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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

17 **Abstract**

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

37

## 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 prophylactically 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

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

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

## 84 **The eusocial framework of social immunity**

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

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

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

## 106 **The limit of the eusocial framework**

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

111 and/or separate evolutionary pathways of collective defences against pathogens across group living  
112 species [7,8]. Moreover, this restriction to eusocial systems opened scope for several important  
113 misconceptions concerning the link between social immunity and social evolution. For instance, it  
114 might suggest that 1) reproductive division of labour is essential to allow the evolution of social  
115 immunity, 2) the presence of social immunity should lower investments into individual immunity in  
116 eusocial species and finally, that 3) social immunity does not have counterparts in non-eusocial species  
117 [6,9,10,24–26]. In the following part, we clarify these three misconceptions using recent empirical  
118 findings and demonstrate why they call for considering social immunity as a broader phenomenon  
119 that is not exclusive to eusocial species [7,8].

### 120 ***On the importance of reproductive division of labour***

121 One misconceptions possibly fostered by the eusocial framework is that the direct fitness costs of  
122 performing social immunity are so high for a donor individual that they should prevent the evolution  
123 of social immunity in groups where the donors' fitness relies on their own reproduction. In other  
124 words, the net benefits of performing social immunity should only be present in groups where donor  
125 individuals forego personal reproduction, i.e. in eusocial species with reproductive division of labour  
126 [25]. The first issue with this prediction is that it neglects that some forms of social immunity are not  
127 only unlikely to provide significant fitness costs to donors (e.g. the use of self-produced secretion to  
128 sanitize the nest, the removal of fresh corpses from the nest [6]), but may also provide direct benefits  
129 to donor individuals. These direct benefits have been recently revealed in allogrooming, a textbook  
130 example of social immunity [6,8]. This behaviour has long been thought to be exclusively costly for  
131 donor individuals, because it increases their risk of being exposed to the pathogens present on the  
132 recipient individuals. In an elegant study conducted in the ant *Lasius neglectus*, however, Konrad *et al*  
133 [35] demonstrated that allogrooming provides direct benefits to both recipients and donors, as it  
134 allows donors to prime their own immune system and thus boost their defences against future  
135 pathogen exposure. Interestingly, a follow-up study recently showed that these direct benefits are



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

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

#### 154 ***On the relaxed selection on individual immunity in eusocial species***

155 A second misconception possibly fostered by the eusocial framework is that the emergence of social  
156 immunity should relax selection on individual immunity and thus, that individual immunity should be  
157 less efficient and/or involve a lower number of genes in eusocial compared to non-eusocial species  
158 [38,39]. The interest of this prediction resided in the fact that it was relatively easy to test empirically.  
159 Unfortunately, the results were at odds with this prediction. On one hand, physiological studies  
160 showed that antimicrobial peptides (a component of individual immunity) are more effective in

161 eusocial compared to solitary sister species in bees [40] and trips [41]. On the other hand, the recent  
162 accumulation of genomic studies comparing insects with different levels of social organization reports  
163 no general association between eusociality and the number and/or expression of immune-related  
164 genes across ants, bees and termites (reviewed in [42]). Hence, shifting the unit of selection from  
165 individual to superorganism may not affect the selection pressures exerted on individual immunity  
166 [43]. Interestingly, this apparent absence of a general link between individual and social immunities  
167 suggests that the emergence of social immunity does not reduce, but instead complements individual  
168 defences against pathogens.

### 169 ***On the absence of social immunity in non-eusocial species***

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

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

186 colony [52,53], whereas the avoidance of contaminated areas is classically considered as a form of  
187 social immunity in eusocial insects [6]. Similarly, experimental exposure to pathogen spores did not  
188 trigger higher levels of allogrooming between workers in the ants *Formica selysi* and *Myrmica rubra*  
189 [11,54], and co-founding queens of the ant *Lasius niger* perform only very little allogrooming and did  
190 not exhibit a better resistance against pathogens when compared to solitary queens [55]. The claim  
191 derived from the eusocial framework and stating that social immunity is “necessary and essential to  
192 protect the entire reproductive entity and maximize its fitness” [25] should therefore be taken with  
193 caution. Arguably, social immunity encompasses a great diversity of forms [6,8], so that the absence  
194 of evidence for one form of social immunity should not be considered as an evidence for the absence  
195 of any form of social immunity. Nevertheless, the above findings warn us on the risk to over-  
196 interpreting the expression of certain behaviours as social immune responses on the sole basis that  
197 they are present in a eusocial species.

