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Evolutionary feedbacks between insect sociality and microbial management

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Fitness-determining interactions with microbes — in particular fungi — have often been considered a by-product of social evolution in insects. Here, we take the view that both beneficial and harmful microbial consortia are major drivers of social behaviours in many insect systems — ranging from aggregation to eusociality. We propose evolutionary feedbacks between the insect sociality and microbial communities that strengthen mutualistic interactions with beneficial (dietary or defensive) microbes and simultaneously increase the capacity to defend against pathogens (i.e. social immunity). We identified variation in habitat stability — as determined by breeding site predictability and ephemerality — as a main ecological factor that constrains these feedbacks. To test this hypothesis we suggest following the evolution of insect social traits upon experimental manipulation of habitat stability and microbial consortia.

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Social management of microbes by insects

Since their evolutionary origin insects co-occur with microorganisms (e.g. [1,2]). The resulting interactions range from harmful to beneficial. Insects have evolved a strikingly diverse array of behavioural and physiological strategies both to combat microbial pathogens, parasites or competitors and to effectively transmit and promote those microbes that benefit them as essential dietary supplements, substrate degraders, or defence agents [3,4,5••]. The tricky part is that keeping the 'harmfuls' in check and propagating the 'beneficials' often need to be accomplished simultaneously (Box 1). In this article, we argue that social interactions between insects — from simple collective feeding to complex division of labour (Figure 1) — provide strong means to construct high-quality microbial environments for insect fitness by selectively favouring the beneficial microbes, while keeping the harmful microbes suppressed.

Coevolution of insect sociality and beneficial microbes

Insects show a fascinating array of behaviours (Figure 1) that promote beneficial microbes in their vicinity [4,10–13]. If the collective execution of these behaviours further improves the growth of the beneficials. This can start a positive evolutionary feedback process between the partners; every amelioration in the social selection and propagation of these microbes may feed back on insect fitness, with the potential of tightening the insect–microbe mutualism even more (Figure 2a). Interestingly, this process may speed up during this co-evolution as within species relatedness is expected to increase, which reinforces investments in the mutualism as the benefits are likely to profit relatives [14]. In the end, kin selection in combination with the proposed feedback may lead to the highest level of interspecific and intraspecific cooperation, namely obligate mutualism in the context of insect eusociality. In fungus-farming ant and termite societies, for example, characterized by a complex caste system, millions of workers and just a few reproductive individuals fully rely on each other and their farmed fungus for subsistence [13]. However, as pointed out by Korb [15], crucial experimental tests that allow differentiation between direct and indirect fitness gains of collective behaviours are still scarce.

Coevolution of insect sociality and harmful microbes

The success of insect–microbe mutualisms is frequently challenged by invasion of non-beneficial microbes that harm either the insects (e.g. as pathogens, parasites or toxin-producers) or their beneficial microbial partners (e.g. as pathogens or resource-competitors). Insects have evolved the neurophysiological ability to identify such microbial threats and various strategies to prevent establishment of harmful microbes in their habitats, ranging from simple avoidance of infested habitats [16] to physical, for example, grooming, weeding [17], or chemical suppression of microbial invaders [18,19••] (Figure 1). Like for beneficial microbes, we argue that collective

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Glossary
Cooperation: exchange of beneficial traits between partners of the same or different species, which increases the direct fitness of each partner
Symbiosis: a close and often long-term interaction between two different species, which makes no statement about the fitness effects and thus includes mutualism, commensalism and antagonism
Sociality: behavioural interactions between partners of the same species, which are often related, thereby increasing the inclusive fitness of each partner
Interspecific mutualism: exchange of beneficial traits between partners of different species, thereby increasing the direct fitness of each partner
Collective behaviour (= Semisociality): aggregation of mostly unrelated individuals of the same species, which are usually driven by direct fitness gains
Parental care (= Subsociality): behavioural investment of the parents into the direct fitness of their offspring
Facultative eusociality: social organization defined by overlapping offspring generations and helping offspring that is capable of own reproduction but partly refrains to do so
Obligate eusociality: social organization defined by overlapping offspring generations and presence of morphologically specialized castes of workers and reproductives
Co-evolution: selective pressures between species or traits that are reciprocally exerted, thereby affecting each other's evolution
Vertical transmission: passing of symbiont from parents to offspring
Horizontal transmission: uptake of symbiont from the environment
Partner choice: preferential interaction with a beneficial subset of partners. Choice can be made in response to honest signalling of partner quality or by imposing a cost to partners to screen out cooperators
Sanctions (= Policing): imposing a penalty on a non-cooperative partner
Partner-fidelity feedback: improvement of the fitness of a partner of the same or different species, which improves its phenotypic ability to return the aid
Kin selection: form of natural selection that favours behaviour, which may decrease an individual's direct fitness but benefits that of their kin (who share a proportion of their genes)

