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1 **A data-driven simulation of the trophallactic network**  
2 **and intranidal food flow dissemination in ants.**

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## **Abstract**

Food sharing can occur in both social and non-social species but is crucial in eusocial species in which only some group members collect food. This food collection but also intranidal food distribution through trophallactic (i.e. mouth-to-mouth) exchanges are fundamental issues in eusocial insects. However, the behavioural rules underlying the regulation and the dynamics of food intake and the resulting networks of exchanges are poorly understood. In this study, we provide new insights into the behavioural rules underlying the structure of trophallactic networks and food dissemination dynamics within the colony. We build a simple data-driven model that implements interindividual variability and division of labour to investigate the processes of food accumulation/dissemination inside the nest, both at the individual and collective levels. We also test the alternative hypotheses (no variability and no division of labour). Division of labour with inter-individual variability predicts contrary to other models the food dynamics and exchange networks. We establish the links between the interindividual heterogeneity of the trophallactic behaviours, the food flow dynamics and network of trophallactic events. Despite the relative simplicity of the model rules, efficient trophallactic networks may emerge as the ones observed in ants leading to better understanding of evolution of such societies.

40

## Introduction

41 Food sharing is not the most obvious advantage of group living but can occur in different species  
42 (Isaac 1978; Kaplan et al. 1985; Stevens and Gilby 2004). Evolutionary origins of food sharing  
43 have been studied using the predictions of reciprocal altruism (Trivers 1971), biological markets  
44 (Noë and Hammerstein 1995) and multilevel selection (Traulsen and Nowak 2006). Food  
45 exchange is central to eusocial species such as ants, termites, bees and even naked mole  
46 rats (Anderson 1984; Jarvis et al. 1994; Nowak et al. 2010). In eusocial species, only a restricted  
47 number of individuals forage and retrieve food for the rest of the colony forming trophallaxes  
48 (i.e., mouth-to-mouth food exchange) networks (Quque et al. 2021). Indeed, insect societies may  
49 be seen as social networks whose structure is shaped by individual (nodes) behaviours and  
50 interactions (edges) between individuals, including food sharing. While different networks  
51 (colonies) may allocate the same total amount of time to a task (such as brood care or food  
52 collection), the time investment or the efficiency (i.e. quantity of food exchanged per interaction)  
53 could be quite different between nodes (Dornhaus et al. 2012; Tenczar et al. 2014) according to  
54 their interactions and the emergent hierarchical and modular property of the trophallaxes  
55 networks (Quque et al. 2021). The topology of social networks drives information transmission  
56 (Aplin et al. 2014; Atton et al. 2014), food stock building (Sendova-Franks et al. 2010) and  
57 influences a range of collective outcomes, such as the transmission of parasites and pathogens  
58 (Hamede et al. 2009; VanderWaal et al. 2014; Stroeymeyt et al. 2018; Romano et al. 2020). Food  
59 stock building in social insects involves networks of food sharing interactions through  
60 trophallactic events, during which not only food is transferred (LeBoeuf 2017). A small fraction  
61 of the workers (the foragers) collect the food that is distributed to the nonforaging part of the  
62 colony, which in turn disseminates the food (Howard and Tschinkel 1981; Pinter-Wollman et al.

63 2013). A chain of demands, whose origins are principally the larvae and the queen, fine-tunes the  
64 foraging activity to the colony's needs (Cassill et al. 1998; Dussutour and Simpson 2008). No  
65 single worker has a comprehensive understanding of the nutritional status of the whole colony.  
66 Instead, colony-level nutritional regulation is an emergent property resulting from numerous  
67 individual behaviours (e.g., foraging and disseminating) modulated by local information (such as  
68 individual crop content (Seeley 1989)). In such a process, the interindividual variability of the  
69 responses may affect the collective outcomes and performance of the colony (Adler and Gordon  
70 1992; Robinson et al. 2008; Pamminger et al. 2014; Delgado et al. 2018).

71 Many studies have focused on interindividual variability in searching behaviour and in food  
72 collection efforts (e.g., in honeybees (Spaethe and Weidenmüller 2002; Tenczar et al. 2014),  
73 bumblebees (Crall et al. 2018), and ants (Dornhaus 2008; Robinson et al. 2008; Beverly et al.  
74 2009; Campos et al. 2016; Pask et al. 2017)). However, the intertwining of the interindividual  
75 heterogeneity with the food dissemination activity and the division of work and the resulting  
76 trophallactic networks at the intranidal level remain far less studied. Some empirical works  
77 revealed the colony-level dynamics of food sharing and accumulation as well as the negative  
78 feedbacks that regulate the food flow entering the nest (Buczowski and Bennett 2009; Buffin et  
79 al. 2009a, 2012). The absence of individual identification in such studies limits the inquiries  
80 between the level of workers' contributions and colony food management. The recent  
81 technological improvement in automating individual identification (Mersch et al. 2013; Gernat et  
82 al. 2017; Crall et al. 2018; Greenwald et al. 2018a; Richardson et al. 2020; Wild et al. 2021)  
83 allows better investigations of the individual behaviours involved in food exchanges. A first  
84 study analysing the whole trophallactic network showed a spatial re-organisation of worker  
85 positions in the presence of starvation, accelerating the food stock recovery (Sendova-Franks et

86 al. 2010). Network resilience (i.e. capacity to maintain the food exchange whilst removing central  
87 individuals) and efficiency (i.e. how fast the food is transmitted from foragers to peripheral  
88 individuals) are stable with colony size but increase in the presence of broods, presumably in  
89 response to the nutritional needs of larvae (Quque et al. 2021). Other studies focused on the  
90 individual behavioural rules regulating the food exchanges (Bonavita-cougourdan and Gavioli  
91 1981; Greenwald et al. 2015, 2018a), refuting some classical assumptions about this phenomenon  
92 which was commonly viewed as a deterministic process (Cassill and Tschinkel 1999; Gregson et  
93 al. 2003; Buffin et al. 2009b; Sendova-Franks et al. 2010). In particular, the authors showed that  
94 1) the donor does not deliver its entire crop load, nor does the recipient fill up to its crop capacity;  
95 2) the food flow during a trophallactic event can be bidirectional; and 3) foragers are able to leave  
96 the nest even if their crops are not completely empty.

97 Moreover, a high level of variability is observed in the amount of food transferred during a  
98 trophallactic exchange for the crop contents of a given recipient as well as in the crop load of the  
99 foragers exiting the nest (Greenwald et al. 2018a). These variabilities prevent any clear  
100 conclusions about the relationships between the crop content and the nest-leaving behaviour or  
101 the amount of food transferred during an exchange. The consequences of this stochasticity on  
102 food flow dynamics and food spreading speed are not straightforward to assess empirically and  
103 are therefore overlooked (Gräwer et al. 2017).

104 In the context of foraging activity, a widely accepted behavioural categorisation distinguishes the  
105 individuals visiting, even once, the food source and bringing the food back to the nest (foragers)  
106 and the individuals staying inside the nest (non-foragers). However, the link between this  
107 categorisation and the respective contributions of each caste (foragers vs. non-foragers) in  
108 intranidal food dissemination and the characteristics of the trophallactic network are far from

109 clear. How intra-caste variability in food exchange behaviour affects food dissemination within  
110 the context of the trophallactic network is also poorly understood.

