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

3 Olivier Bles¹, Jean-Louis Deneubourg¹, Cédric Sueur^{2,3} and Stamatios C. Nicolis¹

4 1. Center for Nonlinear Phenomena and Complex Systems (Cenoli) - CP 231, Université libre de Bruxelles (ULB),
5 Campus Plaine, Boulevard du Triomphe, Building NO - level 5, B-1050 Bruxelles, Belgium

6 2. Université de Strasbourg, CNRS, IPHC, UMR 7178, Strasbourg, France

7 3. Institut Universitaire de France, Paris, France

8 Corresponding author: cedric.sueur@iphc.cnrs.fr

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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; Pamminer 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 α , 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 β , corresponding to the inverse of this time.

155

156

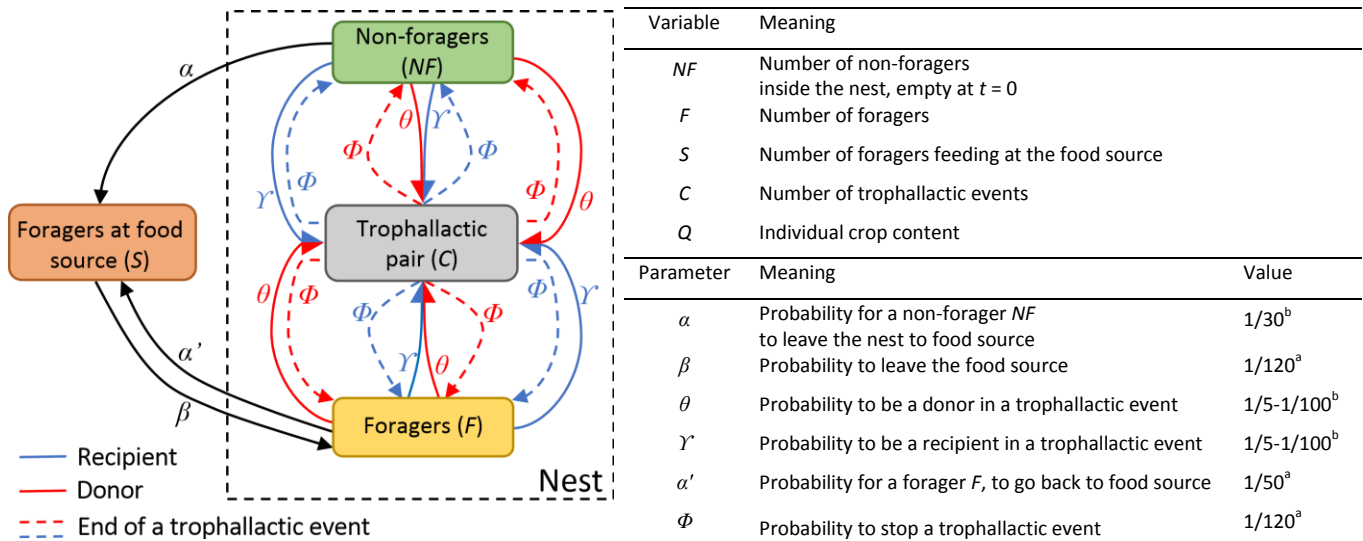


Figure 1: Flow diagram of the model, variables and parameters. The square boxes representing the states of individuals (NF , F , S , C). Black arrows are state-transition rates; coloured arrows represent the formation of a trophallactic pair, the red one being the donor and the blue one the receiver. On the right part of the figure, variables and parameters are defined and value of parameters implemented are indicated. ^aParameters estimated from the experiments presented in the material and methods section or derived from the literature (Mailleux et al., 2010, 2006). ^bParameters 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 θ_i (as donor) or γ_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 Φ 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 θ or Y to give or to receive
 176 food and the probability Φ 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 γ_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 θ_i to give and γ_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 θ_i to give and γ_i to receive food

207 between the individuals with a standard deviation, respectively, equal to the mean probabilities of
208 θ_i and γ_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 ε equal to θ or γ] (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 1st time. These two
217 values, before and after the 1st 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 1st 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.
	θ_F	1/11	1/10	1/6	1/10	1/11	1/9
	θ_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- α). 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 θ to give and γ 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.

