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Editorial: Microbial Drivers of Sociality – From Multicellularity to Animal Societies

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Editorial on the Research Topic

Microbial Drivers of Sociality – From Multicellularity to Animal Societies

MICROBES—AN ECOLOGICAL DRIVER OF SOCIAL EVOLUTION

While sociality is present in a taxonomically diverse number of species, most animals remain solitary (Bourke, 2011). Over the last centuries, this apparent imbalance in social and non-social animals has led to a great deal of research aimed at shedding light on the biotic and abiotic factors explaining the emergence and maintenance of sociality in nature (West et al., 2015). Among them, microbes were quickly identified as a major problem for the evolution of social life, because frequent contact between group members typically facilitates the transmission of pathogens, high nest fidelity favours the establishment of microbial pathogens close to their social hosts and, finally, because social groups often exhibit limited genetic diversity and thus limited genetic resistance against certain pathogen strains (Schmid-Hempel, 1998; Cremer et al., 2007). However, this long-standing view has changed considerably over the last few years. Recent research indeed revealed that group living may be more effective than solitary living to limit the risk of infection by pathogenic microbes because group living also allows the development of an additional layer of defence against pathogens in the form of social immunity (Cremer et al., 2007; Cotter and Kilner, 2010). Under strong pressure from pathogens, microbes could therefore promote, rather than hinder, the evolutionary transition from solitary to group living (Meunier, 2015; Biedermann and Rohlfs, 2017). Moreover, we are increasingly aware that many microbes provide essential benefits to their hosts by performing critical digestive, physiological, and reproductive functions (Engel and Moran, 2013; McFall-Ngai et al., 2013). The need to access beneficial microbes may thus have played a role in the expression of frequent and tight interactions between conspecifics and ultimately promoted social evolution (Wilson, 1971; Onchuru et al., 2018). Finally, a growing number of studies suggest that microbes could enforce the aggregation and expression of cooperative behaviours of the hosts to increase their chance of reaching new hosts and may therefore be involved in the evolution of host sociality (Lewin-Epstein et al., 2017) (but see Johnson and Foster, 2018).

In this Research Topic, we aimed to provide an overview of these recent advances and the potential limitations of our understanding of the roles of microbes in the social evolution of hosts. The collection of articles presented here responds to these objectives by focusing on five major points: (1) a potential limit in our understanding of the roles of microbes in social evolution comes from the multiple definitions of sociality and the persistent boundaries between research communities, (2) the access to social immunity does not necessarily modify investment into

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individual immunity, (3) further researches are needed to explore the wide diversity of social immunity in non-eusocial species and to shed light on the mechanisms of recognition of microbial pathogens in social groups, (4) habitat quality can be a prime candidate to explain the association between microbes and social evolution, and (5) the necessity to acquire symbionts from conspecifics could be a key evolutionary driver of sociality. In the following parts, we will briefly summarise how the studies contained in this Research Topic address these five points and then conclude on potential future directions of research.

On the Multiple Definitions of Sociality and the Necessity to Break Boundaries Between Research Communities

Social life is not only present in various organisms but also in all kinds of forms: simple aggregations of individuals, facultative or obligatory parental care, cooperatively breeding groups and super-organismal eusocial societies (Bourke, 2011). However, research on animal sociality has long focused exclusively on the fascinating eusocial organisation of certain hymenopteran and isopteran insects, hampering our general understanding of the evolution of all forms of social life in nature (Elgar, 2015; Meunier and Steiger, 2018). Somewhat surprisingly, the results of our call for this Research Topic suggest that this bias is being corrected: 7 of the 16 published articles are based on non-eusocial systems (**Table 1**). All else being equal, this indicates that the research community studying the link between microbes and social evolution has moved away from exclusive eusocial model systems. However, the results of our call also point out existing partitions between communities, as we only managed to receive two non-insect articles and unfortunately none on a non-eukaryotic system (**Table 1**). This bias may come from the fact that the editors of this special issue are mostly working on insect models, and have failed to reach out and/or to attract members of the other communities. This bias may also stem from the multiple definitions of sociality present in the literature (Rubenstein and Abbot, 2017), which are often very specific to each community, and which may have—for instance—excluded vast communities of researchers studying family life and aggregation behaviours much more frequent in non-insects species.

