Bipartite network analysis of task-ant associations reveals task groups and absence of colonial diurnal activity

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Abstract
Division of labour is the key factor leading to higher-order systems such as cooperative animal groups. How division of labour is achieved without a central control is one of the most fascinating questions in behavioural ecology and complex systems science. Social insects are one of the best examples of complex self-organised systems through local interactions. However, it is difficult to comprehensively understand division of labour due to the chronological and individual variation in behaviours, and the differences between social environments. Thus, it is imperative to quantify individual behaviours and integrate them into colony levels. Here, we demonstrate that network analyses on individual-behaviour relationships can be valid for characterising the task allocation patterns. We recorded the behaviours of all individuals with verified age in colonies of monomorphic ant and analysed the individual-behaviour relationship at individual, sub-network, and network-levels. We detected the "task groups" including subsets of individuals and behaviour, and the patterns of task groups were consistent throughout the day. We also found a relationship between the age and the characteristics of individuals within the network. These findings suggest that bipartite network analyses can untangle the complex task allocation patterns and provide novel insights into understanding how division of labour is achieved.

Keywords
Network analysis, Division of labour, Community detection, Social insect, *Diacamma*, Age polyethism

1. Introduction

How the simple elements at a lower level, for example, a single cell and an individual, can evolve to higher-level systems, for instance, multicellular organisms and animal groups, through natural selection has been a central question in evolutionary biology [1]. Such systems often exhibit division of labour through efficient task allocation, in which different elements perform different tasks [2]. It has been considered that division of labour can be a primary advantage for social evolution [3, 4]. Therefore, it is crucial to understand how they achieve division of labour.

Social insects are one of the most sophisticated examples of division of labour because individuals exhibit a reproductive division of labour between queen(s) and workers; and among workers various tasks are allocated. For example, task allocation for nursing, foraging, nest defence, or cleaning is accomplished without central controls in a colony [5-7]. To elucidate how such colonies achieve task allocation through interactions among individuals, we need to reveal the behavioural rules underlying it. However, it is difficult not only to determine the behavioural rules but also to describe and quantify the individual behavioural patterns. The difficulty in measuring these parameters arises from the fact that a large number of individuals comprise a colony, and that the behavioural differences depend on internal states, experience, colony size, demands from the nestmates, or environment, that can change across time [8-14]. Moreover, colonies generally consist of individuals with different characteristics such as morphology, age, physiology, and spatial position [15-17]. Therefore, the methods to extract useful information from such complexity (i.e. many elements and high variation) and to integrate them to understand the complex social systems are strongly required.

Over the past two decades, network analysis has developed as a useful tool for analysing complex systems in various fields, including ecology, social science, and animal behaviour [10, 18-27]. The network perspective assumes that systems are comprised of nodes (i.e. elements) and links (i.e. the relationship between elements). The quantification of networks makes it possible to provide the information on the structure of systems or characteristics of each individual within the network. Previous studies on ant interaction networks revealed the individual variation in the number of links [23, 28], the module (i.e., subnetwork) which is a functional unit within a colony depending on tasks such as foraging and nursing [16], and the spreading dynamics of information, food, or disease [24-30]. These illustrated examples suggest that network analyses can inform about characteristics at various scales, from individuals to subnetwork and colony-level, based on complex datasets, and may provide new insights into understanding social insects.

Most network analyses in animal societies, show relationships among individuals within a group, although it can be applied to any elements and relationships. A previous study suggested that the task allocation patterns in social insects can be described as a bipartite network (figure 1), which has two node classes and the links are established only between nodes in different classes [31, 32]. Workers are connected to the tasks they are engaged in, and tasks are linked to several workers that perform them [31, 32]. In the present study, we demonstrate that bipartite network analysis could be an effective approach to characterise the task allocation in social insect colonies. In particular, we focused on a multi-level scale (network, subnetwork, and individual) for individual-task relationships through the network analysis.