111 In this study, we attempt to fill this gap by developing a data-driven model of trophallactic  
112 networks that implements interindividual variability and division of labour. We also tested the  
113 alternative hypotheses (no variability and no division of labour). These models are based on  
114 empirical data collected from the food exchange process in colonies of the ants *Lasius niger* [see  
115 “summary of the behavioural experiments” section]. Our goal is to identify the minimal set of  
116 rules governing the trophallactic and foraging behaviours and to capture the main features of the  
117 food exchange process of our experimental ant colonies. The model includes four activities:  
118 departure from the nest, food collection, travel back to the nest and food exchange  
119 (donation/reception).

120 While some levels of variability are often expected to enhance foraging success (Campos et al.  
121 2016), here we explore the effects of two levels of variability of the trophallactic behaviour on  
122 the food spreading:

123 (i) resulting from the existence of forager- and non-forager-specific behaviours. We will  
124 first assume that non-forager and forager trophallactic behaviours are identical and  
125 will thus consider one behavioural caste (OC) which corresponds to a null hypothesis.  
126 We will next explore the case where a differentiation of non-forager and forager  
127 trophallactic behaviours occurs after the first visit of the foragers at the food source  
128 and will thus consider two behavioural castes (TEC), which corresponds to what is  
129 observed in ants.

130 (ii) occurring within castes. In this case, individuals of each caste have a probability of  
131 performing a trophallactic event drawn from a particular distribution. Three common

132 probability distributions will be tested, namely, the delta distribution, uniform  
133 distribution and exponential distribution making varying the probability to give or  
134 receive food (explanations are given in the “Material and methods” section).with  
135 exponential distribution being closer to what is observed in ants as foragers give more  
136 than the received and vice-versa with non –foragers.

137 In “Material and methods” section, we formulate the main model and its different versions;  
138 “Results” section is devoted to the analyses of the model and its comparison with experiments.  
139 Finally, we discuss the biological relevance of the model predictions, particularly the link  
140 between the interindividual variability and the participation of each ant in collective food  
141 management.

## 142 **Materials and Methods**

### 143 **Model description**

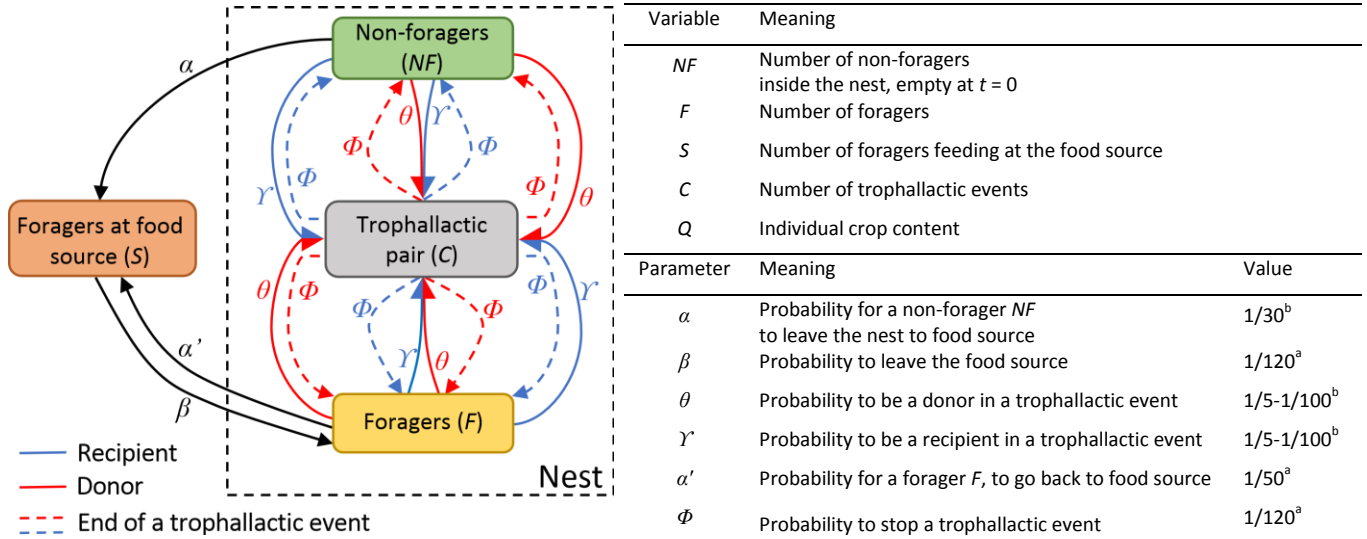
144 To capture the essence of food collection and storage dynamics as well as intranidal trophallactic  
145 network properties in *L. niger*, we developed an agent-based model. A general overview and the  
146 relationship of the main variables of the model is given in Figure 1. At the beginning of each  
147 simulation ( $t=0$ ), the colony only contains non-forager individuals *NFs* with a crop content equal  
148 to zero,  $[Q_i(0) = 0]$ . The food source access is unrestricted, and the quantity of food is unlimited.  
149 At each timestep  $t$ , every non-forager in the nest, selected in a random order, can leave the nest  
150 and start to feed at the food source with a probability per time unit  $\alpha$ , which is the inverse of the  
151 mean time spent before leaving the nest. Each individual visiting the food source at least once is  
152 considered to be a forager *F* for the rest of the simulations. After a time spent at the food source,



153 the foragers  $F_s$ , containing an amount of food  $Q$  proportional to the time spent feeding, go back  
 154 to the nest with a probability  $\beta$ , corresponding to the inverse of this time.

155

156



**Figure 1:** Flow diagram of the model, variables and parameters. The square boxes representing the states of individuals ( $NF$ ,  $F$ ,  $S$ ,  $C$ ). Black arrows are state-transition rates; coloured arrows represent the formation of a trophallactic pair, the red one being the donor and the blue one the receiver. On the right part of the figure, variables and parameters are defined and value of parameters implemented are indicated. <sup>a</sup>Parameters estimated from the experiments presented in the material and methods section or derived from the literature (Mailleux et al., 2010, 2006). <sup>b</sup>Parameters estimated by fitting on the experiments.

157

158 At each timestep  $t$ , every individual  $i$  ( $i=F, NF$ ) in the nest can randomly exchange food  
 159 respectively, as donor or receiver, with a probability  $\theta_i$  (as donor) or  $\gamma_i$  (as receiver), which are  
 160 increasing/decreasing functions that depend in a sigmoidal way on the current crop content  $Q_i$   
 161 (Greenwald et al. 2015, 2018a):

