



Microbial Influence on Plant–Insect Interaction

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Abstract

Plants and insects live in a microbial world, and the co-existence have shaped their ecology and evolution. These microbial allies play an essential role in the health, well-being, and vigor of their hosts and are often considered as “hidden players” in plant–insect interaction. The present chapter attempts to cover the contribution of microbes as drivers of plant–insect interaction where the microbial companions directly or indirectly influence the plant–insect interaction. The chapter also emphasizes the diversity of microbial communities linked with both plants and insects and their contribution toward plant–insect interaction from an ecological standpoint. It further deals with the recent updates on the use of microorganisms in pest management and the implications of microbes as a toolbox in future IPM strategies.

Keywords

Microbes · Metagenomics · Hidden allies · Toolbox · Host–microbe interaction · Microbe-associated molecular patterns (MAMP) · Symbiosis · Mycorrhiza-induced resistance (MIR) · Herbivore-induced plant volatiles (HIPVs)

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1 Introduction

The co-existence of plants and insects evolved over 400 million years and shaped the ecosystem. Both plants and insects are engaged in an arms race where plant defenses against insect herbivory, while insects evolve strategies to overwhelm them. Phytophagous insects (generalists and/or specialists) attack diverse plant species for herbivory. In response, plants produce an array of defensive compounds known as plant secondary metabolites to cope with their enemies. Glucosinolates, alkaloids, terpenoids, and phenolics are classic secondary metabolites serving as defensive compounds (Papadopoulou and van Dam 2017), which are either constitutively expressed in plants or induced in response to herbivory (Wu and Baldwin 2010). To counteract these plant defenses, insects secrete elicitors with their salivary secretions that decoy the defense responses (Fürstenberg-Hägg et al. 2013) or detoxify them (Ceja-Navarro et al. 2015).

In the last two decades, biologists have been keen on exploring the role of microbes in shaping the ecology of plants and animals. Studies have revealed that microbial communities associated with plants and insects play an essential role in health, well-being, and vigor of their hosts and are often considered as “hidden players” in plant–insect interaction (Douglas 2018; Sugio et al. 2014); (Biere and Bennett 2013). Various microbial communities (e.g., mycorrhizal fungi, rhizobacteria, root endophytic fungi) promote plant growth and protect them against a wide range of diseases by inducing resistance in systemic tissues (Induced Systemic Resistance – ISR) (Pineda et al. 2010; Van Wees et al. 2008). Furthermore, microbes have profound effects on insect feeding efficiency by helping to digest food or detoxifying entomotoxic compounds, modulating host growth, development, behavior, etc. Microbial allies of insects affect the plant defense mechanisms by either suppressing or counteracting the plant defense response (Sugio et al. 2014; Zhu et al. 2014). Microbes may engage in altering plant metabolisms and/or defense systems that significantly impact the plant–insect interaction either benefiting the plants or insects. Recent advances in high-throughput omics technology have opened up fascinating research area with the possibilities to conduct global analysis on the composition and functional capabilities of microbial symbionts that may contribute to the health and fitness of their host. The fast-moving scientific developments offer excellent potential for in-depth investigation of the fundamental processes and manipulation of the microbiota for effective microbial therapies.

The present chapter attempts to cover the role of microbes as drivers of plant–insect interaction where microbial associates directly or indirectly influence the plant–insect interaction. This chapter centers on the diversity of microbial communities and their contribution to plant–insect interaction from an ecological perspective. It further deals with the recent updates on the use of microorganisms in pest management and the implications of microbes as a toolbox in future IPM strategies.

2 Microbial Contribution in Shaping the Tri-Trophic Interactions in an Ecosystem

A diverse spectrum of microbes are often allied to plants and insects, and the nature of their association may vary from pathogenic to mutualistic interaction depending on underlying ecological factors. Symbiotic microorganisms live in the close interface with the host either permanently or for a considerable part of host's life cycle and play a key role in their diversification and evolutionary stability (Salem et al. 2015). Most of the intracellular symbionts show maternal inheritance where the symbionts are vertically transmitted from mother to the offspring. The horizontally transmitted symbionts are however transmitted directly from the environment or other conspecific or heterospecific host individuals (Kikuchi et al. 2007). The pathogenic interactions may also shift to the beneficial relationship over the course of time such as *Wolbachia* infection in *Drosophila simulans*, leading to an increase in the fecundity over uninfected females (Weeks et al. 2007).

Apart from the two-way interactions between microbes and their hosts (plants or insects), microbes are also engaged in a multi-trophic interaction where microbes interact with plants and insects simultaneously (Biere and Bennett 2013; Biere and Tack 2013). For example, the aphid–barley interaction depends on the interacting aphid species and bacteria present in rhizosphere (Tétard-Jones et al. 2007, 2012). The development of next-generation sequencing (NGS) technologies has enabled assessing the microbial diversity in different ecosystems. Meta-genomic and meta-transcriptomic sequencing combined with bioinformatic tools have assisted in exploring the taxonomic and functional diversity of hitherto hidden microbial association in a given environment (Douglas 2018).

2.1 Microbial Diversity Allied with Plants

Plants harbor diverse microbial communities in different compartments such as the rhizosphere (near the roots), phyllosphere (plant surface like leaves), and endosphere (within the plant and root tissues) (Andreote and e Silva 2017). Microbial communities associated with plants, both belowground and aboveground, benefit their host by aiding in the better uptake of nutrients from the soil for plant growth, increased tolerance to environmental stress (saline stress, drought, and occurrence of heavy metals) (Pineda et al. 2010), and protection against the pathogen (Bulgarelli et al. 2013). Some microbes are also capable of synthesizing plant growth–promoting hormones (Contreras-Cornejo et al. 2009; Van Loon 2007).

2.1.1 Microbes Enhancing Plant Growth and Nutrient Uptake

Plant-associated microbes such as the nitrogen-fixing bacteria (*Rhizobium*, *Bradyrhizobium*, *Mesorhizobium*, *Ensifer* (*Sinorhizobium*), and *Azorhizobium*) are widely studied for its interaction with the host and biogeochemical function (Batterman et al. 2013). The symbiotic association with plants helps in the better nutrient uptake and enables fixing atmospheric nitrogen required for plant growth.

