Original Article

Title

Worker-behavior and behavior-behavior interaction networks in the trap-jaw ant *Odontomachus chelifer* (Latreille, 1802)

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Abstract

Division of labor is among the main factors to explain the evolutionary success of social systems, from the origins of multicellularity to complex animal societies. The remarkable ecological success of social insects seems to have been largely driven by ergonomic advantages stemming from the behavioral specialization of workers. However, little is known about how individuals and their correspondent behavioral repertoire are related to each other within a division of labor context, as this relationship can be viewed as a complex network. Applications of network theory in the study of social insects are almost exclusively used to analyze behavioral interactions between individuals, rather than to the study of relations among individuals and behaviors. Here, we use a new approach to the study of the organization of the behavioral repertoire of ant colonies, which consider both individual-task interactions and task-task interactions, besides colony time budgets. Our study investigates for the first time the organization of division of labor in colonies of the trap-jaw ant *Odontomachus chelifer* (Latreille 1802). Data from all the behavioral acts (including inactivity) performed within three queenright colonies of different sizes (n = 7, 30, and 60 workers) were studied under controlled laboratory conditions. Each ant within the colonies was individually marked and observed by scan sampling in 10 min intervals for 10 h each (n = 5820 behavioral acts). We describe the network topologies in terms of centrality, specialization, modularity, and nestedness. This study shows that workers of *O. chelifer* interact in structured networks composed of specialists and generalists with consistent organization, even across colonies of different sizes. Our results underscore the potential of the use of complex networks in order to discover and study novel organizational patterns of social groups in animal behavior.

Keywords: Division of labor, polyethism, task allocation, Formicidae, Ponerinae.

Introduction

Division of labor is a property of social systems thought to have been favored by natural selection that occurs in a variety of phenomena, from subcellular level to complex animal societies (Maynard Smith & Szathmáry 1997). In particular, the remarkable ecological success of social insects seems to have been largely driven by the ergonomic advantages stemming from division of labor, such as individual specialization and parallel task execution (Oster & Wilson 1978, Robinson 1992, Traniello & Rosengaus 1997, Beshers & Fewell 2001, Rocha & al. 2014, Avril & al. 2016). Division of labor in social insects can be broadly defined as "any behavioral pattern that results in some individuals in a colony performing different functions from others" (Michener 1974). Uncovering general principles of the division of labor requires the estimation of the contribution from individual workers toward the completion of colony tasks (Beshers & Fewell 2001). Therefore, insights about the organization of the division of labor in social insects might be obtained through the view of the relationship between workers and their corresponding behavioral performance, or between tasks, as a complex network.

A complex network is described as a system of interacting nodes (within a social insect colony, workers or tasks connected by links), that communicate with each other, displaying patterns of connection that are neither purely regular nor purely random (Newman 2003). In social insects, the network concept itself has been present in the literature for a long time, especially considering the interaction between individuals, i.e. social interactions (Gordon 2010). Even then, empirical data that explicitly describe interaction networks in social insect colonies have been only recently studied (e.g., Bhadra & al. 2009, Naug 2008, 2009, Sendova-Franks & al. 2010, Pinter-Wollman & al. 2011, Waters & Fewell 2012, Mersch & al. 2013). While social interaction networks are an interesting approach to understand the behavioral influence of one individual on another, it does not reflect explicitly how workers interact with the tasks performed by it. In the literature there are several theories and evidence of the division of labor exhibited by ant colonies, yet there is still a lack of studies that reflect the empirical complexity exhibited by the interactions of workers and tasks within a colony. This lack of knowledge may hinder the understanding of the organization of division of labor, and even the extent to which several mechanisms proposed to explained division of labor are consistent. In order to fulfill this gap, one could use a framework considering networks in different ways. For instance, we could envision tasks as nodes and individual workers as links (such as symbolic dynamics) (Fewell 2003). Charbonneau & al. (2013) presented one empirical analysis of task-task interaction networks (unipartite networks) in order to identify dynamics of task switching within a colony of the ant *Temnothorax rugatalus* using betweenness centrality, to measure how central is the role of one task compared to others. The results showed that ants wander throughout the nest between tasks rather than directly switch among the other tasks. Recently, Pasquaretta & Jeanson (2018) proposed the use of bipartite networks to represent interactions between workers and tasks. Moreover, the authors quantified the bipartite network in the context of division of labor, using specialization and modularity measures, which consider the specialization of nodes and the strength of division of a network into groups, respectively.

Here, we use a new approach beyond interaction social networks, which consider both workers-task interactions and task-task interactions, besides usual colony time budgets. Such an integrative approach offers results that are complementary to each other, showing possible hidden pattern dynamics in the formation of complex behavioral interactions. For instance, the degree of specialization observed in the worker-task network could derive groups to be compared (e.g. specialists and generalists) in the task-task networks. Besides the network metrics used in the previously mentioned studies, we also considered new theoretical concepts developed in community ecology, such as nestedness, and expanding the use of modularity for task-task interactions. A nested network structure is observed when specialists mainly interact with a proper subset of the nodes of generalists. Nested networks are generally robust against random node loss (i.e., loss of workers or tasks, depending on the type of network) (Thébault & al. 2010), while networks with a high degree of specialization are more vulnerable (Kaiser-Bunbury & al. 2017). Regarding modularity in task-task networks, the division of the network in groups that are more related to each other (modules) is similar to the concept of roles developed by Hölldobler & Wilson (1990), stated as a "set of behavioral acts, linked by relatively high transition probabilities".

Inactivity may occur as a result of time delays associated with searching for or switching tasks (Leighton & al. 2017). Thus, we also use inactivity as links in the task-task networks to quantify its influence.

Our study uses the trap-jaw ant *Odontomachus chelifer* (Latreille 1802) as a model organism. We investigate the organization of division of labor in colonies of *O. chelifer*. In the congener *O. brunneus,* dominant ant individuals are more likely to reside in the central areas of the nest, where they take care of the brood, while subordinate individuals are pushed towards the edge, where they are more likely to forage (Powell & Tschinkel 1999). This process of division of labor has been called "Interaction-based task allocation" (Powell & Tschinkel 1999). Similarly, the division of labor in *O. chelifer* could be based on interactions between workers resulting in spatial fidelity and we take this into account. Thus, we address the following questions: (1) Is the division of labor in *O. chelifer* also derived from "Interaction-based task allocation"? (2) What is the individual role of the behaviors and workers described by the network analysis (i.e., specialization, centrality, modularity and nestedness)? (3) What is the difference between the task interactions of specialists and generalists?

Methods

Field Collection and Culture Methods: The species chosen for this study is the ant *Odontomachus chelifer* (Latreille 1802). The genus *Odontomachus* (Ponerinae) is characterized by large body size (≈ 12-15 mm in length) and a powerful articulated jaw, usually forming small colonies (Latreille 1804, Patek & al. 2006, Spagna & al. 2008). The species is distributed from Mexico to the northeast of Argentina (Brown 1976) and it has a generalist diet (Raimundo & al. 2009, Núñez & al. 2011). In our study, five colonies of *Odontomachus chelifer* were collected in forest fragments at the campus of the Universidade Federal do Paraná and the Museu de História Natural do Capão da Imbuia, Curitiba, Paraná, Brazil. The colonies usually had less than 100 workers (mean ± sd: 38 ± 24). In the laboratory, colonies were transferred to artificial plaster nests, where they were kept under stable environmental conditions (20^0C under constant light with 600≈lux and humidity at 60%). Internal dimensions of the cavity were 19.5 x 15 x 2 cm (width x depth x height) divided in two chambers. All the colonies were supplied with water *ad libitum*, pieces of mealworms and an artificial diet (Bhatkar & Whitcomb 1970). In all colonies, ants arranged themselves in a pattern similar to that observed by Powell & Tschinkel (1999) for *O. brunneus*, where the chamber furthest from the entrance contained the brood and queen, creating three distinct zones: the "brood zone", "broodless zone" (all the other areas within the nest), and "foraging zone" (area outside the nest). These three artificial delimited zones were used to record the general location of each individual. Colonies were allowed to adjust within laboratory conditions for one month before the beginning of observations. All workers were marked individually with combinations of oil-based Testors® paint (one spot on the head, one on the mesosoma, and two on the gaster) for individual worker recognition. All colonies were allowed to adjust to laboratory conditions for at least one month before any focal workers were marked, and the colonies were left for an additional week after marking before observations began.

Behavioral observations: Three queenright monogynous colonies of the five collected in the field were chosen for observation based upon their apparent health and status (i.e., a large brood pile and the presence of a queen). Each worker from the three colonies (n = 60, 30, and 7 workers, henceforth colonies A, B, and C, respectively) was observed through scan sampling at 10-min intervals for ten hours, divided into two observations by an interval of two days (five hours each; between 09:00 and 19:00 *per* trial). In each trial, we systematically scanned each zone chamber, noting the behavioral state and location of each marked worker in order to assure the correct behavioral notation of all the ants. The observations were recorded with a digital camcorder (JVC GZ-HM320SUB) placed above the colonies. After the videos were analyzed, all the recorded behaviors (11,633 recorded activities) were double-checked by a second person to ensure accurate recordings of ant identities across the observations. Individual behavioral repertoires were created and classified across the spatial zones (see Tab. 1 for a complete list of the behavioral acts and definitions). Furthermore, some behavioral acts that could be classified as dominance interactions

were observed but given that they were uncommon (n < 10), such behaviors were not included in the behavioral categories considered but were briefly described in the results.

Networks: Networks were depicted as adjacency matrices, in which an element within the matrix a_{ij} with a value equal to zero means the absence of interaction, and any value ≥ 1 indicates the number of interactions between the elements of the network. Two different kinds of networks were considered in this study: worker-task networks (WTNs) and task-task networks (TTNs). WTNs characterizes the relationship between two sets of nodes; workers and their respective task repertoires. It is an undirected bipartite graph, in which links (edges) are defined whenever an individual performs a specific task. Differently, TTNs connects every task to the one performed immediately after it, with workers as links. It is a unipartite di-graph, representing temporal and directional interaction between each task. Networks were analyzed considering all the tasks observed as nodes, excluding inactivity behavior. Inactivity is not a task, so it was disregarded as a node. Also, when inactivity was maintained as a node it had a high recurrence of the interaction with tasks, which could make the detection and understanding of the network patterns harder to interpret. Nevertheless, we quantified inactivity influence in two ways. The first one was calculated as the normalized proportion of the raw inactivity for each ant (named *Ii*) during behavioral observations. The second one is a variation of the TTNs, where tasks were linked by the frequency of inactivity behaviors between them (i.e., TTNs of inactivity). Thus, the link between two nodes (tasks) of the TTNs of inactivity was quantified as the presence (1) or absence (0) of the behavioral interaction, and inactivity was the additional (1 + *n*) or the only weight of the link.

