Chapter 7
The Extended Microbiota: How Microbes Shape Plant-Insect Interactions

Zyanya Mayoral-Peña, Roberto Álvarez-Martínez, Juan Fornoni, and Etzel Garrido

Abstract Microorganisms were the first forms of life on Earth and are now part of all living organisms, but the role they played during the evolution of multicellular species is still a mystery. Among other biotic interactions, plants and their herbivorous insects have always occurred under a microbial milieu. During the past 20 years, our understanding of how microorganisms shape the ecology and evolution of plant-insect interactions has increased rapidly. However, the extent to which plant-associated microbes influence insect performance and how insect-associated microbes influence plant defenses remains largely unexplored. Here, we will highlight the potential reciprocal feedbacks between the microbiotas of plants and insects that could affect their interaction. We also bring attention to how network theory can help us understand the potential interactions within and between microbiotas. Finally, we will point out some promising directions for future experimental studies in order to better understand microbe-insect-plant interactions.

Keywords Defense · Microbiota · Network theory · Plant-insect interactions · Resistance · Tolerance

Despite the historical pairwise perception of the coevolutionary process between plants and herbivorous insects, the environment surrounding plants and their consumers is far from sterile; thus all their interactions take place under a microbial milieu that can significantly alter the ecology and evolution of both plants and insects (Felton and Tumlinson 2008). Metagenomic studies have accelerated our understanding of the fundamental role played by microorganisms in the survival

Z. Mayoral-Peña · R. Álvarez-Martínez · E. Garrido (✉)
Unidad de Microbiología Básica y Aplicada, Facultad de Ciencias Naturales, Universidad Autónoma de Querétaro, Santiago de Querétaro, Querétaro, Mexico
e-mail: etzel.garrido@uaq.mx

J. Fornoni
Departamento de Ecología Evolutiva, Instituto de Ecología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

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and adaptation of plants (Partida-Martínez and Heil 2011; Pineda et al. 2013) and their herbivorous insects (Chu et al. 2013; Chung et al. 2013; Asplen et al. 2014; Sharpton 2018). Nowadays, we also acknowledge that microorganisms can mediate biochemical communication between plants and insects (Hansen and Moran 2013). Indeed, the field of microbe-insect-plant interactions has been rapidly expanding over the past two decades with excellent reviews about the ecological implications of microorganisms (Biere and Bennet 2013; Biere and Tack 2013; Casteel and Hansen 2014; Sugio et al. 2015; Mason et al. 2019). However, the extent to which plant-associated microbes influence insect performance and how insect-associated microbes influence plant defenses remains largely unknown (but see Schausberger 2018 for induced resistance). Our aim is to provide a conceptual framework to fill this gap through the understanding of possible reciprocal feedbacks between the microbiotas of plants and insects that could affect their evolution. First, we will discuss how the holobiont concept came to be and whether this view actually helps us in understanding the ecology and evolution of hosts and their interactions. Next, we will review evidence about how the phyllosphere affects insect performance and possible feedbacks between the insect microbiota and plant defenses. We will finally point out how network theory can shed light into evaluating coevolutionary processes between the microbiotas of plants and insects.

From Microbes Through Holobionts to Plant-Insect Interactions

Our understanding of how microorganisms can shape the ecology and evolution of plant-insect interactions has been increasing rapidly since the last 20 years. However, along with all these advances came a general confusion in the terms and concepts frequently used in the context of the host-microbe interactions. The term holobiont was coined by Lynn Margulis (1990) to describe the intimacy between a host and its microbial symbiont. While this term was initially developed to explain the origin of eukaryotic cells, it was latter extended to include other obligatory symbioses (O'Malley 2017). At the beginning of this century, and under the umbrella of the hologenome theory of evolution, the term holobiont was redefined as a host (plant or animal) together with all its associated microorganisms upon which natural selection can operate (Zilber-Rosenberg and Rosenberg 2008; Theis et al. 2016; Rosenberg and Zilber-Rosenberg 2018). Along with this new view of holobionts, other concepts were commonly used although not always with the same meaning. Thus, in 2015 Marchesi and Ravel proposed clear definitions which we will follow throughout this review. The microbiota refers to the assemblage of microorganisms present in a defined host. The microbiome includes the host, all its microorganisms, their genomes, and the surrounding environmental conditions. The hologenome can then be defined as the sum of the genetic information of the host and its microbiota. While there is now plenty of evidence supporting the hologenome hypothesis of