These endosymbionts form nitrogen-fixing nodules in the roots of the leguminous plants on expressing the rhizobial nodule-forming (*nod*) and nitrogen-fixing (*nif*) genes which are generally located on “symbiosis islands” (Ling et al. 2016). By definition, “symbiosis islands” are the mobile, integrative, conjugative elements that carry genes that enable them to expunge from the chromosome to form closed circular molecule that eventually conjugate and recombine into recipient chromosomes through horizontal gene transfer (HGT) from bacteria present in soil to host leguminous plants (Haskett et al. 2016; Ling et al. 2016). These mobile elements bear various novel traits such as antibiotic resistance, virulence, biofilm formation, degradation of aromatic compounds, and symbiosis (Ling et al. 2016; Okubo et al. 2016). For example, the transfer of the “symbiosis island” of 500 kb from *Mesorhizobium loti* to *Lotus corniculatus* and its integration into a phenylalanine-tRNA gene of the host plant chromosome resulted in root nodule formation and nitrogen-fixation in lotus plant (Ramsay and Ronson 2015). A similar example of such symbiotic interaction was documented in *S. rostrata*-*Azorhizobium caulinodans* system where the “symbiosis island” of *A. caulinodans* on integration to glycine-tRNA gene of *S. rostrata*-induced host nodulation (Ling et al. 2016).

Another interesting symbiotic association, observed between microbes present in plants and soil, is the arbuscular mycorrhizal symbiosis (Hammer et al. 2014; Richardson et al. 2009) where arbuscular mycorrhizal fungi (AMF, obligate biotrophs) belonging to the phylum Glomeromycota colonize on the cortical cells of the plant root. The AMF profit from the host carbon compounds to obtain metabolic energy (Gianinazzi et al. 2010), and in exchange caters better uptake of water and mineral nutrients (such as nitrogen and phosphorous) (Baum et al. 2015; Gutjahr and Parniske 2013) leading to increased host plant biomass, higher tolerance to abiotic stress (salinity, drought, heavy metals) (Singh et al. 2011) and protection against plant diseases (Bernardo et al. 2017). Enhanced plant growth determines increased food supply and improved nutrient quality for the herbivores and in turn influences the plant–insect interaction. Conversely, beneficial microbes accelerate the plant regrowth after herbivory by facilitating the nutrient and water uptake (Herman et al. 2008; Kempel et al. 2009; Kula et al. 2005).

2.1.2 Microbes-Induced Resistance in Plants

Plant defenses against pathogen attack can be either constitutively expressed in plants (passive resistance) or induced after the infection or herbivore attack (induced resistance). Microbes such as plant growth-promoting rhizobacteria (PGPR) and fungi (PGPF) (Segarra et al. 2009; Van Wees et al. 2008) as well as mycorrhizal and endophytic fungi (Stein et al. 2008) often initiate induced systemic resistance (ISR) to mitigate biotic and abiotic stresses in plants (Pozo and Azcón-Aguilar 2007; Shikano et al. 2017; Trillas and Segarra 2009). Induced systemic resistance involves activation of jasmonic acid and ethylene signaling pathways (Van der Ent et al. 2009) either by priming of plant defense genes in response to pathogen or insect attack (Conrath et al. 2001) or on interaction between non-pathogenic microbes with the plant roots. For instance, the establishment of arbuscular mycorrhizal symbiosis activates and boosts plant basal defense mechanisms on pathogen attack through

Mycorrhiza-induced Resistance (MIR) (Pozo and Azcón-Aguilar 2007; Song et al. 2015). Based on transcriptomic and proteomic profiling, Fiorilli et al. (2018) demonstrated that the wheat–AMF association was not only benefiting the wheat plant in mineral nutrition but also protecting them against the pathogen (*Xanthomonas translucens*). Mycorrhizal colonization on plant root induces systemic defense responses via microbe-associated molecular patterns (MAMPs) recognition (Zamioudis and Pieterse 2012). It is interesting to note that the host plant initially perceives this mycorrhizal interaction as a putative pathogen by plant MAMP-recognition receptors and activates MAMP-triggered immunity (MIT) response as the first line of defense to prevent further invasion (Jones and Dangl 2006; Millet et al. 2010). This MIT response induced by mycorrhizal invasion results in transcriptional and hormonal changes that leads to the accumulation of hydrolytic enzymes (chitinase, glucanase), reactive oxygen species in roots, and activation of phenylpropanoid metabolism (García-Garrido and Ocampo 2002; Pozo and Azcón-Aguilar 2007) in the host plant, leading to the establishment of the symbiosis (Schouteden et al. 2015).

Interestingly, plant pathogens also invade plant tissues through stomata and thus stomatal closure is a part of innate immunity (Melotto et al. 2006). *Pseudomonas syringae* overwhelms this innate defense by the release of phytotoxin Coronatine (COR) (Zheng et al. 2012) that activates the Jasmonic acid signaling pathway, enabling the reopening of the stomatal pores. Plant-associated microbes have been reported to influence plant metabolic processes to block pathogen invasion (Kumar et al. 2012). A recent study documented that the plant growth–promoting fungi *Penicillium simplicissimum* induces systemic resistance to protect *Arabidopsis thaliana* against the pathogen *Pseudomonas syringae* by altering the plant metabolic processes (Desclos-Theveniau et al. 2012; Du et al. 2014). The MYB44 gene product of endophytic fungi acts as stomata-specific enhancer of the plant Abscisic acid (ABA) signaling pathway that promotes stomatal closure thereby by blocking the entry of pathogen through stomata (Hieno et al. 2016; Montillet et al. 2013).

2.1.3 Microbial Toxin Production Against Insects

Microbes colonizing on plants can produce toxic compounds that can be harmful for insects during herbivory (Bizzarri and Bishop 2008; Monnerat et al. 2009). The crystal-like proteins (delta- endotoxins) produced by gram-positive bacteria *Bacillus thuringiensis* (Bt) on sporulation is known to have insecticidal activity (Palma et al. 2014). These endotoxins constitute Cry (crystal) and Cyt (cytosolic) group of proteins that interact synergistically to have a potential insecticidal effect (Butko 2003). The inactive Cry protoxins are ingested and proteolytically cleaved to yield shorter active toxins of 55–60 kDa in the insect midgut (Bravo et al. 2007). There are several models proposed for the mechanism behind the toxicity of Cry protein (Jurat-Fuentes and Crickmore 2017). It is generally believed that the active toxic molecules bind to specific receptors such as cadherin-like proteins, glycosylphosphatidylinositol (GPI)-anchored Alkaline phosphatase (ALP), and GPI -anchored aminopeptidase (APN) at the surface of midgut, forming pores on the membrane, increasing its permeability, and disrupting the transmembrane ionic gradient, resulting in cell lysis