## 198 **What is and what is not a form of social immunity?**

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

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

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

## 232 **Conclusion**

233 In this review, we emphasized that individuals living either in facultative/temporary groups or in  
234 obligatory/permanent colonies can all perform defences against pathogens that may not only help  
235 themselves, but also their group members. The presence of these defences in such a large diversity of  
236 social systems recently made necessary the shift from a eusocial to a broad conceptual framework of  
237 social immunity [6–8,24,25]. This shift has generated novel works using the term ‘social immunity’ in  
238 a few subsocial insects such as the European earwig (e.g. [45,60,61]) and the burying beetle (e.g.  
239 [59,62,63]). Here, we claim that it is crucial to expand these first works to a taxonomically broader  
240 number of non-eusocial species. The resulting studies would first allow us to disentangle whether the  
241 selection pressures favouring the emergence of social immunity have either secondarily evolved to  
242 limit the inherently high risk of pathogen exposure in species with an obligatory and permanent social  
243 life (i.e. some forms of social immunity derive from eusociality), or whether they remained constant  
244 after the evolutionary shift from solitary to group living (i.e. social immunity is an ancestral process)  
245 [7,8]. Interestingly, it would also allow testing an alternative evolutionary scenario positing that the  
246 general risk of pathogen exposure for a solitary individual could have selected for the emergence of  
247 group living in order to obtain an additional line of defence such as social immunity [64]. Second, a  
248 taxonomically broader number of studies on social immunity would allow us exploring the potential  
249 trade-off between social and individual immunity across group-living species [65] and thus shed light  
250 on the dependent or independent evolutionary drivers of these two lines of anti-pathogen defences  
251 across animals. For instance, it would allow us to address questions such as whether certain types of  
252 pathogens are more likely to apply selection pressure onto individual instead of social immunity, or  
253 whether these two lines of defences necessarily trade-off across social systems [65]. Finally, non-  
254 eusocial species could offer experimental opportunities that are not available in eusocial species and  
255 thus allow exploration of novel factors possibly underlying the expression of social immunity. For  
256 instance, a recent study in the European earwig allowed to demonstrate that the recent (but not  
257 prolonged!) social isolation of group-living adults induces a stress that specifically lowers their  
258 resistance against pathogens, whereas comparing the effects of pathogens on necessarily-newly

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

## 266 **Conflict of interest statement**

267 The authors declare no conflict of interest.

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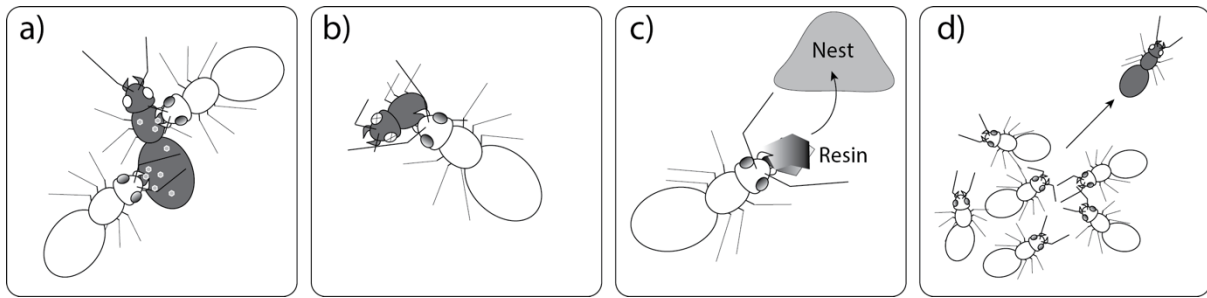
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410 **Figure 1** | Four classical examples of social immunity that can be found in ant colonies. (a) Two workers  
411 groom an infected nestmate (grey) to remove external pathogens. (b) A worker carries a corpse (grey)  
412 away from the nest. (c) 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].

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436 In particular, they claim that pathogens could serve as promoters of social evolution by favoring  
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