Network metrics: We tested a series of measures from network analysis in the WTNs and TTNs, all analyses were performed using R 3.6.0 (R Development Core Team 2019). Graph visualization was created using both the IGRAPH and BIPARTITE packages (Csardi & Nepusz 2006, Dormann & al. 2009). We explored the organization within the networks, i.e., the roles of individual nodes (node-level metrics), as well as on a global scale (network-level metrics). Each metric had its values compared to the ones obtained from random networks generated by a specific null model (each null model used in our study is explained in another section). The chosen metrics could be divided into five categories: Specialization (only for WTNs), centrality (only for TTNs), modularity and nestedness (for both WTNs and TTNs).

1) Specialization: We used two specialization network measures based on interaction frequencies in the WTNs: the *d'* and H_2' metrics (Blüthgen & al. 2006), which represents scale-independent indices to characterize specialization in ecological networks at node and group-levels, respectively. Originally, both measures were proposed to quantify specialization in ecological plant-pollinator networks. The *d'* index is derived from Kullback-Leibler distance (such as Shannon's diversity index) and quantifies how strongly a task (or worker) deviates from a null model which assumes task allocation in proportion to the workers and tasks available (more details; Blüthgen & al. 2006). The *d'* index ranges from 0 (no specialization) to 1 (full specialization) and can be calculated at worker level (d'_{indv}) or task level (d'_{task}). For the entire network, the degree of specialization considering both parties (e.g. tasks and workers) can be determined with the H_2' index (Blüthgen & al. 2006, 2008). H_2' was used in the context of division of labor for the first time by Pasquaretta & Jeanson (2018). It describes to which extent the worker-task interactions deviate from those that would be expected from a neutral configuration given the workers and tasks marginal totals. H_2' ranges between 0 (no specialization) to 1 (specialization). The *d'* and H_2' measures were calculated by the R package BIPARTITE in R (Dormann & al. 2008). Furthermore, we distinguished specialists from generalists, where individuals with d'_{indv} values above the median of the colony were considered specialists, and below it, generalists. Thus, we create TTNs of specialists and generalists with similar size for each colony. Here, we used the term specialists to mean simply "concentrate on," without requiring that it be accompanied by increased performance efficiency or an implicit reason to occur (as suggested by Jeanne 2016). Furthermore, Gorelick et al. (2004) created two indices based on normalized mutual entropy, which have been used in several empirical and theoretical studies of division of labor (e.g. Jeanson & al. 2007, Dornhaus 2008, Santoro & al. 2019). While they were not created in the context of network theory, they are implemented in adjacent matrices such as graphs. These metrics quantify

specialization from individuals and tasks and were named DOL_{indv} and DOL_{task}, respectively. The two indices range between 0 (no division of labor) to 1 and were indirectly compared to the H_2' index.

2) Centrality: We used betweenness centrality and degree centrality to study the patterns of flow information across tasks (TTNs). Betweenness centrality is a measure of how often a node is located on the shortest path (geodesic) between other nodes in the network (Freeman 1979). Thus, it measures the degree to which the node (task) functions as a potential point of control of communication (i.e., bridge) among the other nodes within a network. In unweighted networks (where the original betweenness centrality was proposed), all links have the same weight, thus the shortest path for interaction between two nodes is through the smallest number of intermediate nodes. Differently, most of the new centrality measures proposed for weighted networks have been solely focused on edge weights, and not on the number of links, a central component of the original measure. Due to this issue, we use the betweenness centrality proposed by Opsahl & al. (2010), which considers both the number and the strength of links (weight). The relative importance of these two aspects in the metric is controlled by the tuning parameter (α), which goes from 0 to 1. We set alpha to 0.5 to consider both factors with the equal proportions. In order to differentiate nodes with higher betweenness centrality from the others, tasks with a betweenness centrality above the third quartile of the data (<75%) were considered bridges. Degree centrality was applied to the TTNs of inactivity and used to describe the latency of the activity among the tasks, i.e., the higher the degree centrality of a node, the higher the latency (inactivity) around it. Originally, degree centrality is simply the count of how many connections (i.e., links) a node has in a binary network. The degree has generally been extended to the sum of weights in weighted networks (Barrat & al. 2004, Newman 2004, Opsahl & al. 2008) and labeled node strength. In order to combine both degree and strength, we used the degree centrality metric proposed by Opsahl & al. (2010), which as the betweenness centrality proposed by the same authors, uses a tuning parameter (α) to set the relative importance of the number of ties compared to link weights. The α tuning parameter was set to 0.5 to consider both factors with equal proportions. Degree centrality was divided as in and out-degree centrality for directed graphs (such as TTNs of inactivity). As the names imply, in-degree point toward and out-degree away from the given node. Tasks with an in-degree and out-degree centrality above the third quartile of the data (<75%) were regarded as inactivity hubs (i.e., with inactivity converging to the node) or inactivity spreaders (i.e., with inactivity leaving the node), respectively. While we computed centrality measures for all observed tasks and compared each of them with a null model (Tab. 3, 4 and 5), in our results we only report tasks considered bridges, inactivity hubs and spreaders. Betweenness centrality and degree centrality were calculated using the R package TNET (Opsahl 2009).

3) Modularity: Modularity was proposed by Newman (2006) to compute the strength and number of modules within a network, and it has been studied across different biological scales (Lorenz & al. 2011). Modules can be defined as groups of tightly connected nodes that are sparsely connected to other nodes in the network (Newman 2006). The modularity (Q) ranges from 0 (community structure not different from random) to 1 (complete separation between modules). There are different algorithms available to detect modules in weighted bipartite and unipartite networks (Clauset & al. 2008, Dormann & Strauss 2014, Beckett 2016). In the WTNs, the DIRTLPAwb+ algorithm for optimizing bipartite modularity was used (Beckett 2016) and implemented in the R package BIPARTITE (Dormann & al. 2008). We normalized the bipartite modularity values following Pasquaretta & Jeanson (2018). The algorithm used to search for modules in the TTNs is the Louvain method developed by Clauset & al. (2008) and implemented in the R package IGRAPH (Csardi & Nepusz 2006).

4) Nestedness: We used two different metrics to estimate nestedness of the WTNs and TTNs. The first metric was the weighted nestedness metric based on overlap and decreasing fill (WNODF), which is a modified version of the nestedness metric based on overlap and decreasing fill (NODF) that consider weighted bipartite networks instead of only binary ones (Almeida-Neto & al. 2008, Almeida-Neto & Ulrich 2011). WNODF nestedness score ranges from 0 (non-nested) to 100 (perfectly nested) and it was applied to the WTNs. The nestedness in the TTNs was quantified by the UNODF, the unipartite version of the NODF metric (Cantor & al. 2017). In completely non-nested networks, UNODF = 0, while in perfectly nested networks UNODF tends towards 1. Directed networks (such as the ones of this study) will have

two different UNODF values (and interpretations), because the interactions in matrix elements a_{ij} and a_{ij} represent different things. These two different UNODF values could be divided in nestedness among rows (UNODFr) and nestedness among columns (UNODFc). UNODFr measures nestedness computing the pairwise overlap among rows and UNODFc the pairwise overlap among columns. Since the calculation of UNODF is made through binary networks, we measured the UNODF index for different cut-off values (such as Cantor & al. 2017). The metric was calculated without a cut-off to include all data (named UNODF 1), but also considering a cut-off of 10% of the data (named UNODF 2), in order to exclude tasks which were not so frequent considering all others. WNODF and UNODF were calculated using the R packages BIPARTITE and UNODF, respectively (Dormann & al. 2009, Cantor & al. 2017).

Statistical analysis and comparison with nulls models: G-test goodness of fit (including post-hoc pairwise comparisons) was used to compare the frequency of behavioral acts (Sokal & Rohlf 1981). The statistical null hypothesis considers that the number of observations in each task is equal to that predicted by a uniform discrete distribution of the data, and the alternative hypothesis is that the observed numbers differ from this expected distribution. No correction for the multiple comparisons was applied (Rothman 1990, Saville 1990). Correlation between *d'* and *Ii* was tested (Spearman correlation). There are several null models to generate random networks, simpler or more sophisticated (Farine 2017). The Paterfield's algorithm was used in the WTNs, as suggested by Pasquaretta & Jeanson (2018) for the division of labor for bipartite networks. This model generates random networks constraining the marginal sums (i.e., worker performance and behavior need are maintained), but links are randomly assigned between workers and behaviors. There is no null model recommended in the literature for unipartite networks (TTNs) in a division of labor context, thus we considered three different null models extensively used in the literature and that had important properties to be considered in our work. To compare the values of modularity and betweenness centrality obtained in the original TTNs with the ones obtained from random networks, we used the link and weight reshuffling null model developed by Opsahl & al. 2008. Such model consists of reshuffling the network topology while preserving degree distribution. The importance of maintaining the network degree distribution is that most real-world degree distributions are naturally skewed rather than having a uniform or Poisson distribution. Thus, preserving the same degree distribution of the original network makes the null model more realistic and comparable to the original network. In order to compare degree centrality, we used the weight reshuffling null model, also developed by Opsahl & al. (2008). The weight reshuffling procedure consists of reshuffling the weights globally in the network (Opsahl & al. 2008). This null model maintains the topology of the observed network. Therefore, the number of ties originating from a node does not change. The null models used to verify nestedness were first developed for bipartite networks, so we used an adapted version of a model widely used in bipartite biological networks, named null model 2 (Bascompte & Jordano 2007) for unipartite binary networks (in our study, modified versions of the weighted TTNs; Cantor & al. 2017). In this null model, the probability that a link connects two nodes is proportional to their corresponding degree. A conveniently property of this model is that it preserves key network features, such as the network size, connectance and degree distribution. The statistical significance of all the network measures compared to the random networks was evaluated based on the *Z*-score:

$$Z = \frac{X_{emp} - X_{rand}}{SD_{rand}},$$

where X_{emp} is a metric extracted from the empirical networks (n = 1000), X_{rand} is the average value of the same metric obtained from random networks and SD_{rand} is the standard deviation of the metric obtained from the randomized networks. The *p* values from all the analyses were considered significant at $p \leq 0.05$, but also described at different levels as well when necessary (i.e., ≤ 0.01 and ≤ 0.001). All the statistical analyses and null models were performed by the R software 3.6.0 (R Core Team 2019). The R packages RVAIDEMEMOIRE and STATS were used to compute the G-test and Spearman correlation, respectively (R Core Team 2019, Hervé 2020). The null models for WTNs were created by the R package BIPARTITE (Dormann &

al. 2008). Two packages were used to create null models for TTNs, the TNET package was used to create the link and weight reshuffling model, and the weight reshuffling model (Opsahl 2009), the UNODF package was used to create the adapted null model 2 (Cantor & al. 2017).

Results

Our results are divided in the data originated from the behavioral repertoire (colony time budgets) and the information extracted from network analyses (WTNs and TTNs). We analyzed 5748 behavioral acts (10400 including inactivity), WTNs (Fig. 1) resulting in 5816 interactions, and TTNs (Fig. 2, 3, and 4) resulting in 5917 interactions.