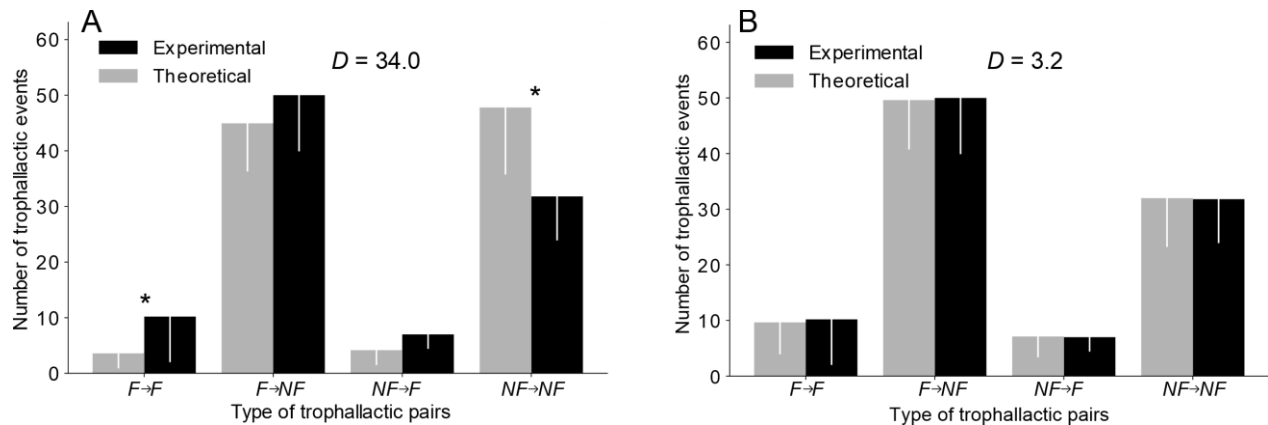


Figure 2: Comparison of the number of each type of trophallactic pairs between the experiments and the simulations implemented with a Delta distribution in the OC version (A) and in the TEC version (B). * = MW with a $p < 0,05$. Error bar = standard deviation. D = Sum of the difference of the number 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

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

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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

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

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

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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).