and insect death (Pigott and Ellar 2007). Alternatively, the interaction of the Cry toxin with cadherin receptor triggers a signaling cascade involving protein G, adenylate cyclase and protein kinase A, as well as induces the activation of mitogen-activated kinases such as MAPK p38-triggering cell apoptosis (Zhang et al. 2006). More recently, Portugal et al. (Portugal et al. 2017) demonstrated that the binding of Cry toxin to specific receptors activates the phosphorylation of MAPK p38, disrupting the calcium ion influx through pore formation, which leads to cell death. Among different groups of Cry toxins (de Maagd et al. 2003), Cry1A toxin binds to cadherin protein receptors of most lepidopteran species (such as *Manduca sexta*, *Bombyx mori*, *Heliothis virescens*, *Helicoverpa armigera*, *Pectinophora gossypiella*, and *Ostrinia nubilalis*) (Pigott and Ellar 2007). The use of Cry toxins into transgenic crops for targeted and effective pest control has significantly reduced the use of chemical insecticides (Bravo et al. 2011). Another well-characterized rhizospheric bacteria, *Pseudomonas protegens*, secretes an antimicrobial compound that on ingestion promotes apoptosis in insects (Haas and Keel 2003; Loper and Gross 2007). In addition to the endotoxins, insecticidal proteins are also secreted during bacterial vegetative growth phase known as Vip (vegetative insecticidal proteins) (de Maagd et al. 2003; Estruch et al. 1996) that can be categorized into four groups Vip1, Vip2, Vip3, and Vip4 depending on their amino acid sequences (Chakroun et al. 2016; Zack et al. 2017). Vip1 and Vip2 are binary insecticidal proteins that are toxic to Coleopteran and Hemipteran species (Bi et al. 2015; Chakroun et al. 2016) whereas Vip3 targets against Lepidopteran insects (Song et al. 2016). However, Vip4 protein is not yet reported to have insecticidal activity (Chakroun et al. 2016).

2.2 Microbial Diversity Allied with Insects

Insect-associated microbes colonize mostly in the external cuticle and the gut. However, they can breach the exoskeleton and the gut to gain access to the hemocoel and within the specialized insect cells. Microbial communities present in insect influence several aspects of insect ecology, behavior, and physiology such as responses to the utilization of plant nutrients, immunity, reproduction, detoxification of defensive plant compounds, and protection against natural enemies (Oliver et al. 2010).

2.2.1 Microbes Providing Essential Nutrients

Insects along with other animals are unable to synthesize the essential amino acids and co-factors obligatory for many metabolic enzymes to function. In addition to these essential amino acids, insects cannot synthesize sterols that contribute to membrane architecture (Behmer and Nes 2003). Most insects derive these essential nutrients from their diet while feeding on plant sap. These insects constitute large populations of specific microorganisms localized in specialized cells, called bacteriocytes, within their body. The microbial symbionts present in most of the plant sap-feeding insects (hemipterans) are transmitted vertically from mother to

their offspring via ovaries to the cytoplasm of each egg at oviposition that provides essential amino acids and/or vitamin cofactors that are limiting in host diet. Furthermore, the gut symbionts that are deposited externally over the eggs are acquired by the feeding offsprings (Buchner 1965). For instance, the bacterial endosymbiont, *Buchnera aphidicola*, in aphids is a model for such association where the bacterial symbiont is localized in metabolically active *Buchnera* cells and uses the insect body as its habitat and in return provides essential nutrients to its host (Wang et al. 2018). Upon the elimination of the symbiotic bacteria by the antibiotic treatment, the capability to synthesize essential amino acids is lost in aphids (Douglas et al. 2001).

Similarly, the symbiotic association of gall midges with fungi is essential for invading the plant stem to access the vascular tissue for nutrients and development of gall (Rohfritsch 2008). The close association of termites with microbes is also one of the best-studied symbiotic relationships in insects. The ability of the termites to harness and feed on nitrogen-deficient wood-based diet is due to the presence of unique consortium of microbes living in the termite gut. The microbial cellulolytic enzymes play a critical role in the digestion by enhancing its digestive efficiency (Peterson and Scharf 2016). The presence of mutualistic gut symbiont *Erwinia dacicola* in the olive fruit fly *Bactrocera oleae* benefits the host by providing essential amino acids and protease enzymes to digest the food (Capuzzo et al. 2005). Furthermore, in ants, cockroaches, and termites microbial allies recycle the nitrogenous wastes to essential amino acids (Douglas 2015). The resident microbes often produce glucosyl hydrolase that degrades plant cellulose and hemicellulose to short-chain fatty acids to provide a readily available nutrient source to insect host (Berenbaum 1980; Calderón-Cortés et al. 2012).

2.2.2 Microbes Influencing Insect Immunity

Microbes often contribute to insect innate immunity wherein gut microbes regulate the expression of immune genes (Johnson 2015a). The bacterial symbionts such as *Wolbachia pipientis*, *Spiroplasma* species, and *Hamiltonella defensa* either vertically or horizontally transmitted to the host have shown to influence host immunity (Engel and Moran 2013). For example, the facultative symbiont *H. defensa* protects aphids against the parasitoid through bacteriophage-encoded gene expression (Oliver et al. 2010). Similarly, *Spiroplasma* present in *Drosophila neotestacea* imparts resistance against the parasitic nematode (Jaenike et al. 2010). Furthermore, in mosquitoes, the gut microbiota activates the innate epithelial immunity against *Plasmodium* infection whereas the elimination of the microbiota renders the mosquitoes susceptible to infection (Dong et al. 2009). Over the years, *Wolbachia* infection is considered parasitic to insects as they contribute to cytoplasmic incompatibility, leading to reproductive disruption. Nevertheless, studies suggested that *Wolbachia* infection in *Drosophila* also deliberates antiviral protection leading to the higher survival of the flies (Johnson 2015b). The presence of *Wolbachia* in *Drosophila* induce antiviral resistance against a wide range of RNA viruses (Dicistroviridae, Nodaviridae, Flaviviridae, Togaviridae, and Reoviridae) but not DNA viruses (Teixeira et al. 2008). The reduction of the viral load and the anti-viral protection is reported to be due to the competition between the symbiotic bacteria

and the viruses for the cellular resources (Caragata et al. 2013). Alternatively, the symbiotic association of *Wolbachia* affects the reactive oxygen species (ROS) levels, a key player in the insect immune system. The increase in ROS levels stimulates the Toll pathway, imparting anti-viral protection (Pan et al. 2012). Other studies reported the proliferation of *Wolbachia* inside the insect body suppresses the viral infection by inducing host immune responses by stimulating the miRNA expression (Hussain et al. 2011), thereby leading to cell death in insect (Brackney 2017; Terradas and McGraw 2017). However, the exact mechanism behind the antiviral protection by *Wolbachia* is still poorly understood (Yixin et al. 2017) (Fig. 1).

