

Author running head: *M. Quque et al.*

Title running head: *Hierarchical networks in Lasius niger*

Correspondence: Cédric Sueur, CNRS, IPHC UMR718, 67087 Strasbourg, France. Tel: +33388107453; fax: +33388107456; email: cedric.sueur@iphc.cnrs.fr

* Equal contribution of these authors.

ORIGINAL ARTICLE

Hierarchical networks of food exchange in the black garden ant *Lasius niger*

Martin Quque^{1,*}, Olivier Bles^{2,*}, Annaëlle Bénard³, Amélie Héraud¹, Bastien Meunier⁴, François Criscuolo¹, Jean-Louis Deneubourg^{2,*} and Cédric Sueur^{1,5,*}

¹Université de Strasbourg, CNRS, IPHC UMR718, Strasbourg, France;

²Centre for Non-linear Phenomena and Complex Systems (Cenoli)–CP 231, Université libre de Bruxelles (ULB), Bruxelles, Belgium;

³Université de Bourgogne Franche-Comté, Dijon, France;

⁴Université de Rennes 1, Rennes, France;

⁵Institut Universitaire de France, Paris, France

Abstract

In most eusocial insects, the division of labour results in relatively few individuals foraging for the entire colony. Thus, the survival of the colony depends on its efficiency in meeting the nutritional needs of all its members. Here, we characterise the network topology of a eusocial insect to understand the role and centrality of each caste in this network during the process of food dissemination. We constructed trophallaxis networks from 34 food-exchange

experiments in black garden ants (*Lasius niger*). We tested the influence of brood and colony size on (i) global indices at the network level (*i.e.* efficiency, resilience, centralisation and modularity) and (ii) individual values (*i.e.* degree, strength, betweenness and the clustering coefficient). Network resilience, the ratio between global efficiency and centralisation, was stable with colony size but increased in the presence of broods, presumably in response to the nutritional needs of larvae. Individual metrics highlighted the major role of foragers in food dissemination. In addition, a hierarchical clustering analysis suggested that some domestics acted as intermediaries between foragers and other domestics. Networks appeared to be hierarchical rather than random or centralised exclusively around foragers. Finally, our results suggested that networks emerging from social insect interactions can improve group performance and thus colony fitness.

Key words insects; network evolution; self-organisation; social evolution; social network analyses

Introduction

There are many well-known advantages to living in societies: protection against predators, more efficient discovery of food sources and better access to information (Krause & Ruxton, 2002). Another benefit of group living is food sharing (Isaac, 1978; Kaplan *et al.*, 1985; De Waal, 1989; Stevens & Gilby, 2004). Food sharing can occur in both social and non-social species, and its evolutionary origins have been studied using the predictions of reciprocal altruism (Trivers, 1971), biological markets (Noë & Hammerstein, 1995) and multilevel selection (Traulsen & Nowak, 2006).

Food exchange is central to many animal societies, including eusocial species such as ants, termites, bees and even naked mole rats (Anderson, 1984; Jarvis *et al.*, 1994; Wilson & Hölldobler, 2005; Nowak *et al.*, 2010). In eusocial species, only a restricted number of individuals forage and retrieve food for the rest of the colony. Castes can be distinguished by

their behaviour and even by their proteome (Quque *et al.*, 2019). Given that trophallaxis, the mouth-to-mouth transfer of food, is the mechanism of food exchange, the exchange of food facilitates social recognition via the exchange of informative colony-specific hydrocarbons (Boulay *et al.*, 2000), information on the location of food resources (Gil & De Marco, 2005; Frasnelli *et al.*, 2012) and even immune-related molecules (Hamilton *et al.*, 2010; LeBoeuf *et al.*, 2016). In the black garden ant (*Lasius niger*), the only food exchanged—aphid honeydew (*Aphidoidea* sp.)—is stored exclusively in the crop of individuals (Buffin *et al.*, 2009). The foragers give food to non-forager workers (i.e., nest workers, hereafter called domestics), which may then transfer the food to other domestics, including caretakers of larvae. These chains of exchanges allow food to be disseminated throughout the nest, from the entrance to the deepest chambers (Lee Cassill & Tschinkel, 1999; Wilson & Eisner, 1957).

At the entrance of the nest, the interactions between forager ants are fundamental as they regulate the dynamics of food harvesting (Gordon, 1996; Pinter-Wollman, 2015; Pinter-Wollman *et al.*, 2011; Schafer *et al.*, 2006). However, domestics possess essential information on the colony's needs. Exchange between foragers and domestics is spatially confined within an area close to the entrance of the nest in both the wild (Tschinkel & Hanley, 2017) and the laboratory (Mersch *et al.*, 2013). For instance, in *Pogonomyrmex badius*, foragers represent less than 5% of ants inside the nest 20 cm from the entrance and are completely absent in regions 70 cm from the entrance (Tschinkel & Hanley, 2017). This observation illustrates the spatial fidelity of castes and how this fidelity may affect network topology (Pinter-Wollman, 2015; Pinter-Wollman *et al.*, 2011) through differences in the connectivity between colony members (Jeanson, 2012; Mersch *et al.*, 2013).

To maximise fitness, the number of trophallaxes necessary to transfer food from foragers to the queen and larvae needs to be minimised to make the process of food exchange as fast as possible. Thus, efficient food exchange networks should be favoured by selection given

the restricted roles of each caste and their spatial distribution within the colony (Sueur *et al.*, 2019). However, ants do not have a single, optimal social network topology (Camazine *et al.*, 2003). Each colony member does not have to evaluate the needs of workers and the role of their activities in a task, as the trophallactic interactions spread relevant information through the entire colony (Grüter *et al.*, 2006). Nevertheless, ants are known to have collective cognition (Couzin, 2009) or swarm intelligence (Bonabeau *et al.*, 1999). As a result, simple interaction rules can explain the construction of complex structures, such as the Towers of Hanoi (Reid *et al.*, 2011) and how ants make bridges (Reid *et al.*, 2015). Stroeymeyt *et al.* (2018) showed that the interactions of ants can be modified to mitigate the spread of disease, as the network centralities of ants are critically important for the transmission of infections (Romano *et al.*, 2016). This behavioural plasticity permits the topology of the interaction network to be modified so that the network can become less efficient (for definitions of network efficiency, see Ek *et al.*, 2015; Pasquaretta *et al.*, 2014; Romano *et al.*, 2018) and more modular to prevent epidemics. This social immunity is well known in eusocial insects (Cremer *et al.*, 2007; Cremer, 2019; Liu *et al.*, 2019; Małagocka *et al.*, 2019) but has also been documented in other taxa, such as primates, where this phenomenon has been called the social bottleneck hypothesis (Nunn *et al.*, 2015; Romano *et al.*, 2020; Romano *et al.*, 2018). Despite the central role that trophallactic interactions play in the regulation of food flow in eusocial species, the way that chains of demands are established and how they ultimately impact network topology have been largely unexplored. Furthermore, most previous studies on these subjects have not considered the individuality and identity of the trophallactic partners (Buffin *et al.*, 2012). One of the first studies to analyse the entire trophallactic network demonstrated a spatial reorganisation of worker positions facing starvation that accelerated the recovery of food stocks (Sendova-Franks *et al.*, 2010). Waters and Fewell (2012) identified individuals and antenna interactions in *Pogonomyrmex californicus* and

concluded that the regulatory motif of interactions they observed supports the hypothesis that eusocial insects are shaped by selection for network patterns that integrate functionality at the group (*i.e.* colony) level rather than at the individual level. Lastly, Greenwald *et al.* (2015, 2018) assessed the role of foragers and non-foragers in the dissemination of food; however, these studies did not take into account the global state of the colony or conduct a thorough analysis of the network topology of trophallactic interactions.

Given that self-organisation results in the emergence of adapted complex systems (Camazine *et al.*, 2003; Fisher & Pruitt, 2020), we tested for the efficiency of trophallaxis networks in garden black ants. Specifically, we evaluated whether food was exchanged non-randomly (e.g., unpredictability in the direction and time of trophallaxes), expecting that the pattern of food dissemination maximises the speed with which food circulates through the colony. In addition, we conducted laboratory experiments in which we monitored the behaviour of foragers in colonies of varying sizes and with and without broods. Overall, we tested for the effects of three main factors: brood presence, the forager/domestic ratio and behaviour (which were also response variables) and colony size. Each ant was followed during the entire test using QR codes (Garrido-Jurado *et al.*, 2014; Stroeymeyt *et al.*, 2018), and all trophallaxes were scored. We used social network analyses to study the efficiency of food dissemination. Combining experimentation with network analyses, especially in social insects, is a powerful tool for studying the evolution of complex systems (Charbonneau *et al.*, 2013; Mersch, 2016; Sueur & Mery, 2017). We made three major alternative hypotheses concerning the network properties of trophallactic exchanges (Fig. 1):

(A) Interactions are random, and foragers have the same social centralities as domestics.

