



New developments in microbial interspecies signaling

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There is a growing appreciation that in addition to well-documented intraspecies quorum sensing systems, small molecules act as signals between microbes of different species. This review will focus on how bacterial small molecules modulate these interspecies interactions. We will particularly emphasize complex relationships such as those between microbes and insects, interactions resulting in non-antagonistic outcomes (i.e. developmental and morphological processes), how co-culture can lead to the discovery of new small molecules, and the use of known compounds to evoke unexpected responses and mediate crosstalk between microbes.

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Introduction

Historically, interspecies interactions have focused on growth-inhibitory interactions, yet a variety of phenotypic outcomes other than antibiosis are possible, including alterations in developmental processes such as sporulation and biofilm formation or production of secondary metabolites (Figure 1). Over the years, studies of antibiosis have undoubtedly led to a deeper understanding of how microbes relate to a major component of their natural environments—their fellow microbes—as well as to the discovery of clinically useful compounds. Examining interspecies interactions using a broader framework that encompasses both alternative signals and more diverse responses will accordingly continue to advance these vital fields.

The past few years have seen a surge of studies [1,2] covering all aspects of these possible interactions (Figure 1). Detecting phenotypic or developmental bio-

modulation between two organisms can indicate when they are communicating via small molecules, and thus can denote the presence of overlooked compounds. In other cases, signaling has been shown to occur via ‘repurposed’ compounds—known molecules that are functioning in an unexpected manner. One exciting potential result of interspecies interactions is the induction of novel secondary metabolite production by the responding organism. Thus, examination of microbial relationships can lead to the discovery of new molecules—in some cases as the small molecule mediating the interaction, and in others as the consequent *result* of two microbes interacting.

The scope of this article will be limited primarily to microbial interactions, although a few studies are referenced that highlight the complex relationship that microbes have with multicellular eukaryotes, and all demonstrate how little we understand of the complicated interplay occurring between microbes and the potential chemical eavesdropping occurring between them (Table 1).

Alliances and antagonisms

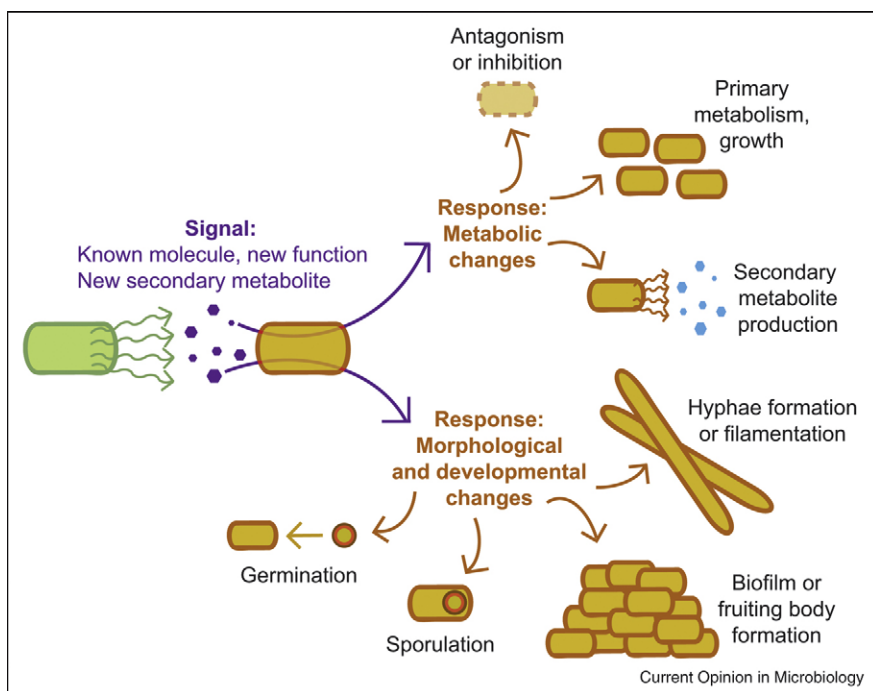
Microbial-eukaryotic

Here we focus on insects that have evolved specific associations with fungi and bacteria, a biological context that has selected the evolution of myriad antagonistic and beneficial interactions that highlight microorganisms’ ability to exert exquisite biological specificity in mediating their interactions.