162

$$\theta_i = \frac{\theta_i(0) \cdot Q_i^n}{k^n + Q_i^n} \quad (1)$$

163

$$Y_i = \frac{Y_i(0) \cdot k^n}{k^n + Q_i^n} \quad (2)$$

164 where  $k$  is a threshold value of the amount of food carried (as individuals may have different  
165 thresholds, (Greenwald et al. 2018b)) and  $n$  controls the steepness of the functions (Amé et al.  
166 2006; Sueur and Deneubourg 2011). A high value of  $n$  leads to a rapid decreasing (increasing)  
167 probability to accept (give) food when the value of  $Q_i$ , the amount of food carried by the  
168 individual  $i$ , approaches the value of  $k$ . The probability that two individuals exchange food  
169 depends on the product of their individual interaction probabilities. Furthermore, the food flow is  
170 directional from the donor to the receiver and cannot be reversed during a single trophallactic  
171 event. The probability  $\Phi$  for a trophallactic pair to be separated is equal and constant for both  
172 individuals; however, when the donor is empty, the trophallactic event is stopped. For simplicity,  
173 we imposed that the quantity of food exchanged is proportional to the duration of the  
174 trophallactic event (Greenwald et al. 2015). The individual maximal carrying capacity is not  
175 imposed but results from the product of the individual probability  $\theta$  or  $Y$  to give or to receive  
176 food and the probability  $\Phi$  to separate a trophallactic pair. The probability of leaving the nest also  
177 decreases with the crop content  $Q$ :

178

$$\alpha_i = \frac{\alpha_i(0) \cdot k^n}{k^n + Q_i^n} \quad (3)$$

179 with  $\alpha_i(0)$  representing the maximum probability of leaving (when  $Q=0$ ). After the first visit to  
180 the food source, this maximum probability  $\alpha'_i(0)$  increases ( $\alpha'_i(0) > \alpha_i(0)$ ). The literature suggests  
181 only a weak link between the crop content and the probability of food exchange or the probability  
182 to leave the nest (a wide range of the probability to exchange food or to leave the nest is observed  
183 for a given crop content (Greenwald et al. 2015, 2018a)); therefore, we fixed the values of  $n$  and  
184  $k$  as follows:  $n = 2$  (smooth increasing/decreasing of the probability to give/receive with an

185 increasing crop content) and  $k = 120$  (which corresponds to the mean quantity of food exchanged  
186 during one trophallactic event, see the next section for details on experimental procedure). Given  
187 these parameter values, individuals leave the nest with variable crop content, according to  
188 experiments from (Greenwald et al. 2018a).

189 We compared the dynamics of food dissemination at the intranidal level and the properties of  
190 trophallactic networks in two versions of the model, which differed only in their assumptions  
191 concerning the individual probability of giving or receiving food through a trophallactic event  
192 between foragers and non-foragers:

193         A. In the first version, we made a one-caste assumption (OC version). All individuals of  
194 the colony were indistinguishable in terms of their probabilities to give and receive food through  
195 a trophallactic event ( $\theta_F = \theta_{NF}$  and  $\gamma_F = \gamma_{NF}$ , respectively).

196         B. In the second version of the model, we made a two emergent castes assumption (TEC  
197 version); at the beginning of the simulation, all the individuals are non-foragers *NFs*. When a  
198 non-forager *NF* leaves the nest to go to the food source, it becomes a forager *F* and, having new  
199 information about the food availability, now behaviourally differs from the non-foragers *NFs* in  
200 terms of the probabilities to give and receive food through a trophallactic event ( $\theta_F \neq \theta_{NF}$  and  $\gamma_F$   
201  $\neq \gamma_{NF}$ , respectively).

202 In both versions of the model, we tested three hypotheses entailing an increasing level of  
203 interindividual variability in the probability  $\theta_i$  to give and  $\gamma_i$  to receive food: (i) Delta probability,  
204 we tested a delta probability distribution where all the individuals have the same intrinsic  
205 probability to exchange food (this corresponds to a simple but null hypothesis); (ii) Uniform  
206 probability, we tested a uniform distribution of the probability  $\theta_i$  to give and  $\gamma_i$  to receive food

207 between the individuals with a standard deviation, respectively, equal to the mean probabilities of  
208  $\theta_i$  and  $\gamma_i$ ; and (iii) Exponential distribution, we tested for the effect of individual variation in  
209 trophallaxis probability on the food flow entering the nest and the individual inequality in  
210 trophallactic activity since ants vary in their probability to give/receive food following a  
211 decreasing exponential law [  $f(x) = \varepsilon \cdot e^{\left(\frac{-x}{\varepsilon}\right)}$ , with  $\varepsilon$  equal to  $\theta$  or  $\gamma$  ] (this corresponds to what  
212 is observed in ants with foragers giving more and receiving less than non-foragers). In (i), (ii) and  
213 (iii) the intrinsic individual probabilities of giving and receiving food through a trophallactic  
214 event are attributed at the beginning of each simulation and do not change over time in the one-  
215 caste (OC) version of the model. In the two-castes (TEC) version, the individual threshold is  
216 updated to a forager ( $F$ ) value after the ant visits the food source for the 1<sup>st</sup> time. These two  
217 values, before and after the 1<sup>st</sup> visit to the food source, are not correlated.

218

## 219 **Summary of the behavioural experiments**

220 From five large mother colonies (>1000 ants) of *L. niger* (collected in Brussels, Belgium, autumn  
221 2016), we created five queenless and broodless subcolonies of 50 randomly chosen workers. Ants  
222 were individually labelled with an ArucoColor tag (<https://sites.google.com/site/usetrackerac/>)  
223 allowing automatic identification of ants. Each tag was stuck onto the abdomen, had a side length  
224 of 0.8 mm, weighed 0.1 mg (corresponding to less than 5% of the average mass of an adult  
225 worker or less than 10% of the amount of food a worker carries (Mailleux et al. 2000)) and was  
226 printed on waterproof paper at a resolution of 1200 dpi. The tags were hand-cut using a scalpel  
227 and a steel ruler as guide. Following a 5-min acclimatisation period, the labelling was not  
228 observed to impede the ants' behaviours, movement or interactions. Each subcolony was

229 introduced in the experimental setup between 15 to 18 days prior to the first experiment; the  
230 setup was composed of a one-chamber nest (56 x 41 x 2 mm) covered by a glass window. This  
231 duration was long enough to stabilise the task repartition among individuals. A single access  
232 route (4 x 3 x 2 mm) leads to the foraging area (61 x 49 x mm) containing a 0.3 M sucrose  
233 solution and water *ad libitum*. The walls of the foraging area were covered in Fluon® to prevent  
234 the ants from escaping. The subcolonies were kept at 22 ±3°C and 60 ±5% relative humidity,  
235 with a 12:12 h constant photoperiod. After 4 days of starvation, we introduced 3 mL of a 1 M  
236 sucrose solution. The ants were filmed for 90 min, starting 30 min before food source  
237 introduction. Each colony was tested once. The video data were recorded using a Panasonic®  
238 Lumix DMC-GH4-R mounted with a 30 mm Olympus® ED lens capturing 25 frames/s at the  
239 definition of 4180\*2160 p. We discriminated foragers (*Fs*) from non-foragers (*NFs*). An  
240 individual was considered a forager if it spent at least five consecutive seconds feeding at the  
241 food source during the experiment. Each minute, we performed a scan-sampling (Altmann 1974)  
242 of all the trophallactic interactions, identifying the donor, the receiver and the X and Y spatial  
243 positions of the trophallactic event (contact point of the mandibles of both ants). A trophallactic  
244 event was recorded when ants engaged in mandible-to-mandible contact for greater than 5 s. The  
245 directionality of food flow and the role of the donor and the receiver were determined by the  
246 characteristic body posture and the mandible position (Cassill and Tschinkel 1999; Greenwald et  
247 al. 2015). A trophallactic event involving the same individuals on two or several consecutive  
248 scans was considered as a single trophallactic event of two or several min lengths. Raw empirical  
249 data, codes as well as supplementary figures (Fig.Sx) and tables (tables) are available in Zenodo  
250 (<https://doi.org/10.5281/zenodo.6396637>). A complete description of the results is presented in  
251 (Planckaert et al. 2019).