First, it is important to note that the number of task groups within a colony is one of the fundamental factors in task allocation research. [10] suggested that "task performance is a continuous variable and hence neither dichotomous nor discrete". In other words, most individuals show several behaviours, and there may be few specialist individuals. Moreover, as the classification of tasks was dependent on arbitrary criteria, it is unclear what distinct task groups are [15]. In the present study, we propose that a community detection method can be valid for the classification of task groups. By using this, we quantify the degree of specialisation within the colony, detect subnetworks (modules), and obtain the information about the number

of task groups (figure 1). Once the network was divided into subnetworks, we investigated which tasks and individuals can be united (figure 1c).

Moreover, finding the task groups can reveal the subnetwork structure, namely, the degree of task group connection with each other. For example, the workers' tasks could change in the order of brood-care, guarding, and forage, or brood-care, cleaning, and forage [16, 33]. In these cases, the task group of brood-care may be less connected with that of the forage group.

Finally, an individual's role within the network can be unveiled by calculating metrics for each node. In particular, revealing the connection of individual characteristics, such as age, or body size, with the individual role within a network is crucial for understanding the mechanisms of task allocation. For example, we can investigate whether individuals belonging to the same task groups share some common individual characteristics. Here, we focus on age as a biological trait because behavioural variations in social insects are largely generated by age differences [4]. Moreover, we can compare the metrics obtained from network analysis among individuals with different characteristics (e.g. caste) or different networks (e.g. year, season, colony, and the time of day).

In the present study, we observed all colonial individuals with verified age in a ponerine ant (*Diacamma* sp.) and analysed individual-task networks. We quantitatively analysed three distinct levels: the network, subnetwork, and node (individual level) and addressed the questions of how task groups were distributed among workers, using network analysis, and revealed the roles of workers. We also analysed whether the age of individual or the time of day affects the pattern of task groups. This study shows that network analysis for individual-task networks can lead to a comprehensive approach for understanding task allocation in complex social systems.

2. Materials and Methods

2.1. Insects

The ponerine ant, *Diacamma* sp., from Japan (the only species of the genus *Diacamma* found in Japan) is a monomorphic ant. The colony size of this ant species is 20 to 200 workers. Young workers (typically 0–30 days of age) stay inside the nest and care for the brood (i.e. eggs, larvae, and pupae), whereas workers older than 30 days of age start to forage outside the nest for various terrestrial invertebrates [34]. The lifespan of individuals is about a year in this focal ant [35].

2.2. Colony setup

Five colonies of *Diacamma* sp. were excavated in Sueyoshi Park (Naha) and Kenmin-no mori (Onna), Japan, and maintained in the laboratory in artificial plastic nests that were filled with moistened plaster as previously described [36]. The colonies were maintained at 25 °C under 16L/8D (light phase, 07:00–23:00). By covering the top of the nest with a red film, the inside-nest environment was kept under dim red light. Reared colonies were fed chopped mealworms and crickets three times a week. The colonies consist of a single mated-female (gamergate) and workers. Colony size was 38–167 individuals (including queen); however, data could not be obtained for some individuals because of the loss of tags or death (table S1). To understand the relationship between the role of individuals in a colony and the age, we marked newly eclosed workers about once a month to record the age of each individual. Detailed information about the colonies is provided in table S1.

2.3. Observation of behaviour

To keep the uniqueness of each individual, we attached 2D barcode tags (2.0 mm × 2.0 mm) to individuals by instant glue (3M Scotch, liquid glue multipurpose, Product No. 7004). The photos of the arena including the colony and foraging area were taken every second with a CCD camera (FLIR©Grashopper®3, GS3-U3-123S6C-C, 3000 × 4000 pixels) under a constant dim-red light. Experiment nests filled with moistened plaster (20.0 × 10.0 × 5.0 cm) had an entrance (diameter = 1.0 cm) to connect the foraging arena (37.0 × 25.0 × 11.5 cm). The details of the experimental setup are provided in figure S1. During the observation period, we fed crickets at random times and provided water at all time.