Confirmation of this null hypothesis would suggest that trophallaxes do not play an important role in food exchange. We did not expect to find random networks.

(B) Food exchange occurs exclusively between foragers and domestics. This hypothesis predicts that foragers should show higher centralities than domestics.

(C) Foragers transfer food to domestics, but some intermediary domestics are involved in the chain of food dissemination. This hypothesis predicts that these intermediary domestics should show forager-like centralities. Thus, these intermediary individuals would provide the link between the source (foragers) and the final destination of food.

We used different social network indices to assess these predictions (see Table S1). We expected colony size to affect the network topology, as previous studies have shown that centralisation and modularity increases with colony size (Pasquaretta *et al.*, 2014; Nunn *et al.*, 2015). Efficiency should be stable because, theoretically speaking, efficiency should decrease with network size (Romano *et al.*, 2018); however, ants are capable of modifying their division of labour depending on the size of the colony (Jeanson *et al.*, 2007; Holbrook *et al.*, 2011; Modlmeier *et al.*, 2019). Furthermore, the presence of broods is expected to modify the structure of the network, as broods affect both the nutritional needs of the colony and thus the demand for foragers (Portha *et al.*, 2002). Because the presence of broods adds a level of food dissemination, brood presence should have an impact on both individual and global network indices with either the same ratio of foragers contributing more work (e.g., via higher efficiency and higher centralisation) or more foragers decentralising the network.

Materials and methods

Ant colony setup

We created 52 queenless subcolonies of 11 to 120 workers, with and without broods (see details below) from 12 wild and large mother colonies (> 1000 ants) of *Lasius niger* collected in Brussels, Belgium during the autumn of 2016. We formed the subcolonies after the colonies had been in the lab for 18 months years to decrease the potential effect of temporal

polyethism. We tested queenless colonies for simplicity; several studies have shown that the absence of the queen does not affect the interactions between workers and the shape of the food dissemination network (Holbrook *et al.*, 2011; Jeanson, 2012; Bazazi *et al.*, 2016; Bles *et al.*, 2018).

These colonies were tested in an experimental enclosure (Fig. 2A). The dimensions of the experimental enclosure were $17.5 \times 12.5 \times 5$ cm. The walls of the foraging area were covered with Fluon®, in addition to a glass covering the tray, to prevent ants from escaping. Ants were placed in these trays for 10 days so that they could acclimate until the repartitioning of tasks among individuals stabilised. Although the division of labour is flexible according to the needs of the colony, several other studies have suggested that 10 days is enough for the caste of each ant to stabilise (Sendova-Franks & Franks, 1993; Huang & Robinson, 1996; Amdam *et al.*, 2005; Baker *et al.*, 2012). The colonies were kept at 22 ± 3 °C and $60\% \pm 5\%$ relative humidity, with a constant 12 : 12 h photoperiod.

The experimental enclosure was divided into two parts: the nest area and the feeding area. Two food sources were placed in the feeding area at equal distances relative to the nest entrance: 0.3 mol/L of milk powder and 0.3 mol/L of sucrose. The position of the food sources relative to the nest entrances (*i.e.* left or right) was randomised. Ants were starved for 5 days in the nest area before experiments to increase foraging activity and the rate of trophallaxis. The experiments ran for one hour. Video data were recorded using a Panasonic® Lumix DMC-GH4-R mounted with a 30-mm Olympus® ED lens capturing 25 frames/s at a resolution of 4180×2160 p.

Ant identification through QR codes

Labelling of ants with Aruco tags (QR codes, Garrido-Jurado *et al.*, 2014), along with the software USETracker (<https://sites.google.com/site/usetrackerac/>), allowed individual ants to

be identified continuously (Fig. 2B). Ants were placed in the freezer until they were inert (about one minute). Each unique tag was then stuck to the abdomen and had a side length of 0.8 mm, weighed 0.1 mg (corresponding to approximately 5% of the average mass of an adult worker or less than 10% of the amount of food that a worker carries) and was printed on waterproof paper at a resolution of 1200 dpi. The tags were hand-cut using a scalpel and a steel ruler as a guide. Following a 5-min acclimatisation period, the labelling did not appear to impede the ant behaviours, movements or interactions. We discriminated foragers from domestics. An individual was considered a forager if it spent at least 5 consecutive seconds feeding at the food source (not in the feeding area but at either one of the two food sources or both) during the experiment. This discrimination was possible by analysing the position of each individual per frame during the experiment (see Fig. S1).

Data scoring

Each trophallaxis that occurred in the entire observation area, its duration as well as the identities (unique tag) and caste (forager *vs.* domestic) of both the donor and the receiver ant were scored. A trophallactic event was recorded when ants engaged in mandible-to-mandible contact for greater than 2 seconds (the minimum time needed to exchange a piece of food). The directionality of the food flow and the role of the donor and the receiver were determined by body posture and mandible positions: The donor opens her mandibles and displays a droplet of sucrose solution between them while the receiver turns and moves her head forward to receive it (Greenwald *et al.*, 2015; Lee Cassill & Tschinkel, 1999).

We only analysed videos where 100% of the trophallaxis interactions could be identified. Of the 52 experimental runs, a total of 34 videos were analysed. Each of the 12 colonies was tested 2.8 ± 1.1 times (min = 1, max = 5). On the 34 videos, broods were present in 21 colonies and absent from 13 (proportion per colony: 0.66 ± 0.24). The colony size ranged

from 11 to 120 ants (mean = 42 ± 26). Colony replications were incorporated into the statistical analyses. Different observers scored the videos; however, we found that there was weak inter-observer bias, as an inter-observer reliability test on eight videos revealed that the minimum score that we observed was 88.5% (generally, reliability scores greater than 80% are considered sufficient; Hartmann, 1977; Watkins & Pacheco, 2000; Borgeaud *et al.*, 2016).

Social network measures

General statements For each test, an edgelist was created with the trophallaxis time from individual i to individual j as the edge strength. The network was directed and weighted. We then calculated different individual and global measures using the ANTs (Sosa *et al.*, 2018) and igraph (Csardi & Nepusz, 2006) R packages. We avoided measures that were not interpretable with the directionality of the edges (see Mersch, 2016; Sueur *et al.*, 2011; Sosa *et al.*, 2020); instead, we selected those that allowed us to make expectations based on our three aforementioned hypotheses. Table S1 shows the different indices and their associated expectations.

Global network measures The global measures included maximum modularity, the centralisation index, global efficiency and resilience. Maximum modularity is the strength of subgrouping or division of a network into modules or clusters (Newman, 2004). It ranges from 0 to 1 with 0 corresponding to a network where all individuals are equally connected and indices close to 1 corresponding to networks where the number and strengths of connections between individuals of different subgroups are low. The centralisation index captures the strength of centralisation of a network towards one or several individuals and how these central individuals gather relationships (Sueur *et al.*, 2012; Pasquaretta *et al.*, 2014). It ranges from 0 to 1 with 0 for corresponding to an equal network (*i.e.* all individuals are equally connected) and 1 for a star network (*i.e.* individuals are all connected to a single

central individual). Global efficiency is the strength or speed of the exchange of entities—information or food—throughout the network (Latora & Marchiori, 2001; Ek *et al.*, 2015). Specifically, global efficiency equals $N/(I \times D)$ where N is the number of nodes, I is the number of edges and D is the network diameter. In other words, global efficiency indicates how quickly an entity is transmitted from the spreader (*i.e.* source) to the most peripheral individual in the group via the fewest number of connections. Global efficiency can range from 0 to 1, with more efficient networks having values closer to 1 (Romano *et al.*, 2018). Finally, we calculated resilience by dividing global efficiency by the centralisation index (Naug, 2009; Puga-Gonzalez *et al.*, 2019). Resilience assesses whether the strength or speed of the exchange of food can be maintained in the absence of central individuals, generally called bridges or hubs (Kitsak *et al.*, 2010).

Individual network measures The individual network measures included the degree (the number of edges of a node; *i.e.* the number of individuals giving or receiving trophallaxes from an ant), strength (the total time of trophallaxes of an ant; here we considered in-strength, the total time of trophallaxes received, and out-strength, the total time of trophallaxes given), betweenness (the number of shortest paths passing by a node; *i.e.* how many individuals an ant connects) and the clustering coefficient (whether individuals with which an ant exchanges food also exchange food). Detailed explanations of these different measures have been provided by previous reviews and books on animal networks (Whitehead, 1997; Croft *et al.*, 2008; Sueur *et al.*, 2011; Sosa *et al.*, 2020)

Statistical analysis

Food exchanges We first analysed the direction of trophallaxes between foragers and domestics. We used the ratio between the in-strength and out-strength to assess whether one

caste gave more than it received (ratio > 1) or received more than it gave (ratio < 1). We used a student t -test to test for differences between the two castes.