252

253 **Model calibration and comparison of the model output with the**

254 **experimental results**

255 The model was calibrated with values of parameters derived from the experiments (see previous  
256 section), and the parameters given in Figure 1 and Table 1 so that the model reproduces the  
257 following experimental results: 1. the mean number of foragers; 2. the mean number of  
258 trophallactic events; and 3. the proportions of the 4 different types of trophallactic pairs ( $F \rightarrow NF$ ;  
259  $F \rightarrow$ ;  $NF \rightarrow$ ;  $NF \rightarrow F$ ). Therefore, the simulations were run for 3600 timesteps (with each timestep  
260 equal to 1 s) with 53 individuals, corresponding to the duration of the experiment and the mean  
261 size of the experimental colonies. Simulations were repeated 1000 times. For each simulation, the  
262 start/end time of each trophallactic event, as well as the identity and role of each individual in the  
263 trophallactic pairs (the donor/receiver) were extracted. The complete trophallactic network of  
264 each simulation (N=1000) and each experiment (N=5) was built, allowing us to analyse and  
265 compare the food dissemination dynamics, the properties of the networks of food exchanges and  
266 the participation of individuals in the trophallactic events. Classical tools of social network  
267 analysis in animal societies (Wey et al. 2008) were also used to characterise the global properties  
268 of each trophallactic network as well as the role of each individual in the network (see the next  
269 section for details on data analysis). The survival curve of the 1<sup>st</sup> arrival to the food source in the  
270 experiments is well fitted by a power law distribution of  $\alpha_i(0)$ , the individual probability to leave  
271 the nest in the model (Figure S1). This suggests that few individuals have a high probability of  
272 visiting the food source, and most of them have a low probability.

273 We evaluate the goodness-of-fit of these three outputs between the experiments and both versions  
274 of the model (OC and TEC), each tested with the three distributions (delta, uniform, exponential)

275 of the probability  $\theta_i(0)$  to give and  $Y_i(0)$  to receive food through a trophallactic event. Only the  
 276 version of the model (OC or TEC) that best met this first “selection filter” was considered for  
 277 more detailed analysis. A local sensitivity analysis of the selected parameter values is provided  
 278 (Figure S6).

279

	Parameters	One caste (OC)			Two emergent castes (TEC)		
		Equal	Uniform	Exp.	Equal	Uniform	Exp.
	$\theta_F$	1/11	1/10	1/6	1/10	1/11	1/9
	$\theta_W$				1/33	1/32	1/32
	$Y_F$	1/60	1/50	1/56	1/11	1/9	1/9
	$Y_W$				1/38	1/28	1/27
Results	Experiments (mean+/-s.d)						283
Number of trophallactic events	99.0+/-17.4	100.1	98.7	100.5	101.0	99.5	98.4
Number of foragers	12.2+/-1.9	12.2	12.6	12.2	12.3	12.4	12.5

286 **Table 1:** The upper part of the table shows the parameters values of the two versions of the model and three  
 287 distributions. Only the parameters that vary between models are shown. The lower part of the table shows the  
 main experimental and the theoretical results of the foraging activity. See the text for further explanation.

## 288 Statistical and social network analysis

289 A Mann-Whitney U test (MW) was used to compare the theoretical and experimental numbers of  
 290 each type of trophallactic pair ( $F \rightarrow NF$ ;  $F \rightarrow F$ ;  $NF \rightarrow NF$ ;  $NF \rightarrow F$ ; Figures 2, S3 and Table S1). A  
 291 Kolmogorov-Smirnov test (KS) was used to analyse the deviation between the theoretical and the  
 292 experimental distributions of the number of trophallactic events among the colony members  
 293 (Figures 3, S4.A-C and S5) and the cumulative number of trophallactic events (Figures 4.A and  
 294 S4.D-F). To quantify the degree of inequality in trophallactic activity among the workers, we  
 295 plotted the cumulative distribution of total trophallactic events performed in each trial in the form

296 of a Lorenz curve (Tenczar et al. 2014) (Figures 4.B and S4.G-I). Such a curve displays the share  
297 of trophallactic activity (Y axis) accounted for by x% of the workers (sorted by the number of  
298 trophallactic events per individual) in the colony. A perfectly equitable distribution of foraging  
299 activity would correspond to the line  $Y=X$ . The Gini coefficient (Figures 4.C and S4.J-L) is  
300 known as the ratio between the area below the experimental Lorenz curve and the triangular area  
301 below the perfect equality case  $Y=X$  and provides a measure of the degree of inequality in the  
302 distribution of trophallactic activity, ranging from 0 (perfect equality) to 1 (perfect inequality).  
303 Social network analysis was performed on both the theoretical and experimental results. The  
304 nodes correspond to individuals (Figure S2, red = foragers; green = non-foragers), and the edges  
305 represent trophallactic events directed from the donor to the receiver. We performed weighed (i.e.  
306 including the number of interactions between two nodes) and directed (i.e., including the  
307 direction of exchanges) analyses. Social network analyses were performed at both the individual  
308 level and the functional category (foragers/non-foragers) level. The length of the edge conveys no  
309 information. At the individual level, we calculated the betweenness, the closeness and the  
310 clustering coefficients of each individual (Sosa et al. 2020). Betweenness centrality (Figures 5.C  
311 and S4.S-U) is an estimate of how important an individual ant is to the promotion of connectivity  
312 across the entire colony and this value measured by the number of times an individual acts as a  
313 bridge along the shortest path between two other ants (Dell et al. 2014). Closeness centrality  
314 (Figures 5.B and S4.P-R) is based on the distance (measured by shortest paths) from an  
315 individual to every other individual in the colony; the more central an ant is, the lower its total  
316 distance is from all the other ants (Wey et al. 2008). The clustering coefficient (Figures 5.D and  
317 S4.V-X) allows us to determine the existence of “communities” in a network, such as node pairs  
318 with many more edges between them than with other ones (Saramäki et al. 2007). To assess the  
319 effect of network structure on food spreading speed, we measured the efficiency (Figures 5.A and



320 S4.M-O), defined as the multiplicative inverse of the shortest path distance between all pairs of  
321 nodes (Latora and Marchiori 2001; Buhl et al. 2004) and measuring how fast an entity (here the  
322 food) is transmitted into the network. Concerning the food spreading speed, we compared the  
323 mean theoretical  $T_{50}$  and experimental  $T_{50}$  (time when half the trophallactic events were realised,  
324 Figures S4.Y- $\alpha$ ). To statistically quantify whether experimental values were different from the  
325 simulations (concerning the  $T_{50}$ , the Gini coefficient and the social networks metrics:  
326 betweenness, closeness clustering, and efficiency coefficients), we used Z-tests (ZT) to compare  
327 the experimental mean (N=5) to the corresponding theoretical mean (200 mean scores from 5  
328 randomly selected simulations among 1000 simulations). A Kruskal-Wallis (KW) analysis  
329 revealed that the degree (KW,  $H=0.70$ ,  $p>0.95$ ), out-degree (KW,  $H=1.83$ ,  $p=0.77$ ), in-degree  
330 (KW,  $H=0.66$ ,  $p>0.95$ ), betweenness (KW,  $H=9.10$ ,  $p=0.06$ ), closeness (KW,  $H=3.98$ ,  $p=0.41$ )  
331 and eigenvector (KW,  $H=0.93$ ,  $p=0.91$ ) distributions among colony members were homogeneous  
332 between the five experiments; therefore, we merged and averaged the experimental results for the  
333 calibration of the model and for the comparison between the experimental and theoretical results.  
334 The level of significance was set at  $p<0.05$ . All simulations were conducted on Python 3.6; all the  
335 analyses were performed with NetworkX 2.1, PyGraphviz 1.4, NumPy 1.14, SciPy 1.0.0 and  
336 Matplotlib 2.2.2.