Following the identification of individual ants using a tag-based tracking system (BugTag, Robiotec Ltd.), we conducted five-minute visual observations every 3 hours (a total of 8 daily observations) for consecutive 3 days and recorded one behavioural state by an observer analysing the videos. Behaviour in each observation was classified as either inactive (completely immobile), walking (active), egg-care, larva-care, pupa-care, and foraging (outside the nest) following a previous study [34]. In our definition, inactive was defined as completely immobile during the 5 minute observation. Walk indicates an active state staying inside the nest, but not engaging in brood-care and foraging. It included self-glooming, allo-glooming, eating inside the nest, trophallaxis [37], and aggressive behaviour [23]. Behaviour as brood-care included carrying the brood or performing the brood grooming. Note that the colonies had different brood conditions, shown in table 1. Foraging included walking outside the nest, carrying food, eating food and drinking water.

2.4. Constructing bipartite networks

We constructed a bipartite network with weights for each colony from the behavioural data as defined above (figure 1*a,b*). The nodes represent ant individuals and behaviours, and the links represent the behaviour of an individual (figure 1*b*). Note that the behaviour data was separated by day (i.e. day 1, day 2, and day 3) to examine the consistency of patterns across different days (figure 1*a*). In particular, it is considered that the fine resolution for constructing networks in division of labour is 24 hours [15, 16]. The weights on the links in each day represent the

number of executions of the behaviour (maximum 8 per day). The row and column of an adjacency matrix for a colony represent individuals and behaviours (e.g. foraging of day 1, foraging of day 2, foraging of day 3, nursing of day 1), respectively (figure 1*a*). The detailed information of each network is shown in table 1.

2.5. Community detection in bipartite network

To quantify the modules which is a functional units, inindividual-behaviour networks, we adopted community detection methods which can classify the node sets into sub-networks through maximising modularity [38, 39]. Modularity indicates the degree of the link density within a given set of nodes and the link sparsity between nodes belonging to different sets. The maximised modularity provides the information of the extent to which the network has module-like structures, and the classification obtained from maximising the modularity indicates the number of modules and the structure of sub-networks. Note that behaviours in a module obtained from this analysis can be interpreted as a "task group". In addition to the links, weights can be important information about the extent to which an individual contributes to a certain task and reflect the roles of individuals within a colony. Hence, to assess the module structures, we used the modularity defined for bipartite networks with quantitative interaction strength (i.e., weights) [40]. The definition of the modularity Q_W for such networks is as follows:

$$Q_w = \frac{1}{M}\sum_{i=1}^{r}\sum_{j=1}^{s}\left(A_{ij} - E_{ij}\right)\delta(g_i, h_j) \quad (1)$$

where M is the total weight of the network, A_{ij} is $r \times s$ matrix including the number of behaviour execution, and E_{ij} is the expected value from a random network with the same degree distribution. r and s represent the number of rows (i.e. individuals) and columns (i.e. behaviours) of A_{ij}, respectively. For the weighted bipartite networks, E_{ij} is $y_i z_j/M$ where y_i and z_j are the total weights of individual i and behaviour j, respectively [40]. The δ is a delta function that outputs 1 if i and j are in the same module (g_i and h_j represent module annotation to which i and j belong, respectively) and 0 if they are in different modules. Thus, when the links or weights within modules are larger than expected values, Q_W becomes larger.

The maximisation of the modularity was conducted using an algorithm DIRTLPAwb+ developed by [9]. This method is more robust than a previously proposed algorithm, QuanBio for bipartite networks with weights [9]. We ran the algorithm by using computeModules function implemented in "bipartite" package ver. 2.11 of R 3.4.3. To compare the empirical results with those of random networks, we used null models which have the same marginal totals with empirical one, but the number of links can vary (r2d null model). Moreover, to compare the modularities among networks, the value was normalised by the maximum value of modularity in the possible network configuration with the same total weight [9, 32]. To do so, we used a specific function provided by previous study [32] and finally obtained the normalised modularity ranging from 0 to 1. The p-value for modularity was calculated by identifying the position of empirical modularity in the distribution of the 1000 modularities obtained from the null model.

