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Insect–microbe interactions: the good, the bad and the others

Editorial overview

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The past quarter century has seen a dramatic rise in our understanding of the mechanistic basis of insect–microbe interactions. Though not unique in living in close proximity to microbes, it is not difficult to appreciate that insects partly owe their success to being very adept at dealing with them. Studying the response of insects to pathogens has revealed the nature of receptors, signalling cascades and effectors that comprise insect immune systems. Despite not being ‘adaptive’ in the classical immunological sense, insect immunity is clearly multi-faceted, specific and highly effective. Significant progress has also been made on the microbial side with the identification of a variety of virulence mechanisms that enable microbes to evade, suppress or resist the insect’s immune system. Equally, understanding the basis of insect host resistance to microbes has strong implications for limiting the ability of insects to vector diseases that impact human health or destroy crops, while facilitating the development of better strategies to protect beneficial insects, including pollinators.

The majority of interactions between insects and microbes are commensal or mutualistic, not pathogenic in nature. It has long been appreciated that certain insects incorporate and harness the vast metabolic potential of microbes for their own benefit, such as the mutualistic bacterium *Buchnera*, which supplies its aphid host with essential amino acids that plant saps lack. Increasingly, we are beginning to appreciate that insect–microbe symbioses are much more diverse and widespread than was initially thought. The microbial flora that colonize insect guts are not only important for the provision of nutrients, but also have recently been implicated in the ability of insects to resist infection. Endosymbiotic *Wolbachia* have long been studied for their ability to manipulate the reproduction of their host, but their ability to confer their hosts with resistance to viral infection, a feature which in large part explains why they are so prevalent, was overlooked until just several years ago.

In this edition of *Current Opinions in Microbiology* we have brought together a series of reviews that cover some aspects of insect–microbe interactions. They not only reveal the recent advances in the field but also reflect the diverse nature of interactions between insects and microbes.

It has long been recognized that insects are rather resistant to microbial infection due to effective physical barriers, including their cuticle or the gut peritrophic matrix as well as a robust, multi-faceted immune response. A subset of entomopathogenic bacteria such as *Bacillus thuringiensis*, *Serratia entomophila*, *Photorhabdus* spp. and *Xenorhabdus* spp. has the capacity to breach insect barriers either by themselves or (as is the case for *Photorhabdus* spp. and *Xenorhabdus* spp.) with the assistance of nematodes, invading and proliferating within their host. Initial studies of these bacteria have mostly focused on their insecticidal toxins, with the goal of developing bio-pesticides. Recent studies have been revealing the additional layers of complexity involved in the infection process. In this issue, Nielsen-Leroux *et al.* describe the mechanisms used by the entomopathogenic bacteria, *B. thuringiensis*, *Photorhabdus luminiscens* and *Xenorhabdus* spp. to infect insects — from initial colonization of the gut and hemolymph — to exploitation of the insect cadavers and elimination of bystanders. An emerging trend is that a diverse range of entomopathogens use common strategies to invade and exploit their hosts.

Entomopathogenic fungi have the capacity to penetrate insect cuticles through the production of chitinases and lipases. They are important pathogens of insects in the wild and as such attractive agents for controlling crop pests and disease vectors. The study of entomopathogenic fungi has recently benefited from the development of genetic and genomic tools. In their review, Fang *et al.* examine how, with a comprehensive understanding of virulence mechanisms and other aspects of fungal biology, it has recently become possible to engineer novel and more potent entomopathogenic fungal strains that could increase the potential of this method of insect control.

Bubonic plague is now widely believed to be the cause of the Black Death that swept through Europe in the 14th century and killed an estimated 25 million people, representing 30–60% of the European population. Bubonic plague is a zoonotic disease caused by a gram-negative bacterium, *Yersinia pestis*, circulating mainly among small rodents and transmitted to humans through fleas. In their review, Chouikha and Hinnebusch examine the mechanistic basis of adaptations that enable *Y. pestis* to colonize the flea midgut. Interestingly, *Y. pestis* had to gain certain functions, including biofilm formation and resistance to antibacterial activity, but also lost certain functions, namely insecticidal activity.