Behavioral repertoire: The behavioral repertoire performed by the workers was composed of 11 tasks (Tab. 2), inactivity, and dominance interactions (which will be described in the following section). The frequency of inactivity compared to the tasks was significantly higher across all colonies. Over the observation period, 81% of workers were inactive in colony A ($G_{(59)} = 650$; $P < 0.001$), 83% in colony B ($G_{(29)} = 243$; $P < 0.001$) and 61% in colony C ($G_{(6)} = 26.9$; $P < 0.001$). Among the tasks, walking and self-grooming had frequencies significantly higher considering all the colonies (colony A, $G_{(10)} = 747.03$, $P < 0.001$; colony B, $G_{(8)} = 233.96$; $P < 0.001$; colony C, $G_{(6)} = 138.78$; $P < 0.001$). Brood care also had a higher frequency than the other tasks but limited to the colony A and B, and feeding and foraging/patrolling only in colony C.

Description of dominance interactions: We observed three rare behaviors (n < 10) that could be characterized as dominance interactions, which are named as rapid antennation, aggressive grooming, and aggressive contact. Rapid antennation began with 'antennal dueling', where two workers met head-on and displayed rapid antennal striking behavior for approximately 5 s. Rapid antennation also occurred in a side-on form, in which one worker rapidly antennated the thorax or gaster of another one, often leading to antennal drumming. Aggressive grooming consisted of a dominant worker grooming a subordinate one, with rapid antennation directed to the head and thorax of the subordinate worker, whilst maintaining a raised body posture, similarly to the "aggressive interaction" described for *O. brunneus* (Powell & Tschinkel 1999). Aggressive contact started with rapid antennation between two workers (≈ 5s) and evolved into an interaction where a dominant worker physically carries a subordinate one through the jaws for a few minutes (≈ 5min). During the aggressive contact, the dominant worker repeatedly tries to bite the subordinate, but no injury or deaths resulted from such behavior where observed.

Task Performance and Spatial zones: As expected, brood care (including carrying brood) was exclusively limited to the brood zone and foraging/patrolling behavior was exclusively limited to the foraging zone. In general, all the other behaviors, including the dominance interactions were performed in every zone.

Specialization: We found that H_2' values in the colonies were significantly higher than the H_2' obtained from random networks (Fig. 5, Colony A, $Z = 29.3$, $P < 0.0001$; Colony B, $Z = 15.8$, $P < 0.0001$; Colony C, $Z = 10$, $P < 0.0001$). The DOL_{indv} values in the colonies (Fig. 6) were also significantly higher than the correspondent ones obtained from random networks (Colony A, $Z = 28.9$, $P < 0.0001$; Colony B, $Z = 15.4$ $P < 0.0001$; Colony C, $Z = 9.8$, $P < 0.0001$). Following the same trend, DOL_{task} values (Fig. 6) were higher than the ones from random networks (Colony A, $Z = 3.2$, $P < 0.0001$; Colony B, $Z = 2.8$ $P = 0.005$; Colony C, $Z = 9.8$, $P = 0.001$). The distribution of d'_{indv} and d'_{task} values, as well as the *Ii* index were clearly skewed (Fig. 7), with similar median values between the colony A and B, and lower values in colony C. There was no observed correlation between the d'_{indv} and the correspondent *Ii* values from each colony (Colony A, r_s: -0.03, $P = 0.76$; Colony B, r_s: -0.35, $P = 0.06$; Colony C, r_s: 0.57, $P = 0.10$).

Centrality: The centrality measures allowed us to identify the influence of each task (i.e., bridges, inactivity hubs and spreaders) within TTNs. In colony A, walking and self-grooming were bridges when considering either all workers, generalists and specialists. Brood care was also a bridge behavior when

considering all workers and generalists, but not specialists (Fig. 2A). In colony B, self-grooming and grooming were bridge behaviors for all workers and specialists, while self-grooming and brood-care were the bridges for generalists (Fig. 2B). Differently, feeding was the only bridge behavior in colony C for all workers and specialists, while walking and foraging/patrolling were bridges for the generalists (Fig. 2C). The bridge behaviors of self-grooming (colony A and B), walking (colony A), and feeding (colony C) had betweenness centrality values significantly different from the ones obtained by the null model (among specialists; Fig. 2 and Tab. 3).

In colony A, walking was the only common inactivity hub when considering all workers, generalists and specialists (Fig. 3A). In addition, self-grooming was also an inactivity hub for all workers and generalists and grooming was only an inactivity hub for all workers. In colony B, self-grooming and grooming were inactivity hubs considering all workers and specialists, and brood care was an inactivity hub for the generalists (Fig. 3B). In colony C, walking and feeding were common inactivity hubs for all workers and specialists, and generalists had walking and foraging/patrolling as inactivity hubs. Also, in this colony self-grooming was a hub for the specialists (Fig. 3C). In colony A, the inactivity hubs, self-grooming (for generalists) and walking (for specialists) were significantly different when compared to random networks (Fig. 3 and Tab. 4). In colony B, all the inactivity hubs from generalists and specialists, along with the grooming behavior for all workers, were significantly higher than the expected from random networks (Fig. 3 and Tab. 4). In colony C, the identified inactivity hubs were not statistically different than the random networks, except for walking among generalists (Fig. 3 and Tab. 4).

Self-grooming was an inactivity spreader present in all workers, generalists, and specialists in colony A (Fig. 4A). In addition, brood care and feeding were inactivity hubs from all workers and generalists, while walking and grooming were inactivity hubs among specialists (Fig. 4A). In colony B, grooming and brood care were inactive spreaders for all workers and generalists, and grooming only for specialists (Fig. 4B). In colony C, foraging/patrolling and feeding were inactivity spreaders among all workers and generalists, and specialists had walking and feeding behaviors as spreaders (Fig. 4C). In colony A, self-grooming and feeding among all workers and generalists were significant inactivity spreaders compared to random networks. In addition, brood care was a significant inactivity spreader for generalists and walking for specialists (Fig. 4 and Tab. 5). In colony B, the brood-care behavior when considering all workers and generalists, and grooming behavior for the specialists, were the inactivity spreaders significantly different from the null model (Fig. 4 and Tab. 5). In colony C, feeding for the specialists was the inactivity spreader statistically higher than random networks (Fig. 4 and Tab. 5).

Modularity: Modularity values for the WTNs (Q_{norm}) in all the colonies (Fig. 5) were significantly higher than the Q_{norm} obtained from random networks (Colony A, $Z = 29.7$, $P < 0.0001$; Colony B, $Z = 12.54$, $P < 0.0001$; Colony C, $Z = 6.25$, $P < 0.0001$). WTNs were organized into four modules in colony A and C and six modules in colony B, and the composition of the modules (number of individuals and tasks interacting) differed between all colonies (Fig. 1). TTNs modularity values were not significantly higher compared to those obtained from random networks in colony A and C, but significant in colony B for all workers, generalists, and specialists (Fig. 8). TTNs in colony A were organized into three modules in all workers and generalists, with only two modules in specialists (Fig. 2). All TTNs were organized in two modules in colony B and C (Fig. 2). The composition of the modules (the interacting tasks) within each colony differs with each worker composition (all workers, generalists, and specialists).

Nestedness: Nestedness (WNODF) value was significantly lower than the ones obtained from random networks (also known as an anti-nested pattern, but there are criticism about using this term, see Almeida-Neto & al. 2006) in colony A, while the values in colony B and C were not statistically significant (Fig. 5, Colony A, $Z = -5$, $P < 0.0001$; Colony B, $Z = -1.64$, $P < 0.0001$; Colony C, $Z = -1.65$, $P < 0.0001$). Nestedness (UNODF) values revealed that in general, the colonies did not have a nested structure in both the cut-off conditions considered from TTNs. However, a nested structure was significantly present when considering all workers in colony A (UNODFc 1, $Z = 2.59$, $P < 0.009$) and C (UNODFr 1, $Z = 2.39$, $P < 0.01$). TTNs were significantly less nested than randomized networks for specialists in colony B (UNODFr 1, $Z = -2.48$, $P < 0.01$ and UNODFr 2, $Z = -2.23$, $P < 0.01$) and C (UNODFc 1, $Z = -2.93$, $P = 0.003$ and UNODFc 2, $Z = -2.8$, $P = 0.005$).

Discussion

This study shows that colonies of *Odontomachus chelifer* interact in structured networks with consistencies even across colonies of different sizes. In short, inactivity is the most performed behavior in *O. chelifer*, where the performance of some tasks such as walking and self-grooming is more frequently observed than the others. Dominance interactions are present but rarely observed, despite the presence of a few tasks specific to certain spatial locations. Specialists diverged significantly from generalists, with self-grooming and feeding having a distinct role as bridges across the colonies. Complex patterns such as modularity, nested and significantly not nested structures were observed in WTNs and TTNs. Our results are manifold and will be discussed with detail in turn.

Inactivity by a large margin is the most recurrent behavior observed in all the colonies of *O. chelifer*. High inactivity frequency among ant workers (< 50% *per* colony) is a very widespread phenomena observed in several ant species, both in field and laboratory studies (Lindauer 1952, Hölldobler & Wilson 1990, Herbers 1983, Herbers & Cunningham 1983, Cole 1986, Schmid-Hempel 1990, Dornhaus 2008, Dornhaus & al. 2008, Dornhaus & al. 2009, Charbonneau & Dornhaus 2015). However, the role of inactivity is rarely considered to comprehend task allocation strategies or colony organization (for exceptions, see Herbers 1981, Fresneau 1984, Cole 1986, Corbara & al. 1989, Retana & Cerdá 1990, Retana & Cerdá 1991, Charbonneau & Dornhaus 2015). It appears as already discussed in the literature, that inactivity could have larger importance in the context of division of labor, since it was observed that even some workers specialize in inactivity (Charbonneau & Dornhaus 2015). In *O. chelifer*, while some workers were clearly more inactive than others, the degree of inactivity performed by a worker did not directly influenced its specialization. This suggest that while inactivity is the most performed behavior, its influence on task allocation is not quantified by its simple execution. The role of inactivity as a link between task switching will be discussed further through the analysis of inactivity hubs and spreaders. Self-grooming and walking were the most performed tasks by the workers in all the colonies. Self-grooming is a self-maintenance (cleaning) task and a regulator of chemical signaling from hydrocarbons constituents (Soroker & al. 1998, Lahav & al. 1999). The hydrocarbon constituents of the postpharyngeal gland are sequestered by internal transport as well as from the body surface by self-grooming (Soroker & al. 1994, 1995a,b). Thus, the link between the postpharyngeal gland and body surface enables the ants continuously to refresh, and subsequently update their epicuticular hydrocarbons. The chemical signaling made by cuticular hydrocarbonates and enhanced by self-grooming is probably a mechanism to maintain reproductive skew within the colonies. The fertility signal from chemical signaling communicates information that increase the individuals' fitness (Keller & Nonacs 1993). Walking have innate importance in the performance of other tasks, based upon the consequent movement of the ant to a designated task outside its position (Charbonneau & al. 2013), so it is not surprising that is one of the most performed tasks by the workers. Moreover, brood-care had significant frequency in the larger colonies (A and B) and foraging/patrolling in the smaller one (C). Ants extensively present in the brood zone could have a higher reproductive status due to a close relationship with brood care and the production of eggs. This phenomenon is observed in *O. brunneus,* where social rank based on reproduction (proximity of allocated zone to the brood) is correlated to ovarian condition (Powell & Tschinkel 1999, Smith & al. 2012). In addition, a valid hypothesis for the significant frequency of foraging/patrolling behavior in colony C is that since this specific colony is smaller than the other ones, the activities of the colony are focused on food income in order to develop the colony ergonomically further. It is known that the capacity of flexibility in task allocation in ants appears to be very high, adjusting itself with the colony's needs (Robinson & al. 2009, Charbonneau & Dornhaus 2015). Colony size could influence this adaptation as evidenced in the literature, where smaller groups might be slower to answer to colony needs, and consequently the workforce gets more attached to a temporary task (such as foraging to supply food intake to the colony) than necessary (Pacala & al. 1996, Thomas & Elgar 2003, Jeanson & al. 2007, Holbrook & al. 2011). Moreover, the descriptions of the few dominant behaviors observed in *O. chelifer* are similar to the ones observed in *O. brunneus* (Powell & Tschinkel 1999). While dominance interactions could have a role in the division of labor (i.e., reinforcing dominance/submission among workers), they were rare and not extensively observed in *O. chelifer*, which suggests that dominant behaviors are not a crucial process or the only one responsible for the division of

