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Current Opinion in Insect Science

How resident microbes modulate ecologically-important traits of insects

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The microbiota inhabiting insects influence a wide range of ecologically-important traits. In addition to their better-known roles in nutrient provisioning and degrading plant polymers, there is emerging evidence that microorganisms also aid herbivores in countering plant defenses. The latter can be mediated by enzymes that degrade plant allelochemicals or via the modulation of plant signaling pathways. Symbionts are also increasingly recognized to protect insects from attack by a wide range of natural enemies. Underlying mechanisms are poorly understood, but some microbes produce antimicrobials or toxins, while others modulate insect immune responses. Ecologically-relevant symbioses can exhibit dynamic variation in strength and specificity of conferred phenotypes, transfer key traits among unrelated insects, and have effects that extend to interacting players and beyond.

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Current Opinion in Insect Science 2014, **4**:1–7

This review comes from a themed issue on **Molecular physiology**

Edited by **Angela E Douglas**

For a complete overview see the Issue and the Editorial

Available online 12th August 2014

doi:10.1016/j.cois.2014.08.001

Introduction

As the most diverse and abundant animals on Earth, insects perform important roles in terrestrial ecosystems as decomposers, recyclers, pollinators, herbivores and natural enemies [1]. Insects have also evolved for more than 400 myr, and persist today, in a microbial world resulting in an astonishing array of insect–microbe interactions [2,3]. Many interactions, including those involving uncultivable microbes and diverse microbial communities, were difficult to study before the availability of modern molecular techniques, resulting in a worldview that largely emphasized interactions among multicellular eukaryotes. Today, our perspective is undergoing a sea change, and there is a rapidly growing appreciation that microorganisms are key players influencing insect function, ecology, and evolution.

Insects form persistent associations with many microbial groups, and the major types of interactions are found in Table 1. In general, surfaces exposed to the environment, including the gut, are colonized by extracellular microbes, but the particular areas infected, the duration and specificity of the association, and effects on the insect are highly variable [2]. Many microbial associates are acquired from the environment each generation, but others are maternally transmitted with high fidelity and persist over long periods of time [3]. In the latter, insect and symbiont fitness are tightly linked, and many microbes invade and persist in insect populations by conferring net benefits, although some spread by manipulating insect reproduction in ways that favor infected matrilines, and a few employ both strategies [4,5]. Here we focus on the microbial residents of insects that influence resource acquisition and insect defense (Figure 1), emphasizing the diversity of conferred phenotypes and recent progress in understanding functional mechanisms.

Microbe-modulated resource acquisition

Many of the most successful insect groups are herbivorous or xylophagous, which present major challenges to resource acquisition, including low nitrogen content, indigestible components, and chemical defenses [6,7]. Plant tissues vary greatly in nitrogen content and the availability of essential amino acids, and it has long been known that insect groups specializing on nitrogen poor substrates, such as plant sap, require infection with nutrient-provisioning microbial partners [6,7]. These *obligate intracellular symbionts* (Table 1) have highly reduced genomes, yet retain the specific metabolic machinery, lost ancestrally in animals, allowing for subsistence on restricted diets [6,7]. In some groups, dual obligate symbionts occur, each with reduced genomes encoding nutritional pathways that complement the capabilities of the other [8]. Nutrient provisioning was the sole role assigned to obligate intracellular symbionts until the recent discovery that the Asian citrus psyllid, *Diaphorina citri*, has one obligate symbiont, *Carsonella*, dedicated to nutrient provisioning, and a second, *Profftella armatura*, likely functioning as a protective symbiont, with a large fraction of its small genome dedicated to polyketide toxin biosynthesis [9••].

The *gut microbiota* (Table 1) of insects are associated with more diverse roles in resource acquisition [2]. Many

Table 1

Major types of insect–microbe interactions.