2.2.3 Microbes Influencing Detoxification of Plant-Defensive Compounds

Microbes are considered as the drivers promoting plant specialization in herbivorous insects (Janson et al. 2008). The acquisition of symbiotic microbes enabled the different sap-feeding insects to colonize on several plants. Plant-defensive secondary metabolites (terpenoids, phenolics, alkaloids, glucosinolates, and alliinins) are an essential determinant in plant–insect interaction. The ability of the insects to detoxify these toxic plant allelochemicals is often attributed to microorganisms associated with insects (Boone et al. 2013; Douglas 2013; García-Fraile 2018; Howe et al. 2018). Some herbivores often neutralize toxic phenolic compounds by increasing their gastrointestinal mucus production, by recruiting the gut microorganisms for degradation, and/or by secreting phenol-binding proteins in the saliva (Dearing et al. 2005). Insect symbionts can inhibit or counteract the host plant defenses through the direct or indirect production of enzymes targeting plant-defensive compounds (Broderick et al. 2004; Dowd and Shen 2011). The symbiotic fungus, *Leucocoprinus gongylophorus*, is present in the nest of the leaf-cutting ant, *Acromyrmex echinatior*, and aids to overwhelm plant-defensive phenolic compounds. Precisely, leaf-cutting ants preferentially feed on the fungal hyphae called gongyliidia that expresses the laccase coding genes. On ingestion, the laccase molecules pass through the gut of these ants, released on defecation onto the ingested plant materials, and degrade plant defense compounds, for example, flavonoids and tannins (De Fine Licht et al. 2013).

Similarly, Ceja-Navarro et al. (2015) demonstrated the role of gut microbiome of the coffee berry borer (*Hypothenemus hampei*) in the detoxification of toxic plant alkaloid (Caffeine). *H. hampei* is a devastating insect pest of coffee that resulted in 80% crop loss on infestation. Caffeine, produced by the coffee plants, acts as a defense mechanism in response to herbivory. Interestingly, the coffee borer *H. hampei* possesses a core gut microbiota that is responsible for detoxification of caffeine in the insect gut and supports the survival of the insect in a hostile environment. The gut bacteria such as *Pseudomonas* possess caffeine demethylase genes that aid in caffeine detoxification. Upon treatment with antibiotic that confiscates the insect gut microflora, eliminates the caffeine degradation ability of the beetle. However, the re-inoculation of *Pseudomonas* strain re-establishes the caffeine detoxification ability, thus certifying the pivotal role of microbial associates

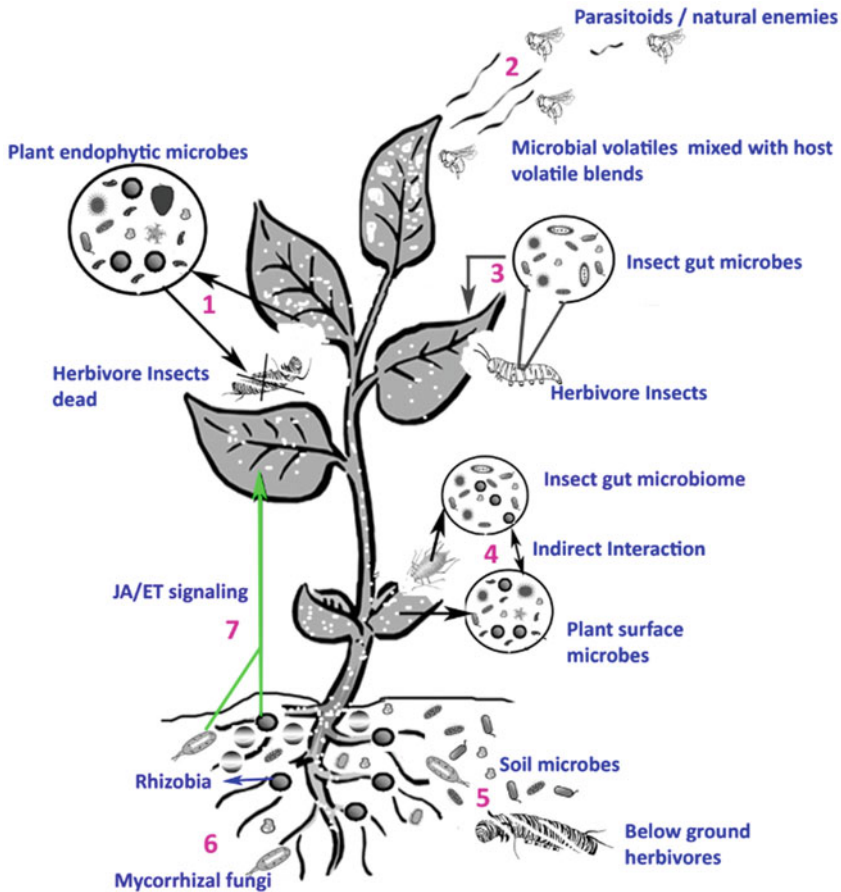


Fig. 1 The tri-trophic interactions between plant-microbe-insect. (1) Plant endophytic microbes producing toxin against insect herbivore. (2) Microbial volatiles mixed with host plant volatiles attract parasitoids. (3) Insect gut microbiome enables detoxifying defensive plant compounds. (4) Indirect interaction between the plant endophytes and insect gut microbiome wherein the insect ultimately confiscates the plant defenses. (5) Soil microbes produce different metabolites that are detrimental to belowground herbivores. (6) Plant growth-promoting rhizobia as well as mycorrhizal fungi interact with plant roots, influencing the JA/ ET signaling pathways inducing resistance against aboveground herbivores

in caffeine degradation. Similarly, gut microbiota of the velvet bean caterpillar *Anticarsia gemmatilis* is involved in the production of serine and cysteine proteases and contributes to the insect's tolerance to dietary protease inhibitors in soy plant (Pilon et al. 2013). Another interesting study showed that in the mountain pine beetle, *Dendroctonus ponderosae*, females initiate mass colonization through the production of aggregation pheromone trans-verbenol (Vité and Pitman 1968) by confiscating the host plant defense mechanisms. The trans-verbenol is a product of