labor in *O. chelifer.* Perhaps dominant interactions are important in a larger scale of time, or during few exceptions that demand a kind of control within the colony between workers (such as sudden changes in the food supply of the colony), or even in parallel with other kinds of behavioral control which do not demand physical contact (e.g. self-grooming). In addition, aggression (dominance interactions) and signaling by cuticular hydrocarbons enhanced by self-grooming are two possible modalities used to regulate reproduction in *O. chelifer*. They are both strong indicators of reproductive capacity (for aggression this was already discussed for vertebrates: Hrdy & Hrdy 1976; and insects: West-Eberhard 1967).

We observed that the division of labor of *O. chelifer* is organized through the significant presence of specialization within all colonies studied. The connection between specialization and subsequent better task performance is scarce and contradictory in the literature (O'Donnell & Jeanne 1992, Dornhaus 2008, Russell & al 2017, Santoro & al. 2019), but specialization must be important for other reasons within the colony organization. Specialization must be expected when you have interaction-based task allocation, such as observed for *O. brunneus* (Powell & Tschinkell 1999) and possibly to some degree (as already discussed) for *O. chelifer.* Behavioral roles are naturally restricted to particular zones of the colony, therefore, allocation to a particular zone, through dominance interaction (or other processes, such as fertility signaling by self-grooming), ensured role specialization. We hypothesized that the tasks which had more specialization across the colonies (brood care and foraging/patrolling) are the most affected by this kind of dynamics. Risky and costly tasks for social insects, such as solitary foraging/patrolling (O'Donnell & Jeanne 1992, Perry & al. 2015) are made by specialists in *O. chelifer*, that inserted in the context of interaction-based task allocation have a lower social rank (i.e., a higher distance of the brood zone). Brood care specialization may also be the result of a reproductive hierarchy, differently than foraging/patrolling, brood care and carrying brood are probably performed by workers with higher social rank (within the brood zone). Moreover, the skewed distribution of d'_{indv} values clearly show that some workers are more specialists than others, where the worker force of the colony is composed by a mix of generalists and specialists, such pattern appears to be widespread in social insects (e.g., Jandt & al. 2009, Santoro & al. 2019). A partial division of labor, where generalists coexist with specialists could be structurally important for the division of labor, for instance, such arrangement could generate more flexibility in the performance of tasks (Jandt & al. 2009). A mathematical model developed by D'Orazio & Waite (2007) demonstrates that errors committed by generalist workers are few compared with the success of the group in general, thus the inefficiency and error-prone generalists may also be a fundamental feature of many of the social insect systems, as observed in wasps (Forsyth 1978, Jeanne 1986, Karsai & Wenzel 2000) and stingless bees (Hofstede & Sommeijer 2006). Moreover, there is a lot of possible explanation for the presence of specialization within colonies of eusocial insects, for instance, increased spatial efficiency, as hypothesized for ants (Sendova & Franks 2005), or reduction of other switching costs (Chittka & al. 1997). It is also possible that specialization optimizes material flow in multistep tasks, (Jeanne 1986). Any of these processes may create colony-level fitness benefits the division of labor, and even without improvement in individual efficiency.

While the interpretation of significance for the network-level metrics is quite intuitive, for instance, a significant positive nestedness Z-score indicates that the network is nested, and a significant negative one indicates a value less nested than randomized networks, this is not the case for node-level metrics, such as the betweenness and degree centrality (in and out-degree) measures from tasks. A problem observed for centrality measures is that even a node with a negative Z-score, still have a higher centrality value than the other ones within the random network. Thus, we evaluate the significance of the comparison of the empirical centrality values (which were classified as bridges, inactivity hubs, and spreaders) to the random networks as simply a significant difference, rather than an attempt to interpret a positive or negative z-score. Information flow across tasks was intermediated by a set of different nodes (bridges), which varied accordingly to each colony. Self-grooming had a prominent role (i.e., bridge) in the larger colonies (A and B), as well as feeding in the smaller colony (Colony C) considering all workers and specialists, but only significant in the later ones. Differently, Charbonneau & al. 2013 observed that walking had higher betweenness centrality compared to all other tasks for *Temnothorax regutalus* being a significant bridge in our classification. This suggests that *O. chelifer* workers did not wander around the

nest as much to switching tasks (with exception of specialists in colony A, in which walking was a significant bridge as well). Self-grooming as a bridge between tasks gives evidence to the already discussed hypothesis of self-grooming as a reproductive regulator, with a crucial role for the maintenance of task allocation of the colony. Thus, self-grooming could be performed between tasks to ensure reproductive status between workers, for instance, maintaining nurses (i.e., workers performing brood care and carrying brood) as nurses, and foragers as foragers. In colony C, however, feeding is a significant bridge. This gives another perspective of the phenomena of higher food intake in colony C, which occur between other tasks and that the bridge role is adjustable to the colony needs. Specialists caused a more significant change in the dynamics of the colonies (compared to the random networks), which shows that specialists were more responsible for the dynamic patterns of information flow observed across the tasks of the colonies than generalists. Inactivity hubs and inactivity spreaders varied a lot across the colonies without a visible pattern of occurrence of tasks. However, the significant nodes of generalists and specialists varied greatly between them, and a pattern could not be observed. While such difference might not mean something other than a random structural organization, it could be an implicit view of the inherent difference between switching tasks by generalists and specialists.

Modularity analysis offers the great advantage of providing a quantitative method to identify modules of preferentially interacting workers and tasks and among tasks. WTNs presented significant modularity, which means the existence of exclusive interactions between workers and tasks. Modularity is thought to increase stability in ecological communities (May 1972; Krause & al. 2003; Teng & McCann 2004; however, see Pimm 1979). The existence of modules in WTNs might generate stability as well: if a worker is lost, another one from the same module could replace it minimizing the loss of a possible specialist. Differently, TTNs presented mixed results, with only colony B showing significant modularity. Among the modules of colony B, the association between them appears to be random, with the exception of brood care and carrying brood. They are usually performed intermittently between each other, frequently classified together as nursing behavior in the literature. The apparent randomness of the modular composition within TTNs could indicate the capacity of task flexibilization across the colonies of *O. chelifer*.

WTNs were not nested, and colony A even was significantly less nested than randomized networks. The lack of a nested structure may indicate that the division of labor dynamics is vulnerable to worker loss, although the relatively low degree of specialization present in the colonies (i.e., $H'_2 \leq 0.40$) might increase robustness (Pocock & al. 2012) and the workers within modules might fulfill similar interaction functions. Non-nested structures have been often observed in weighted ecological networks, and anti-nested patterns while rarer in nature (Staniczenko & al. 2013), were observed in interactions between fungi and plants (Bahram & al. 2014, Toju & al. 2014, 2015, Jacobsen & al. 2018), which could be explained by competitive exclusion (Toju & al. 2015). While competitive exclusion does not make sense in the context of division of labor, it could be analogous to the formation of strict modules without much connection with other nodes, since colony A had higher modularity compared to the other colonies. Some significant nested structures occurred in TTNs in colony A and C, considering all workers, while specialists in colonies A and C significantly had less nested structures than randomized networks in both cut-off conditions. Nestedness implies a hierarchy in the linking rules of the network system, so there is heterogeneity in the number of interactions among its elements. Furthermore, in ecological systems a nested structure is related to stability (e.g., Memmott & al. 2004, Burgos & al. 2007, Bastola & al. 2009). The presence of nestedness in task allocation of ants could be viewed as a steady process, where individual adaptation could slightly change due to the necessities of the colony at some specific interval of time. Therefore, workers concentrate on some specific behaviors, but new ones could be performed trough colonial necessity. This pattern is foreseen by some mathematical models in social insects (e.g., Wilson 1985, Robinson 1987a, 1987b, 1992, Robinson & Page 1988, Calabi 1988, Detrain & Pasteels 1991, 1992, Page & Robinson 1991, Bonabeau & al. 1996). However, when comparing specialists and generalists, it is expected that the behavioral repertoire of specialists is less diversified than generalists due to its own behavior (specialization in only certain tasks), which could be the reason for the existence of significant anti-nested or non-nested patterns among them.

The view of the ant colony as a complex system is not something new (Gordon 2010), but such view needs the use of a conceptual framework which capture simultaneously the complexity present within patterns of the colony as well as provides tools to analytically interpret the observed behavioral processes. The use of worker-task and task-task interactions constitute another layer of complexity for exploring the mechanisms that underlie individual variation within a network. It should be emphasized that this not exclude the assumption that interaction among workers (social interactions) are involved in task allocation, which could be analyzed together with worker-task and task-task interactions. The use of network concepts such as specialization, centrality, modularity and nestedness proved to be interesting for the description of the roles of the behaviors and workers in the organization of the division of labor. Furthermore, as previously suggested by Lewinsohn & al. (2006), simultaneously looking at several network patterns can substantially advance our understanding of the architecture of networks as well. A hindrance to the development of studies like this is the difficulty to account and quantify the real number of the tasks displayed by all the workers of the colony. Our study is still based on manual annotation of behaviors, while such approach is effective, it is time demanding and impractical for larger colonies or periods of time. Clever approaches such as the use of spatial fidelity for the determination of task performance (Mersch & al. 2013), while interesting to the study of several behavioral phenomena, it falls short to determine correct task performance or include behaviors that probably have an impact in colony organization (e.g., self-grooming, feeding). New improvements in approaches using automatic tracking by machine learning (which could encode and quantify behaviors; see Hong & al. 2015) could provide alternatives for this experimental gap. We expect even more holistic studies in the future, comparing species with different colony sizes to help the description of individual differences between workers.

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Tab. 1: List of possible behavioral acts observed in the colonies (divided in two classes; tasks and inactivity), the acronym used in the figures and tables, and detailed descriptions of each behavior.