Attine ants grow fungal cultivars as food, and have been shown to have co-evolved with both their food cultivar and actinomycetes that help protect their food from being infected by a parasitic *Escovopsis* fungus [3]. There is specificity in both the attraction and repulsion between these two sets of fungi and these conflicting forces explain why in natural environments particular *Escovopsis* fungi infect only a restricted set of the food fungi [4]. Although the active compounds driving these responses are not yet known, *Escovopsis* spp. are attracted to and grow especially on cultivars that are hosts to that parasite, and the food cultivars produce compounds that actively inhibit the growth of other *Escovopsis* strains [4].

The southern pine beetle, *Dendroctonus frontalis*, exemplifies another example of the intriguing symbioses between the insect, fungal, and bacterial worlds. The beetle is symbiotically associated with an *Entomocorticium* sp. fungus that helps nourish the beetles’ larvae, but an antagonistic fungus, *Ophiostoma minus*, can outcompete

Figure 1



Schematic illustrating potential interspecies interactions. An interaction between two microbes is illustrated on the left of the figure, with the green microbe producing a signal (purple hexagons) that causes the orange microbe to respond in one of the manners illustrated on the right. The signals discussed here fall primarily into two classes: known metabolites (such as peptidoglycan, antibiotics, and intraspecies signals) that cause unexpected responses affecting other microbial species, and novel secondary metabolites; in some cases the signals are still unknown. Upon detecting the signal, the responding organism may experience changes in metabolism (growth inhibition or stimulation, or production of new small molecules) or morphological and developmental changes (alterations in cell shape or morphology; production of biofilms or fruiting bodies; or specialized processes such as sporulation and germination). More than one response is possible to a single signal.

this beneficial symbiont to the detriment of the beetle larvae [5^{••}]. An actinomycete bacterium mediates the retention of the beneficial fungus by producing mycangimycin, a novel linear polyene peroxide antifungal that selectively inhibits only the antagonistic fungus and not the symbiotic one [5^{••}]. This discovery shows that examining insect symbioses can reveal not only new biology but also interspecies signaling molecules, some of which will be chemically novel.

The importance of how the larger microbial context can influence biological activity was highlighted in a study that overturned a long-asserted understanding regarding the mechanism of the anti-insecticidal activity of *Bacillus thuringiensis*. The presence of the insect midgut microbiota (in particular an *Enterobacter* sp.) was shown to be required for anti-insecticidal activity, and the *B. thuringiensis* toxin alone—in the absence of enteric bacteria—was insufficient to kill insects [6[•]].

The biology of the fungus *Fusarium* also underscores the significance of microbial context. Some strains act as plant pathogens, while others are protective agents against pathogenic *Fusarium* strains [7]. The non-pathogenic

Fusarium are associated with a consortium of endosymbiotic bacteria that alter fungal gene expression and eliminate their ability to invade plants [7]. The protective capacity of these non-pathogenic strains is explained because *Fusarium* associated with its endosymbionts—but not the endosymbionts alone—produce volatile sesquiterpenes that repress virulence genes in pathogenic *Fusarium* strains [8].

Microbial–microbial

Two recent studies follow-up on phenomena described years ago. *Pseudomonas aeruginosa* and *Staphylococcus aureus*, two human-associated bacteria, have been known since the 1950s to have a paradoxical relationship in which 4-hydroxy-2-heptylquinoline-*N*-oxide (HQNO) produced by *P. aeruginosa* suppresses the respiration of *S. aureus*, but also increases its resistance to antibiotics in co-culture. It was shown that HQNO selects for small colony variants—a form of *S. aureus* that conveys antibiotic resistance [9]. HQNO was only detected in the sputum of cystic fibrosis patients infected with *P. aeruginosa*, highlighting the potential relevance of the interaction of these pathogens in clinical cases [9].

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