On the Links Between Individual and Social Immunities

A long-standing question about the link between microbial pathogens and social evolution is whether access to additional defences against microbial pathogens (i.e., social immunity) necessarily comes with reduced investment in individual immunity. Five manuscripts of this Research topic illustrate the complexity of this question and the diversity of answers that can be given. First, Meusemann et al. used genomic and transcriptomic data from eight termite species, representing wood-dwelling and foraging species, plus 14 other winged insects (Pterygota) and found that differences in the types of sociality do not reflect differences in the intensity of natural selection on immune genes. Instead, they found evidence for a genome-wide pattern of relaxed selection on these genes in termites. Second, Baeuerle et al. used experimental approaches on 14 bumblebee species to show that the investment in an external defence against pathogens (in the venom) does not trade-off against the investment in internal immune defence present in the hemolymph. Third, Esparza-Mora et al. revealed in a termite that inhibiting an external enzyme capable of degrading entomopathogenic fungi does not trigger collective defences such as allogrooming, but instead reduce defensive cannibalistic behaviours. This suggests that the individual immune system is linked to certain collective immune behaviours in this termite. Fourth, Cole and Rosengaus emphasised the importance of social environment on pathogen resistance, as they showed that the presence of a king may help to mitigate the negative effects of a queen's infection during colony foundation in a dampwood termite. Finally, Pull and McMahon propose a comprehensive review of social immunity and emphasise that "superorganism immunity" may fulfil an analogous function to the immune system of Metazoa.

On the Diversity of Social Immunity and Mechanisms of Recognition of Microbial Pathogens

The recent proposal that social immunity is not specific to eusocial systems (Cotter and Kilner, 2010; Van Meyel et al., 2018) opened numerous questions about the diversity of its forms, the type of immune benefits provided by the social environment and the mechanisms mediating the recognition of pathogenic microbes in social species. Two manuscripts of this Research Topic offer an overview of these questions. First, Trienens and Rohlfs investigated forms of social immunity in groups of fruit fly larvae. They showed that larvae suppress the invasion of a harmful fungus by the summative effect of individuals at high densities and that larger groups of larvae at the same density can control fungal growth more efficiently. This indicates a potential collective defence against habitat invasion by pathogenic fungi in insects that exhibit mere aggregation behaviour. Second, Goes et al. reviewed the literature on leaf-cutting ants' social immunity to investigate how workers protect their fungal garden against harmful microbes. They reveal that workers discriminate against harmful microbes *via* chemical cues originating from the antagonistic microbe and/or semiochemicals released by the fungus-garden during harmful interactions, as well as *via* associative learning when workers connect the microbe cues with damage in the fungus garden.

On the Key Role of Habitat Quality in the Association Between Microbes and Social Evolution

Several articles dealt with the issue that habitat can shape interactions of animals with microbes, which in turn affects the animal's social behaviour. Three of these articles specifically looked at wood as a substrate for insects, which is acknowledged to be very favourable for the evolution of sociality because of its structural resistance and longevity compared to the life of an insect (Hamilton, 1978; Kirkendall et al., 2015). In a review article, Dillard and Benbow argue that two additional factors may

TABLE 1 | Articles included in our Research Topic.

References	Type	Study organism(s)	Level of sociality
Cole and Rosengaus	Research article	*Zootermopsis angusticollis* (Blattodea)	Eusociality
Meusemann et al.	Research article	Various Blattodea	Various levels of sociality
Tragust et al.	Research article	*Lasius niger* (Hymenoptera)	Eusociality
Baeuerle et al.	Research article	14 species of bumblebees (Hymenoptera)	Eusociality
Sinotte et al.	Review	Eusocial insects in general	Eusociality
Esparza-Mora et al.	Research article	*Reticulitermes flavipes* (Blattodea)	Eusociality
Figueiredo and Kramer	Review	Animals in general	All levels of sociality
Nalepa	Review	Lower termites and *Cryptocercus* spp. (Blattodea)	Eusociality and subsociality
Dunn et al.	Review	Hominins	Different levels of sociality
Bratburd et al.	Review	Social insects	Different levels of sociality
Trienens and Rohlfs	Research article	*Drosophila melanogaster* (Diptera)	Aggregation
Goes et al.	Review	Attini (Hymenoptera)	Eusociality
Biedermann	Research article	*Xyleborus affinis* (Coleoptera)	Cooperatively breeding
Pull and McMahon	Review	Eusocial insects in general	Eusociality
Dillard and Benbow	Review	Various wood-dwelling insects	Different levels of sociality
Nuotclà et al.	Research article	*Xyleborinus saxesenii* (Coleoptera)	Cooperatively breeding

