



Social immunity: why we should study its nature, evolution and functions across all social systems

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1 **Social immunity: Why we should study its nature, evolution and**
2 **functions across all social systems**

3 **Short title: The group-living framework of social immunity**

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11 **Highlights**

- 12 • Social immunity offers protection against pathogens in group living species
- 13 • Mostly studied in eusocial insects, it can be found in many social systems
- 14 • Studying its presence in more non-eusocial systems would provide major benefits
- 15 • It would help deciphering evolutionary pathways of individual and social immunity
- 16 • It would help better understanding the roles of pathogens in social evolution

Abstract

Mounting defences against pathogens is a necessity for all animals. Although these defences have long been known to rely on individual processes such as the immune system, recent studies have emphasized the importance of social defences for group-living hosts. These defences, called social immunity, have been mostly studied in eusocial insects such as bees, termites and ants, and include, for instance, mutual cleaning and waste management. Over the last few years, however, a growing number of works called for a broader exploration of social immunity in non-eusocial species. In this review, we summarise the rationales of this call and examine why it may provide major insights into our current understanding of the role of pathogens in social evolution. We start by presenting the original conceptual framework of social immunity developed in eusocial insects and shed light on its importance in highly derived social systems. We then clarify three major misconceptions possibly fostered by this original framework and demonstrate why they made necessary the shift toward a broader definition of social immunity. Because a broader definition still needs boundaries, we finally present three criteria to discriminate what is a form of social immunity, from what is not. Overall, we argue that studying social immunity across social systems does not only provide novel insights into how pathogens affect the evolution of eusociality, but also of the emergence and maintenance of social life from a solitary state. Moreover, this broader approach offers new scopes to disentangle the common and specific anti-pathogen defences developed by eusocial and non-eusocial hosts, and to better understand the dependent and independent evolutionary drivers of social and individual immunity.

38 Introduction

39 During its life cycle, every animal encounters large numbers of pathogens such as viruses, protozoans,
40 bacteria, helminths and fungi [1]. Pathogen infections often have dramatic consequences in a host,
41 ranging from premature death to the modification of a broad set of fitness-related physiological,
42 morphological and behavioural traits [2]. To limit the costs of pathogen infection, hosts have thus
43 developed a multitude of defences encompassed in the term individual immunity [2–4]. In insects,
44 these defences typically rely on physiological changes limiting pathogen development into the host
45 body (i.e. immune system) [2,5] and on behavioural processes reducing the risk of pathogen exposure
46 and infection, for instance, by prophylactively or therapeutically consuming food sources with anti-
47 pathogenic properties, a process called self-medication [4].

48 Over the last decades, a growing number of studies has revealed that protection against
49 pathogens may not only rely on the defences exhibited by the host itself, but also on defences
50 generated by its surrounding relatives [6–8]. Textbook examples of this *social immunity* typically come
51 from eusocial insects such as bees, ants and termites (Figure 1) [6,8–10]. One of these examples is
52 allo-grooming, a behaviour frequently reported in eusocial insects, during which workers groom each
53 other to remove the pathogens present on the cuticle [11]. Another example encompasses sanitary
54 behaviours, during which workers remove food waste and/or cadavers from their colony to prevent
55 the development of microbial pathogens, as found in many bees, ants and termites [12–15]. Social
56 immunity can also be illustrated by social isolation, during which infected individuals leave their colony
57 [16,17] or reduce contacts to the brood [18,19] to limit the transfer of pathogens to colony members.
58 Finally, ant and termite workers frequently use self-produced secretions to sanitize the nest walls
59 and/or the brood [20–22], which is also a common form of social immunity (for an exhaustive list of
60 all the classical forms of social immunity, please refer to [6,8]).

61 The discovery of social immunity rapidly led to major advances in our understanding of why
62 and how eusocial insects are efficiently protected against pathogens [6,9,23]. It also gave rise to two

evolutionary scenarios on the role of social immunity in the evolution of group living. The first scenario posited that social immunity is a phenomenon that has secondarily derived from eusocial systems and thus only plays a role in the consolidation of complex, permanent and obligatory forms of group living exhibiting reproductive division of labour (thereafter called the *eusocial framework*) [6,24,25]. The other (more recent) scenario postulates that social immunity is an ancestral phenomenon that can be found in many forms of group living and thus, that social immunity also plays a key role in the early emergence and maintenance of group living from a solitary state (thereafter called the *group-living framework*) [7,8].