We used linear mixed models (package lme4 in R, Bates *et al.* 2014) to test for the effect of brood presence and colony size on global variables, such as the number of trophallaxes, the duration of trophallaxes and the forager/domestic ratio. Colony origin was included as a random effect. Data for all response variables were normally distributed (Shapiro-Wilk normality test, $W > 0.93$, $P > 0.074$). Therefore, all models were type-III ANOVAs using Satterthwaite's method and had normally distributed residuals.

Global and individual network measures We then analysed the effect of brood presence, the number of individuals and the forager/domestic ratio for the global network measures (e.g., centralisation, global efficiency, modularity and resilience) as well as the caste (forager or domestic) for the individual network measures (e.g., degree, strength, betweenness and the clustering coefficient). Because data on the interactions and the network measures were not independent, we used Monte Carlo Markov Chain GLMM (package MCMCglmm in R, Hadfield, 2010). This approach is a powerful and standard technique for comparing statistical models based on the original data observed to distributions of null models based on randomised data (Pasquaretta *et al.*, 2014; Balasubramaniam *et al.*, 2018; Sosa *et al.*, 2019). We ran MCMCglmm models for a minimum of 43 000 iterations after a burn-in of 3000 to minimise autocorrelation and a thinning interval of 10 (*i.e.* one out of every 10 iterations in the Markov chain was used to estimate the posterior distribution of the parameters). We also assessed the robustness of the parameter estimates by checking the stability of the models. For all models, we assessed for approximate convergence of the MCMC chain (chain stability). We evaluated a final model's validity by assessing the distribution of residuals through residual normality distribution plots. The 95% credible intervals were calculated using Bayesian methods in the MCMCglmm package. We used a

Poisson law for the degree and strength and a zero-inflated Poisson law for the betweenness and clustering coefficient. Modularity followed a normal law while centralisation, global efficiency and resilience followed a log-normal law.

We then used individual network measures and the function PCA and HCPC of the FactormineR package in R to perform a hierarchical clustering analysis using principal components analysis to assess the presence of intermediary domestics. The HCPC function permitted us to determine whether some domestics acted as intermediaries (*i.e.* whether certain domestics had higher strength, in-strength, out-strength, degree and betweenness relative to other domestics). We also performed Pearson correlations between the different individual network measures.

All tests were conducted on R 3.6 (R Development Core Team, 2009). The significance level was set at 0.05. Results are shown as mean \pm stdv [median].

Results

Food exchange

At the individual level, foragers spent more time giving than receiving food ($t = 75.7$, $df = 33$, $P < 0.0001$, Table 1). The opposite pattern was observed for domestics ($t = -138.1$, $df = 33$, $P < 0.0001$) (Fig. 3). However, Figure 3 shows a high level of variability among both foragers and domestics: some foragers spent more time receiving than giving and some domestics spent more time giving than receiving. This result was also recovered at the global (Fig. 3) and test levels (Fig. S2).

At the colony level, the mean duration of trophallaxes (31.7 ± 12.8 s, corrected by colony size) was not influenced by the presence of broods ($df = 29.9$, t value=1.34, $P = 0.189$) nor by colony size ($df = 29.9$, t value = 2.03, $P = 0.051$, Fig. S3). The total number of trophallaxes (77.6 ± 49.1) significantly increased with colony size ($df = 30$, t value=7.62, $P < 0.0001$, Fig.

S4A) but did not change significantly with brood presence ($df = 30$, t value = 1.32, $P = 0.197$). However, the number of trophallaxes corrected by colony size (mean number: 2.04 ± 1.13) did not change with colony size ($df = 30$, t value = 0.51, $P = 0.613$) showing that the effect was more or less linear. This corrected number of trophallaxes did not change with brood presence ($df = 30$, t value = 1.31, $P = 0.197$). Lastly, the forager/domestic ratio (0.47 ± 0.21) was not influenced by colony size ($df = 27.7$, t value=1.02, $P = 0.315$) but was increased when broods were present ($df = 28.6$, t value = 3.07, $P = 0.005$, Fig. S4B).

Global network measures

Four illustrations of trophallaxis networks are shown in figure 4. The number of ants negatively influenced network centralisation (l-95% CI = -0.017 , u-95% CI = -0.008 , $P < 0.001$, Fig. 5A) and global efficiency (l-95% CI = -0.02 , u-95% CI = -0.0001 , $P = 0.04$, Fig. 5C), positively influenced modularity (l-95% CI = -0.001 , u-95% CI = 0.005 , $P = 0.002$, Fig. 5B) and did not impact resilience (l-95% CI = -0.009 , u-95% CI = 0.013 , $P = 0.626$). However, resilience increased in the presence of broods (l-95% CI = -1.51 , u-95% CI = -0.14 , $P = 0.026$, Fig. 5D); in contrast, brood presence had no effect on the other global network measures (centralisation: l-95% CI = -2.40 , u-95% CI = -1.47 , $P = 0.116$; modularity: l-95% CI = -0.125 , u-95% CI = 0.11 , $P = 0.882$; global efficiency: l-95% CI = -1.20 , u-95% CI = 0.013 , $P = 0.059$). The forager/domestic ratio did not influence the global measures ($P > 0.225$; Fig. S5). Results of all statistical tests are shown in the supplementary material.

Individual network measures: Distributions of individual network measures (table 1) are shown in Figure S6. Local peaks were observed for foragers and domestics in the distributions for degree, out-strength and clustering coefficient. The degree decreased in the presence of broods (l-95% CI = -0.057 , u-95% CI = 0.293 , $P = 0.001$) and decreased with

colony size (l-95% CI = -0.004 , u-95% CI = -0.0004 , $P = 0.015$). Domestics had a lower degree than foragers (l-95% CI = -0.370 , u-95% CI = -0.197 , $P < 0.0001$). Strength was negatively influenced by the forager/domestic ratio (l-95% CI = -3.061 , u-95% CI = -1.576 , $P < 0.0001$). Surprisingly, caste did not influence strength. Foragers had a higher betweenness than domestics (l-95% CI = -0.590 , u-95% CI = -0.067 , $P = 0.013$). Betweenness also increased with the forager/domestic ratio (l-95% CI = -0.590 , u-95% CI = -0.066 , $P = 0.013$) and with colony size (l-95% CI = 0.016 , u-95% CI = 0.028 , $P < 0.0001$) but decreased in the presence of broods (l-95% CI = -0.284 , u-95% CI = -0.066 , $P = 0.012$). Similar to betweenness, the clustering coefficient was lower in the presence of broods (l-95% CI = -0.014 , u-95% CI = 0.083 , $P = 0.002$) and decreased with colony size (l-95% CI = -0.002 , u-95% CI = -0.001 , $P < 0.0001$). All other variables had no effect on the clustering coefficient. Results of all statistical tests are provided in the supplementary material.

A hierarchical clustering analysis following a principal components analysis confirmed the presence of three clusters in the domestics. Details of this analysis are provided in the supplementary material (Fig. S7). All individual network measures, as well as brood presence, colony size and the ratio foragers/domestics, significantly affected the clustering. Cluster 3 was composed of domestics with higher strength, in-strength, out-strength, degree and betweenness compared with the other two clusters identified.

Correlations between individual network properties showed that only in-strength and out-strength ($r = 0.03$; $P = 0.246$, $n = 1096$), as well as betweenness and the clustering coefficient ($r = 0.02$; $P = 0.513$, $n = 1096$), were not correlated. All other indices were correlated ($0.10 < r < 0.73$; $P < 0.0005$, $n = 1096$, Fig. 6, Table S2)

Discussion

The goal of this study was to understand the organisation of trophallaxes in black garden ants, assess the topology of the trophallaxis network and characterise variation in the centralities among foragers and domestics. Consistent with expectation, our results showed that the trophallaxis network in black garden ants was not random and that the directionality of this network was oriented from foragers to domestics. The high betweenness and out-strength values indicated that intermediary domestics existed. In addition, local peaks and clusters were observed in the distribution of some domestic centralities. These intermediary individuals provided the link between the source (foragers) and the final destination of food. This division of labour resulted in a food dissemination chain in the form of a hierarchical network. We also observed high variability among individuals, consistent with previous studies that have examined the distribution of activities (specifically, the percentage of time foraging, distributing food or working inside colonies on a per-individual basis) among workers (Kolmes & Sommeijer, 1992; Dornhaus *et al.*, 2009; Tenczar *et al.*, 2014; Quevillon *et al.*, 2015; Bles *et al.*, 2018).