Symbiont types	Transmission	Insect host range	Major roles
Obligate intracellular symbionts: Ancient, highly-specialized associations, restricted tissue tropism. Usually bacteria, some fungi.	Strictly vertical	Present in many hemipteran groups feeding exclusively on phloem, xylem, and vertebrate blood. Also found in carpenter ants, cockroaches, tsetse flies, some Psocodea, and Coleoptera.	Nutrient provisioning, possibly defense
Heritable facultative symbionts: Mostly intracellular, some extracellular, and some both. Usually bacteria.	Primarily vertical, occasionally horizontal	Widespread across insects, although infections are often sporadic within and among host lineages.	Host protection, reproductive manipulation, and some likely mediate herbivore-plant interactions
Gut microbiota: Extracellular. Mostly bacteria, some fungi and other eukaryotic microbes	Usually environmentally acquired with varying specificity, but also social transmission	Widespread across insects, but highly variable in terms of microbial diversity. Associations are often more specific and specialized in some groups including xylophages and social insects.	Breakdown cellulose and other plant polymers, nutrient provisioning, nitrogen recycling and fixation, detoxify plant defenses and pesticides, protect against ingested pathogens
Environmental associates: Mutualistic associations between insects and environmental microbes, including plant pathogens that confer benefits to insect vectors. Often fungi, bacteria, and viruses.	Environmental and social	Leaf-cutter ants, sap-feeding Hemiptera, xylophagous insects	Food source, mediate resource acquisition, counter plant defenses

groups, but especially xylophages, carry gut associates that, often in conjunction with insect-produced enzymes, break down lignocellulose, making insect–microbe collaborations major players in terrestrial carbon cycling [2]. In a few cases, gut symbionts are known to recycle nitrogenous waste or fix atmospheric nitrogen for insect nutrition, and some likely provision nutrients directly, including essential amino acids and vitamins [2]. For instance, the extracellular gut symbiont *Ishikawaella*, found in the herbivorous plataspid *Megacopta punctatissima*, rivals intracellular nutritional symbionts in degree of specialization, including a sharply reduced genome that retains pathways for the biosynthesis of essential nutrients [10].

Plants employ a range of tactics to defend against insect herbivory, including the production of repellant and toxic secondary metabolites. In turn, insects have countered with an array of behavioral and intrinsic physiological responses, including the detoxification of defensive allelochemicals. The interplay between plant chemical defenses and insect counter-responses impacts herbivore diet breadth and has played a major role in the coevolutionary diversification of plants and phytophagous insects [1]. In addition to intrinsic mechanisms, recent studies hint that microbes may frequently assist insects in the detoxification of plant allelochemicals. For example, several bacterial species found in the gut of the mountain pine beetle, *Dendroctonus ponderosae*, a major pest of lodgepole pine, encode pathways involved in the detoxification of terpenes, a widespread chemical defense in conifers [11•]. Another example occurs in the leaf-cutter ants, which cultivate a symbiotic fungus for consumption of plant material in their nests. In at least one case, laccase enzymes produced by the fungus *Leucocoprinus* are consumed by the ant, passed through gut, and deposited on top of fungus garden where they break down plant phenolics [12•].

Resident microbes have also been shown to modulate inducible plant signaling pathways involved in herbivore defense. The Colorado potato beetle, *Leptinotarsa lycopersicum*, for example, uses orally secreted bacteria to elicit the plant's antibacterial salicylic acid pathway, which interferes with the induction of the jasmonic acid pathway, resulting in the suppression of plant defenses against herbivory [13•]. There is also growing evidence that many plant pathogens are simultaneously beneficial symbionts of the insects that vector them. A viral pathogen of tobacco, for example, vectored by the whitefly, *Bemisia tabaci*, suppresses defenses aimed at herbivores, including terpene synthesis [14]. And in tomatoes, herbivore-related plant defensive pathways are suppressed when the plant pathogen *Liberibacter psyllarous* and its vector, the tomato psyllid *Bactericera cockerelli* co-occur, relative to the insect feeding alone [15].

Economically important plants are often chemically defended against insect herbivory by human applied insecticides, and again, insects have a very successful