In this study, we review recent empirical data across eusocial and non-eusocial (i.e. group living species that do not exhibit a eusocial organisation) insects to emphasize why it is now time to study the nature, evolution and functions of social immunity across all social systems. Specifically, we first present the origin and implications of the eusocial framework in our current understanding of anti-pathogen defences in eusocial insects. We then discuss the rationales of the recent call for a switch from a eusocial to a group living framework by shedding light on three major misconceptions that can be fostered by the eusocial framework. In a final part, we stress that understanding social immunity requires boundaries in its definition and thus propose a newly defined group-living framework detailing three criteria that could allow discriminating what is a form of social immunity, from what is not. Overall, we argue that expanding the number of studies on social immunity in a broad taxonomical spectrum of non-eusocial species would provide novel major insights into our general understanding of the common and specific solutions developed by each type of social host to counteract infections and thus, into the role of pathogens in social evolution.

The eusocial framework of social immunity

The eusocial framework of social immunity emerged at the beginning of the 21th century as the result of works conducted by researchers investigating how eusocial insects limit the inherently high risks of

pathogen exposure and transmission between colony members [6,9,10,26]. The central idea of this framework is that social immunity mimics the individual immunity of multicellular organisms when the unit of selection has shifted from the individual to the colony [23,27]. In other words, social immunity has “evolved in convergence with individual immunity to protect the entire reproductive entity (i.e. the superorganism, [28]) and maximize its fitness” [25]. Three examples typically illustrate this parallel between personal and social immunity in eusocial insects. First, wood ants, honeybees and stingless bees collect and incorporate plant resin with antimicrobial properties into their nests to limit the development of microbial pathogens [29–31], a process mimicking individuals’ self-medication process to fight an infection [32]. Second, honeybee workers can fan their wings simultaneously to increase the temperature of their hive and thereby eliminate heat-sensitive pathogens [33], a process mimicking the fever exhibited by a body to fight an infection. Finally, workers of the ant *Lasius neglectus* administer antimicrobial poison inside infected cocoons to prevent pathogen replication and establishment within the colony, just like the individual immune system targets and eliminates infected cells from host body [34].

The accumulation of results supporting the parallel between individual and social immunity in eusocial insects rapidly led to the adoption of the eusocial framework by researchers interested in collective defences against pathogens. This adoption then fostered the claim that social immunity is “necessary and essential to eusocial systems” [25] and thus, that social immunity should be considered as a major and unique social parameter once eusociality has emerged [6,9,24,25].

The limit of the eusocial framework

One pillar of the original eusocial framework is thus that all collective defences against pathogens employed by individuals living in non-eusocial groups are not social immunity, but instead reflect non-derived defences such as communal disease defences and parental care [24,25]. This boundary between eusocial and non-eusocial species rapidly became a major issue in deciphering the common

and/or separate evolutionary pathways of collective defences against pathogens across group living species [7,8]. Moreover, this restriction to eusocial systems opened scope for several important misconceptions concerning the link between social immunity and social evolution. For instance, it might suggest that 1) reproductive division of labour is essential to allow the evolution of social immunity, 2) the presence of social immunity should lower investments into individual immunity in eusocial species and finally, that 3) social immunity does not have counterparts in non-eusocial species [6,9,10,24–26]. In the following part, we clarify these three misconceptions using recent empirical findings and demonstrate why they call for considering social immunity as a broader phenomenon that is not exclusive to eusocial species [7,8].