Variation in global network values: The rise of intermediate workers

The mean duration of a trophallaxis (tendency) and the total number of trophallaxes increase with colony size and were not influenced by the presence of a brood. Moreover, the forager/domestic ratio was not influenced by colony size (as was found in Dornhaus *et al.*, 2009 but in the presence of a queen) but increased in the presence of a brood. This finding demonstrates the behavioural plasticity of ants and their capacity to respond to changes in the demand for food by the colony, regardless of its size and composition (Portha *et al.*, 2002; Mailleux *et al.*, 2011; Tenczar *et al.*, 2014). When broods are present during experiments, domestics can become foragers to address the increased protein needs of the brood (Lee

Cassill & Tschinkel, 1999; Dussutour & Simpson, 2008, 2009). In contrast, when broods are absent, foragers can become domestics (Sendova-Franks & Franks, 1993; Huang & Robinson, 1996; Amdam *et al.*, 2005; Baker *et al.*, 2012). This adaptability is also supported by our global network measures. Network efficiency is an important network parameter contributing to the success of colonies (Sendova-Franks *et al.*, 2010; Waters & Fewell, 2012; Stroeymeyt *et al.*, 2018). Colony members are known to modulate their interactions, and thereby the network, based on food availability and the needs of the colony (Sendova-Franks *et al.*, 2010; Pinter-Wollman *et al.*, 2011), the spread of disease (Stroeymeyt *et al.*, 2018) and group/colony size (Pasquaretta *et al.*, 2014; Romano *et al.*, 2018). The relationship between network efficiency and network size is non-linear, as there are different peaks of efficiency at different values of modularity based on group size (Romano *et al.*, 2018). This non-linearity is interpreted as an adaptive mechanism for optimising the social transmission of information and impeding the transmission of pathogens (Waters & Fewell, 2012; Nunn *et al.*, 2015; Sueur *et al.*, 2019; Romano *et al.*, 2020).

We found that global efficiency decreases with colony size. However, resilience—the ratio between efficiency and centralisation—was stable with colony size but increased in the presence of a brood, presumably in response to the needs of the larvae. Improving or maintaining network resilience while ensuring reproduction, can increase the ability of the colony to recover from cascading failures (*i.e.* breaks in the transmission chain, Wang & Xiao, 2016). Moreover, modularity increases with colony size. Interestingly, caste-specific adaptations to colony size might also occur, and the role of intermediary domestics may be crucial. For example, intermediary domestics may stabilise the link between foragers and domestics, promoting network resilience with increasing group size. Indeed, the hierarchical clustering analysis revealed the presence of a cluster of intermediary domestics with higher strength, in-strength, out-strength, degree and betweenness compared with other domestics.

In sum, our global measures indicate—similar to the findings of Stroeymeyt *et al.* (2018) for disease—that the food dissemination process and interactions at the colony level are highly flexible and depend on colony size and needs. All subcolonies used had been in the lab for 18 months to decrease the potential effect of temporal polyethism. The possibility of a potential age effect was also minimised by the fact that we conducted multiple tests with different colony sizes as well as the 10-day buffer that we provided to colonies before scoring interactions. Moreover, ants can continually adapt to the needs of colonies as individuals change castes—even to changes from foragers to domestics (Sendova-Franks & Franks, 1993; Huang & Robinson, 1996; Amdam *et al.*, 2005; Baker *et al.*, 2012). Thus, we believe that the effect of temporal polyethism on our findings was negligible.

Variation in individual network values: Towards a decentralised and hierarchical organisation

We found that foragers had higher degree and betweenness but the same strength and clustering coefficient as domestics (see supplementary material for detailed statistics). This pattern is consistent with foragers giving more than they received and domestics receiving more than they gave (Quevillon *et al.*, 2015). Because foragers gave more food to more ants than domestics did, they also had a higher betweenness (degree and betweenness are correlated). Thus, the degree, betweenness and out-strength values clearly indicate that foragers were the ones distributing food in the network, supporting the centralised network hypothesis. This finding was further confirmed by the fact that betweenness increased with the forager/domestic ratio. Specifically, foragers became more important for food exchange as the number of intermediaries decreased, and when intermediaries were few, the number of foragers increased. However, the fact that foragers had a similar strength and clustering coefficient compared with domestics suggested that there were connections between

domestics and that the network was not highly centralised, allowing the trophallaxis network to retain its adaptability and resilience. Decentralisation was supported by the decrease in strength (but not degree) as the forager/domestic ratio increased. Specifically, foragers gave less per trophallaxis when their number was higher or domestics served as intermediaries by giving more when the number of foragers was low. While the trophallaxis network was not randomly organised, the presence of intermediary ants, confirmed by the local peaks and the hierarchical clustering analysis, indicated that the form of the trophallaxis network was most consistent with the hierarchical network hypothesis. Trophallaxes were clearly directed in different steps and levels, which made the networks hierarchical.

Social network and brood

The presence of a brood did not influence individual strength. Strength was quite stable given that no parameter, except the forager/domestic ratio, affected it. Strength reflects the duration of trophallaxis of an individual, and this should depend more strongly on intrinsic characteristics (Greenwald *et al.*, 2018), such as the quantity of food present in the social stomach. The crop capacity is generally stable between individuals measured at distinct foraging events (Greenwald *et al.*, 2018). Thus, foragers should always transfer stable quantities of food but some might occasionally give large quantities of food to domestics and at other times several small quantities of food. Our results highlight that the pattern of food distribution is independent of colony size and the presence of a brood. In contrast to expectation, the degree and betweenness of foragers and intermediary domestics did not increase in the presence of a brood. This finding may stem from increases in the number of foragers. As a consequence of such a decentralised organisation, the degree and betweenness *per* individual decreases. Thus, a more decentralised and resilient network with intermediary domestics may arise, preventing food exchange from being concentrated to a small number of

foragers. The change in the forager/domestic ratio in the presence of a brood indicated that the system balances foraging and caregiving effort (Schafer *et al.*, 2006; Mailleux *et al.*, 2011). The mechanisms underlying the responses of the system, namely behavioural plasticity of the workers, reinforce the hypothesis that the network was more hierarchical than centralised (Middleton & Latty, 2016).

Social network and colony size

An increase in colony size negatively influenced the degree and the clustering coefficient of ants, positively affected their betweenness and had no effect on their strength. These results corroborate the findings of several previous studies (Naug, 2009; Pasquaretta *et al.*, 2014; Puga-Gonzalez & Sueur, 2017). As colony size increases, the probability of interactions between each pair of ants inherently decreases, resulting in a decrease in network density and as consequence, in the clustering coefficient. However, in larger colonies, as the network becomes more centralised, the mean individual betweenness should decrease. This expectation should hold if interactions are more or less random but not directed towards specific individuals as trophallaxes often are. Thus, one explanation that might explain our finding of betweenness decreasing with colony size is that in larger colonies, some individuals—either foragers or intermediary domestics—become more important in the transfer of food, allowing us to reject the random network hypothesis. Because some domestics had an out-strength/in-strength ratio greater than one (Fig. 3), our data most strongly support the hierarchical network hypothesis.

Conclusion

Behavioural flexibility and decentralised control (the presence of several individuals per caste) are parameters characterising the organisational resilience of ants (Middleton & Latty,

2016). Several studies have already demonstrated the presence of decentralised but hierarchical networks in mammals (Hill *et al.*, 2008). Various hierarchical networks have been described in nature ranging from protein complexes (Ravasz *et al.*, 2002), to neural networks (Chatterjee & Sinha, 2007; Clune *et al.*, 2013), to animal groups (Hill *et al.*, 2008) and to organisation in social insects (Linksvayer *et al.*, 2012). Hierarchical networks are more resilient than centralised networks but less costly in terms of connections (time to find partners and exchanges) than complete networks (Banavar *et al.*, 1999; Bode *et al.*, 2010; Guimera *et al.*, 2001; Barabasi *et al.*, 2003; Ravasz & Barabási, 2003). Changes in our global network measures, such as efficiency, centralisation or resilience, may ultimately result in increases in group performance as mentioned by Sueur (2012) and described by Fontanari and Rodrigues (2016). The two latter authors hypothesised that the collective cognition behind the complex systems built by social insects suggests that the topology of social networks is selected to optimise problem-solving competence at the group level. However, although individuals are selected and not the group or networks, feedbacks exist between these two levels (Farine *et al.*, 2015; Fisher & McAdam, 2017). This process of multilevel selection previously described as “collective social niche construction” by Sueur *et al.* (2019) deserves increased attention. Indeed, study of this process promises to enhance our understanding of the evolutionary mechanisms contributing to the emergence of complex systems.

Acknowledgments

MQ was funded by the Ministère Français de l’Enseignement Supérieur et de la Recherche. OB was funded by the Fonds pour la Recherche dans l’Industrie et dans l’Agriculture and the Van Buuren Fund (Belgium). CS is a junior member of IUF (Academic Institute of France) and a fellow of USIAS (University of Strasbourg Institute for Advanced Studies).