facilitate prolonged parent-offspring contact and cooperative behaviours in insects. First, the low nutritional value of wood selects for associations with nutrient-enriching microbes that need to be transferred to offspring, which is often through social contact. Furthermore, insects compete with many antagonistic microbes in this habitat and collective defence is often better to keep them in cheque. A research study by Biedermann found evidence for collective pathogen defence in a cooperatively breeding, fungus-farming ambrosia beetle. Delayed dispersing female offspring showed more social hygienic behaviour at places within the nest with higher abundances of antagonistic fungi. Nuotclà et al. showed in a closely related ambrosia beetle species with a similar social system that the two nutritionally important fungal mutualists of this species vary in their relative abundance depending on the dryness of the wood substrate. Interestingly this fed back on the social behaviour and the delayed dispersal periods of daughters in this facultatively eusocial beetle. Finally, a study by Tragust et al. on founding *Lasius niger* ant queens showed that queens exposed to pathogens invest simultaneously in formic acid defence and higher worker production. Surprisingly there was no measurable trade-off between this individual immune defence and reproduction at an early nest stage, but this may have effects on later fitness.

On the Role of Symbionts as Promoters of Hosts' Social Evolution

The growing awareness that microbes residing on and in a host can provide it with major benefits has recently stimulated a great number of experimental and theoretical research on the impacts of symbionts in the social evolution of hosts. This is illustrated by five articles in this Research Topic. First, Bratburd et al. examined the general role of defensive microbial symbionts in host protection against pathogens in terms of behavioural and immune responses and discussed why insects are good models to study issues relating to human health and agriculture. Second, Dunn et al. used a comparative approach to study how microbiomes of hominins have changed over evolutionary time, questioning their impact on the evolution of several host functions and discussing the possibility that prosocial microbes promoted hominin social behaviour. Third, Nalepa discussed why symbiont transmission *via* proctodeal trophallaxis and sociality are likely to have entangled evolutionary histories and conclude that the vertical transmission of gut microbes (flagellates) and the origin of host subsociality are two sides of the same coin in termites. Fourth, Sinotte et al. explored the link between the division of labour and symbiosis in social insects. Their review suggests that structured microbiomes have evolved in parallel to social complexity, and predicts that mature social insect colonies with the most extreme division of labour shows the strongest distinction between caste microbiomes. This suggests that caste-specific microbiomes may enhance symbiotic benefits and the efficiency of division of labour. Finally, Figueiredo and Kramer took another perspective and focused on the microbes themselves. Their review describes cooperation and conflict within the microbiota. They discuss how these parameters can affect animal hosts and conclude that an explicit consideration of social dynamics within symbiont communities is crucial to advance our understanding of how microbes shape animal function and evolution.

CONCLUSION

Overall, this Research Topic emphasises the multiple roles of microbes in the social evolution of their hosts, which range from obstruction to promotion. It also illustrates why group-living animals specifically face an intense tug-of-war between the necessity to limit the inherently high risk of pathogen infection and transmission within the nest as well as the necessity to protect and efficiently transmit essential symbionts within the nest and to dispersing sexuals. The outcome of this war can

have profound impacts on the life-history traits of a given species. Finally, it also points out that although our current understanding of the link between microbes and social evolution is based on a wider range of social systems and is thus becoming more comprehensive, it still needs to bring together the results of all research communities studying different organisms. We believe that this Research Topic is a first step toward achieving this goal.

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