On the importance of reproductive division of labour

One misconceptions possibly fostered by the eusocial framework is that the direct fitness costs of performing social immunity are so high for a donor individual that they should prevent the evolution of social immunity in groups where the donors' fitness relies on their own reproduction. In other words, the net benefits of performing social immunity should only be present in groups where donor individuals forego personal reproduction, i.e. in eusocial species with reproductive division of labour [25]. The first issue with this prediction is that it neglects that some forms of social immunity are not only unlikely to provide significant fitness costs to donors (e.g. the use of self-produced secretion to sanitize the nest, the removal of fresh corpses from the nest [6]), but may also provide direct benefits to donor individuals. These direct benefits have been recently revealed in allogrooming, a textbook example of social immunity [6,8]. This behaviour has long been thought to be exclusively costly for donor individuals, because it increases their risk of being exposed to the pathogens present on the recipient individuals. In an elegant study conducted in the ant *Lasius neglectus*, however, Konrad *et al* [35] demonstrated that allogrooming provides direct benefits to both recipients and donors, as it allows donors to prime their own immune system and thus boost their defences against future pathogen exposure. Interestingly, a follow-up study recently showed that these direct benefits are

pathogen-specific in that workers immune-primed with one type of pathogen preferentially direct their future allogrooming behaviours toward individuals infected with the same compared to a different pathogen [36].

The second issue with this prediction is that it overlooks the central role of kin selection in the evolution of some extreme forms of social immunity and neglects the fact that kin selection also operates in groups of individuals undergoing personal reproduction [37]. This central role can be illustrated by the self-exclusion of infected workers (figure 1), another textbook example of social immunity reported in ants and bees [16,17]. This behaviour reflects that infected workers leave their nest to die alone and thereby limit the infection of their colony members. The evolution of such a behaviour typically relies on kin selection, as it becomes adaptive only if it allows the genes of the sacrificed individual to be passed on to the next generation by one or more of the saved group members, i.e. only if the benefactor and the beneficiaries are genetically related. Based on the same reasoning, such a sacrificial behaviour could *in principle* evolve in subsocial (family) groups if the self-exclusion of infected offspring significantly improves the reproduction of their related siblings. Whether such sacrifices occur in non-eusocial species is, however, unexplored so far. Overall, social immunity is thus not necessarily associated with net fitness costs for donor individuals and it is therefore possible for social immunity to evolve in group-living species without reproductive division of labour.

On the relaxed selection on individual immunity in eusocial species

A second misconception possibly fostered by the eusocial framework is that the emergence of social immunity should relax selection on individual immunity and thus, that individual immunity should be less efficient and/or involve a lower number of genes in eusocial compared to non-eusocial species [38,39]. The interest of this prediction resided in the fact that it was relatively easy to test empirically. Unfortunately, the results were at odds with this prediction. On one hand, physiological studies showed that antimicrobial peptides (a component of individual immunity) are more effective in

eusocial compared to solitary sister species in bees [40] and trips [41]. On the other hand, the recent accumulation of genomic studies comparing insects with different levels of social organization reports no general association between eusociality and the number and/or expression of immune-related genes across ants, bees and termites (reviewed in [42]). Hence, shifting the unit of selection from individual to superorganism may not affect the selection pressures exerted on individual immunity [43]. Interestingly, this apparent absence of a general link between individual and social immunities suggests that the emergence of social immunity does not reduce, but instead complements individual defences against pathogens.

On the absence of social immunity in non-eusocial species

A third misconception possibly fostered by the eusocial framework is that social immunity is exclusive to eusocial species. A recent study, however, revealed that 11 of the 30 anti-pathogen defences found in eusocial insects and classically considered as forms of social immunity [6] can also be found in non-eusocial insects [8] (see also [7]). For instance, the use of self-produced components with antimicrobial properties as colony material is not only present in ants and termites [29,44], but has been reported in nests of the wood cockroach *Cryptocercus punctulatus*, the European earwig *Forficula auricularia* and the Burying beetle *Nicrophorus vespilloides* [45–47]. Sanitary behaviours consisting in the removal of waste and feces material from the colony can also be found in several non-eusocial species with high nest fidelity (reviewed in [48]), such as the subsocial cricket *Anurogryllus muticus* [49]. Finally, allogrooming is a behaviour frequently observed in arthropod species where parents remain with juveniles after egg hatching (e.g. [50,51]), even if its role against pathogen infection needs to be further explored.