References

- Amdam, G.V., Aase, A.L.T.O., Seehuus, S.C., Kim Fondrk, M., Norberg, K. and Hartfelder, K. (2005) Social reversal of immunosenescence in honey bee workers. *Experimental Gerontology*, 40(12), 939–947.
- Anderson, M. (1984) The evolution of eusociality. *Annual Review of Ecology and Systematics*, 15, 165–189.
- Baker, N., Wolschin, F. and Amdam, G.V. (2012) Age-related learning deficits can be reversible in honeybees *Apis mellifera*. *Experimental Gerontology*, 47, 764–772.
- Balasubramaniam, K.N., Beisner, B.A., Berman, C.M., De Marco, A., Duboscq, J., Koirala, S., Majolo, B., MacIntosh, A.J., McFarland, R. and Molesti, S. (2018) The influence of phylogeny, social style, and sociodemographic factors on macaque social network structure. *American Journal of Primatology*, 80, e22727.
- Banavar, J.R., Maritan, A. and Rinaldo, A. (1999) Size and form in efficient transportation networks. *Nature*, 399(6732), 130.
- Barabasi, A.L., Dezso, Z., Ravasz, E., Yook, S.H. and Oltvai, Z. (2003) Scale-free and hierarchical structures in complex networks. *Modeling of Complex Systems: Seventh Granada Lectures* Vol. 661 (eds. P.L. Garrido & J. Marro), pp. 1–16. AIP. <https://doi.org/10.1063/1.1571285>.
- Bastian, M., Heymann, S. and Jacomy, M. (2009) *Gephi: An Open Source Software for Exploring and Manipulating Networks*.
- Bates, D., Maechler, M., Bolker, B. and Walker, S. (2014) lme4: Linear mixed-effects models using Eigen and S4. *R Package Version*, 1(7), 1–23.
- Bazazi, S., Arganda, S., Moreau, M., Jeanson, R. and Dussutour, A. (2016) Responses to nutritional challenges in ant colonies. *Animal Behaviour*, 111, 235–249.
- Bles, O., Deneubourg, J.L. and Nicolis, S.C. (2018) Food dissemination in ants : Robustness of the trophallactic network against resource quality. *Journal of Experimental Biology*, 221(24), jeb192492.

- Bode, N.W.F., Wood, A.J. and Franks, D.W. (2010) Social networks and models for collective motion in animals. *Behavioral Ecology and Sociobiology*, 65, 117–130.
- Bonabeau, E., Dorigo, M. and Theraulaz, G. (1999) *Swarm Intelligence: From Natural to Artificial Systems*. Oxford University Press.
- Borgeaud, C., Sosa, S., Bshary, R., Sueur, C. and van de Waal, E. (2016) Intergroup variation of social relationships in wild vervet monkeys: A dynamic network approach. *Frontiers in Psychology*, 7, 915.
- Boulay, R., Hefetz, A., Soroker, V. and Lenoir, A. (2000) *Camponotus fellah* colony integration : Worker individuality necessitates frequent hydrocarbon exchanges. *Animal Behaviour*, 59, 1127–1133.
- Buffin, A., Denis, D., Van Simaey, G., Goldman, S. and Deneubourg, J.L. (2009) Feeding and stocking up: Radio-labelled food reveals exchange patterns in ants. *PLoS ONE*, 4, e5919.
- Buffin, A., Goldman, S. and Deneubourg, J.L. (2012) Collective regulatory stock management and spatiotemporal dynamics of the food flow in ants. *The FASEB Journal*, 26, 2725–2733.
- Camazine, S., Deneubourg, J.L., Franks, N. R., Sneyd, J., Theraula, G. and Bonabeau, E. (2003) *Self-Organization in Biological Systems*. Princeton University Press.
- Charbonneau, D., Blonder, B. and Dornhaus, A. (2013) Social insects: A model system for Nnetwork dynamics. *Temporal Networks* (eds. P. Holme & J. Saramäki), pp. 217–244. Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-36461-7_11
- Chatterjee, N. and Sinha, S. (2007) Understanding the mind of a worm: Hierarchical network structure underlying nervous system function in *C. elegans*. *Progress in Brain Research*, 168, 145–153.
- Clune, J., Mouret, J.B. and Lipson, H. (2013) The evolutionary origins of modularity. *Proceedings of the Royal Society B: Biological Sciences*, 280(1755), 20122863. <https://doi.org/10.1098/rspb.2012.2863>
- Couzin, I.D. (2009) Collective cognition in animal groups. *Trends in cognitive sciences*, 13, 36–43.
- Cremer, S. (2019) Social immunity in insects. *Current Biology*, 29, R458–R463.

- Cremer, S., Armitage, S.A.O. and Schmid-Hempel, P. (2007) Social immunity. *Current Biology*, 17, R693–R702.
- Croft, D.P., James, R. and Krause, J. (2008) *Exploring Animal Social Networks*. Princeton University Press.
- Csardi, G. and Nepusz, T. (2006) The igraph software package for complex network research. *International Journal of Complex Systems*, 1695, 1–9.
- De Waal, F.B. (1989) Food sharing and reciprocal obligations among chimpanzees. *Journal of Human Evolution*, 18, 433–459.
- Dornhaus, A., Holley, J.A. and Franks, N.R. (2009) Larger colonies do not have more specialized workers in the ant *Temnothorax albigipennis*. *Behavioral Ecology*, 20, 922–929.
- Dussutour, A. and Simpson, S.J. (2008) Carbohydrate regulation in relation to colony growth in ants. *Journal of Experimental Biology*, 211, 2224–2232.
- Dussutour, A. and Simpson, S.J. (2009) Communal nutrition in ants. *Current Biology*, 19, 740–744.
- Ek, B., VerSchneider, C. and Narayan, D.A. (2015) Global efficiency of graphs. *AKCE International Journal of Graphs and Combinatorics*, 12, 1–13.
- Farine, D.R., Montiglio, P.O. and Spiegel, O. (2015) From individuals to groups and back: The evolutionary implications of group phenotypic composition. *Trends in Ecology & Evolution*, 30, 609–621.
- Fisher, D.N. and McAdam, A.G. (2017) Social traits, social networks and evolutionary biology. *Journal of Evolutionary Biology*, 30, 2088–2103.
- Fisher, D.N. and Pruitt, J.N. (2020) Insights from the study of complex systems for the ecology and evolution of animal populations. *Current Zoology*, 66, 1–14.
- Fontanari, J.F. and Rodrigues, F.A. (2016) Influence of network topology on cooperative problem-solving systems. *Theory in Biosciences*, 135, 101–110.
- Frasnelli, E., Iakovlev, I. and Reznikova, Z. (2012) Asymmetry in antennal contacts during trophallaxis in ants. *Behavioural Brain Research*, 232, 7–12.

- Garrido-Jurado, S., Muñoz-Salinas, R., Madrid-Cuevas, F.J. and Marín-Jiménez, M.J. (2014) Automatic generation and detection of highly reliable fiducial markers under occlusion. *Pattern Recognition*, 47, 2280–2292.
- Gil, M. and De Marco, R.J. (2005) Olfactory learning by means of trophallaxis in *Apis mellifera*. *Journal of Experimental Biology*, 208, 671–680.
- Gordon, D.M. (1996) The organisation of work in social insect colonies. *Nature*, 380, 121.
- Greenwald, E.E., Baltiansky, L. and Feinerman, O. (2018) Individual crop loads provide local control for collective food intake in ant colonies. *eLife*, 7, e31730.
- Greenwald, E., Segre, E. and Feinerman, O. (2015) Ant trophallactic networks: Simultaneous measurement of interaction patterns and food dissemination. *Scientific Reports*, 5, 12496.
- Grüter, C., Acosta, L.E. and Farina, W.M. (2006) Propagation of olfactory information within the honeybee hive. *Behavioral Ecology and Sociobiology*, 60, 707–715.
- Guimera, R., Arenas, A. and Diaz-Guilera, A. (2001) Communication and optimal hierarchical networks. *Physica A: Statistical Mechanics and its Applications*, 299(1–2), 247–252.
- Hadfield, J.D. (2010) MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software*, 33, 1–22.
- Hamilton, C., Lejeune, B.T. and Rosengaus, R.B. (2010) Trophallaxis and prophylaxis: Social immunity in the carpenter ant *Camponotus pennsylvanicus*. *Biology Letters*, 7, 89–92.
- Hartmann, D.P. (1977) Considerations in the choice of interobserver reliability estimates. *Journal of Applied Behavior Analysis*, 10, 103–116.
- Hill, R.A., Bentley, R.A. and Dunbar, R.I. (2008) Network scaling reveals consistent fractal pattern in hierarchical mammalian societies. *Biology Letters*, 4, 748–751.
- Holbrook, C.T., Barden, P.M. and Fewell, J.H. (2011) Division of labour increases with colony size in the harvester ant *Pogonomyrmex californicus*. *Behavioral Ecology*, 22, 960–966.
- Huang, Z.Y. and Robinson, G.E. (1996) Regulation of honey bee division of labour by colony age demography. *Behavioral Ecology and Sociobiology*, 39, 147–158.