337

## 338 **Results**

### 339 **Evaluation of the quality of the calibration of the models**

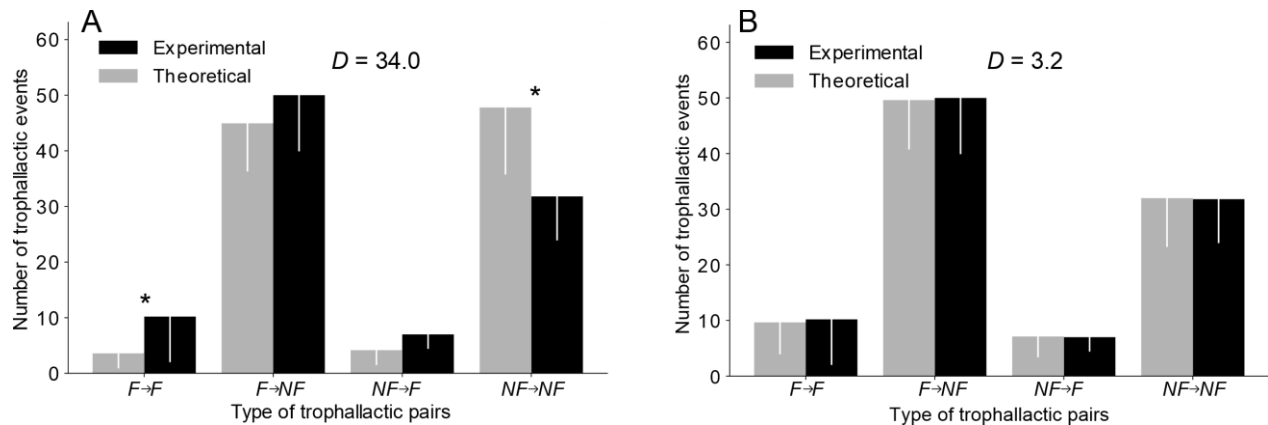
340 The values of the probability  $\theta$  to give and  $\gamma$  to receive a food through a trophallactic event that  
341 best fit the experimental outputs are presented in Table 1. Both model versions (OC and TEC)

342 closely reproduced the empirically measured number of trophallactic events while respecting the  
343 number of foragers, although they were not explicitly imposed at the beginning of the simulation.  
344 This result is independent of the distribution (delta, uniform, exponential) of the individual  
345 probability to give/receive that was implemented (Table 1).

346

347 We then determined to what extent each type of trophallactic pair ( $F \rightarrow F$ ,  $F \rightarrow NF$ ,  $NF \rightarrow F$ ,  
348  $NF \rightarrow NF$ ) contributes to the total number of trophallactic events. The OC version, whatever the  
349 distribution implemented, systematically reproduced the proportion of each type of trophallactic  
350 pair ( $F \rightarrow F$ ,  $F \rightarrow NF$ ,  $NF \rightarrow F$ ,  $NF \rightarrow NF$ ) with a lower accuracy than did the TEC version (Figures  
351 2, S3 and Table S1): the OC version, whatever the distribution, significantly overrated the  
352 number of  $NF \rightarrow NF$  exchanges and underestimated the number of  $F \rightarrow F$  exchanges (MW:  $p < 0.05$   
353 in each case, see also Figure S3 and Table S1 for details on statistical analysis), while the TEC  
354 version, whatever the distribution, reproduced the number of each type of trophallactic pairs  
355 (MW,  $p > 0.2$  in each case, see Figures 2, S3 and Table S1 for details on statistical analysis).

356 As the OC version failed to reproduce the experimentally observed proportions of each type of  
357 trophallactic pair, in the rest of the paper, we will focus on the TEC version.



**Figure 2:** Comparison of the number of each type of trophallactic pairs between the experiments and the simulations implemented with a Delta distribution in the OC version (A) and in the TEC version (B). \* = MW with a  $p < 0,05$ . Error bar = standard deviation.  $D$  = Sum of the difference of the number of trophallactic pairs of each type ( $F \rightarrow F$ ,  $F \rightarrow NF$ ,  $NF \rightarrow F$ ,  $NF \rightarrow NF$ ) between the experiments and the simulations. See Figure S3 for the Uniform and Exponential distributions and Table S1 for details.

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### Individual contributions to food dispersion / accumulation

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After investigating the trophallactic activity at the colony level, we analysed the way each ant

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participated in trophallactic exchanges. Our main interest was to understand whether

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interindividual variability in trophallactic activity was required to fine-tune the experimental

364

distribution of trophallactic activity/contribution to food dissemination. Figure 3.A and Figures

365

S4.A-C show the distribution of the number of trophallactic events executed by all the ants, both

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at the theoretical and experimental levels. While a KS test indicated a significant improvement of

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the fitting along with an increasing level of interindividual variability implemented in the model

368

(exponential > uniform > delta), only the TEC exponential version was not significantly different