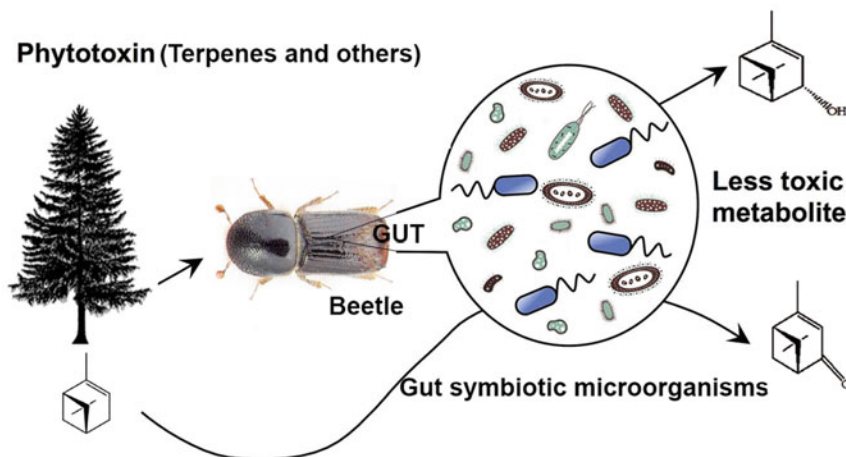


Fig. 2 Figure illustrating the contribution of the bark beetle gut microbiome in plant toxin detoxification

oxidative degradation of plant secondary defense compound monoterpene α -pinene (Renwick et al. 1976).

Recent studies have reported symbiont-mediated terpene degradation and verbenone production in beetles (Fig. 2) (Berasategui et al. 2017; Cao et al. 2018). Shotgun DNA sequencing on the gut microbiome of the mountain pine beetle revealed the presence of terpene-degrading bacteria belonging to genera *Pseudomonas*, *Rahnella*, *Serratia*, and *Burkholderia* (Adams et al. 2013).

2.2.4 Impact on Insect Pheromone Production and Reproduction

Pheromones are chemical compounds that serve as cues/signals for communication between individuals of the same species. These chemical compounds are involved in courtship, mating, defense, trail marking, aggregation, kin recognition, etc. (Howard and Blomquist 2005; Regnier and Law 1968). Though pheromones are generally encoded by insect gene, studies have shown that host-associated microbes also play a significant role in modulating their host chemical profiles, mating preference, and social behavior (Engl and Kaltenpoth 2018). Such modulation of the chemical signals occur either directly by influencing the biosynthetic pathway of pheromone production (Marshall et al. 2016) or by manipulating the host metabolic pool and allocating resources into pheromone production (Engl et al. 2018). The microbial symbiont in saw-toothed grain beetle *Oryzaephilus surinamensis* modulates the cuticle synthesis, resulting in the thinner cuticle and thereby rendering the beetles more susceptible to desiccation (Engl et al. 2018). Several insects exhibit reduced attractiveness and fecundity on the disruption of resident microbes with antibiotic treatment. This suggests a microbial role in mate choice and sexual communication (Ben-Yosef et al. 2008). For instance, the disruption of gut microbiota by the administration of antibiotics in Tephritid fruit fly, *Ceratitis capitata*, showed

increased oviposition rates of females under nutritional stress as well as prolonged mating latency in males on a standard diet (Ben-Yosef et al. 2008). The reduced attractiveness of the female oriental fruit flies, *Bactrocera dorsalis*, to the males on antibiotic treatment could be reversed by the re-establishment of the gut microbiota into the female flies through feeding (Engl and Kaltenpoth 2018). Another fascinating example showed that *Drosophila* flies reared on different diets exhibit a strong mating preference where flies fed on the same diet preferred to mate with each other but not with flies reared on a different diet (Sharon et al. 2010). Such preference in mate choice could be mediated by diet itself or by diet-associated gut microbial shifts. Sharon et al. (2010) showed evidence of resident gut bacteria influencing the mating preference in *D. melanogaster*, which could be abolished by antibiotic treatment. Interestingly, the lost preference for mate choice could be re-established by infecting the axenic *D. melanogaster* flies with the microbiota of the healthy flies on a diet. However, this study was controversial as several researchers tried to replicate the experiment that had conflicting results where the assortative mating pattern was only observed in inbred fly lines before the transfer to different diets (Najarro et al. 2015). Others showed no stability of the results within the replicates (Arbutnott et al. 2016). Thus, extensive research is needed to elucidate the factors influencing the mating preference and success in *D. melanogaster*.

Microbes-associated with insects often manipulate host reproduction by feminizing genetic males, inducing parthenogenesis or male killing, and by inducing cytoplasmic incompatibility (i.e., reproductive sterility when infected males mate with uninfected or infected females with a different symbiont strain) (Hughes et al. 2012; Miller and Schneider 2012; Werren et al. 2008). *Wolbachia*, *Arsenophonus*, *Cardinium*, *Rickettsia*, and *Spiroplasma* are among the universal reproductive manipulators that influence host reproduction (Engelstädter and Hurst 2009). *Spiroplasma* in pea aphid induces male killing to prevent competition with the infected females and avoidance of inbreeding depression (Simon et al. 2011). Increased female bias in infected female whiteflies was observed due to the invasion of *Rickettsia* (Himler et al. 2011) that swayed the population dynamics of whiteflies. The virus LbFv decreases the competitive ability of the parasitoid *Leptopilina bouhardi* to infect *Leptopilina heterotoma* by manipulating the reproductive behavior of the parasitoid (Patot et al. 2012). Reproductive manipulators may serve as novel targets to be exploited in the development of alternative control strategies. These reproductive manipulators indirectly impact the plant–insect interactions by regulating the population dynamics and in so doing minimize the genetic diversity and/or recombination rates in infected species (Engelstädter and Hurst 2009) which in turn influence their co-evolutionary dynamics and functioning of ecological networks (Ferrari and Vavre 2011).

