Symbionts in insect biology and pest control
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Within the last decade, the importance of the microbiome has become increasingly evident, not just in humans (Blaser, 2014; Yong, 2016), but as much in insects (Douglas, 2018). The microbiome is defined as the collection of microorganisms, their genomes, and the surrounding environment (Marchesi & Ravel, 2015). A vast number of studies investigating various organisms have revealed that the microbiome not only harbours disease-causing agents and antagonists but also symbionts and other microbes with a beneficial role for their host. Examples of such facilitating functions include the processing of indigestible food substrate, the supply of essential nutrients, the support of immune defence functions against parasites and pathogens, and in some cases even the entire replacement of obligate physiological functions of their hosts. Knowledge of the composition of insects’ microbiomes, and understanding modifications and interactions within them, is important for insect pest control and large-scale insect rearing, as applied in, for instance, the sterile insect technique (SIT) and disease-free feed production.

The microbiome of insects consists of members from multiple kingdoms: bacteria, archaea, fungi, viruses, and protozoa. In this special issue of the journal, a range of invited contributors explore the interactions between these microbiome components and their insect host. Gurung et al. (2019) review the composition of pest insects’ microbiomes and their impact on fitness and behaviour of the hosts. These microbes do not exclusively interact with their host, yet may also be engaged in interactions with each other. This is nicely illustrated by Gonella et al. (2019) who review the interactions between symbionts of phloem-feeding phytophagous insects. These insects may act as vectors of bacterial phytopathogens when they move from infected to uninfected (or infected) host plants. However, the outcome of the intra-microbe interactions can substantially affect the insect vector competence and consequently the spread of diseases.

The microbiome composition of a given insect species may depend on multiple factors, e.g. its geographical location and the type of food eaten. Also human-inflicted modifications and treatments, as they, for instance, occur in insect mass-rearings, can have an impact. Morera-Margarit et al. (2019) characterise the bacterial microbiota composition of the black vine weevil, Otiorhynchus sulcatus (Fabricius) (Coleoptera: Curculionidae), across four geographically separate locations in the UK. A single operational taxonomic unit phylogenetically related to Candidatus Nardonella accounted for 81% of the total sequencing reads for all tested insects. Koskinioti et al. (2019) investigate differences of the gut bacterial profile of two wild olive fruit fly populations, Bactrocera oleae Rossi (Diptera: Tephritidae), in association with their geographic origin and with changes that occurred after introduction into a laboratory environment. They look specifically at changes after the first exposure of the wild adult flies to artificial diet with and without antibiotics. This is relevant for SIT practice, for which mass-reared insects are exposed to radiation to render them infertile, prior to their release into the environment where they compete for mates with wild flies. Irradiation, however, is likely to not only affect the fertility of the insects but may also cause changes in the composition of the bacterial community of treated insects. Stathopoulou et al. (2019) analyse the bacterial profile of larvae and adults of the oriental fruit fly, Bactrocera dorsalis (Hendel), an important fruit pest, as well as changes in pupae after gamma radiation. After irradiation the taxonomic diversity of the bacterial community is higher compared to that in non-irradiated B. dorsalis samples, suggesting the
disturbance of intra-microbiome and/or microbiome-host interactions.

North American yellowjacket species (Hymenoptera: Vespidae) are found to be associated with the yeast species *Hanseniaspora uvarum* and *Lachancea thermotolerans*, and are attracted by brewer's yeast, *Saccharomyces cerevisiae* (all Saccharomycetaceae). Babcock et al. (2019) analyse the headspace volatiles of *H. uvarum* and *L. thermotolerans* cultures and test the attraction of whole yeast culture volatile blend as well as a synthetic blend of 18 headspace components in field experiments. Both yeast appear to attract yellowjackets if grown on yeast peptone dextrose (YPD) agar infused with grape juice but not if these yeasts are grown on YPD agar deployed alone or with grapes, and the synthetic blend is differently attractive to different Vespidae species.