Class	Behavioral acts	Acronym	Description
Task	Antennation	at	Contact with another worker with the antenna
	Brood care	bc	Manipulating brood
	Carrying brood	cb	Moving brood
	Carrying debris	cd	Carrying/manipulating a stone within the nest in any way
	Carrying food	cf	Manipulating food inside and outside the nest
	Feeding	fd	Feeding inside nest (brought back by foragers)
	Foraging/Patrolling	fp	Located outside of the nest (foraging)
	Grooming	g	Grooming another ant
	Be groomed	bg	Be groomed by another ant
	Self-grooming	sg	Grooming itself
	Walking	wl	Walking within the nest
Inactivity	Inactivity	in	When the ant is immobile within the nest (more than 10s)

Tab 2. Frequencies of the tasks observed in the colonies (A, B and C). The value (represented in %) is followed by the *P*-value (expressed as significant in bold) of the specific post-hoc *G-test*.

Tasks	Colony A (*N*= 3605)	*P-values*	Colony B (*N*= 1775)	*P-values*	Colony C (*N*= 368)	*P-Values*
wl	18.4% (N=122)	***P*<0.001**	22.7% (N=66)	***P*<0.001**	43.6% (N=62)	***P*<0.001**
sg	23.5% (N=156)	***P*<0.001**	27.6% (N= 80)	***P*<0.001**	22% (N= 31)	***P*<0.001**
at	1.5% (N=10)	ns	4% (N= 11)	ns	2.1% (N= 3)	ns
bg	1.6% (N=11)	ns	12.4% (N= 36)	ns	----------	----------
fd	21.7% (N=144)	***P*<0.001**	----------	----------	14.8% (N= 21)	***P*<0.001**
g	4% (N=26)	ns	6% (N= 17)	ns	----------	----------
bc	23.2% (N=154)	***P*<0.001**	19.3% (N= 56)	***P*<0.001**	0.7% (N= 1)	ns
cb	2% (N=13)	ns	7% (N= 22)	ns	----------	----------
cd	1.6% (N=11)	ns	0.3% (N= 1)	ns	----------	----------
fp	1.6% (N=11)	ns	0.3% (N= 1)	ns	14.8% (N= 21)	***P*<0.001**
cf	0.09% (N=6)	ns	----------	----------	0.2% (N= 3)	ns

Tab 3. Betweenness centrality values from the TTNs of all the colonies (A, B and C). The tasks (nodes) of all workers, generalists and specialists are considered. The tasks considered bridges due to betweenness centrality values above the third quartile of the data (<75%), The Z-score and *P*-values (expressed as significant in bold) are also exposed.

All workers	A	Z-score	*P*-values	B	Z-score	*P*-values	C	Z-score	*P*-values
wl	**14**	-1.49	0.13	0	-0.62	0.53	5	1.19	0.23
sg	**36**	0.91	0.36	**17**	1.03	0.29	0	0	1
g	0	0	1	**8**	**0.05**	0	---	----------	----------
bg	0	0	1	5	-0,14	0.88	---	----------	----------
bc	**14**	1.92	**0.05**	2	0	0.99	0	0	1
cb	0	0	1	3	1.77	0.07	---	----------	----------
fd	0	0	1	---	----------	----------	**6**	-0,93	0.35
cf	0	0	1	---	----------	----------	0	----------	----------
fp	0	0	1	0	0	1	5	-1,26	0.20
cd	0	0	1	---	----------	----------	---	----------	----------
at	---	---------	----------	0	0	1	0	0	1
Generalists	A	Z-score	*P*-values	B	Z-score	*P*-values	C	Z-score	*P*-values
wl	**6**	-1.15	0.24	0	0	1	**9**	-0.53	0.58
sg	**23**	0.85	0.39	**20**	0	1	0	0	1
g	0	0	1	0	0	1	---	----------	----------
bg	0	0	1	0	0	1	---	----------	----------
bc	**11**	0	1	**9**	0	1	0	0	1
cb	0	0	1	0	0	1	---	----------	----------
cd	0	0	1	---	----------	----------	---	----------	----------
cf	0	0	1	---	----------	----------	0	0	1
fd	0	0	1	---	----------	----------	2	-0,65	0.51
fp	---	---------	----------	---	----------	----------	**13**	1.50	0.13
at	---	---------	----------	---	----------	----------	0	0	1
Specialists	A	Z-score	*P*-values	B	Z-score	*P*-values	C	Z-score	*P*-values
wl	**3**	-3.35	**0.0007**	0	-0,9	0.36	4	0.38	0.70
sg	**4**	-2.7	**0.006**	**16**	4.24	***P*<0.0001**	3	0.06	0.95
g	0	0	1	**14**	1.12	0.25	---	----------	----------
bc	0	-0.65	0.51	0	0	1	---	----------	----------
cb	0	-0.67	0.50	13	1.52	0.12	---	----------	----------
fp	0	-1.16	0.24	0	0	1	4	1	**0**
fd	0	-1.83	**0.05**	---	----------	----------	**7**	1	**0**
bg	---	---------	----------	5	-0,94	0.34	---	----------	----------
at	---	---------	----------	0	0	1	0	1	1
cf	---	---------	----------	---	----------	----------	3	1	**0**

Tab 4. Degree centrality values (In-degree) from the TTNs of all the colonies (A, B and C). The tasks (nodes) of all workers, generalists and specialists are considered. The tasks considered inactivity hubs due to in-degree centrality values above the third quartile of the data (<75%), The Z-score and *P*-values (expressed as significant in bold) are also exposed.

All workers	A	Z-score	*P*-values	B	Z-score	*P*-values	C	Z-score	*P*-values
wl	**37**	1.58	0.11	13.5	-0.56	0.56	**11.9**	0.71	0.47
sg	**36.3**	1.33	0.18	**27.2**	1.25	0.20	8.9	0.03	0.97
at	3.3	-1.81	0.06	13.6	-0.59	0.55	2.9	-1.64	0.09
g	**18.2**	0.28	0.77	**17.6**	**0.001**	0.99	-----	----------	----------
bg	12.6	-0.42	0.57	10.3	-0.68	0.49	-----	----------	----------
bc	18.1	0.31	0.75	17.3	-0.13	0.88	0	0	1
cb	11.7	-0.81	0.41	7.3	0.89	0.37	-----	----------	----------
cd	4.3	-1.29	0.19	2.1	-0.7	0.48	-----	----------	----------
fp	4.5	-1.23	0.21	3.2	0.19	0.84	8.8	0.006	0.99
cf	2.8	-0.47	0.63	-----	----------	----------	7.3	0.70	0.48
fd	-----	----------	----------	-----	----------	----------	**8.8**	0.006	0.99
Generalists	A	Z-score	*P*-values	B	Z-score	*P*-values	C	Z-score	*P*-values
wl	**16.3**	0.58	0.56	11.5	-0.01	0.98	**7.4**	0.31	0.75
sg	**27.1**	-3.11	**0.001**	11.5	0.03	0.96	5.5	0.10	0.91
g	16.2	1.87	0.06	9.2	-0.89	0.37	-----	----------	----------
bg	8.1	-0.46	0.63	4.2	-0.42	0.67	-----	----------	----------
bc	16.1	0.42	0.66	**12.3**	2.36	**0.01**	0	0	1
cb	8.3	-2.88	**0.003**	6	-2.3	**0.02**	-----	----------	----------
cd	4.1	-1.24	0.21	-----	----------	----------	-----	----------	----------
cf	2.5	-0.42	0.67	-----	----------	----------	2.1	0.71	0.47
fd	15.1	0.01	0.98	-----	----------	----------	5.1	-4.61	***P*<0.0001**
fp	-----	----------	----------	-----	----------	----------	**6.9**	-1.54	0.12
at	3.2	-1.73	0.08	2.8	-1.81	0.07	-----	----------	----------
Specialists	A	Z-score	P-values	B	Z-score	P-values	C	Z-score	*P-values*
wl	**26.5**	2.13	**0.03**	13.2	-3.49	**0.0004**	**6.9**	1.53	0.12
sg	18.3	0.98	0.32	**22.7**	2.92	**0.003**	**8**	0.45	0.64
g	3.3	-1.56	0.11	**17.2**	8.78	***P*<0.0001**	-----	----------	----------
bc	7.3	-0.47	0.63	13.1	3.18	0.001	-----	----------	----------
cb	5.7	-1.44	0.34	7.1	-0.62	0.53	-----	----------	----------
fp	4.1	-0.99	0.31	-----	----------	----------	3.1	-1.02	0.30
fd	14.4	0.43	0.66	3.2	-5.25	***P*<0.0001**	**7.5**	-0.11	0.90
bg	4.4	-0.69	0.48	10.1	3.56	0.003	-----	----------	----------
at	1.2	-1.55	0.11	13.4	11	***P*<0.0001**	2.8	-1.44	0.14
cf	0	0	1	-----	----------	----------	4	5.17	***P*<0.0001**

Tab 5. Degree centrality values (Out-degree) from the TTNs of all the colonies (A, B and C). The tasks (nodes) of all workers, generalists and specialists are considered. The tasks considered inactivity spreaders due to out-degree centrality values above the third quartile of the data (<75%), The Z-score and *P*-values (expressed as significant in bold) are also exposed.

All workers	A	Z-score	*P*-values	B	Z-score	*P*-values	C	Z-score	*P*-values
wl	13.5	-4,64	***P*<0.0001**	6.5	-3,39	***P*<0.0001**	6.5	0.64	0.51
sg	**24.5**	-2,49	**0.01**	11.1	-2,58	**0.009**	7	0.08	0.92
at	9.3	-0,44	0.65	9.4	-1,14	0.25	4.1	-1,61	0.10
g	17.5	0.05	0.95	**20.3**	-0,1	0.91	-----	----------	----------
bg	11.7	0.58	0.56	17.5	1.17	0.24	-----	----------	----------
bc	**21.5**	1.48	0.14	**20**	2.18	**0.02**	2.5	-3,34	**0.0008**
cb	14.1	1.45	0.14	17.8	17.8	0.20	-----	----------	----------
cd	9.9	-0,17	0.85	4.7	1.59	0.11	-----	----------	----------
fp	10.3	-0,007	0.99	4.8	1.73	0.08	**11**	0.01	0.98
cf	10.7	1.89	**0.05**	-----	---------	----------	6.9	0.62	----------
fd	**22.6**	3.47	**0.0005**	-----	---------	----------	**12.6**	1.67	0.09
Generalists	A	Z-score	P-values	B	Z-score	P-values	C	Z-score	*P*-values
wl	11.6	-4.21	***P*<0.001**	6.5	-3.39	***P*<0.0001**	3.6	-2.54	**0.01**
sg	**18**	-4.34	***P*<0.001**	11.1	-2.58	**0.009**	4.5	-1.28	0.19
g	12.2	0.03	0.96	**12**	0.35	0.72	-----	----------	----------
bg	10.2	0.61	0.53	11.4	1.61	0.10	-----	----------	----------
bc	**19**	1.61	0.10	**13**	2.88	**0.003**	1.8	0.01	0.99
cb	12.6	-1.05	0.29	3.5	-4.16	***P*<0.0001**	-----	----------	----------
cd	4.4	1.27	0.20	-----	---------	----------	-----	----------	----------
cf	4.5	1.27	0.20	-----	---------	----------	1.7	-0.22	0.82
fd	**19**	3.21	**0.001**	-----	---------	----------	**7.2**	-1.3	0.19
fp	-----	----------	----------	-----	---------	----------	**8.2**	1.33	0.18
at	5.5	-0.36	0.71	-----	---------	----------	-----	----------	----------
Specialists	A	Z-score	P-values	B	Z-score	P-values	C	Z-score	P-values
wl	**11.6**	-4.17	***P*<0.0001**	6.5	-3.48	**0.0005**	**6.5**	1.57	0.11
sg	**15.4**	-1.53	0.12	11.1	-2.6	**0.01**	5.1	-0.45	0.64
g	**11.8**	0.56	0.57	**20.3**	-2.54	**0.01**	-----	----------	----------
bc	7.1	1.30	0.19	15.4	2.05	**0.03**	-----	----------	----------
cb	3.7	-1.28	0.19	17	2.76	**0.005**	-----	----------	----------
fp	7.9	1.78	0.07	-----	---------	----------	4.7	-3.25	**0.001**
fd	8.5	2.30	**0.02**	-----	---------	----------	**7.8**	7.80	***P*<0.0001**
bg	9.9	1.11	0.26	13.8	1.21	0.12	-----	----------	----------
at	5.3	-0.08	0.93	9.4	-1	0.30	3.9	4.94	***P*<0.0001**
cf	4.1	1.37	0.16	-----	---------	----------	4.3	5.88	***P*<0.0001**