- Isaac, G. (1978) The food-sharing behavior of protohuman hominids. *Scientific American*, 238, 90–109.
- Jarvis, J.U., O’Riain, M.J., Bennett, N.C. and Sherman, P.W. (1994) Mammalian eusociality: A family affair. *Trends in Ecology & Evolution*, 9, 47–51.
- Jeanson, R. (2012) Long-term dynamics in proximity networks in ants. *Animal Behaviour*, 83, 915–923.
- Jeanson, R., Fewell, J.H., Gorelick, R. and Bertram, S.M. (2007) Emergence of increased division of labour as a function of group size. *Behavioral Ecology and Sociobiology*, 62, 289–298.
- Kaplan, H., Hill, K., Cadelina, R.V., Hayden, B., Hyndman, D.C., Preston, R.J., Smith, E.A., Stuart, D. E. and Yesner, D.R. (1985) Food sharing among ache foragers: Tests of explanatory hypotheses [and comments and reply]. *Current Anthropology*, 26, 223–246.
- Kitsak, M., Gallos, L.K., Havlin, S., Liljeros, F., Muchnik, L., Stanley, H.E. and Makse, H.A. (2010) Identification of influential spreaders in complex networks. *Natural Physics*, 6, 888–893.
- Kolmes, S.A. and Sommeijer, M.J. (1992) A quantitative analysis of behavioral specialization among worker stingless bees (*Melipona favosa* F.) performing hive duties (Hymenoptera, Apidae). *Journal of the Kansas Entomological Society*, 65, 421–430.
- Krause, J. and Ruxton, G.D. (2002) *Living in Groups*. Oxford University Press.
- Latora, V. and Marchiori, M. (2001) Efficient behavior of small-world networks. *Physical Review Letters*, 87, 198701.
- LeBoeuf, A. C., Waridel, P., Brent, C.S., Gonçalves, A.N., Menin, L., Ortiz, D., Riba-Grognuz, O., Koto, A., Soares, Z.G. and Privman, E. (2016) Oral transfer of chemical cues, growth proteins and hormones in social insects. *eLife*, 5, e20375.
- Lee Cassill, D. and Tschinkel, W.R. (1999) Regulation of diet in the fire ant, *Solenopsis invicta*. *Journal of Insect Behavior*, 12, 307–328.
- Linksvayer, T.A., Fewell, J.H., Gadau, J. and Laubichler, M.D. (2012) Developmental evolution in social insects: Regulatory networks from genes to societies. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 318, 159–169.

- Liu, L., Zhao, X.Y., Tang, Q.B., Lei, C.L. and Huang, Q.Y. (2019) The mechanisms of social immunity against fungal infections in eusocial insects. *Toxins*, 11, 244.
- Mailleux, A.C., Buffin, A., Detrain, C. and Deneubourg, J.L. (2011) Recruitment in starved nests: The role of direct and indirect interactions between scouts and nestmates in the ant *Lasius niger*. *Insectes Sociaux*, 58, 559.
- Małagocka, J., Eilenberg, J. and Jensen, A.B. (2019) Social immunity behaviour among ants infected by specialist and generalist fungi. *Current Opinion in Insect Science*, 33, 99–104.
- Mersch, D.P. (2016) The social mirror for division of labour: What network topology and dynamics can teach us about organisation of work in insect societies. *Behavioral Ecology and Sociobiology*, 70, 1087–1099.
- Mersch, D.P., Crespi, A. and Keller, L. (2013) Tracking individuals shows spatial fidelity is a key regulator of ant social organisation. *Science*, 340(6136), 1090–1093.
- Middleton, E.J. and Latty, T. (2016) Resilience in social insect infrastructure systems. *Journal of the Royal Society Interface*, 13(116), 20151022.
- Modlmeier, A.P., Colman, E., Hanks, E.M., Bringenberg, R., Bansal, S. and Hughes, D.P. (2019) Ant colonies maintain social homeostasis in the face of decreased density. *eLife*, 8, e38473.
- Naug, D. (2009) Structure and resilience of the social network in an insect colony as a function of colony size. *Behavioral Ecology and Sociobiology*, 63, 1023–1028.
- Newman, M.E.J. (2004) Analysis of weighted networks. *Physical Review E*, 70, 056131.
- Noë, R. and Hammerstein, P. (1995) Biological markets. *Trends in Ecology & Evolution*, 10(8), 336–339.
- Nowak, M.A., Tarnita, C.E. and Wilson, E.O. (2010) The evolution of eusociality. *Nature*, 466(7310), 1057.
- Nunn, C.L., Jordán, F., McCabe, C.M., Verdolin, J.L. and Fewell, J.H. (2015) Infectious disease and group size: More than just a numbers game. *Philosophical Transactions - Royal Society Biological Sciences*, 370(1669), 20140111.

- Pasquaretta, C., Levé, M., Claidière, N., van de Waal, E., Whiten, A., MacIntosh, A.J., Pelé, M., Bergstrom, M.L., Borgeaud, C. and Brosnan, S.F. (2014) Social networks in primates: Smart and tolerant species have more efficient networks. *Scientific Reports*, 4, 7600.
- Pinter-Wollman, N. (2015) Persistent variation in spatial behavior affects the structure and function of interaction networks. *Current Zoology*, 61, 98–106.
- Pinter-Wollman, N., Wollman, R., Guetz, A., Holmes, S. and Gordon, D.M. (2011) The effect of individual variation on the structure and function of interaction networks in harvester ants. *Journal of The Royal Society Interface*, 8(64), 1562–1573.
- Portha, S., Deneubourg, J.L. and Detrain, C. (2002) Self-organized asymmetries in ant foraging: A functional response to food type and colony needs. *Behavioral Ecology*, 13, 776–781.
- Puga-Gonzalez, I., Sosa, S. and Sueur, C. (2019) Social style and resilience of macaques' networks, a theoretical investigation. *Primates*, 60, 233–246.
- Puga-Gonzalez, I. and Sueur, C. (2017) Emergence of complex social networks from spatial structure and rules of thumb: A modelling approach. *Ecological Complexity*, 31, 189–200.
- Quevillon, L.E., Hanks, E.M., Bansal, S. and Hughes, D.P. (2015) Social, spatial, and temporal organisation in a complex insect society. *Scientific Reports*, 5, 13393.
- Quque, M., Benhaim-Delarbre, M., Deneubourg, J.L., Sueur, C., Criscuolo, F. and Bertile, F. (2019) Division of labour in the black garden ant (*Lasius niger*) leads to three distinct proteomes. *Journal of Insect Physiology*, 117, 103907.
- R Development Core Team (2009) *R: A language and Environment for Statistical Computing*. R Foundation for Statistical Computing.
- Ravasz, E. and Barabási, A.L. (2003) Hierarchical organisation in complex networks. *Physical Review E*, 67(2), 026112.
- Ravasz, E., Somera, A.L., Mongru, D.A., Oltvai, Z.N. and Barabási, A.L. (2002) Hierarchical organisation of modularity in metabolic networks. *Science*, 297(5586), 1551–1555.

- Reid, C.R., Lutz, M.J., Powell, S., Kao, A.B., Couzin, I.D. and Garnier, S. (2015) Army ants dynamically adjust living bridges in response to a cost–benefit trade-off. *Proceedings of the National Academy of Sciences USA*, 112(49), 15113–15118.
- Reid, C.R., Sumpter, D.J. and Beekman, M. (2011) Optimisation in a natural system: Argentine ants solve the Towers of Hanoi. *Journal of Experimental Biology*, 214, 50–58.
- Romano, Valéria, Duboscq, J., Sarabian, C., Thomas, E., Sueur, C. and MacIntosh, A.J.J. (2016) Modeling infection transmission in primate networks to predict centrality-based risk. *American Journal of Primatology*, 78, 767–779.
- Romano, Valéria, Shen, M., Pansanel, J., MacIntosh, A.J. and Sueur, C. (2018) Social transmission in networks : Global efficiency peaks with intermediate levels of modularity. *Behavioral Ecology and Sociobiology*, 72(9), 154.
- Romano, V., Sueur, C. and MacIntosh, A.J.J. (2020) The trade-off between information and pathogen transmission in animal societies [Preprint]. *EcoEvoRxiv*. <https://doi.org/10.32942/osf.io/vqt4g>
- Schafer, R.J., Holmes, S. and Gordon, D.M. (2006) Forager activation and food availability in harvester ants. *Animal Behaviour*, 71(4), 815–822.
- Sendova-Franks, A.B., Hayward, R.K., Wulf, B., Klimek, T., James, R., Planque, R., Britton, N.F. and Franks, N.R. (2010) Emergency networking: Famine relief in ant colonies. *Animal Behaviour*, 79, 473–485.
- Sendova-Franks, A. and Franks, N.R. (1993) Task allocation in ant colonies within variable environments (A study of temporal polyethism: Experimental). *Bulletin of Mathematical Biology*, 55, 75–96.
- Sosa, S.O., Pelé, M., Debergue, É., Kuntz, C., Keller, B., Robic, F., Siegwalt-Baudin, F., Richer, C., Ramos, A. and Sueur, C. (2019) Impact of group management and transfer on individual sociality in highland cattle (*Bos taurus*). *Frontiers in Veterinary Science*, 6, 183.
- Sosa, S., Puga-Gonzalez, I., Feng, H.H., Zhang, P., Xiaohua, X. and Sueur, C. (2018) A multilevel statistical toolkit to study animal social networks: Animal Network Toolkit (ANT) R package. *bioRxiv*, 347005.