evolution, whether the holobiont can function as an evolutionary unit is still under debate (Moran and Sloan 2015; Douglas and Werren 2016; Doolittle and Booth 2017; Doolittle and Inkpen 2018). Holobionts are indeed evolving units, but not evolutionary units upon which natural selection can act because a holobiont is better viewed as an ecological community with interactions that range from parasitic to mutualistic, with horizontal and vertical transmission and multiple levels of fidelity among the partners.

In considering the ecology and evolution of holobionts, the fidelity in the transmission of the microbiota along generations is of the most interest. It has been then proposed that the holobiont is constituted by resident microbiota (of vertical transmission), semi-resident microbiota (of vertical and horizontal transmission), and transient microbiota (of horizontal transmission) (Roughgarden et al. 2018). While all three types of microbiota can affect its host fitness (Zakharov 2015; Hurst 2017), the resident microbiota might be more important in evolutionary terms, while the transient microbiota represents an important source of variation affecting the host ecological interactions (Callens et al. 2018; Guégan et al. 2018). In this sense, it is interesting to note that a group of microbes appear to be shared and maintained among most individuals of a single population despite spatial and temporal variation (Roeselers et al. 2011; Lowe et al. 2012; Dougal et al. 2013; Astudillo-García et al. 2017; Kwong et al. 2017). This group of microbes has been termed the core microbiota (Shapira 2016), and while there is still no clear consensus on how to delimit or measure it (Shade and Handelsman 2012; Hurst 2017), considering its function rather than its composition could prove more insightful.

The core microbiota becomes more relevant if functional groups are considered, instead of taxonomic groups, because the latter gives no information about their contribution to the host phenotype (Doolittle and Booth 2017; Foster et al. 2017; Lemanceau et al. 2017). Moreover, considering the functional core microbiota implies that those transient or horizontally transmitted microbes could eventually replace those from the core without altering the host ecology and evolution. Thus, the presence of certain specific lineages of microbes would be sufficient to allow the functional assembly of the holobiont (Roughgarden et al. 2018). This functional contribution could then be relevant even when the microorganisms do not have a common evolutionary history with their host (Catania et al. 2017). Ultimately, the (extended) phenotype expressed by a particular host is the result of not only the presence of different microbes but also their functional contribution. Because this extended phenotype is the one that interacts with the consumers, the functional core microbiota will play a role in plant-insect evolution. Thus, in the context of plant-insect interactions, it is important to understand the effects of the microbiota on its host but also on how this host interacts with other organisms. If the presence/absence of specific lineages in the microbiota affects the fitness of either the plant, the herbivore, or both, a third-party player should be recognized in the battle between plants and herbivorous insects.

The Phyllosphere and Insect Performance

The surface of the leaves is the habitat for large and diverse microbial communities defined as phyllosphere (Ruinen 1956; Lindow and Brandl 2003; Vorholt 2012). All of these microbes are, at some point, inevitably consumed by the insects. While the impact of consuming entomopathogens has been the aim of several studies (Cory and Hoover 2006; Shikano 2017), little is still known about the possible effects of consuming nonpathogenic microbes. Recent evidence suggests that phyllosphere bacteria can indeed colonize the insect midgut (Mason and Raffa 2014; Bansal et al. 2011). Actually, it has been shown that the symbionts in the midgut of the gypsy moth *Lymantria dispar* are mostly obtained from its host plant (Broderick et al. 2004). However, few studies have evaluated the effect of the phyllosphere on insect performance. To our knowledge only two studies have specifically evaluated the effect of the phyllosphere on insect performance.