2.3 Crosstalk in Signaling Pathways – Decoy of Plant Defenses

Plants are armed with a plethora of defense mechanisms to combat against insect and pathogen attack. These defensive mechanisms are either constitutively present or

activated upon insect or pathogen invasion (Pieterse and Dicke 2007). On perceiving the pathogen or insect attack, plants initially retort through its primary immune response and also activate effective systemic broad-spectrum resistance known as induced resistance against attackers (Walters et al. 2007). The phytohormones – salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) – are documented as key players in the regulation of plant defense signaling pathways (Koornneef and Pieterse 2008). In response to pathogen or insect attack, plants emit alarm signals with the production of SA, JA, and ET that contributes to plant defense response. SA-mediated defense responses are generally induced by microbial pathogens whereas insect invasion is usually dissuaded by JA/ET-mediated defenses (Kessler and Baldwin 2002; Thomma et al. 2001). However, in nature plants often encounter raid by different aggressors (pathogens and or herbivores) either simultaneously or by consequent invasion (Stout et al. 2006). Therefore, the crosstalk between the defense signaling pathways delivers a powerful defensive mechanism. These signaling pathways can be either mutually antagonistic or synergistic that allows the plant to combat against its invaders (Bostock 2005). Intriguingly, insect herbivores and pathogens have evolved to decoy the plant defenses for their own benefit by overwhelming the defense mechanisms modulating the plant's signaling network (Pieterse and Dicke 2007). Herbivores often exploit its symbionts to overwhelm the anti-herbivore defenses by dodging the plant perception (Giron and Glevarec 2014; Sugio et al. 2014). For instance, the bacteria present in oral secretion of the Colorado potato beetle, *Leptinotarsa decemlineata*, activate the plant defense response through the stimulation of the SA signaling pathway as a response to microbial pathogen attack which in turn downregulates the JA anti-herbivore response, ensuring improved larval growth (Chung et al. 2013). A similar example, herbivorous silverleaf whitefly nymphs (*Bemisia tabaci*), activates SA signaling pathway as a decoy strategy to overcome JA-mediated defense to enhance larval performance (Zarate et al. 2007). Microbial pathogens often have the ability to produce phytohormones or their functional mimics and thereby manipulate plant signaling network (Robert-Seilaniantz et al. 2007). For instance, *P. syringae* bacteria produce a potent mimic of JA-Ile called coronatine that activates JA-Ile responses and suppresses SA-dependent defenses, resulting in enhanced pathogen growth (Nomura et al. 2005). The induction of SA signaling pathways results in the activation of pathogenesis-related protein encoding genes having antimicrobial activity (van Loon et al. 2006). Some of the prominent molecular players in the crosstalk between SA/JA signaling pathways are the regulatory protein NONEXPRESSOR OF PR GENES1 (NPR1), WRKY transcription factors, glutaredoxin GRX480, and Mitogen-activated protein (MAP) kinases. These regulatory components are essential for the activation of the SA signaling pathway which in turn suppresses the JA-induced response, resulting in overcoming plant defense against herbivore attack (Koornneef and Pieterse 2008).

2.4 Soil Microbial Diversity Influencing the Plant–Insect Interaction

Apart from the plant- and insect-associated microbes, the soil microbial community also plays a crucial role not only in enhancing plant growth and increased tolerance to abiotic stress but also in influencing aboveground insect herbivores through biochemical changes in plant-mediated mechanisms (Pineda et al. 2017). For example, the foliar-feeding *Aphis jacobaea* population depends on the soil microbial communities of its host plant ragwort (*Senecio jacobaea*). A different consortium of free-living soil-borne microbes influences the concentration of amino acids in the plant phloem sap, thereby affecting the aphid population (Kos et al. 2015). Additionally, inoculation of the distinct microbiome in soil manipulates the leaf metabolome of *Arabidopsis*, making it resistant against caterpillar *Trichoplusia ni* (Badri et al. 2013).

Intriguingly, belowground microbes have been shown to influence plant–insect interaction by modulating herbivore-induced plant volatile (HIPV) emission (Pineda et al. 2015). Plants in response to herbivore attack emit varieties of volatile organic compounds (HIPVs) in order to attract the potential predator. For example, the volatiles emitted by *Nerium oleander* plants in response to *Aphis nerii* attack signal the predator *Chrysoperla carnea* which could be altered by the presence or absence of soil microbial communities (Benítez et al. 2017). It was interesting to note *C. carnea* females preferred the HIPV blend emitted from plants grown on soil inoculated with microbes to those emitted from plants grown on control sterile soil (Benítez et al. 2017).

Furthermore, certain beneficial soil microbes can synthesize the phytohormones that enhance the plant growth and can mitigate abiotic stress (salinity, drought, heavy metals) (Egamberdieva et al. 2011; Egamberdieva et al. 2017; Liu et al. 2013). For example, root-colonizing soil bacterium *B. licheniformis* can synthesize indole-acetic-acid (IAA), which promotes wheat plant under saline stress (Singh and Jha 2016). Recent studies have demonstrated a linkage between the leaf microbiome and soil microbial communities (Pineda et al. 2017), wherein belowground microbial entities impact the aboveground insect herbivory as well as the composition of symbiotic “phytobiome” (i.e., plant microbiome). For instance, entomopathogenic fungi (*Beauveria bassiana* and *Metarhizium anisopliae*) that are typically present in soil colonize in different parts of broad bean (*Vicia faba*) plant and enhance plant growth as well as exhibit resistance against insects by translocating nitrogen to the plant from the insect cadavers via their fungal mycelia (Behie et al. 2012; Jaber and Enkerli 2016). Another example of such interaction is observed by a fungus *Trichoderma*, thought to be restricted to the soil, have now been known to colonize on the leaves and can suppress insect pests such as thrips (Muvea et al. 2014).

In the quest for crop protection, there is extensive use of insecticides that pose a threat of insecticide resistance (Whalon et al. 2008). One of the common organophosphorus insecticides used worldwide is fenitrothion that targets acetylcholine esterases and exhibits insect-specific toxicities (Stenersen 2004). Extensive application of such insecticides have led to an increased population of fenitrothion-

degrading microbes in the soil that convert the toxic fenitrothion to non-toxic 3-methyl-4-nitrophenol and utilize it for their growth (Itoh et al. 2018). *Riptortus pedestris* (bean bug), a severe pest of leguminous crops, harbors *Burkholderia* in its midgut in sac-like tissues called “crypts” during its larval second instar stage that enables the bean bug to circumvent the toxic compounds, conferring insecticide resistance (Kikuchi et al. 2005). Notably, such symbiotic association ensures not only host survival but also an increase in body size, growth, and higher fecundity of the host (Kikuchi et al. 2005).