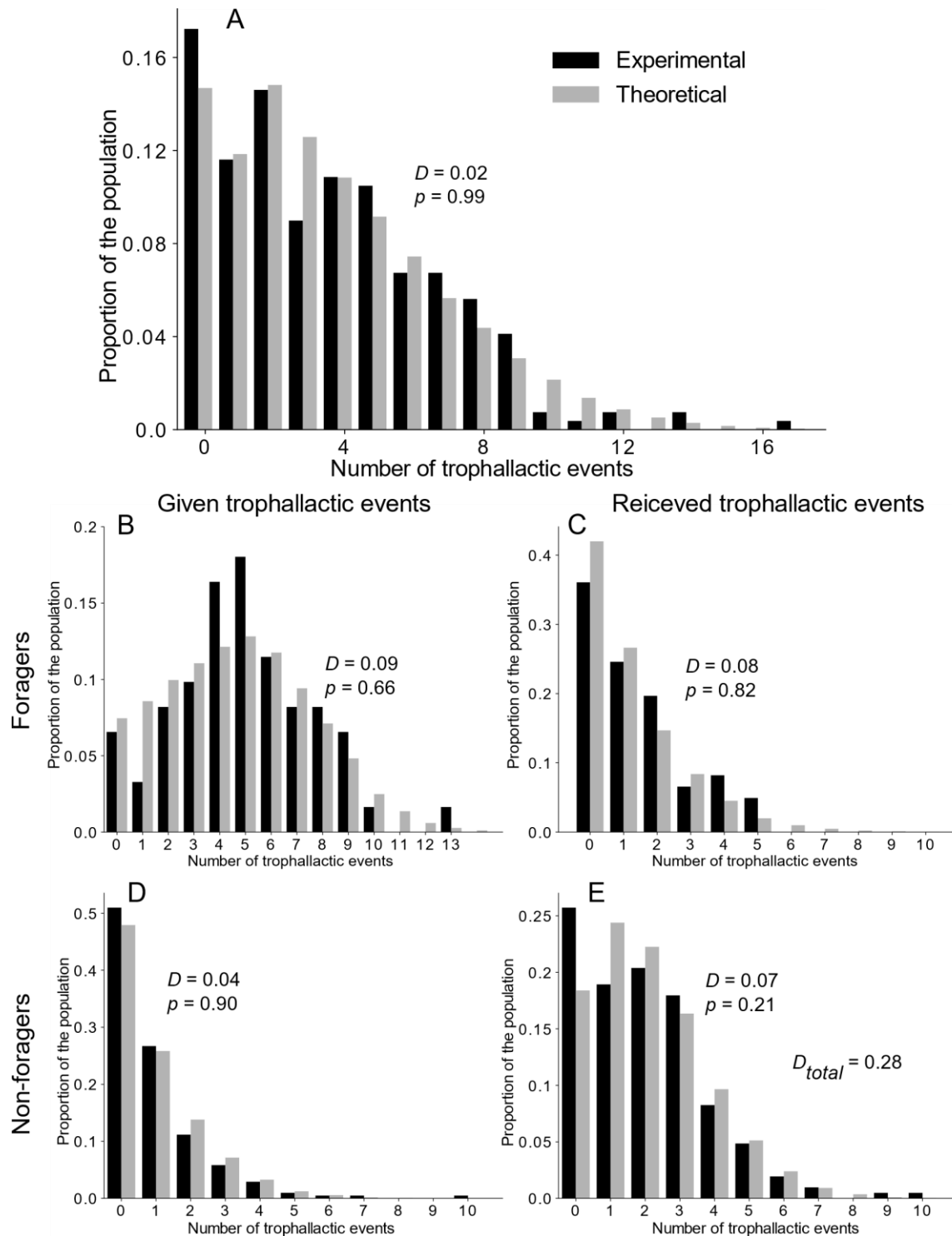


Figure 3: Theoretical and experimental distribution of the number of trophallactic events. A, Distribution of all the trophallactic events at the colony-level. B, C, Respectively, given and received trophallactic events performed by the foragers. D, E, Respectively, given and received trophallactic events 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- α). 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: $Z = -0.9$; $p = 0.39$).

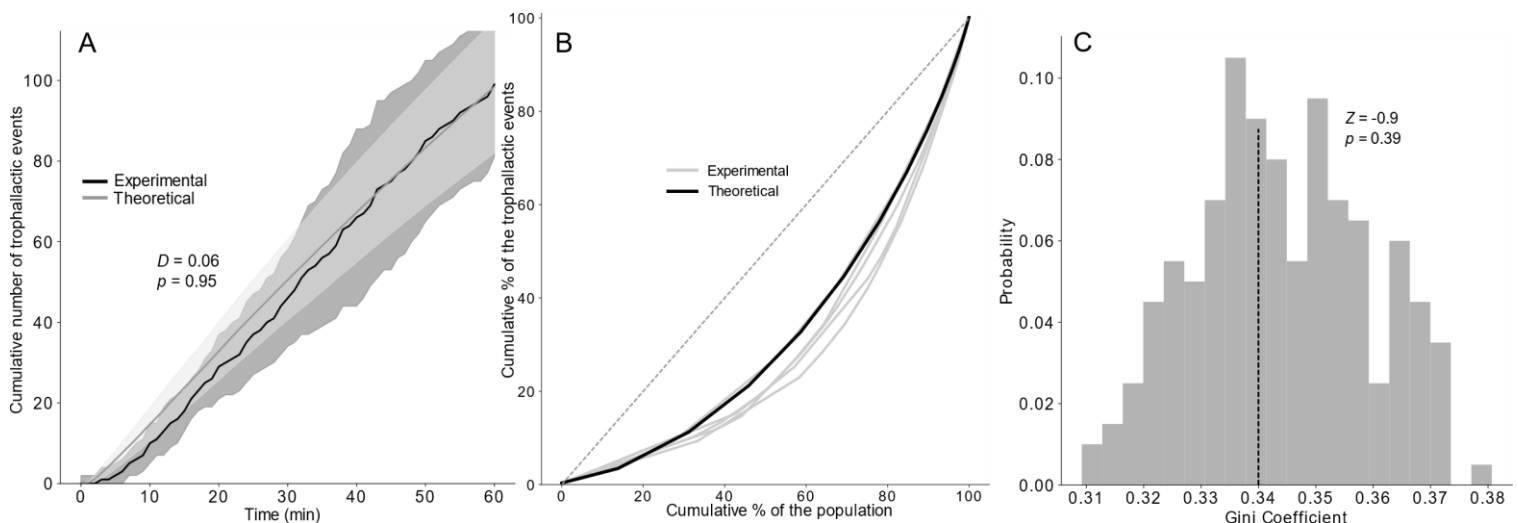


Figure 4: A, Cumulative number of trophallactic events after 1h of experiments or 3600 timesteps from 1000 simulations of the TEC Exponential model and from the experiments (N=5) compared with a KS (D and p -val). Dashed lines represent the time when 50% of the trophallactic events were realized, both 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.