Once we obtain the module structure, the characteristics for each module, that is, at sub-network level can be quantified. The mean total weights q_{ij} of links from individuals belonging to the module i to tasks belonging to the module j represent the relationships among modules. If i equals to j, the value represents the degree of specialisation of the task module. Moreover, we analysed the types of individuals and behaviours that were included in each module as well as the relationship between the modules (figure 1*c*).

To characterise the role of individuals in networks and modules, we calculated the c-score for each individual proposed by [41]. The c-score represents the degree of specialist-generalist in task choice of ant individuals. The definition of c-score c_i for individual i is as follows:

$$c_i = 1 - \sum_{j=1}^{N_M} \left(\frac{d_{ij}}{d_i} \right)^2 \quad (2)$$

where d_i denotes the total weights of links from individual i, d_{ij} denotes the weights of links from individual i to module j, and N_M is the number of modules obtained from modularity analysis. When the c-score is 0, the individual is engaged only in the behaviour of the module the individual belongs to, suggesting that smaller c-score represents more specialised task choice. This value is similar to the participation coefficient in [41], but different from that in the presence of weights.

2.6. Nestedness

We also calculated nestedness to quantify the overlapping structure of bipartite networks as the index of network level. In individual-behaviour networks, we might observe the overlapping structure of executed tasks. In other words, a few generalists (i.e. an individual engaging in various tasks) cover the tasks of specialists. Because the nested structure may be related to the stability of the system [42], it may be one of the most useful indices to characterise the social systems. In individual-behaviour networks, for example, when the specialists for a certain task are lost unexpectedly in a high nestedness colony, the generalists can complement the task, leading to avoidance of the critical function loss at colony level. See the mathematical definition of nestedness in [43]. To calculate nestedness, we used the WNODF algorithm proposed by [44]. This method can quantify nestedness incorporating weights of links and produce correct results compared to WINE [44]. We used the nested function implemented in "vegan" package ver. 2.5 of R 3.4.3.

The three values, WNODF, WNODFc, and WNODFr, were calculated. Then, we compared empirical values with those of null models [44] in which the marginal totals were equivalent to empirical one, but the number of links could vary. The p-value was calculated by identifying the position of empirical data in the distribution of the 1000 values obtained from the null model.

3. Results

We constructed bipartite networks with weights from the observation of each individual's behaviour for three days based on our criteria of behaviours (see Methods). The number of individuals in each network, the number of behaviours, the number of links, and the sum of weights are shown in table 1. Figure 2 shows the visualised bipartite networks with weights by using an alluvial diagram (https://rawgraphs.io/). The visualisation showed that most individuals in the networks were not completely specialised to a certain behaviour for all colonies, that is, many individuals performed multiple behaviours.

3.1. Network level metrics and module structures

First, we focused on the network level properties and calculated nestedness and normalised modularities for five bipartite networks [9, 44]. From the comparison with null models, four out of five individual-behaviour networks had no significant nested structures, while one colony (colony a) had a significantly nested structure (table 1). The comparison of modularity between observed data and null models showed that the significantly high module structures were detected in all networks (table 1). In addition, the normalised modularities ranged from 0.264 to 0.333. This suggests that individual-behaviour networks did not have complete module structures, namely, workers were not completely specialists because the normalised modularity for the case of the complete specialisation should be one. Although task allocation in social insects is considered a specialisation to a specific task, we found that individuals were not completely specialised throughout the day at the behavioural level, that is, several individuals showed multiple behaviours.