- Sosa, S., Sueur, C. and Puga-Gonzalez, I. (2020) Network measures in animal social network analysis : Their strengths, limits, interpretations and uses. *Methods in Ecology and Evolution*, <https://doi.org/10.1111/2041-210X.13366>.
- Stevens, J.R. and Gilby, I.C. (2004) A conceptual framework for nonkin food sharing: Timing and currency of benefits. *Animal Behaviour*, 67, 603–614.
- Stroeymeyt, N., Grasse, A.V., Crespi, A., Mersch, D.P., Cremer, S. and Keller, L. (2018) Social network plasticity decreases disease transmission in a eusocial insect. *Science*, 362(6417), 941–945.
- Sueur, C. (2011) Social Network, information flow and decision-making efficiency: A comparison of humans and animals. *Social Networking and Community Behavior Modeling*. http://www.academia.edu/1271271/Social_Network_Information_Flow_and_Decision-Making_Efficiency_A_Comparison_of_Humans_and_Animals
- Sueur, C., Jacobs, A., Amblard, F., Petit, O. and King, A.J. (2011) How can social network analysis improve the study of primate behavior? *American Journal of Primatology*, 73, 703–719.
- Sueur, C., King, A.J., Pelé, M. and Petit, O. (2012) Fast and accurate decisions as a result of scale-free network properties in two primate species. *Lecture Notes in Computer Science*. <https://docs.google.com/viewer?a=v&pid=sites&srcid=ZGVmYXVsdGRvbWFpbXNjZWRYaWNzdWV1cmFuaW1hbGJlaGF2aW91cnxneDo3OTczZDBiNmRjZWlyYTTFi&pli=1>
- Sueur, C. and Mery, F. (2017) Editorial: Social interaction in animals: Linking experimental approach and social network analysis. *Frontiers in Psychology*, 8, 35.
- Sueur, C., Romano, V., Sosa, S. and Puga-Gonzalez, I. (2019) Mechanisms of network evolution: a focus on socioecological factors, intermediary mechanisms, and selection pressures. *Primates*, 60, 167–181.
- Tenczar, P., Lutz, C.C., Rao, V. D., Goldenfeld, N. and Robinson, G.E. (2014) Automated monitoring reveals extreme interindividual variation and plasticity in honeybee foraging activity levels. *Animal Behaviour*, 95, 41–48.

- Traulsen, A. and Nowak, M.A. (2006) Evolution of cooperation by multilevel selection. *Proceedings of the National Academy of Sciences USA*, 103(29), 10952–10955.
- Trivers, R.L. (1971) The evolution of reciprocal altruism. *The Quarterly Review of Biology*, 46, 35–57.
- Tschinkel, W.R. and Hanley, N. (2017) Vertical organisation of the division of labour within nests of the Florida harvester ant, *Pogonomyrmex badius*. *PLoS ONE*, 12(11), e0188630.
- Wang, Y. and Xiao, R. (2016) An ant colony based resilience approach to cascading failures in cluster supply network. *Physica A: Statistical Mechanics and its Applications*, 462, 150–166.
- Waters, J.S. and Fewell, J.H. (2012) Information processing in social insect networks. *PLoS ONE*, 7(7), e40337.
- Watkins, M.W. and Pacheco, M. (2000) Interobserver agreement in behavioral research : importance and calculation. *Journal of Behavioral Education*, 10, 205–212.
- Whitehead, H. (1997) Analysing animal social structure. *Animal Behaviour*, 53, 1053–1067.
- Wilson, E. and Eisner, T. (1957) Quantitative studies of liquid food transmission in ants. *Insectes Sociaux*, 4, 157–166.
- Wilson, E.O. and Hölldobler, B. (2005) Eusociality: Origin and consequences. *Proceedings of the National Academy of Sciences USA*, 102, 13367–13371.

Manuscript received December 15, 2019

Final version received April 5, 2020

Accepted April 7, 2020

Tables:

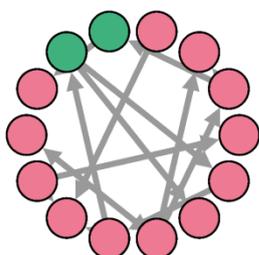
Table 1 Mean \pm standard deviation of individual network measures according to brood (presence/absence) and then caste (foragers/domestics). The relative difference between foragers and domestics is also indicated.

Brood	Presence			Absence		
	Forager	Domestic	Diff(F-D)	Forager	Domestic	Diff(F-D)
Caste						
Degree	3.2 \pm 2.2	2.4 \pm 1.8	0.8	4.1 \pm 2.6	3.2 \pm 2.2	0.9
Instrength	38.7 \pm 68.7	84.2 \pm 111.5	-45.5	90.0 \pm 162.7	94.8 \pm 123.7	-4.8
Outstrength	77.5 \pm 106.2	43.9 \pm 83.3	33.6	113.8 \pm 155 \pm 2	82.3 \pm 128.5	31.5
Strength	123.8 \pm 146.8	120.5 \pm 128.9	3.3	203.8 \pm 223.9	177.1 \pm 188.4	26.7
Betweenness	30.1 \pm 81.1	18.5 \pm 62.0	11.6	55.8 \pm 120.5	35.2 \pm 126.1	20.6
Clust. coeff.	0.08 \pm 0.17	0.06 \pm 0.17	0.02	0.19 \pm 0.26	0.16 \pm 0.26	0.03

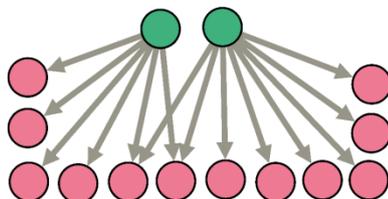
Figure Legends

Fig. 1 Representation of the theoretical networks corresponding to each of the three hypotheses. For each network, there are 14 individuals (two foragers and twelve domestics) as well as fourteen connections (i.e., trophallaxes). (A) Random network for which the trophallaxes are random between individuals, foragers or domestics. (B) Centralised network for which trophallaxes only happen from foragers to domestics; there is one level of interaction. (C) Hierarchical network for which trophallaxes are made first from foragers to domestics and then from these intermediary domestics to other domestics; there are at least two levels of interactions according to the colony size.

A. Random network



B. Centralised network



C. Hierarchical network

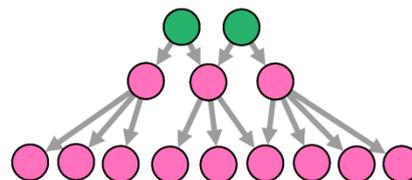


Fig. 2 (A) Experimental setup for testing trophallaxes. Ants are placed in the nest area (on the left) where domestic stay whilst foragers go on the feeding area (on the right) where two food sources are placed: one with protein and one with sugar. The two food sources were randomly attributed. (B) Ants with Aruco tags (QR code) applied on their abdomens.



Fig. 3 Out-strength (total duration of giving food) by in-strength (total duration of receiving food), (A) for all the dataset, (B) for trophallaxes fewer than 100 frames. Blue dots are for foragers whilst red dots are for domestics. Size of the dots represents betweenness. The numbers indicate the foragers (F) or the domestics, on the line (Ratio = 1), under the line (Ratio < 1) or above the line (Ratio > 1).