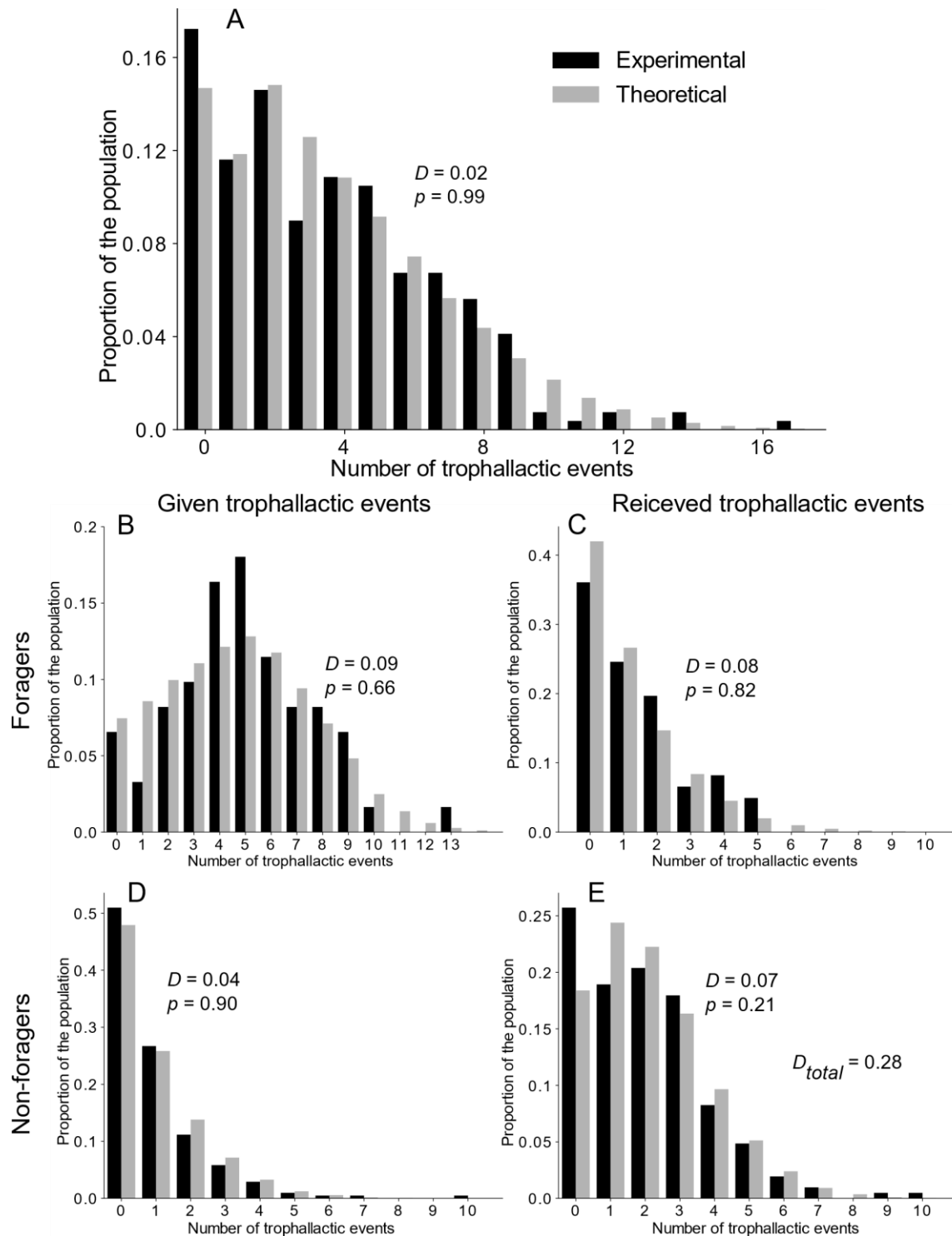
369

from the experiments. Note that the model (with the delta and uniform distributions) always

370

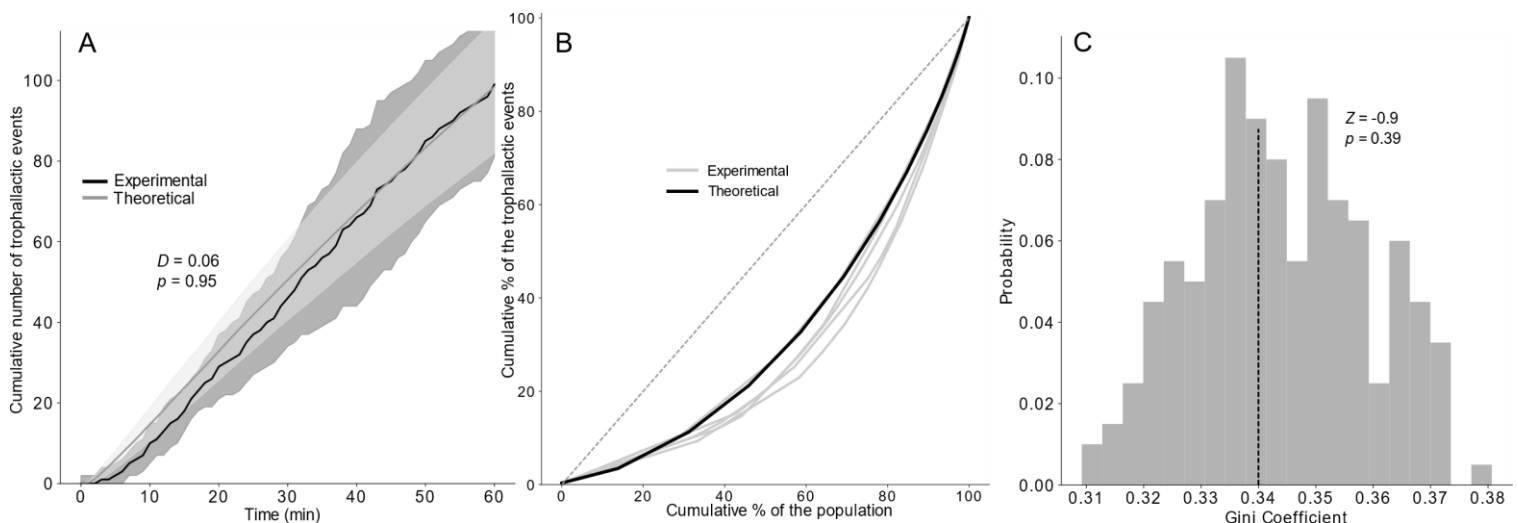
underestimates the proportion of inactive individuals (Figures S4.A-B).

371 We then focused on the distribution of the number of trophallactic events at a finer scale: the  
372 numbers of trophallactic events as donors and receivers, respectively, by the foragers and by the  
373 non-foragers (Figures 3B-E, S5 and Table S2). Only the TEC exponential model was not  
374 different from the experimental distribution of the trophallactic activity for each category (KS,  
375  $p > 0.21$  in each case, see Table S2 for details on statistical analysis).



