion of plant toxins by parasitized caterpillars**. *PLoS One* 2009, **4**:e4796.
37. Grunseich JM, Thompson MN, Aguirre NM, Helms AM: **The role of plant-associated microbes in mediating host-plant selection by insect herbivores**. *Plants* 2020, **9**:6.
38. Gruden K, Lidoy J, Petek M, Podpečan V, Flors V, Papadopoulou KK, Pappas ML, Martínez-Medina A, Bejarano E, Biere A *et al.*: **Ménage à Trois: unraveling the mechanisms regulating plant-microbe-arthropod interactions**. *Trends Plant Sci* 2020, **25**:1215-1226
Up-to-date, mechanistic review on plant-microbe-arthropods interactions.
39. Scully ED, Geib SM, Carlson JE, Tien M, McKenna D, Hoover K: **Functional genomics and microbiome profiling of the Asian longhorned beetle (*Anoplophora glabripennis*) reveal insights**

- into the digestive physiology and nutritional ecology of wood feeding beetles. *BMC Genomics* 2014, **15**:1096.
40. Geib SM, del Mar Jimenez-Gasco M, Carlson JE, Tien M, Jabbour R, Hoover K: **Microbial community profiling to investigate transmission of bacteria between life stages of the wood-boring beetle, *Anoplophora glabripennis***. *Microb Ecol* 2009, **58**:199-211.
 41. Borruso L, Wellstein C, Bani A, Bacchiocchi SC, Margoni A, Tonin R, Zerbe S, Brusetti L: **Temporal shifts in endophyte bacterial community composition of sessile oak (*Quercus petraea*) are linked to foliar nitrogen, stomatal length, and herbivory**. *PeerJ* 2018, **6**:e5769.
 42. Menkis A, Povilaitienė A, Marčiulynas A, Lynikienė J, Gedminas A, Marčiulytė D: **Occurrence of common phyllosphere fungi of horse-chestnut (*Aesculus hippocastanum*) is unrelated to degree of damage by leafminer (*Cameraria ohridella*)**. *Scand J For Res* 2019, **34**:26-32.
 43. Sumarah MW, Miller JD: **Anti-insect secondary metabolites from fungal endophytes of conifer trees**. *Nat Prod Commun* 2009, **4**:1934578X0900401112.
 44. Eberl F, Uhe C, Unsicker SB: **Friend or foe? The role of leaf-inhabiting fungal pathogens and endophytes in tree-insect interactions**. *Fungal Ecol* 2019, **38**:104-112
- Review on interactions between leaf inhabiting fungi and herbivore insects in forest.
45. Miller JD, Sumarah MW, Adams GW: **Effect of a rugulosin-producing endophyte in *Picea glauca* on *Choristoneura fumiferana***. *J Chem Ecol* 2008, **34**:362-368.
 46. Frasz S, Walker A, Nsiama T, Adams G, Miller J: **Distribution of the foliar fungal endophyte *Phialocephala scopiformis* and its toxin in the crown of a mature white spruce tree as revealed by chemical and qPCR analyses**. *Can J For Res* 2014, **44**:1138-1143 <http://dx.doi.org/10.1139/cjfr-2014-0171>.
 47. Beck JJ, Vannette RL: **Harnessing insect-microbe chemical communications to control insect pests of agricultural systems**. *J Agric Food Chem* 2017, **65**:23-28.
 48. Mason CJ: **Complex relationships at the intersection of insect gut microbiomes and plant defenses**. *J Chem Ecol* 2020, **46**:793-807
- Review on how gut microbes can influence interactions between insects and their plants through multiple mechanisms. They provide a clear and forward-looking synthesis on a nascent and still underexplored research field.
49. Giron D, Dedeine F, Dubreuil G, Huguet E, Mouton L, Outreman Y, Vavre F, Simon JC: **Influence of microbial symbionts on plant-insect interactions**. In *Insect-Plant Interactions in a Crop Protection Perspective*. Edited by Sauvion N, Thiéry D, Calatayud P-A. Elsevier, Academic Press; 2017:225-257.
 50. Hulcr J, Stelinski LL: **The ambrosia symbiosis: from evolutionary ecology to practical management**. *Ann Rev Entomol* 2017, **62**:285-303.
 51. Six DL: **Niche construction theory can link bark beetle-fungus symbiosis type and colonization behavior to large scale causal chain-effects**. *Curr Opin Insect Sci* 2020, **39**:27-34.
 52. Hammerbacher A, Schmidt A, Wadke N, Wright LP, Schneider B, Bohlmann J, Brand WA, Fenning TM, Gershenzon J, Paetz C: **A common fungal associate of the spruce bark beetle metabolizes the stilbene defenses of Norway spruce**. *Plant Physiol* 2013, **162**:1324-1336.