Shikano et al. (2015) evaluated the effect of two common bacterial colonizers of the phyllosphere (*Pseudomonas fluorescens* and *P. syringae*) on the performance, immunity, and resistance of the cabbage looper *Trichoplusia ni*. They found that consumption of the phyllosphere bacteria decreased larval growth rate but had no effect on immunity and, while the larval resistance to a baculovirus was not affected, resistance to pathogenic bacteria was concentration-dependent. The phyllosphere, however, can also have positive effects on larval performance. Larvae of the gypsy moth were bigger when consuming diet enriched with bacteria from the phyllosphere of the quaking aspen *Populus tremuloides* compared than when consuming diet enriched with bacteria previously isolated from their own guts (Mason et al. 2014). That is, bacteria that most benefitted larvae were initially foliar residents, suggesting that toxin-degrading abilities of phyllosphere inhabitants indirectly benefit herbivores upon ingestion (Mason et al. 2014). Interestingly, herbivory can in turn influence the phyllosphere. In the plant *Cardamine cordifolia*, the abundance of *Pseudomonas syringae* was higher in herbivore-damaged vs. herbivore-undamaged leaves, while *Pedobacter* spp. and *Pseudomonas fluorescens* infections were negatively associated with herbivory (Humphrey et al. 2014). All this evidence suggest that the composition and provenance of the microorganisms involved in the interaction between plants and insects should be identified before further experimental manipulation aimed at demonstrating their functional role.

The Gut Microbiota and Plant Defenses

In general, plant tissue consumption results in a reconfiguration of the primary and secondary metabolism. Several studies have reported that after damage, those processes related to the primary metabolism such as growth, photosynthesis, carbon assimilation, respiration, and reallocation of resources decrease (Zangerl et al. 2002; Schwachtje and Baldwin 2008), whereas the secondary metabolism,

responsible for the production of chemical defenses, increases (Kessler and Baldwin 2002). These physiological and metabolic changes are closely related to the expression of defensive mechanisms of tolerance and resistance, respectively. It is now recognized that the expression of tolerance is related to changes in primary metabolism that allow tolerant genotypes to reduce the negative effects of herbivory in terms of fitness (Strauss and Agrawal 1999; Stowe et al. 2000; Fornoni 2011). On the other hand, increases in resistance are given by changes in the production and abundance of various secondary metabolites that prevent or limit the loss of foliar tissue (Fritz and Simms 1992; Karban and Baldwin 1997). The triggering of signaling cascades that produce changes in both metabolisms can be either initiated by endogenous biochemical pathways that start when plant cells are damaged (Mithöfer and Boland 2008) or initiated by elicitors of microbial origin present in the regurgitant of herbivorous insects (Felton et al. 2014).

The regurgitant of many insects contains chemical compounds with eliciting properties. Among the substances found in the regurgitant are plant growth promoters such as auxins (Dyer et al. 1995), pectinases (Hori 1975), indoleacetic acid (Miles and Lloyd 1967), epidermal growth factors (Detling and Dyer 1981; Dyer et al. 1995), cytokinins that increase the photosynthetic rate (Giron et al. 2007; Kaiser et al. 2010; Halitschke et al. 2011), and transcription factors involved in the transport of carbon and nitrogen (Steinbrenner et al. 2011) as well as in the reactivation of secondary meristems (Korpita et al. 2014). All these compounds have the potential to alter the tolerance response of plants through different mechanisms. Studies carried out with the tomato plant, *Solanum lycopersicum*, show that plants treated with *Manduca sexta* regurgitant recovered more quickly after a defoliation treatment by increasing their growth rate and the reactivation of secondary meristems (Korpita et al. 2014) probably because of metabolites involved in the transport of carbon and nitrogen that come in contact with the plant cells via the regurgitant (Steinbrenner et al. 2011). Some other studies have shown an effect of the regurgitant on plant traits, but the identity and origin of the particular elicitors are still unknown. For example, in the tobacco plant *Nicotiana attenuata*, it was found that damage by the moth *M. sexta* decreases the photosynthetic rate; however, when consumed by the hemipteran *Tupiocoris notatus*, a specific induction of elevated photosynthetic activity was shown (Halitschke et al. 2011). To our knowledge only one study has indeed shown that the gut endosymbionts are responsible for the production of these elicitors. Such is the case of the Lepidoptera *Phyllonorycter blancardella*, in which its endosymbionts such as *Wolbachia* spp. produce cytokinins that are deposited on the leaves, via regurgitation, leading to the formation of photosynthetically active "green patches" on damaged leaves (Kaiser et al. 2010). If a general pattern where the gut microbiota participates actively in the production of those compounds present in the regurgitant that triggers some tolerance-related trait, it is still to be confirmed.