Whereas (at least) some forms of social immunity can be present in non-eusocial insects, it is also important to stress that (at least) some forms of social immunity are not present in all eusocial insects. For instance, queens of the pharaoh ant *Monomorium pharaonic* and the wood ant *Formica paralugubris* surprisingly prefer habitats contaminated with a pathogenic fungus to establish their

colony [52,53], whereas the avoidance of contaminated areas is classically considered as a form of social immunity in eusocial insects [6]. Similarly, experimental exposure to pathogen spores did not trigger higher levels of allogrooming between workers in the ants *Formica selysi* and *Myrmica rubra* [11,54], and co-founding queens of the ant *Lasius niger* perform only very little allogrooming and did not exhibit a better resistance against pathogens when compared to solitary queens [55]. The claim derived from the eusocial framework and stating that social immunity is “necessary and essential to protect the entire reproductive entity and maximize its fitness” [25] should therefore be taken with caution. Arguably, social immunity encompasses a great diversity of forms [6,8], so that the absence of evidence for one form of social immunity should not be considered as an evidence for the absence of any form of social immunity. Nevertheless, the above findings warn us on the risk to over- interpreting the expression of certain behaviours as social immune responses on the sole basis that they are present in a eusocial species.

What is and what is not a form of social immunity?

The shift from a eusocial to a group-living framework has recently generated some confusion on the boundaries of social immunity, which in turn blurred our general view of its nature, evolution and function across species. Here, we clear up this confusion by proposing a newly defined group-living framework detailing three criteria that can be used to determine whether a given defence is a form of social immunity. First, this defence should help recipient individuals to reduce their risks of infection by pathogens, which refers to anything that can produce a disease such as viruses, bacteria, protozoa, prion, fungus and helminths. This encompasses all the potential steps of an infection, which include direct contact to a pathogen, penetration, development and replication of pathogens into the recipients’ body and ultimately infection-derived death of the host [6,8]. The second criterion is that donors and at least some of the recipients should belong both to the same species and to the same social group. This excludes, for instance, all behaviours and collective processes during which

individuals from one species provide anti-pathogen defences to individuals from another species, as commonly reported in the context of symbiosis and *cleaning symbiosis* in cleaner fishes [56]. Finally, the third criterion is that the defence should be “at least partly” selected for the anti-pathogen benefits it provides to the recipients. This stresses that social immunity is a target of selection and cannot be a simple by-product of individual immunity. This criterion excludes all individual defences that are either passively enhanced by group living (e.g. herd immunity [57]), selfishly driven by the nearby presence of conspecific individuals (e.g. density-dependent prophylaxis [58]) or that only happens to limit the risk of infection of solitary individuals encountered during a life cycle, such as during mating and/or competitive events. This third criterion also clarifies the rationale to separate the nomenclature between individual and social immunity.

Overall, these three criteria can be fulfilled 1) when group living is permanent, obligatory, temporary and/or facultative and 2) in a broad range of species ranging from insects and arachnids, over birds and fishes, to mammals and social microbes [7,8]. Importantly, this absence of a dichotomy between eusocial and non-eusocial systems emphasizes that similar selection pressures are likely to have driven the evolution of comparable forms of social immunity across group living species. For instance, the evolution of the spread of feces with antimicrobial properties on nest walls by eusocial workers in termites [44] is very likely to have evolved under the same selection pressures that the ones selecting for the spread of feces with antimicrobial properties on nest walls by juveniles in family units of burying beetles and earwigs [45,59]. To summarize, social immunity can be defined as “any collective or personal mechanism that has emerged and/or is maintained at least partly due to the anti-pathogen defence it provides to other homospecific group members”, which is an edited definition of social immunity previously formulated by Meunier [8].