2.5 Role of Microbial Volatiles in Plant–Insect Interaction

Similar to plants and animals, microbes also emit a plethora of volatile organic compounds (VOCs) in the course of their metabolic processes (Bitas et al. 2013). These compounds are usually lipophilic in nature that belong to the class of alcohols, aldehydes, esters, terpenoids, thiols, and fatty acid derivatives and have low molecular weight ($<300 \text{ g mol}^{-1}$), low boiling point, and high vapor pressure (0.01 kPa at 20 °C) (Kanchiswamy et al. 2015a, b). The volatile compounds are perceived from a distance as chemical signals to communicate with each other and contribute significantly in multitrophic interaction (Schulz-Bohm et al. 2017). Over the years, the role of microbial volatile compounds (mVOCs) in plant physiology has gained attention. mVOCs affect hormonal balance, metabolism, sugar concentration, and the acquisition of essential nutrients in plants, thereby inducing growth and regulating stress response. For instance, volatiles released from *Bacillus subtilis* have been shown to stimulate growth and salt tolerance in *Arabidopsis thaliana* (Ryu et al. 2003; Zhang et al. 2008a). The underpinning mechanism behind the contribution of VOC in *A. thaliana* was demonstrated using proteome analysis in combination with other biochemical experiments (Kwon et al. 2010). The VOCs released by *B. subtilis* upregulates the iron-regulated transporter 1 (IRT1) gene expression, facilitating the iron uptake from soil. Iron is an essential micronutrient in photosynthesis. Its increased uptake enhances the photosynthesis efficiency and the chlorophyll content thus, inducing plant growth (Fincheira and Quiroz 2018). Salt tolerance in *A. thaliana* in response to mVOCs resulted in the regulation of HKT1 gene that encodes high-affinity Na^+ transporter (Zhang et al. 2008b). Similarly, *Pseudomonas chlororaphis* releases 2, 3- butanediol that induces shoot growth and confers resistance in the tobacco leaves against the soft-rot pathogen *Erwinia carotovora* (Han et al. 2006). The VOC-mediated resistance requires JA/SA/ET signaling pathways (Farag et al. 2013). Apart from the synergistic effect, the microbes also influence antagonistically to plants. Some bacterial species belonging to genera *Burkholderia*, *Pseudomonas*, *Serratia*, *Chromobacterium* release a wide array of volatiles that exhibit phytotoxicity and inhibit plant growth (Bailly and Weisskopf 2012; Kai et al. 2009).

Microbial volatiles are equally crucial to insects and their natural enemies. Insects rely on olfactory cues to locate their host as food resource or as oviposition site and exhibit defense against pathogens (Davis et al. 2013). For instance, the gut bacteria in locust produce antimicrobial phenolic compounds to protect against other

microbial pathogens as well as aggregation pheromone “guaiacol” that promotes mating in locust (Dillon et al. 2000, 2002). In *Rhagoletis pomonella* (apple maggot fly) the oviposition behavior is influenced by the release of volatiles emitted by *Enterobacter agglomerans* present on the fruit (Lauzon et al. 1998). Insects are often attracted to fermented fruit that is inhabited by microbes. The mVOCs emitted enable insects to locate their food source (DeVries 1987). Yeast volatiles have also been reported to modulate sexual behavior and mating in *Drosophila melanogaster* (Gorter et al. 2016). Not only this, microbial volatiles contribute significantly to tri-trophic interaction (Hulcr et al. 2005). The volatiles released by plants or microbes associated with plants provide cues for the natural enemies to locate attacked plants (Hulcr et al. 2005). Interestingly, the yeast volatiles deployed by *Ogataea pini* inhibit the growth of entomopathogenic fungus (*B. bassiana*) on bark beetle. Understanding mVOCs and its role in plant–insect interaction provides a great platform to develop novel, eco-friendly, cost-effective, sustainable pest management strategies (Bitas et al. 2013).

3 Microbes as a Toolbox: Integration of Microbes in Pest Management

The world population is predicted to upsurge from a present population of 6 billion to 9 billion in 30 years, and the need for increased food production to meet the demands of the ever-increasing population is a major challenge (Lacey et al. 2015). Approximately 42% of the total crop loss is caused by pest infestation and is anticipated to rise to 83% without any crop protection (Oerke and Dehne 2004). In the quest of increasing crop yield, farmers have embraced a wide range of conventional pesticides such as organochlorines, organophosphates, carbamates, and pyrethroids. The use of chemical pesticides to control devastating pest has been undoubtedly a great success but suffers from many limitations. Extensive pesticide usage and the constant evolutionary dynamics of insects have led to the selection for pesticide resistance in target species as well as killed a number of non-target beneficial insect species, including pollinators and natural enemies. These chemicals often pollute the surface water and are harmful to birds, humans, and domestic and aquatic animals (Usta 2013). It is high time to reduce the use of chemical pesticides, so as not to gamble with the ecosystem, and to choose an eco-friendly alternative to pest control. As discussed earlier, microbes play a crucial role in host physiology and traits and contribute significantly to plant–insect interaction. Harnessing the potential of the microbes as a toolbox in controlling pests is indeed a smarter alternative approach toward sustainable IPM strategy for crop protection. The development of biocontrol against insect pests by exploiting the microbial potential has progressed tremendously over the last 20 years. However, the European legislation is making continuous efforts to promote the use of biopesticides through policies to restrict the broad-spectrum chemical pesticide practice and ban certain pesticides, but still, it holds no more than 3% of the total global pesticide market (Lacey et al. 2015). The use of microbial entomopathogens in agriculture is an excellent substitute for

chemical fertilizer. Several entomopathogenic microbes are available in the global market as microbial control agents (MCAs) (Lacey et al. 2015). These entomopathogenic microbes easily invade the insect body while feeding where they multiply and confiscate the host, ultimately causing insect death.

Most of the commercially available biopesticides target one specific pest, and although it is advantageous for the safety of the environment and the non-target species, such low range of effectivity has restricted biopesticides to a niche market (Lacey et al. 2015). For example, entomopathogenic viral formulations are commercially available to control insect pests such as codling moth, *Cydia pomonella*, that are highly selective for the target pest and often sensitive to environmental conditions such as solar radiation (Lacey et al. 2008). To achieve commercially successful biopesticides, improvements are needed on the insecticidal activity spectra, persistence to environmental variations, and delivery to target-specific sites of pest occurrence and should be cost-effective (Glare et al. 2012).