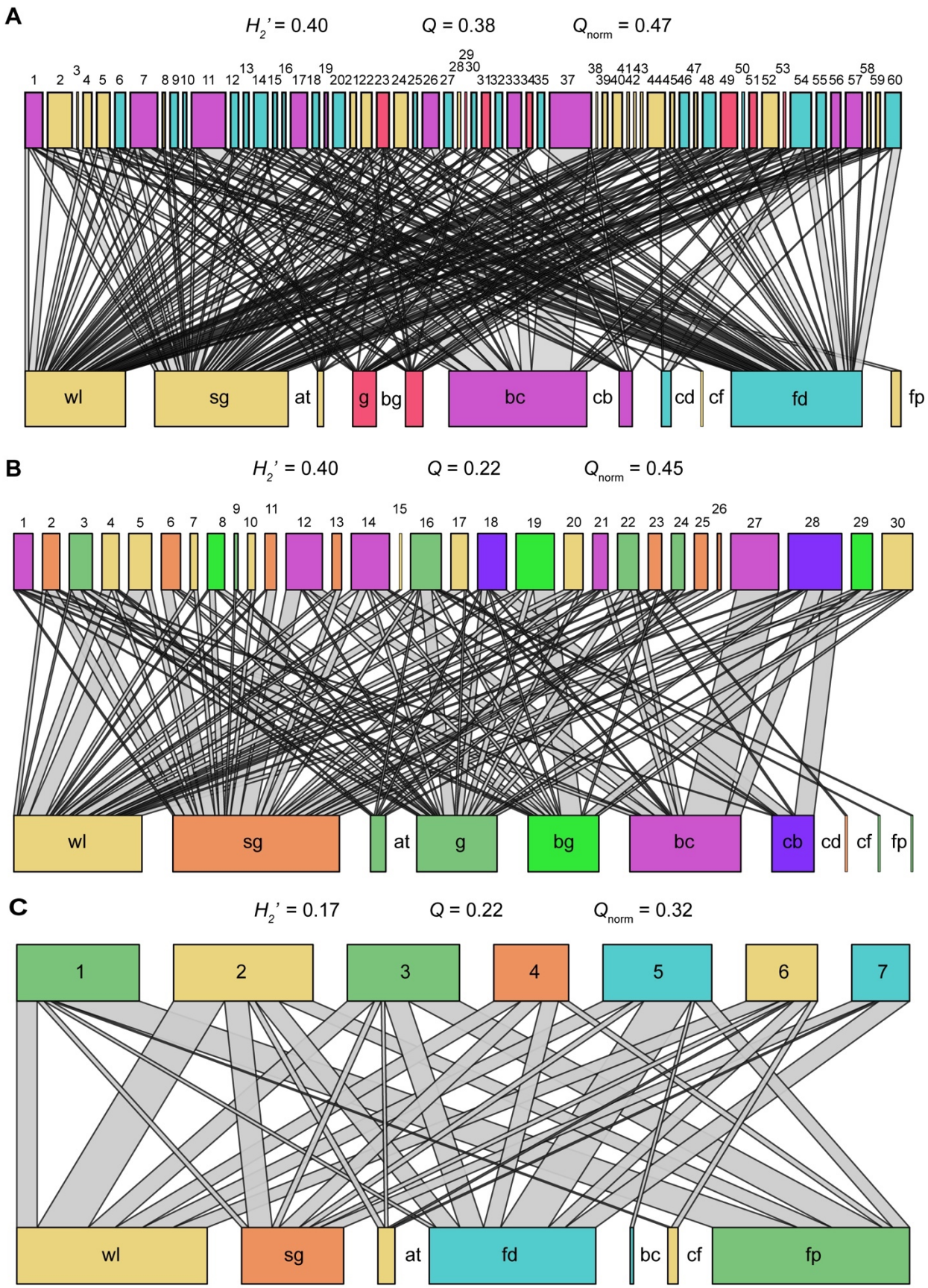

Fig. 1: TWNs graphs from colony A, colony B and colony C. Upper and lower rectangles represent workers and tasks, respectively. The width of each rectangle is proportional to the number of acts and the width of link indicates the frequency of interactions between tasks and workers. For each network, numbers in

upper rectangles represent worker identities. For each network, the value of H_2', Q, and $Qnorm$ are given. The different modules of workers and tasks are identified in different colors.

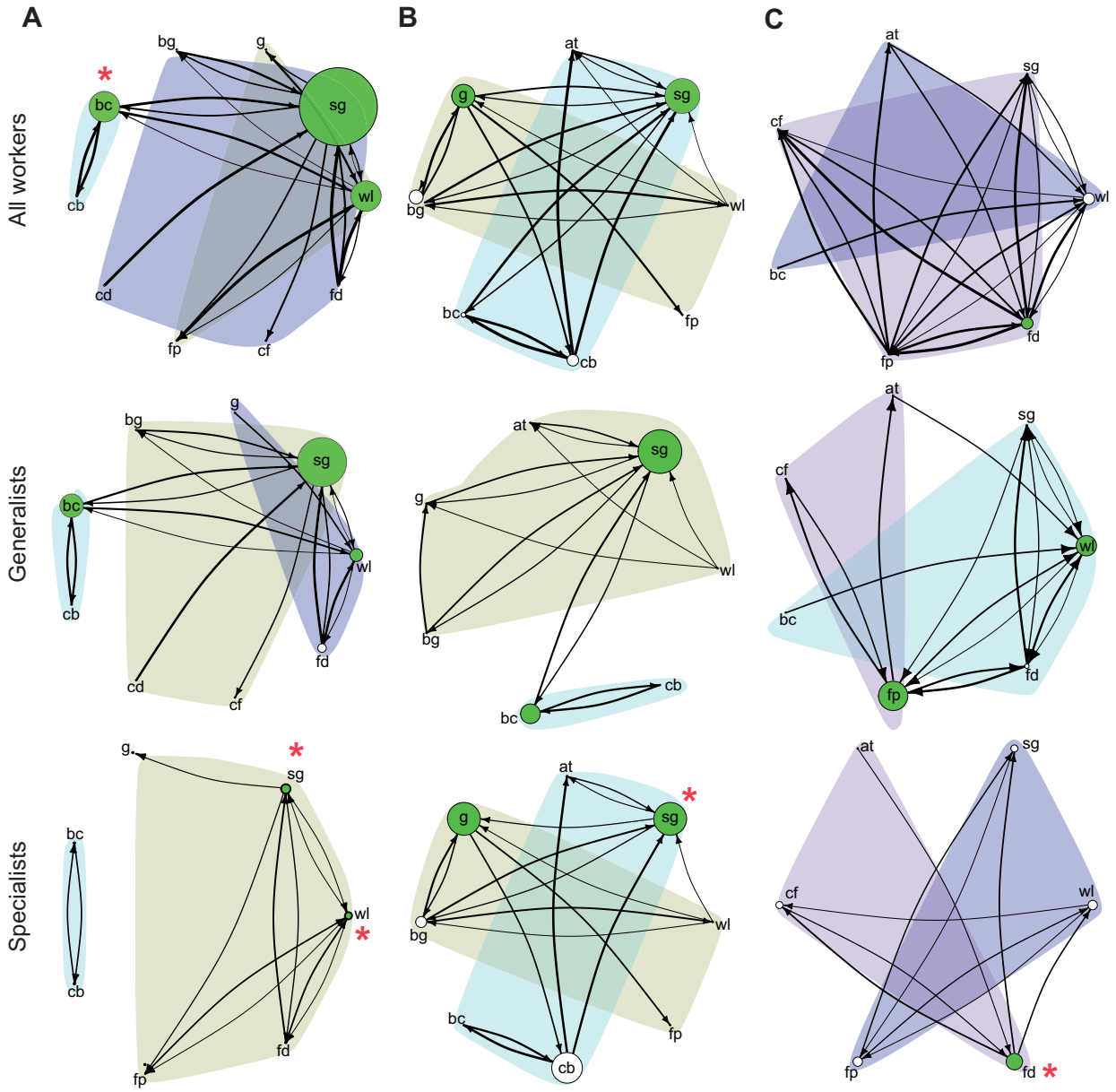

Fig. 2: TTNs graphs from colony A, colony B and colony C. The nodes represent tasks and the links between them the interactions between tasks from the workers. The width of each link indicates the frequency of interactions between tasks and workers. The size of the nodes represents the betweenness centrality values of the nodes (the larger the node, the higher the betweenness centrality value obtained), nodes colored as green are bridges (i.e. nodes with betweenness centrality above the third quartile of the data, <75%). Bridges signaled with a red asterisk (*) are statistically significant compared to the random networks. The different modules of tasks are identified in different colors.