On the other hand, there is also evidence that the regurgitant contains elicitors related to resistance mechanisms such as glucose oxidase (Diezel et al. 2009), polyphenol oxidases (Major and Constabel 2006; Ma et al. 2010), and proteinase inhibitors (Korth and Dixon 1997). The presence of such elicitors can sometimes decrease

(Bede et al. 2006; Lawrence et al. 2008; Weech et al. 2008; Chung and Felton 2011; Chung et al. 2013) or increase plant resistance (Spiteller et al. 2000; Musser et al. 2002; Ping et al. 2007; Diezel et al. 2009). Many studies have even identified the microbial symbionts known to be responsible for affecting plant resistance. The bacterium *Hamiltonella defensa* is a facultative endosymbiont of the whitefly *Bemisia tabaci*, and it is involved in the suppression of JA in tomato plants (Su et al. 2015). Also, in the tomato plant, the larvae of the Colorado potato beetle, *Leptinotarsa decemlineata*, exploit bacteria in their oral secretions to decrease the production of JA and JA-responsive antiherbivore defenses (Chung et al. 2013). In the same study system, applying bacteria isolated from larval oral secretions to wounded plants confirmed that three microbial symbionts belonging to the genera *Stenotrophomonas*, *Pseudomonas*, and *Enterobacter* were responsible for defense suppression (Chung et al. 2013).

Interestingly, the effects of the bacterial symbionts on plant resistance seem to be host-dependent. For example, bacterial isolates from oral secretions of the false potato beetle *Leptinotarsa juncta* belonging to the genera *Pantoea*, *Acinetobacter*, *Enterobacter*, and *Serratia* were found to suppress polyphenol oxidase activity in the non-preferred host tomato, while only *Pantoea* sp. was observed to suppress the same activity in the preferred host horsenettle (Wang et al. 2016). There is even evidence of potential trade-offs among resistance traits mediated by bacterial symbionts. The bacterium *Pantoea ananatis*, isolated from the oral secretions of the armyworm *Spodoptera frugiperda*, downregulates the activity of the proteins polyphenol oxidase and trypsin proteinase inhibitors, but upregulates the peroxidase activity in the tomato plant (Acevedo et al. 2017). In turn, plant chemical defense can also affect the composition and structure of the insect microbial community. In the trembling aspen, *Populus tremuloides*, phenolic glycosides and condensed tannins affected the relative abundances of *Ralstonia* and *Acinetobacter* in the midgut of the gypsy moth *Lymantria dispar* (Mason et al. 2015). Taken together, these examples show the potential feedbacks between insect microbial communities and plant resistance. However, future studies should be designed to specifically test reciprocal feedbacks between the gut microbiota and plant resistance. Overall, all the evidence points at microorganisms modulating the expression of tolerance and resistance mechanisms against herbivory. We visualized two approaches that can complement each other to disentangle the evolutionary role of plant and insect microbiotas: network theory and experimental studies.

Network Theory and Interactions Among Microbiotas

Over the last 20 years, it has been recognized the value and importance of networks in a myriad of applications in biology. The concepts and tools developed from graph theory have provided new insights into evolutionary ecology as well as a valuable conceptual framework to address new challenges. Fundamental concepts from ecological systems – such as communities – to networks of biological interactions

among their components provide a way to summarize large amounts of information within single objects. Perhaps, one of the most successful examples of the application of network theory in biology is plant science where key regulators, functional modules, and novel phenotypes have been identified through gene regulatory networks (Álvarez-Buylla et al. 2007). In the field of microbial evolution, network theory has been used to identify new targets for probiotic treatments (Lemon et al. 2012), find the most influential biotic and abiotic factors that structurally change the structure of the microbial community (Fisher and Mehta 2014), and distinguish the topological properties of microbial networks between health and disease states (Sánchez et al. 2017; Sommer et al. 2017). Microbial networks thus constitute a heuristic tool that could help us model and understand the complexity of the interactions within the microbiota and among microbiotas of interacting hosts.

