New Synthesis: A Holobiontic View on Plant-Insect Interactions

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A considerable proportion of the biomass of plants and animals consists of microbial cells, which when considered together with the host's cells, define the holobiont. The intimate and often obligate relationships between hosts and their associated microbes call into question traditional phyto- or zoocentric views on plant-insect interactions. Instead of considering only the plants' and/or animals' interests in ecological and evolutionary studies, it seems appropriate to ask whether and how the vested interests of their associated microbes, such as survival, proliferation and dispersal, are safeguarded when the macroscopic players interact. Recent findings show that microorganisms are not passive partners but manipulate either the sender or the receiver of signals and/or cues (or initiate signaling by themselves). Accordingly, for plant pathogens, the "host manipulation hypothesis" has been contrasted with the "vector manipulation hypothesis" that addresses either microbe-mediated changes in the plant's phenotype or changes in insect behavior, respectively (Ingwell et al. 2012). These effects could be generalized as a "sender or receiver manipulation hypothesis" in chemical plant-insect communication.

Plant-associated microbes often induce changes in the chemical phenotype of plants or in the plants' responses to insect attacks. Mann et al. (2012) demonstrated that infected *Citrus sinensis* plants emitted higher amounts of methyl salicylate, but less methyl anthranilate and D-limonene than plants not infected by *Candidatus Liberibacter asiaticus* bacteria. Psyllid bugs (*Diaphorina citri*) initially chose infected plants but subsequently—after they became carriers of the pathogen—moved to non-infected plants. This switch was presumably triggered by lower nutrient quality provided by the infected plants. While in this example the sender was manipulated, a study by Ingwell et al. (2012) reported on the manipulation of the receiver's behavioral response towards plant cues. Aphids (*Rhopalosiphum padi*) carrying the Barley yellow dwarf virus preferred healthy winter wheat plants, whereas aphids not serving as vectors chose plants that were already infected with the virus, which also differ in their volatile profiles compared with healthy plants (see references in Ingwell et al. 2012).

The hologenome theory (Rosenberg and Zilber-Rosenberg 2011) proposes that the genetic information of the microbiome associated with a host changes with environmental conditions, affects the host's and the microbes' fitness and can be transmitted to subsequent generations. The

studies mentioned above do not address all aspects required to align plant-insect-microbe tritrophic interactions with the hologenome theory. Furthermore, these studies involve plant pathogens, whose interests may not conform to Rosenberg's and Zilber-Rosenberg's definition (2011). Nevertheless, these studies offer some evidence consistent with the predictions of the theory: 1) the hosts provide a beneficial environment for the microorganisms; 2) the bacterial/viral genome is acquired by the hosts; and 3) the microbes affect phenotypic or behavioral traits of the holobionts as well as (in part) their fitness. Note that these examples provide no information on whether the acquired genes / traits will be transmitted to the next generation, which is an obligate requirement for the theory (Rosenberg and Zilber-Rosenberg 2011). Therefore, it is still too early—and too speculative—to state that plants, animals and their interactions evolve as holobionts, and that acquired traits are passed to future generations in a Lamarckian fashion.

Upcoming questions involve how non-pathogenic microbial communities (i.e., microbiomes, not only individual strains) affect or mediate plant-insect interactions. Additionally, it remains to be elucidated in greater detail how these communities manipulate the senders or receivers of cues / signals, and with which consequences for the ecology and evolution of the holobionts, in realistic communities of multiple senders and receivers. Novel approaches—both computational and experimental—will be required to disentangle microbial and host interests in order to identify where they converge or diverge. Finally, in order to rigorously test the hologenome concept in plant-insect interactions (and elsewhere), stringent experiments will need to address each of the propositions framed in the hologenome concept. Even if "hologenomes"—with all the ambitious expectations on the ecology and evolution of the parties involved—remain a diffuse conception, the idea of joint evolutionary trajectories of microbial communities and their hosts, and how such trajectories are guided by chemistry, will motivate future studies on these fascinating tritrophic interactions.

References

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