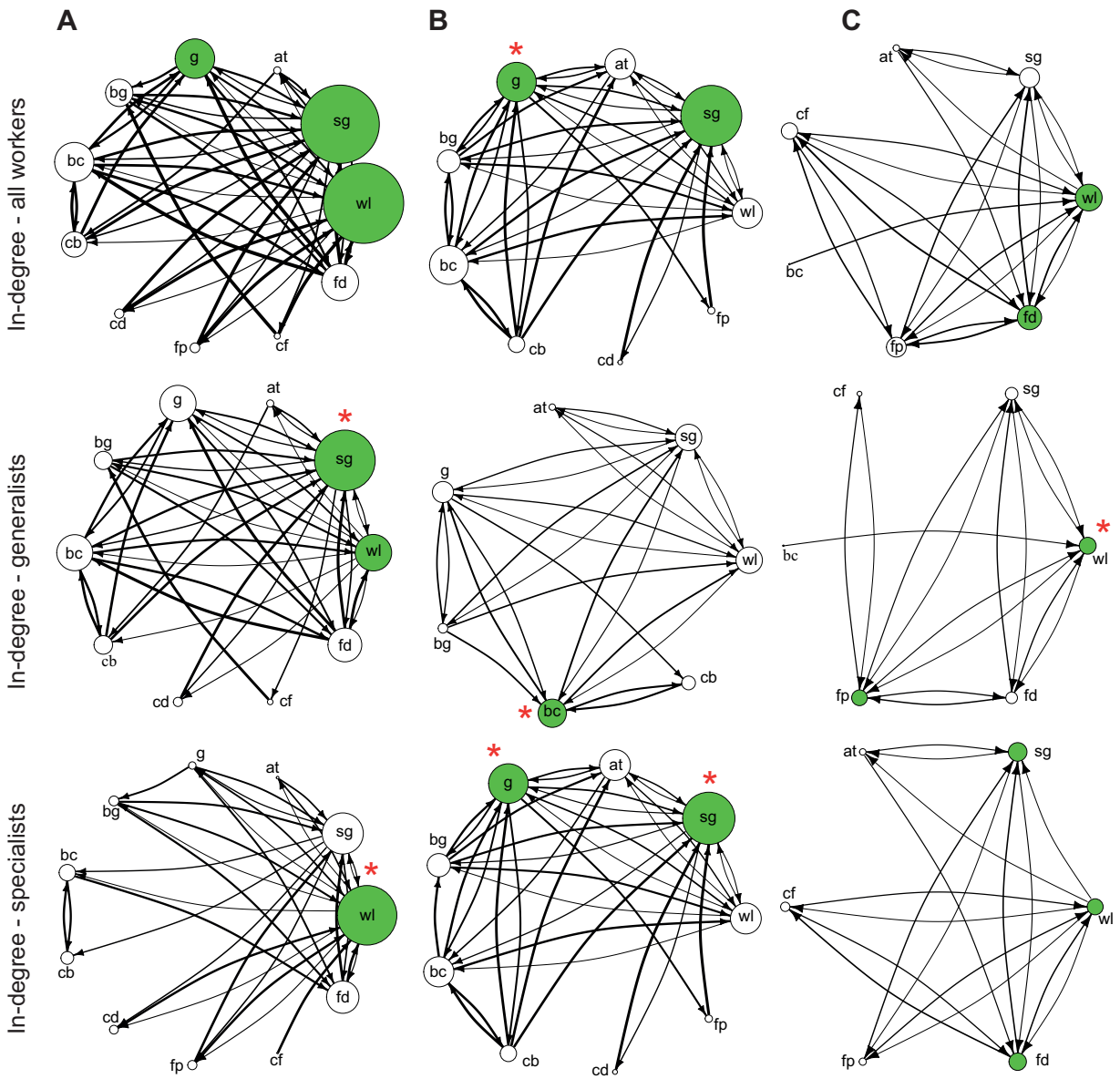

Fig. 3: TTNs inactivity in-degree graphs from colony A, colony B and colony C. The nodes represent tasks and the links between them the inactivity between tasks from the workers. The width of each link indicates the frequency of inactivity between tasks and workers. The size of the nodes represents the in-degree centrality values of the nodes (the larger the node, the higher the in-degree centrality value obtained), nodes colored as green are inactivity hubs (i.e. nodes with betweenness centrality above the third quartile of the data, <75%). Bridges signaled with a red asterisk (*) are statistically significant compared to the random networks. The different modules of tasks are identified in different colors.

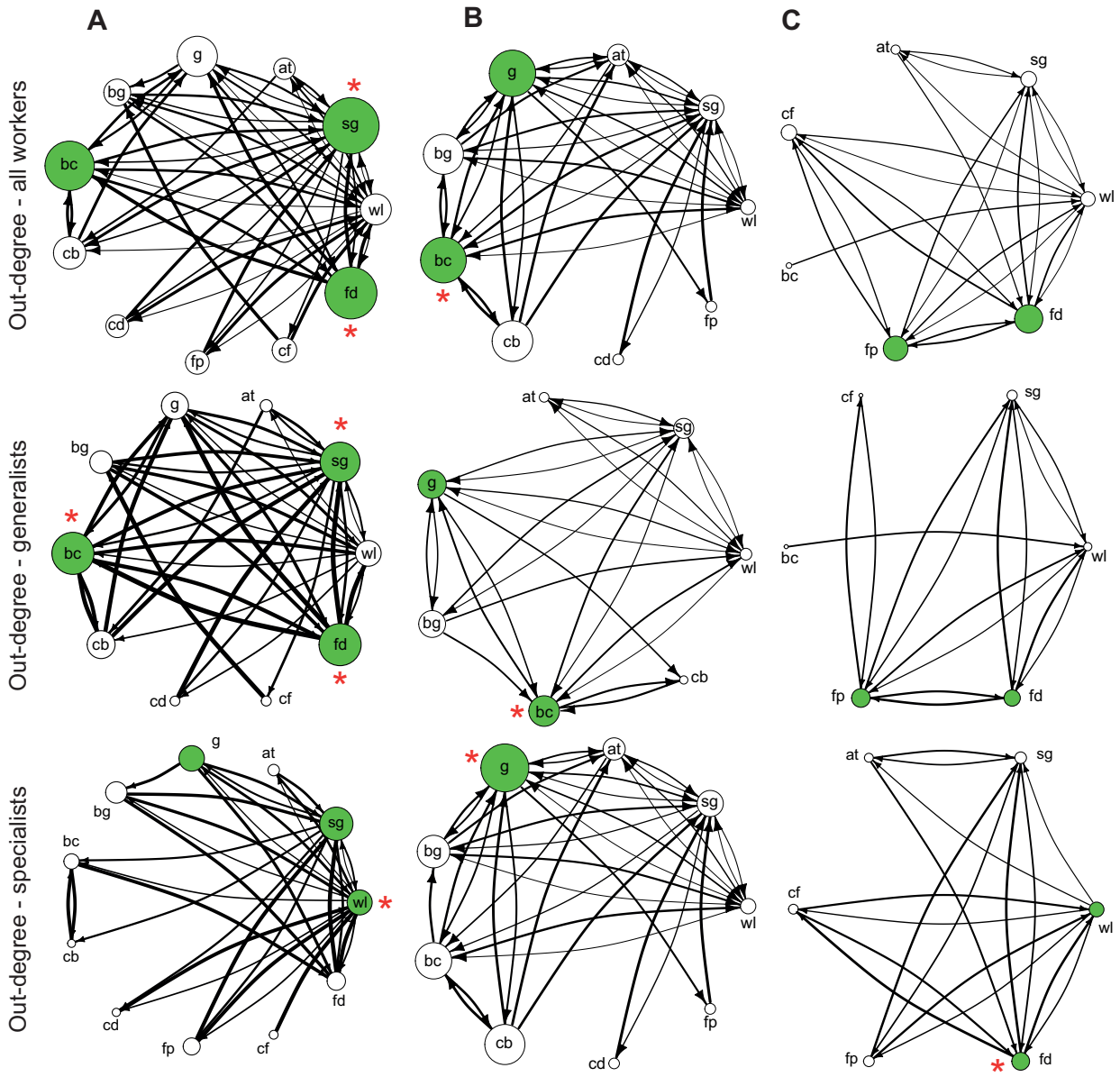

Fig. 4: TTNs inactivity out-degree graphs from colony A, colony B and colony C. The nodes represent tasks and the links between them the inactivity between tasks from the workers. The width of each link indicates the frequency of inactivity between tasks and workers. The size of the nodes represents the out-degree centrality values of the nodes (the larger the node, the higher the out-degree centrality value obtained), nodes colored as green are bridges (i.e. nodes with betweenness centrality above the third quartile of the data, <75%). Bridges signaled with a red asterisk (*) are statistically significant compared to the random networks. The different modules of tasks are identified in different colors.

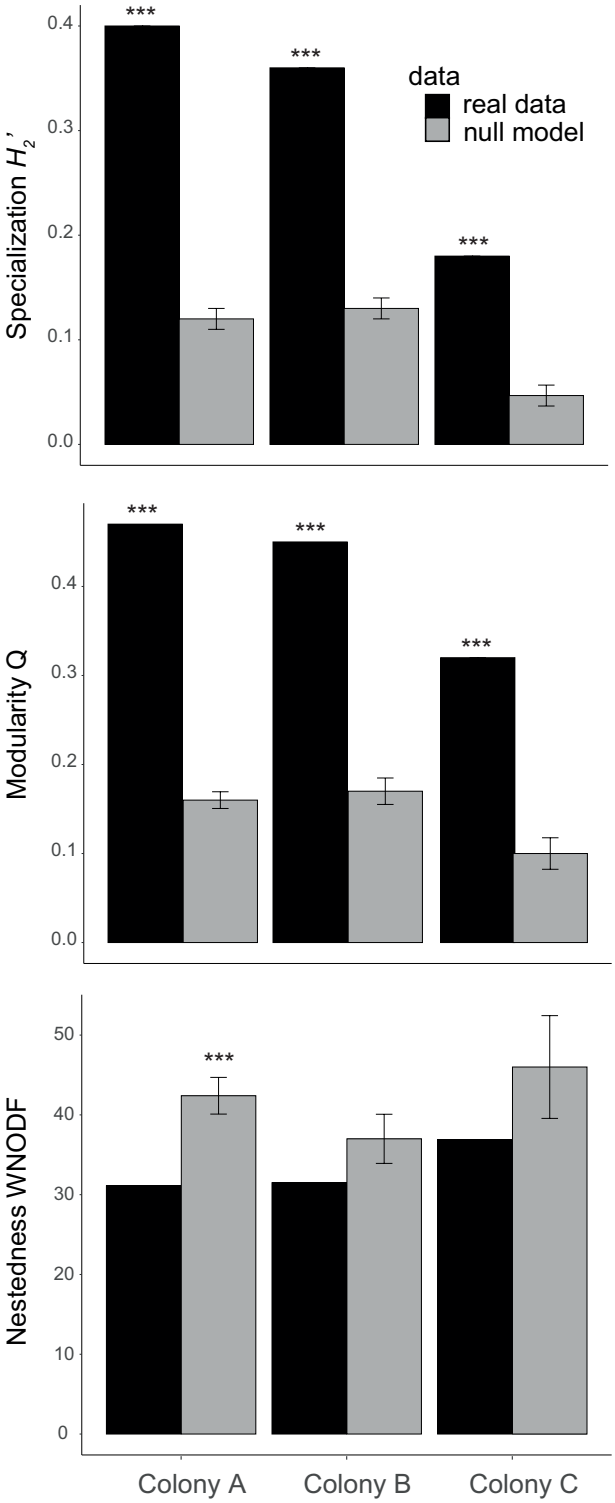

Fig. 5: Network specialization (H_2'), modularity (Q) and weighted nestedness (WNODF) for WTNs from the colonies (A, B and C). Black bars represent the original networks, while grey bars represent networks randomized and the respective standard deviation (SD). The significant statistical differences (Z-score) were signaled by *, ** and *** (p values less than 0.05, 0.01 and 0.001, respectively), non-statistical values were signaled by ns (i.e. non-significant). The asterisks (*) above the bars mean significant differences between the original and the randomized networks or vice and versa.