In general, ecological networks can be divided in static or dynamic networks. Static networks focus on the study of its topological properties: measures of centrality (the relative importance of the nodes, each node representing a particular microorganism), the distribution of links to other nodes (degree distribution), identifying modules or clusters, and finding overrepresented or recurrent subgraphs (motifs). These kinds of networks are useful because they take into account any binary dependence between the elements, that is, the presence-absence of interactions among species. Weighted networks are a generalization of static networks, adding to the edges a measure of the relevance or certainty of its links. This value can be represented by the frequency or the strength of the different interactions. On the other hand, dynamical or evolving networks represent not only the species (i.e., microorganisms) and the topology/strength of the interactions but also the dynamic nature of the whole system (i.e., the holobiont). However, these kinds of networks are more difficult to infer from empirical data because they need a detailed and specific information almost never available. Due to the fact that static networks are much easier to obtain from data, the ample majority of ecological networks belong to this kind.

In microbiome studies, particular approaches have been adapted and combined to infer co-ocurrence networks of OTUs, interaction networks, and a new multi-network approach involving networks of microorganisms with its host. In a seminal paper, Gould and collaborators (2018) mapped the interactions between individual species of bacteria against several fitness traits of its hosts, the fruit fly. They showed that the same bacterial interactions that shape microbial abundances in the microbiota also determine the fly fecundity. In a recent study, Huitzil et al. (2018) proposed an evolutionary computational model in which a network representing the host can adapt in order to perform a predefined function related to its host. In this model, the host network interacts with its microbial network, and these complex interactions can explain the presence of dysbiosis, specialization, and microbial diversity.

One of the most important goals in microbial networks is to identify the so-called keystone taxa in microbial communities and to determine the factors that influence its function in a given environment. The dominant taxa could be the most abundant or the most important, structurally speaking, in terms of the topology of the network. In an extraordinary example, Flores et al. (2013) observed that complex

networks between host and parasites or between bacteria and phages are at the same time, but at different scales, modular and nested. This observation suggests that different evolutionary regimes operate at different scales. The next natural step would be to integrate various layers of information via multiple single networks. This approach is called multilayer networks or multi-networks and could be defined as an amalgamation of networks that interact and evolve with each other (Bianconi 2018). Multilayer network applied to whole holobionts and to the interactions among holobionts could be an extremely valuable tool in understanding microbe-insect-plant interactions. Each one of these networks (plant microbiota network and insect microbiota network) will then form a meta-network, which will undoubtedly be a more realistic approach to the study of ecological interactions among holobionts. Thus, multilayer networks have the potential to take into account multitrophic interactions (Mirzaei and Maurice 2017).

Experimental Studies

To date most studies about microbe-insect-plant interactions have concentrated on the description of the microbiotas within multicellular species as well as in the sources of possible environmental regulation. One of the major assumptions behind these studies is that microorganisms directly affect the survival, performance, and fitness of their hosts as well as the interactions between hosts and other community members. Correlative evidence support this premise but have not yet identified the functional role of most microbial lineages. If microorganisms have the potential to regulate the ecological and evolutionary dynamics between plants and insects, then our technological efforts to reduce or control herbivory levels should not neglect the effects of microorganisms. Pests are usually controlled with the use of insecticides and/or genetically modified crops, whereas the manipulation of microorganisms within plants or insects is still underdeveloped. We highlight two experimental approximations that can shed light into the functional role of microorganisms within the context of a plant-insect interaction. First, performing cross-infection experiments (i.e., reciprocal transplants) of microorganisms from different host populations or environmental conditions can provide relevant information on their role for plant and insect coadaptation to each other. These kinds of experiments are also fundamental to differentiate the relative importance of natural selection and genetic drift in the conformation and function of the microbial communities. Second, experiments where the microbiota composition is manipulated, either the presence/absence or the relative abundance of certain microorganisms, can identify their functional role on the plant-insect interaction. These experimental approximations, among others, will demonstrate whether the understanding and manipulation of plants and insects require the recognition that the evolution of the interaction depends not only upon the plant and insect genetics within a specific environmental context but also on the microbiome as well.

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