Phytoplasmas are insect-vectored bacterial plant pathogens that can have devastating effects on crop yield. *Phytoplasma* are obligate symbionts of plants (growing in the phloem) and sap-sucking insects, the latter being key for their transmission. Phytoplasmas have a broad plant host range, which often depends on which plant species their insect vectors can exploit. Phytoplasmas traverse the gut, pass through the hemolymph and enter the salivary glands of their hemipteran phloem feeding hosts. Similarly to bacterial endosymbionts, phytoplasmas have reduced genomes with limited metabolic capabilities and are not amenable to *in vitro* culture. Despite these limitations Sugio and Hogenhout describe the considerable advances that has been made in the study of phytoplasma genomic organization as well as the identification of specific virulence effector proteins produced by phytoplasma to induce changes in plant physiology. Phytoplasma exemplify insect-associated microbes that are highly specialized for, and almost entirely reliant upon, certain insect host species.

Several insect species carry highly integrated bacteria endosymbionts that provide their host additional metabolic capacity allowing survival on an otherwise nutritionally incomplete diet. Examples include the aforementioned *Buchnera* symbiont of Aphids and *Wigglesworthia* conferring tsetse flies with the ability to use blood meals as their sole food source by providing complex B-vitamins. It has long been recognized that endosymbionts can be lost by rearing insects at higher temperatures. The resulting aposymbiontic insects often suffer drastically reduced fitness. In the light of global warming models that predict a 1.8–4 °C increase in average temperature, Wernegreen discusses the unexpected consequence of climate change on endosymbiontic interactions.

Wolbachia infect 40–60% of all insect species, being amongst the most successful infectious bacteria on earth. As a consequence of their vertical transmission, *Wolbachia* have evolved mechanisms to manipulate the reproduction of their hosts. These manipulations include cytoplasmic incompatibility, which provides *Wolbachia* with a remarkable capacity to spread through insect populations. Their capacity to spread, in conjunction with the protective effect of *Wolbachia* against viruses, makes *Wolbachia* a promising tool for control of disease transmission by insect vectors. Vavre and Charlat describe recent developments in modelling the spread of Wolbachia through insect populations. Predicting the conditions that allow *Wolbachia* to spread through a host population is not only of significant biological interest, but also vital for the implementation of *Wolbachia*-based disease transmission control strategies.

Fungus-farming ants grow fungi for food by providing fungal gardens with various plant-derived substrates. The symbioses between ants associated microbial biofilms and cultivated fungi have been largely popularized as a striking example of symbiosis. Specifically, antibiotic-secreting integumental bacteria were believed to have co-evolved with ants, with a specific role for preventing infection in fungal gardens. These findings have led to appealing analogies being drawn between ant fungiculture and human agriculture. Here, Mueller reports that after re-examination, the interactions between fungus-farming ants and bacteria appear to be more diverse and do not fit entirely with the picture that was initially presented. While we lack the deep understanding of this field to either fully accept or refute the conclusions of this review, we felt that when thoughtfully presented and supported by experimental evidence, expression of contradictory viewpoints is important for scientific advancement.

A common condition of the metazoan gut is to be in association with a number of benign or beneficial microorganisms. Recent studies demonstrate that most insects are associated with a much lower diversity of bacterial taxa than observed in mammals, and that these are acquired from their environment (food, faeces or eggshells). Despite their low number, the influence of these resident microorganisms is profound, altering aspects of host physiology, especially digestive and immune functions. Here, Ricci *et al.* examine our understanding not only of mosquito–microbiota interactions and the implications these have for the general physiology but also immunity of the host insect. Recent advances suggest that by altering or engineering mosquito microbiota it might be possible to decrease their competence as human disease vectors.

Mosquitos of the genus *Anopheles* are the main vectors of the human malaria parasite *Plasmodium falciparum* and as a consequence are the main target for vector control. Wild Anopheles populations are highly heterogeneous in terms of susceptibility to *Plasmodium*. Mitri and Vernick describe the progress in understanding the genetic polymorphisms underpinning mosquito refractoriness to *Plasmodium*. They reveal how a combination of pre-existing genetic variation, pathogen-mediated selective pressure and fitness trade-offs would have shaped the evolutionary response of vectors to pathogens, leading to vector–pathogen specificity. This review highlights how important it is to link our understanding of insect immune function to a wider evolutionary and ecological context.

These diverse reviews reflect the rapid development of research in the field of insect–microbe interactions, and the profound impact this work has for human heath and agricultural productivity. Also reflected is a growing need for a more holistic approach, moving towards more complex models involving the simultaneous study of a variety of microbes and environmental conditions. Progress is likely to be made by studying the interaction between insects and their pathogens in the context of non-pathogenic commensals and mutualists and *vice versa*. Researchers are also increasingly appreciating complicated scenarios in which microbes tend to occupy condition-dependent positions on the spectrum from pathogen to mutualists.