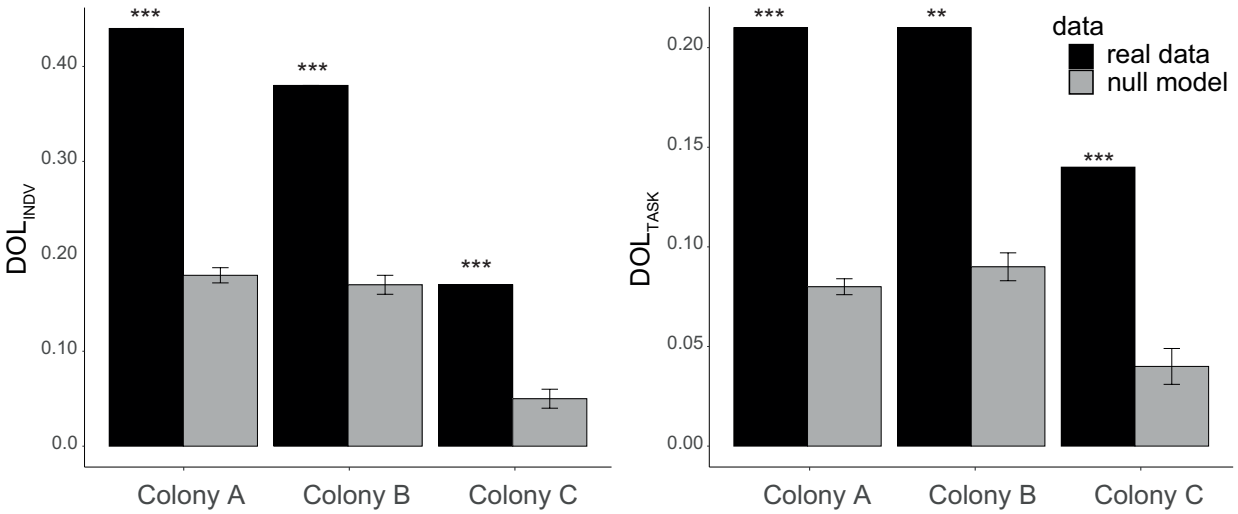

Fig. 6: Network DOL index (DOL_{indv} or DOL_{task}) for WTNs from the colonies (A, B and C). Black bars represent the original networks, while grey bars represent networks randomized and the respective standard deviation (SD). The significant statistical differences (Z-score) were signaled by *, ** and *** (*p* values less than 0.05, 0.01 and 0.001, respectively), non-statistical values were signaled by ns (i.e. non-significant). The asterisks (*) above the bars mean significant differences between the original and the randomized networks or vice and versa.

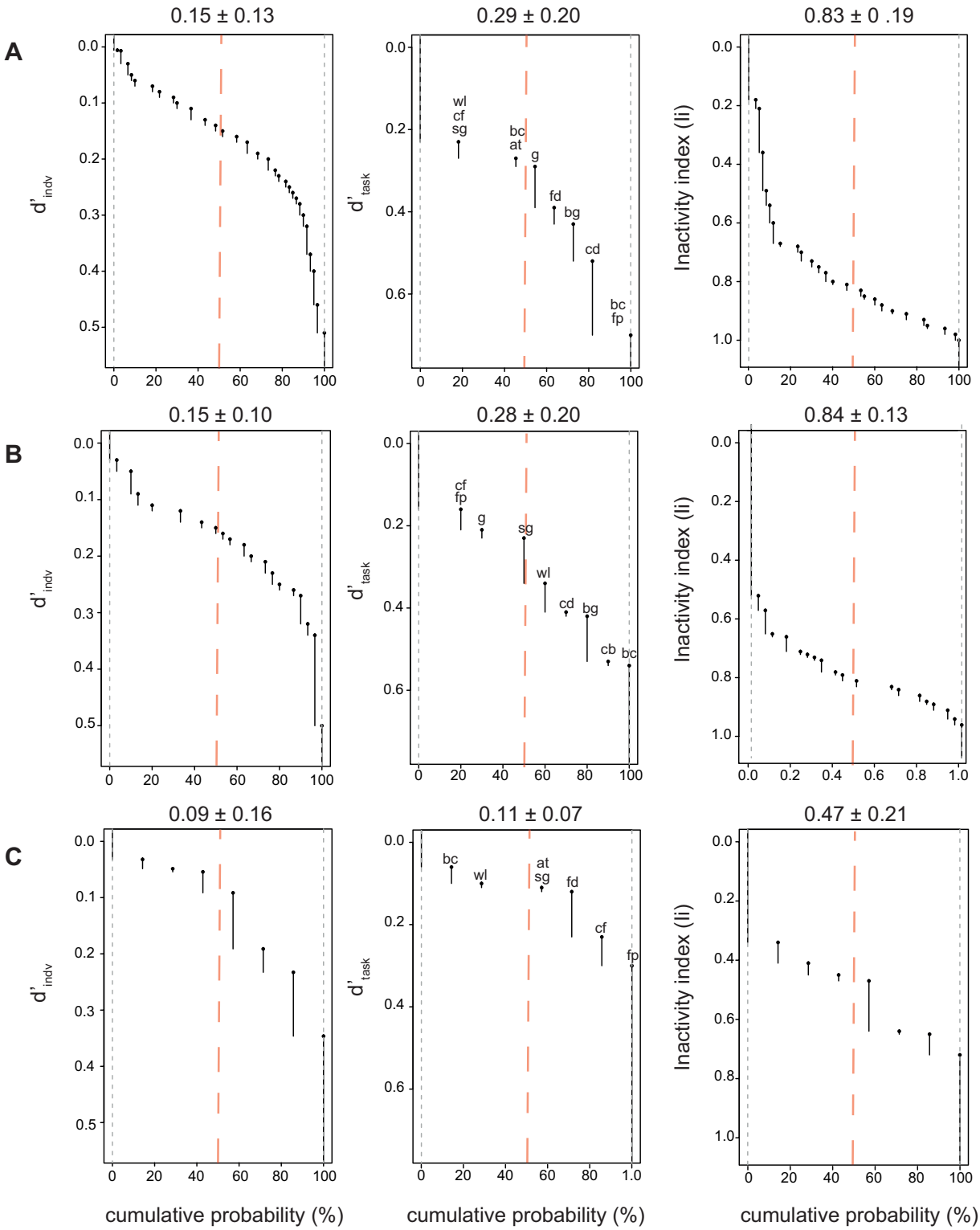

Fig. 7: Data distribution (empirical cumulative distribution) of d'_{indv}, d'_{task} and *Ii* values for WTNs from the colonies (A, B and C) fr each correspondent worker or task. The results were indicated with the median and interquartile range (IQR) of each metric. The numeric values in the d'_{task} are followed by each specific acronym representing the tasks considered (presented in the Tab. 1).

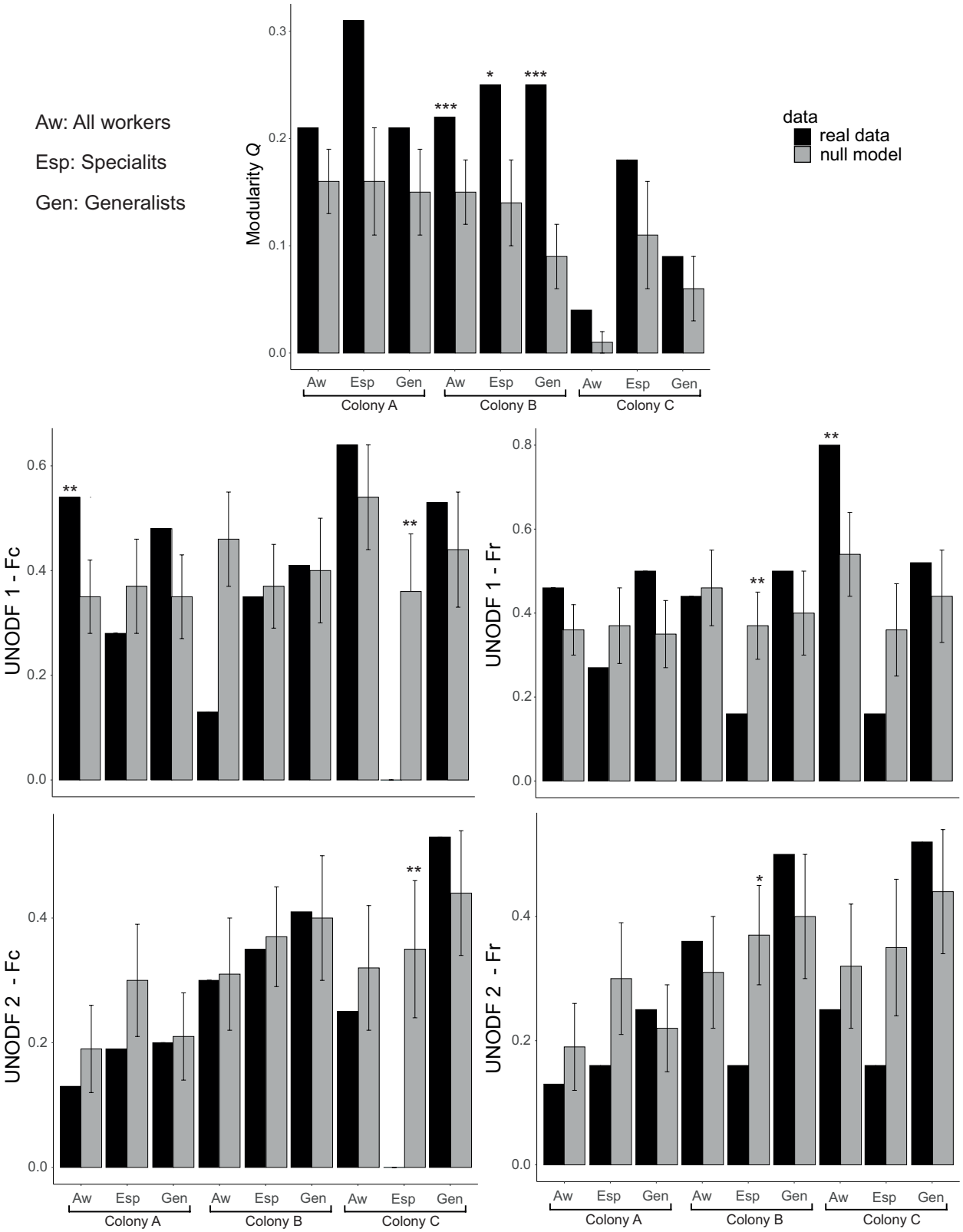

Fig. 8: Network modularity (*Q*) and weighted nestedness (UNODF) for TTNs from the colonies (A, B and C). Black bars represent the original networks, while grey bars represent networks randomized and the respective standard deviation (SD). UNODF 1 is the metric calculated without a cut-off and UNODF 2 is the metric calculated with a cut-off of 10%. The significant statistical differences (Z-score) were signaled by *, ** and *** (*p* values less than 0.05, 0.01 and 0.001, respectively), non-statistical values were signaled by ns (i.e. non-significant). The asterisks (*) above the bars mean significant differences between the original and the randomized networks or vice and versa.