 53. Paniagua Voirol LR, Frago E, Kaltenpoth M, Hilker M, Fatouros NE: **Bacterial symbionts in Lepidoptera: their diversity, transmission, and impact on the host**. *Front Microbiol* 2018, **9**.
 54. Mason CJ, Lowe-Power TM, Rubert-Nason KF, Lindroth RL, Raffa KF: **Interactions between bacteria and aspen defense chemicals at the phyllosphere – herbivore interface**. *J Chem Ecol* 2016, **42**:193-201.
 55. Chung SH, Rosa C, Scully ED, Peiffer M, Tooker JF, Hoover K, Luthe DS, Felton GW: **Herbivore exploits orally secreted bacteria to suppress plant defenses**. *Proc Natl Acad Sci U S A* 2013, **110**:15728-15733.
 56. Wang J, Chung SH, Peiffer M, Rosa C, Hoover K, Zeng R, Felton GW: **Herbivore oral secreted bacteria trigger distinct defense responses in preferred and non-preferred host plants**. *J Chem Ecol* 2016, **42**:463-474.
 57. Frago E, Mala M, Weldegergis BT, Yang C, McLean A, Godfray HCJ, Gols R, Dicke M: **Symbionts protect aphids from parasitic wasps by attenuating herbivore-induced plant volatiles**. *Nat Commun* 2017, **8**:1860.
 58. Kandasamy D, Gershenzon J, Hammerbacher A: **Volatile organic compounds emitted by fungal associates of conifer bark beetles and their potential in bark beetle control**. *J Chem Ecol* 2016, **42**:952-969.
 59. Chakraborty A, Modlinger R, Ashraf MZ, Synek J, Schlyter F, Roy A: **Core mycobiome and their ecological relevance in the gut of five *Ips* bark beetles (Coleoptera: Curculionidae: Scolytinae)**. *Front Microbiol* 2020, **11**.
 60. Kandasamy D, Gershenzon J, Andersson MN, Hammerbacher A: **Volatile organic compounds influence the interaction of the Eurasian spruce bark beetle (*Ips typographus*) with its fungal symbionts**. *ISME J* 2019, **13**:1788-1800
- Interesting study reporting that the fungal symbionts of an economically important bark beetle are able to produce different blends of VOCs that can be recognized by insect specialized olfactory sensory neurons. These microbe produced VOCs could be used by beetles to distinguish between members of its microbial communities and maintain associations that improve their fitness.
61. Gasmi L, Martínez-Solís M, Frattini A, Ye M, Collado MC, Turlings TCJ, Erb M, Herrero S: **Can herbivore-induced volatiles protect plants by increasing the herbivores' susceptibility to natural pathogens?** *Appl Environ Microbiol* 2019, **85**.
 62. Kaplan I: **Attracting carnivorous arthropods with plant volatiles: the future of biocontrol or playing with fire?** *Biol Control* 2012, **60**:77-89.
 63. Jaworski CC, Xiao D, Xu Q, Ramirez-Romero R, Guo X, Wang S, Desneux N: **Varying the spatial arrangement of synthetic herbivore-induced plant volatiles and companion plants to improve conservation biological control**. *J Appl Ecol* 2019, **56**:1176-1188.
 64. Felicijan M, Kristl J, Krajnc AU: **Pre-treatment with salicylic acid induces phenolic responses of Norway spruce (*Picea abies*) bark to bark beetle (*Ips typographus*) attack**. *Trees* 2016, **30**:2117-2129.
 65. Chen Y, Bylund H, Björkman C, Fedderwitz F, Puentes A: **Seasonal timing and recurrence of methyl jasmonate treatment influence pine weevil damage to Norway spruce seedlings**. *New For* 2020, **52**:431-448 <http://dx.doi.org/10.1007/s11056-020-09803-4>.
 66. Mageroy MH, Wilkinson SW, Tengs T, Cross H, Almvik M, Pétriacq P, Vivian-Smith A, Zhao T, Fossdal CG, Krokene P: **Molecular underpinnings of methyl jasmonate-induced resistance in Norway spruce**. *Plant Cell Environ* 2020, **43**:1827-1843
- This study reports that spraying meJA on the bark of mature Norway spruce enhances its resistance against bark beetles and their associated phytopathogenic fungi priming inducible defenses even 35 days after application. A well-designed study and one of the rare examples of plant defense strategies application in natural forest conditions.
67. Saikkonen K, Nissinen R, Helander M: **Toward comprehensive plant microbiome research**. *Front Ecol Evol* 2020, **8**.
 68. Salazar D, Jaramillo A, Marquis RJ: **The impact of plant chemical diversity on plant-herbivore interactions at the community level**. *Oecologia* 2016, **181**:1199-1208.