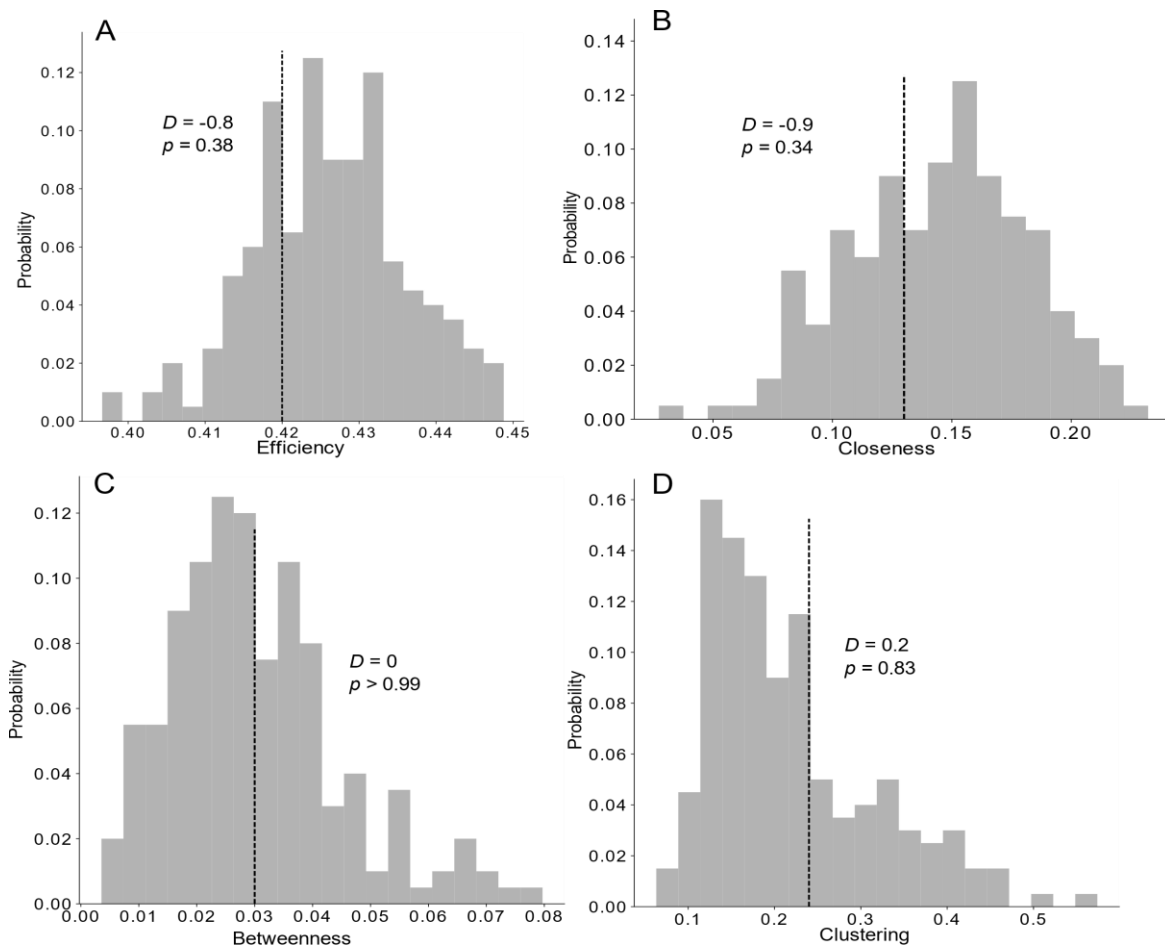
**Figure 3:** Theoretical and experimental distribution of the number of trophallactic events. A, Distribution of all the trophallactic events at the colony-level. B, C, Respectively, given and received trophallactic events performed by the foragers. D, E, Respectively, given and received trophallactic events performed by the non-foragers. Theoretical = TEC Exponential model.  $D$  and  $p$  on figures = statistical values from KS test.  $D_{Total}$  = sum of the KS distance ( $D$ ) from the comparison of distribution in B-E. See Figure S5 and Table S2 for details on statistical analysis of other versions of the model.

378 No difference was found between the dynamics of food accumulation in the simulations and  
 379 experiments in the three versions of the model (KS:  $p > 0.95$  in all cases, see also Figures 4.A and  
 380 S4.D-F for details on statistical analysis). Concerning the spreading speed of food, a Z-test  
 381 indicated no significant difference between the experimental and theoretical  $T_{50}$  (time required to  
 382 reach 50% of the total number of trophallactic events) of the TEC model, regardless of the  
 383 distribution implemented (Figures S4.Y- $\alpha$ ). The next step consisted of testing the ability of our  
 384 model to reproduce the experimentally observed interindividual heterogeneity in the food  
 385 spreading activity, with the majority of the trophallactic events performed by a relatively small  
 386 number of ants. We statistically quantified the heterogeneity in food spreading activity between  
 387 the simulations and experiments using the Lorenz curve and Gini coefficient (Figures 4.B-C and  
 388 S4.G-L). Only the TEC exponential model produced a heterogeneity of the food spreading  
 389 activity as high as that observed in the experiments (ZT:  $Z = -0.9$ ;  $p = 0.39$ ).



**Figure 4:** A, Cumulative number of trophallactic events after 1h of experiments or 3600 timesteps from 1000 simulations of the TEC Exponential model and from the experiments (N=5) compared with a KS ( $D$  and  $p$ -val). Dashed lines represent the time when 50% of the trophallactic events were realized, both in the model and the experiments. Shaded area = standard deviation. B, Lorenz curves showing the cumulative proportions of trophallactic events (y axis) vs. the individual rank (x axis, sorted by the number of trophallactic events performed by each individual), from the simulations (black curve, N=1000) and from the experiments (grey curves, N=5). C, Distribution of the Gini coefficient from the simulations (grey bars, N=1000) and mean from the experiments (dashed lines, N=5) compared with a Z-test ( $Z$ -value and  $p$ -val).

390 We then investigated the characteristics of the trophallactic networks to determine if the structure  
 391 of the empirical networks facilitated food spreading compared with the simulations. Again, only  
 392 the efficiency of the trophallactic networks resulting from the TEC exponential model was not  
 393 significantly different from the empirically measured efficiency (ZT;  $Z=-0.9$ ,  $p=0.38$ ; Figures 5.A  
 394 and S4.M-O). Concerning the closeness, betweenness and clustering coefficients, no significant  
 395 differences were observed between the three distributions (delta, uniform, exponential) in the  
 396 TEC model and the experiments (ZT;  $p>0.05$ ; Figures 5.B-D and S4.P-X). Nevertheless,  
 397 increasing the theoretical interindividual variability (delta>uniform>exponential) leads to a  
 398 higher accordance between theoretical and experimental results for these three coefficients.



**Figure 5:** Distribution of the efficiency (A), closeness (B), betweenness (C) and clustering (D) coefficients measured in the networks of the TEC Exponential model (grey bars, N=1000) and the mean measured from experiments (vertical dashed line, N=5) compared with a Z-test (*Z-value* and *p-val*). See also Figures S4.M-X.

## Discussion

400 We developed and analysed an agent-based model to investigate the mechanisms underlying the  
401 intranidal food spreading in ant nests based on trophallactic exchanges between the colony  
402 members. The keystone hypothesis was that no division of labour is a priori at work as far as  
403 trophallactic exchange is concerned. Rather, the trophallactic processes lead to chains of  
404 exchanges based on random encounters of potential partners.

405 Two versions of the model were tested (OC and TEC, see “Model description” section), each of  
406 which was implemented with three types of probability distributions of giving/receiving food in a  
407 trophallactic event (delta, uniform, exponential). Both versions, regardless of the probability  
408 distribution implemented, fit some of the main outcomes of the experiments: the number of  
409 foragers and the number of trophallactic events (Table 1). In contrast, only the TEC version  
410 (irrespective of the distribution implemented) was able to reproduce the observed pattern of  
411 trophallactic exchanges between the foragers and non-foragers (Table 1, Figure 2 and Figure S3).

412 Based on the Kolmogorov-Smirnov distance (the supremum of the set of distances between the  
413 theoretical and experimental distributions), the TEC exponential model best captured the  
414 individual and collective patterns of the food spreading and, in particular, the interindividual  
415 heterogeneity in the trophallactic activity observed naturally between foragers and non-foragers  
416 (Figure 4, S5 and Table S2).

417 We showed as expected that a behavioural shift in the probability to give/receive food as a  
418 forager in the TEC version of the model and a right-skewed (exponential) distribution of the  
419 probability to give/receive food among all colony members (Table S3) are sufficient to reproduce  
420 the trophallactic networks.