The ambrosia beetle *Megaplatypus mutatus* (Chapuis) (Coleoptera: Platypodidae) damages the leaves of poplar trees. The sex pheromones produced by males contain two substances, sulcatol and sulcate – the first is stored in the males' hindgut, the latter is only present in emissions. Slodowicz et al. (2019) demonstrate that several fungal strains isolated from the beetle’s exoskeleton are able to perform the conversion from sulcatol to sulcate. The fungus *Graphium basitruncatum* (Matsush.) Seift & Okada (Microascales), present in male but not in female exoskeletons, produces the highest amount of this ketone. These results suggest that fungi associated with *M. mutatus* are involved in sex pheromone production in insects.

Some components of the microbiome can be detrimental to their host, such as endosymbionts that manipulate host reproduction. The parasitic endosymbiotic bacterium *Wolbachia* induces parthenogenesis in a whole range of insects, including egg parasitoid *Trichogramma* wasps (Hymenoptera: Trichogrammatidae). Ebrahimi et al. (2019) generate homozygous *Wolbachia*-infected recombinant isofemale lines (RILs) of *Trichogramma pretiosum* Riley to investigate the effect of genetic variation on various life-history traits that are associated with offspring production. It turns out that, as expected, the RILs differ in effectiveness of parasitisation and offspring survival. They further develop methods to track offspring origin, e.g. in competition assays, in which each RIL can be distinguished by its allelic state at one or more loci. This tool can be useful for selecting the best performing individuals in biocontrol approaches.

Jamin & Vorburger (2019) study the effects of the common aphid symbiont *Regiella insecticola* Moran et al. on aphid life-history traits. Commonly, *R. insecticola* does not influence resistance to parasites, yet one specific strain (R5.15) provides strong protection of its host against parasitoid wasps. Three aphid species – the green peach aphid *Myzus persicae* (Sulzer), the pea aphid *Acyrthosiphon pisum* (Harris), and the black bean aphid *Aphis fabae* (Scopoli) (all Hemiptera: Aphididae) – are included in the investigation of potential host life-history costs of protective (R5.15) and non-protective *R. insecticola* strains. After transferring the R5.15 strain to the aphids, not much harm appears to be done to various aphid life-history traits compared to effects by non-protective strains, suggestive – for now – of high benefits at very low costs!

Decreasing hydrolysable tannin concentration and increasing condensed tannin concentration in daimyo oak, *Quercus dentata* Thunberg (Fagaceae), negatively affect the performance of the aphid *Tuberculatus macrotuberculatus* Essig & Kuwana (Hemiptera: Aphididae) (Yao, 2019). Concurrently with the seasonal change in aphid performance also the density of the symbiont *Buchnera aphidicola* Munson et al. decreases, whereas the density of *Wolbachia* sp. remains stable over time. This suggests that *Wolbachia* may occur independently of the metabolism of their host.

There are many opportunities to exploit parts of the insect’s microbiome for human benefit. Agamennone et al. (2019) investigate the potential of a bacterial strain, isolated from the springtail *Folsomia candida* (Collembola: Isotomidae), to serve as a new source of antimicrobial compounds. Identified as *Bacillus toyonensis* Jiménez et al., the isolated strain’s genome is analysed for indication of ‘resistant genes’ and secondary metabolite clusters that may explain the observed inhibitory activity against pathogens of the bacterium and its exudate. Coupled with a high resistance to penicillin, as indicated by resistance genes, the authors claim that this *Bacillus* strain may provide a promising novel source of antimicrobials.

Overall, this special issue provides a broad perspective on the highly diverse roles that microbes may have on insect biology and on their potential for exploitation in insect rearing. It is our strong wish that this set of articles adds fuel to the further development of ‘microbiome science, an exciting and fast-emerging new discipline that is reshaping many aspects of the life sciences’, as it so aptly says on the jacket of the new book of our former board member, Angela Douglas (2018). We could not agree more.

References