Conclusion

In this review, we emphasized that individuals living either in facultative/temporary groups or in obligatory/permanent colonies can all perform defences against pathogens that may not only help themselves, but also their group members. The presence of these defences in such a large diversity of social systems recently made necessary the shift from a eusocial to a broad conceptual framework of social immunity [6–8,24,25]. This shift has generated novel works using the term ‘social immunity’ in a few subsocial insects such as the European earwig (e.g. [45,60,61]) and the burying beetle (e.g. [59,62,63]). Here, we claim that it is crucial to expand these first works to a taxonomically broader number of non-eusocial species. The resulting studies would first allow us to disentangle whether the selection pressures favouring the emergence of social immunity have either secondarily evolved to limit the inherently high risk of pathogen exposure in species with an obligatory and permanent social life (i.e. some forms of social immunity derive from eusociality), or whether they remained constant after the evolutionary shift from solitary to group living (i.e. social immunity is an ancestral process) [7,8]. Interestingly, it would also allow testing an alternative evolutionary scenario positing that the general risk of pathogen exposure for a solitary individual could have selected for the emergence of group living in order to obtain an additional line of defence such as social immunity [64]. Second, a taxonomically broader number of studies on social immunity would allow us exploring the potential trade-off between social and individual immunity across group-living species [65] and thus shed light on the dependent or independent evolutionary drivers of these two lines of anti-pathogen defences across animals. For instance, it would allow us to address questions such as whether certain types of pathogens are more likely to apply selection pressure onto individual instead of social immunity, or whether these two lines of defences necessarily trade-off across social systems [65]. Finally, non-eusocial species could offer experimental opportunities that are not available in eusocial species and thus allow exploration of novel factors possibly underlying the expression of social immunity. For instance, a recent study in the European earwig allowed to demonstrate that the recent (but not prolonged!) social isolation of group-living adults induces a stress that specifically lowers their resistance against pathogens, whereas comparing the effects of pathogens on necessarily-newly

isolated and non-isolated individuals is often used to test for the occurrence of social immunity in eusocial insects [61]. Overall, adopting the group living framework thus opens new perspectives to explore and better understand the common and specific solutions developed by each type of social host to counteract infections and thus, to improve our general understanding of the role of pathogens in the evolution of all forms of social life. Given the comparatively large amount of works on social immunity in eusocial insects, it is now time to further explore social immunity in a larger and taxonomically broader number of non-eusocial species.

Conflict of interest statement

The authors declare no conflict of interest.

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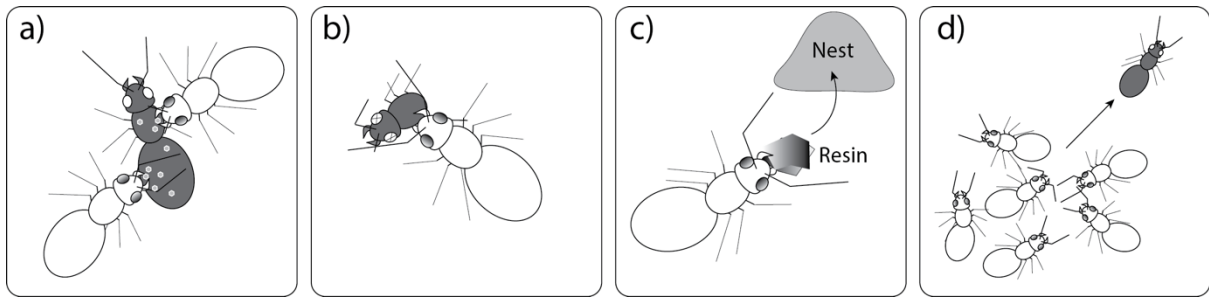
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410 **Figure 1** | Four classical examples of social immunity that can be found in ant colonies. (a) Two workers
 411 groom an infected nestmate (grey) to remove external pathogens. (b) A worker carries a corpse (grey)
 412 away from the nest. (c) A worker collects a piece of resin with antimicrobial properties and brings it
 413 back to its nest. (d) An infected worker (grey) isolates itself from the group to limit the risk of pathogen
 414 spread. References can be found in [6,8].

Highlighted references

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417 immunity and illustrate why they are straightforward in eusocial system with reproductive
418 division of labor. They also discuss the importance to measure fitness effects of social immunity
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430 understand the complexity of social insect immunity.

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431 This empirical study sheds light on the fact that social immunity is not ubiquitous among
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433 to pathogen exposure compared to solitary ones. Notably, co-founding queens also
434 expressed very little allo-grooming and trophallaxis.

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435 In this review, the authors discuss the role of microbes (including pathogens) in social evolution.
436 In particular, they claim that pathogens could serve as promoters of social evolution by favoring
437 cooperation between potential hosts to better fight against infections.