Box 1 Social means of selecting and maintaining beneficial microbes

How do insects choose and maintain the beneficial over the harmful microbes? This is not trivial, as for insects the qualities of the microbes are often hidden (i.e. costly signalling by the microbes is rare; but see examples for mutualist selection in Figure 1 [6•,7,8]) and all potential partners would benefit from being chosen, so even the pathogens have no interest in revealing their true intention [9]. We identified four potential mechanisms that are often socially mediated and thus expected to increase in efficiency during social evolution (Figure 1): First, screening beneficial and harmful microbes by the insects through creation of a group-mediated filtering environment that excludes all but the highest-quality partners (e.g. collective feeding and application of defences). Second, direct collective defence against harmful microbes and sanctioning of cheaters. Third, vertical transmission of beneficial microbes within a social group from adults to offspring, which leads to partner fidelity and thus aligns fitness interests of insects and microbes. Fourth, group-mediated habitat stability and maintenance also leading to prolonged contact and partner fidelity.

behaviours can reinforce the efficacy of individual strategies to suppress harmful microbes via density or group-mediated effects, which has often been termed 'social immunity' [19••,20]. However, in contrast to the common view in the social immunity literature where pathogen defence is regarded as a necessary consequence of increased transmission of pathogens in genetically homogenous family groups, we propose that harmful microbes are a major driver of social evolution in some insects. A feedback loop can be started if, for example, members of a social group profit from the joint suppression of detrimental microbes and are thus selected for staying and helping even more, which again feeds back to an improved suppression of microbes (Figure 2b). Understanding the origin and courses of such feedback loops requires studying facultative eusocial and non-eusocial insect systems.

Constraints on the evolution of stable mutualism and social complexity

Despite the advantages of cooperation, both sociality and mutualism have remained rudimentary in many insect–microbe systems. We suggest that the evolution of more complex social behaviours may be ecologically constrained, predominantly by habitat instability and insect population structure, that is, whether generations overlap and interact, or whether parental and offspring generations are largely discrete and hardly interact. Interestingly, with the transition to eusociality, insects managed to disengage almost completely from these constraints by creating their own habitat [21] (Figure 1). This also relates to regulating microbial communities to support colonial life, such as food-fungus in farming systems. In the following, we illustrate our idea of a common feedback between the social behaviour of insects and their association with microbes by focusing mainly on different insect–fungus systems. Despite the focus on insects and fungi, we note that our ideas should be generally applicable to other animal–fungus or insect–bacteria mutualisms and antagonisms.

Examples of collective fungal management at different levels of sociality

Habitat instability prevents the microbe management-sociality feedback loop to run its course in *Drosophila* fruit flies

Semisocial aggregation is particularly frequent in insects exploiting ephemeral resources, for example dung, carrion, fruits, for larval development (Figure 1). In the *Drosophila* model system, aggregation of unrelated individuals is found *across* distinct breeding patches, often through pheromone-mediated clumping of adults [22], and *within* patches through mutual attraction of larvae [23]. Aggregative egg-laying and larval foraging has been related to first, the suppression of detrimental mould fungi, such as *Aspergillus* sp., *Penicillium* sp. (e.g. [24–26]), and second, the transmission and propagation of beneficial yeasts and bacteria [27,28]. Collective larval

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