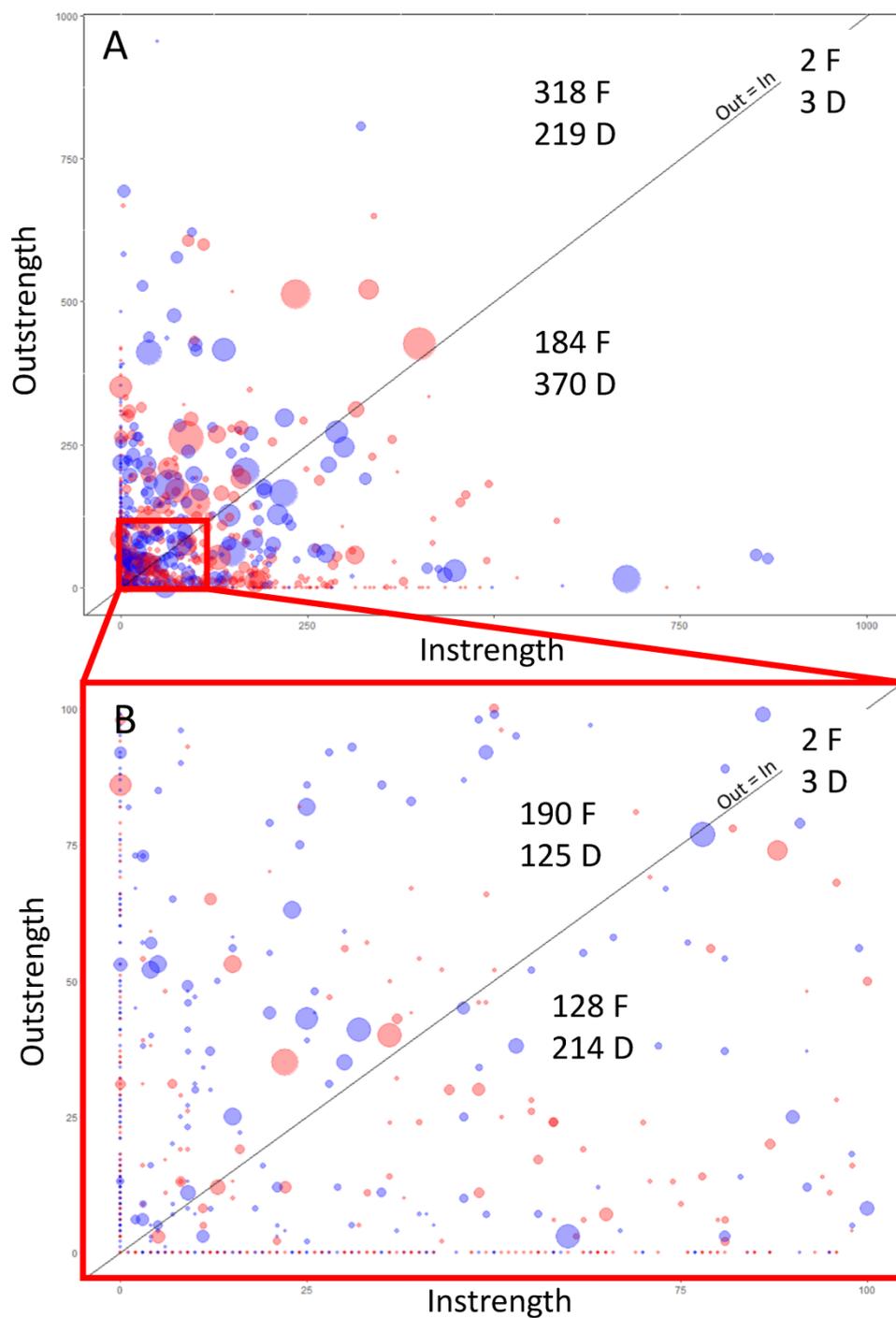
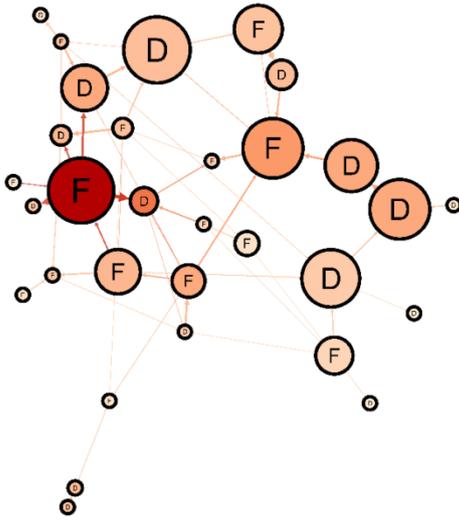
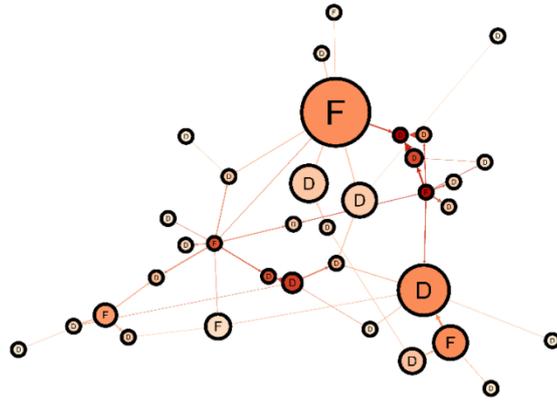


Fig. 4 Illustrations of four trophallaxis networks, with and without brood and with two comparable sizes. D indicates domestics whilst F is for foragers. The size of the nodes corresponds to betweenness (the bigger, the higher) whilst colour fits with the degree (the redder, the higher). Graphs were drawn with Gephi 0.9.2 (Bastian *et al.*, 2009) using the force Atlas 2 package for the spatial visualisation.

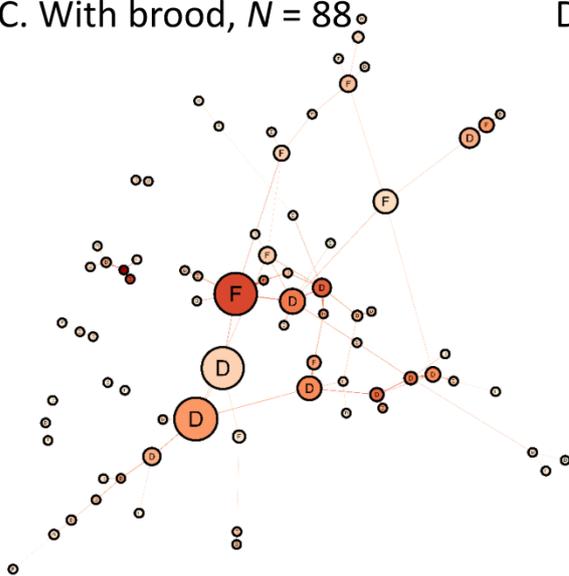
A. With brood, $N = 39$



B. Without brood, $N = 43$



C. With brood, $N = 88$



D. Without brood, $N = 80$

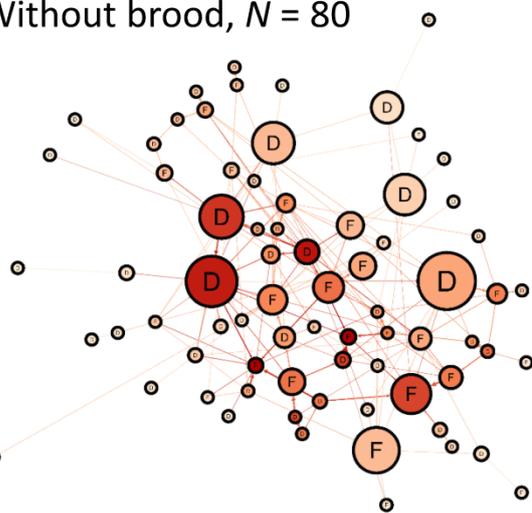


Fig. 5 Effects of factors on global network measures. (A) Number of ants on centralisation. (B) Number of ants on modularity. (C) Number of ants on global efficiency. (D) Presence of Brood on network resilience.

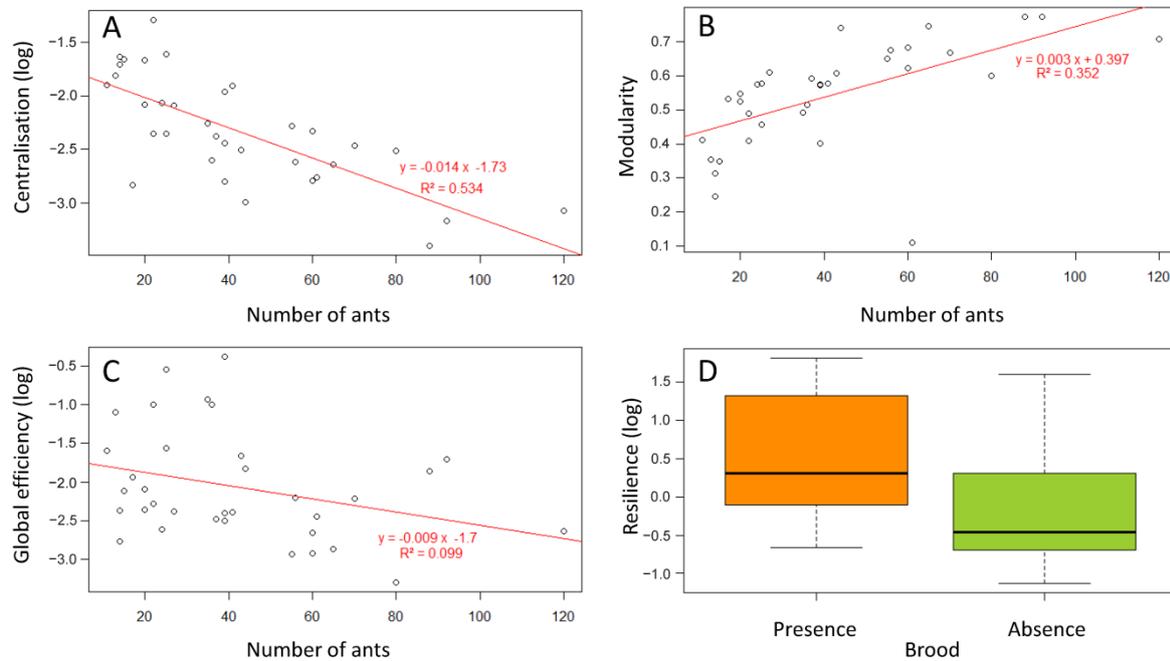


Fig. 6 Correlations matrices between the different individual network measures.