Interestingly, by transferring microbial symbionts from one insect species to another species that do not harbor such microbes naturally can have a drastic effect on the insect physiology and behavior. For instance, *Wolbachia* isolated from *Drosophila* and introduced to mosquitoes by injecting into the *A. aegypti* embryos has remarkably reduced the virus load and viral transmission by mosquitoes (Fraser et al. 2017). Moreover, in addition to suppression of viral transmission, *Wolbachia* infection also causes cytoplasmic incompatibility, leading to reproductive disruption and population reduction (Ferguson et al. 2015; Joshi et al. 2017). This target-specific control strategy could be an effective alternative to control disease outbreaks. Another strategy could either be the mass release of sterile male insect or release of *Wolbachia* infected incompatible females into the environment, resulting in reproductive disruption, thereby controlling the pest population (Nikolouli et al. 2018). However, these strategies suffer certain drawbacks. The mass production of sterile insects is often challenging and not cost-effective. Moreover, environmental factors such as temperature change might have an effect on anti-viral protection and cytoplasmic incompatibility imparted by *Wolbachia* (Ross et al. 2017). Additionally, anti-viral protection depends on the bacterial load that considerably affects the physiology and fitness of the insect host (Martinez et al. 2015).

Megacopta punctatissima, a soybean crop pest, utilizes its gut bacterial symbiont *Ishikawaella* to thrive on soybean. However, a closely related species *M. cribraria* shows high mortality on soybean. Administrating *Ishikawaella* from *M. punctatissima* into the newly hatched nymphs of *M. cribraria* enabled successfully thriving on soybean whereas *M. punctatissima* lost the ability to survive on soybean (Hosokawa et al. 2007). This suggests that the potential of microbial symbionts could be used as an approach for the manipulation of insect host range.

The use of genetically modified (GM) crop variety is expressing microbial endotoxins or inducing RNA interference (RNAi) to target-specific insect species also holds excellent potential against pest control (Zhang et al. 2017). However, it is not feasible to engineer all vulnerable crop varieties as polyphagous pests have a broad host range. Insects do not only attack for feeding but also vectors plant pathogens. An alternative approach to this could be genetically modifying the

microbes to deliver RNA interference to the insect by knocking down the genes essential for insect metabolic processes (Whitten et al. 2016). The delivery of dsRNA for RNA interference can be easily achieved through genetically modifying the microbes that are invariably ingested by the insects where it can proliferate in the gut and spread through feces. For example, administration of the genetically modified bacterial strain, expressing dsRNA against insect α -tubulin gene, to the western flower thrips (*F. occidentalis*) significantly increases the insect mortality (Whitten et al. 2016). However, RNAi technique holds high potential to control insect pest population, though a fundamental problem exists, i.e., dissemination of genetically modified microbes to non-target hosts through horizontal transfer. However, the development of highly specific dsDNA for RNAi to target genes of a particular pest species can mitigate the limitation (Arora and Douglas 2017).

Microbial symbionts are an integral part of the insect life cycle that often influence different aspects: host physiology, behavior, immunity, and reproduction. The elimination of these obligate microbial partners could be a promising strategy to control insect pests. The use of antimicrobial peptides such as melittin, cecropin, or toxin proteins to target obligate symbionts would compromise the insect pest. However, the delivery of such antimicrobial agents to a specific site to target gut symbionts is a challenge. Nevertheless, Husseneder et al. (2016) used genetically engineered *Kluyveromyces lactics* (as a microbial delivery vehicle) that expresses melittin against the termite *Coptotermes formosanus*, which resulted in the elimination of termite gut symbiont thereby losing its cellulose degrading capability.

Furthermore, manipulating the genetic pool of the microorganisms for specific expression in different habitat could provide a much safer strategy to target pest insects. In particular, various entomopathogenic microbes (*Metarhizium* and *Photorhabdus*) have been identified to possess promoters that express toxin gene only in insect habitat (Fang et al. 2011; Münch et al. 2008). Several bacterial suicidal genes are available that degrade in a non-permissive habitat (Li and Wu 2009). The encapsulation of the microbes enables microbial release on insect feeding and in insect gut under particular environmental conditions (such as a change in pH, hydrostatic pressure, or high protease activity) (Arora et al. 2015).

4 Conclusion and Future Perspective

To satisfy the ever-augmenting demands of the growing population, the need for increased food production and crop protection is a major challenge. An army of researchers has been engaged over the years in the development of robust IPM strategies, but most cropping systems to date are hugely dependent on chemical pesticides (Stenberg 2017). There is a clear need for a holistic approach for sustainable pest management as well as to minimize the associated risks. The recent development in technologies has opened up new dimensions in crop protection. The advent of genomics and next-generation sequencing has made it practicable to explore the full spectrum of microbial diversity as there are no longer “hidden players” in plant–insect interaction. The recent advancement in omics technologies

is anticipated to have a considerable impact on the development of biocontrol strategies by harvesting the knowledge in the interaction between insects and their microbial allies. The characterization of microbial diversity together with metabolic fingerprinting plays a crucial role in an in-depth understanding of host–microbe interaction (Douglas 2018). Exploiting microbial partners can serve as a potential candidate for future pest management. Furthermore, recent advancements in RNAi and CRISPR-Cas9 technology have led to breakthroughs in agriculture by manipulating host-associated microorganisms as control strategies against pest insects (Arora and Douglas 2017; Gao 2018). The recent genetic engineering of gut microbiota in honeybee through state-of-the-art CRISPR-CAS9 technology has proven to be an excellent toolkit to characterize and manipulate the gut microbiome in insect host physiology (Leonard et al. 2018). The reproductive alteration mediated by bacterium *Wolbachia* by inducing cytoplasmic incompatibility in the host insect also serves as a potent strategy for pest control (Arora and Douglas 2017). However, it is essential to consider the risk associated with the release of genetically modified microbes to the environment. The application of antagonistic microbes is an alternative eco-friendly approach toward crop protection where the antagonistic microbe competes and/or inhibits the growth of plant pathogens (Feichtmayer et al. 2017). Not only microbes but also microbial-volatile compounds (mVOCs) are potential candidates in biocontrol (Bailly and Weisskopf 2017). It is important to consider that each of these strategies has its limitations that need to be considered in advance. Insects and microbes have a relatively short generation time and are in a constant evolutionary race to overwhelm our control endeavors. The continuous improvement of existing strategies and development of new avenues are pivotal to get rid of crop losses due to insect infestation in future.

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