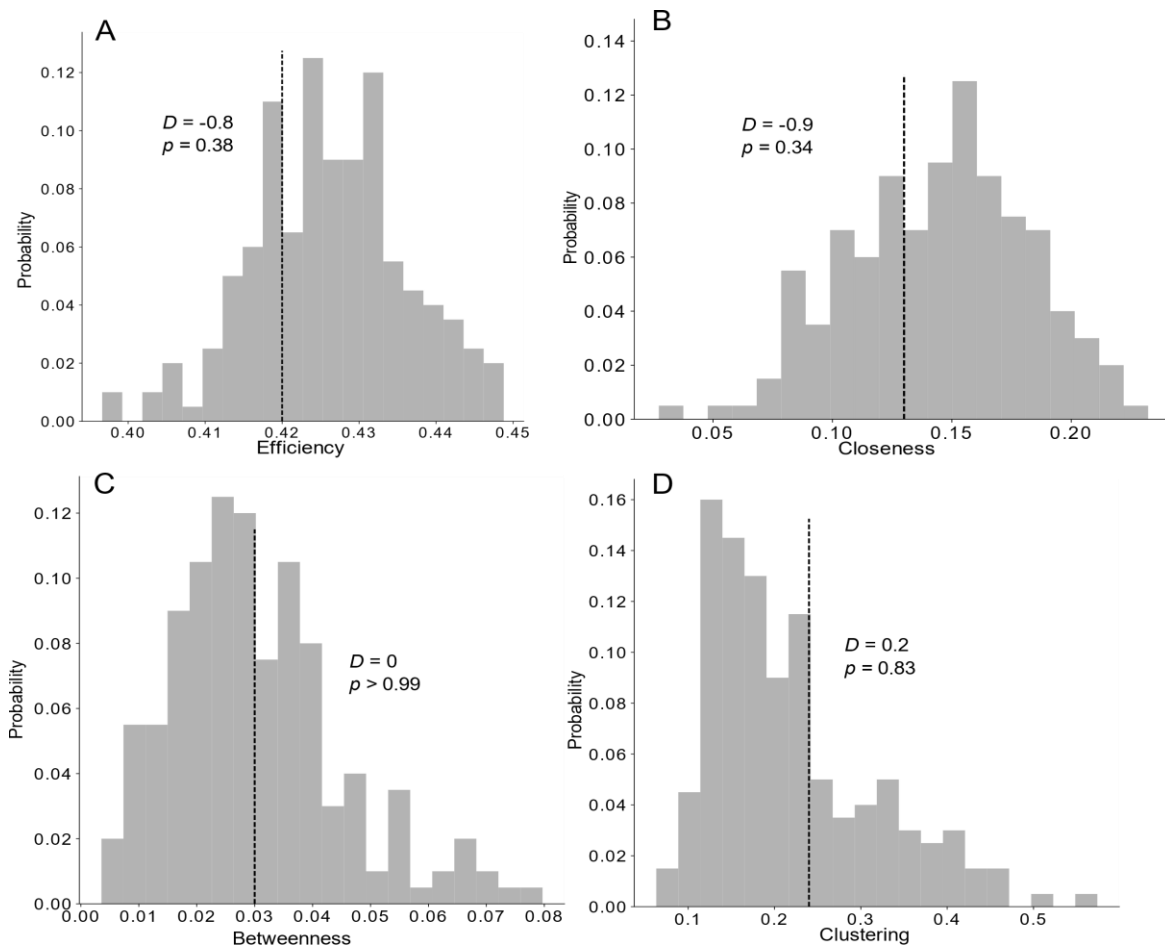


Figure 5: Distribution of the efficiency (A), closeness (B), betweenness (C) and clustering (D) coefficients measured in the networks of the TEC Exponential model (grey bars, N=1000) and the mean measured from experiments (vertical dashed line, N=5) compared with a Z-test (*Z-value* and *p-val*). See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