421 The Gini coefficient revealed that the empirical interindividual level of heterogeneity in  
422 participation in food dissemination activity, both in foragers and non-foragers, was only  
423 generated by the TEC exponential model (Figures S4.J-L). Here, few ants were highly engaged in  
424 trophallactic interactions, which is a common property of many observed networks having scale-  
425 free property (Albert and Barabasi 2002; Naug 2008; Sendova-Franks et al. 2010; Sueur et al.  
426 2012; Crall et al. 2018). This interindividual variability is often considered important as far as  
427 resilience is concerned (Naug 2008), even though the removal of the most engaged nodes can  
428 severely disrupt the system (Barabasi 2002).

429 Classical metrics of social network analysis - revealing role of individuals and topology of food  
430 networks - were also compared between theory and experiment to assess the role of the  
431 underlying network structure and, in particular, whether a non-random mixing of individuals  
432 would be at the origin of a structural organisation or if distinct patterns could play a role in the  
433 regulation of food collection through colony feedback coupled to individual behaviour. The TEC  
434 model, regardless of the distribution of the probabilities, fitted the experimental individual  
435 betweenness, closeness and eigenvector values even for the TEC delta model (Figures S4.M-X).  
436 For this latter model, the distribution of the probability of leaving the nest for the first time,  
437 which is the only source of variability, introduced a slight level of heterogeneity in the number of  
438 trophallactic events that was enough to generate the properties of the experimental networks and  
439 seems to be crucial for leading to efficient trophallactic networks.

440 Indeed, the efficiency of experimental networks was only generated by the TEC exponential  
441 model, as the TEC delta and TEC uniform models displayed a lower efficiency. All versions of  
442 the model assumed random encounters between ants: if the potential donor (receiver) accepts to  
443 give (receive) a trophallactic exchange occurred. This simple hypothesis was sufficient to

444 generate the experimental efficiency of the trophallactic network. One could have assumed  
445 mechanisms of avoidance/attractiveness between partners that had already exchanged food  
446 (Goyret and Farina 2005; Grüter et al. 2013). However, our results suggest that no specific  
447 trophallactic pairs occur except those resulting from the interindividual variability in the  
448 probability to participate in a trophallactic exchange. Therefore, the food accumulated by ants  
449 originates from a large number of randomly encountered nestmates that had regurgitated the food  
450 previously received. Indeed, the model and the experiments showed that approximately 40% of  
451 the given food is given by the non-foragers. The efficiency coefficient is a measure of the  
452 effectiveness of the diffusion of information/food. This metric assumes a network of individuals  
453 with identical needs in which the efficiency is maximal as soon as all the individuals are  
454 connected together. This situation may be far from that of real colonies of social insects, in which  
455 the needs may be different between individuals (Dussutour and Simpson 2009) and the diffusion  
456 of food must satisfy the individual needs. Thus, the effectiveness of food dissemination in the  
457 colony, based on the measure of classical efficiency, suggests an under-optimal connectivity of  
458 the observed network.

459 Increasing the interindividual variability of the probability to give/receive food in a trophallactic  
460 event, keeping the mean probability constant (i.e., increasing the standard deviation of the  
461 uniform distribution), leads to a lower number of exchanges / speed of food accumulation in the  
462 nest for a given time-window (Figure S6). Our theoretical results are consistent with a previous  
463 theoretical work (Nicolis et al. 2003) investigating the relationship between division of labour  
464 (trail-laying behaviour) and efficiency of food recruitment and the subsequent role of positive  
465 feedbacks. These results deviate from the general agreement of the importance of division of  
466 labour in social insects (Oster and Wilson 1978; Hölldobler and Wilson 1990) and from recent

467 experimental results establishing a link between within-group behavioural variation and task  
468 efficiency (e.g., (Pruitt and Riechert 2011)(Modlmeier et al. 2012)). However, we must keep in  
469 mind that our model (and that of (Nicolis et al. 2003)) does not take into account various  
470 ecological and physiological constraints that are omnipresent in such systems and affect the  
471 efficiency of the processes.

472 Other model limitations may have affected the goodness-of-fit of our results. Most obviously, our  
473 model does not capture any effect of the intranidal spatial organisation/occupation (Pinter-  
474 Wollman et al. 2011; Heyman et al. 2016) on the dynamics of food collection and dissemination  
475 in the colony, which are known to be linked to task (Mersch et al. 2013) and to affect collective  
476 response (Crall et al. 2018). A recent stochastic spatial model that neglects interindividual  
477 differences but shares some of our hypotheses provides useful insights into the role of space  
478 during food dissemination (Gräwer et al. 2017). Note that although the spatial segregation of  
479 specialised individuals is thought to optimise performance in social insects (Tofts 1993;  
480 Pamminer et al. 2014), our model is still consistent with experiments.

481 In summary, we investigated the effect of interindividual variation (delta, uniform, and  
482 exponential distributions) of homogeneous (OC) or heterogeneous (TEC) colony models on the  
483 trophallactic networks and food spreading dynamics. The agreement between the theoretical and  
484 empirical data validates the right-skewed behavioural rules used in the model. This analysis  
485 succeeds in accounting for the characteristics of the empirically observed trophallactic networks,  
486 without evoking behavioural rules other than a right-skewed distribution of food dissemination  
487 effort, modulated by the individual crop load. These two hypotheses are in agreement with some  
488 recent empirical work (Greenwald et al. 2018a). Hence, the observed networks of trophallactic  
489 events of ant colonies do not seem to rely on complex behavioural rules involving the transfer of

490 various types of information during the food exchange or the ability to count the number of  
491 trophallactic events executed. Right-skewed distribution of food dissemination effort and  
492 individual crop load are parameters characterizing decentralised control and organizational  
493 resilience of ants (Middleton and Latty 2016). Such decentralized but hierarchical networks also  
494 exist in mammals (Hill et al. 2008). Low clustered but high robust social networks have also been  
495 found in bees (Naug 2008) and is due to the adaptive age polyethism (Wild et al. 2021) as  
496 observed in ants. Such simple non-linear rules conducting to efficient networks have been  
497 described in nature ranging from protein complexes (Ravasz et al. 2002), to neural networks  
498 (Chatterjee and Sinha 2007; Clune et al. 2013) to organization in social insects (Linksvayer et al.  
499 2012; Quque et al. 2021). These properties increase group performance as mentioned by Sueur et  
500 al. (2012) and described by Fontanari and Rodrigues (2016). The collective cognition behind  
501 such complex systems suggests that the topology of trophallactic networks, and more generally of  
502 social networks, is selected through individual self-organised rules to optimize problem-solving  
503 competence at the group level and is described as “collective social niche construction” (Sueur et  
504 al. 2019).

505 The presence of heterogeneity in the food dissemination effort in a more complex social context,  
506 including a queen and larvae that increase the gradient of division of work and the heterogeneity  
507 in nutritional needs among the colony members (Cassill 2003; Dussutour and Simpson 2009),  
508 still requires further investigation. Among these future experimental and theoretical  
509 investigations, priority should be given to the way the colony size affects the global dynamics of  
510 food exchanges and the resulting trophallactic network. Furthermore, the phenomenological  
511 character of our model prevents any conclusion about the origin of the observed behavioural  
512 variability: is it an outcome or an underlying driver of behavioural/network interactions? These

513 challenging questions require further theoretical and experimental investigations and are of major  
514 interest to clarify the link between genetics (Smith et al. 2008), physiology (e.g. proteoms, Quque  
515 et al. 2019), individual experience (Robinson et al. 2008) and social structure.

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