Second, we assessed the module structure of individual-behaviour networks based on the information obtained by maximising modularity. This analysis can tell us the number of modules which can be considered as task groups composed of some individuals and behaviours. The results showed that the number of modules was similar to the number of behaviour types (shown in table 1). The modules were composed of one or two behaviour(s) except for colony a (figure 3), suggesting that individual-behaviour networks had the sub-group structures significantly related to the behavioural categories we defined. Each day most behaviours were found in the same module, suggesting that the module structures were consistent throughout three days (figure 4).

3.2. Network of task groups (modules)

Next, the properties at sub-network (i.e. module) level were quantified. As mentioned above, individuals were not completely specialised to certain behaviour and executed multiple behaviours. Hence, there were weak connections between the modules. To quantify how much the modules were linked with other modules, we calculated the mean weights within and between each module and visualised it as a network of modules (figure 3). The q_{ii} means the mean weights on links from ant individuals belonging to module i to behaviour belonging to module i, and q_{ij} means the mean weights on links from ant individuals belonging to module i to behaviour belonging to module j. In other words, this analysis builds a new network of task groups to inform how task groups interact with each other.

The module size varied among colonies (figure 3). In three colonies, the arrows from non-walk (i.e. forage, brood cares, inactive) to walk modules were thicker than between other modules (figure 3*b,c,d*), suggesting that individuals belonging to the non-walk module sometimes walked. In these colonies, which have a module of inactive ants, the arrows from inactive to non-walk modules (i.e. forage, brood cares) were thin as the arrows from other modules to walk (figure 3*b,c,e*). Like forage and brood-care groups, the module of inactive ants can be treated as a distinct task group. The mean link weights from forage to brood-care modules tended to be small, suggesting that individuals were less likely to engage in both forage and brood-care tasks (figure 3*b,d,e*).

3.3. Individuals' role in network

Finally, we analysed the characteristics of individuals. To evaluate the degree of specialisation for each individual within the colony, *c*-score (i.e. the extent to which the individuals were linked to other modules) was calculated (figure 4). The low *c*-score indicates the strong task specialisation, and vice versa. Although three colonies did not have significantly specialised task groups, the *c*-scores of individuals in the modules of walk and forage were significantly low in two large colonies, compared to those in the other modules, respectively (figure 4*d,e*). This result suggests that some workers specialised in walk and forage, but these patterns between colonies were less consistent.

3.4. Temporal characteristics: daily rhythm

In general, ants show circadian activity rhythms and our focal ant species basically have diurnal activity [45-47]. It is possible that the level of task performance would change between day and night. Therefore, we separated the data into daytime (9:00-18:00) and night-time (21:00-6:00) and assessed the cluster structure of task-individual networks. If task allocation patterns have day and night cycle, there would be clusters of daytime and night-time. The result showed that the detected clusters included both daytime and night-time data, and the modules were separated by behaviour components (figure S2), suggesting that the network structures were consistent throughout the day.

3.5. Relationship with age

The age-dependent changes in behaviours (i.e. forage, brood-care, and inactive) were analysed by regression analysis, by plotting the proportion of executed behaviours as a function of age (figure 5). Positive linear relationships were observed between forage and age in all colonies (a: slope = 0.0004, $R^2 = 0.12$; b: slope = 0.0008, $R^2 = 0.40$; c: slope = 0.0010, $R^2 = 0.24$; d: slope = 0.0010, $R^2 = 0.095$; e: slope = 0.0005, $R^2 = 0.09$; figure 5a,), while there was a negative relationship between brood-care and age except for colony a (b: slope = -0.0004, $R^2 = 0.12$; d: slope = -0.0003, $R^2 = 0.12$; e: slope = -0.0003, $R^2 = 0.15$; figure 5*b*). Although there were large variations between individuals under the same age class, task allocation patterns showed typical age polyethism which is consistent with a previous study on *Diacamma* sp. [34]. Moreover, we compared the age of individuals among modules (figure S3). The forage modules comprised of old workers (figure S3*a,b,c,d*). On the other hand, the modules including brood-care were composed of young workers in the colonies b, and e (figure S3*b,d,e*).

We also showed the proportion of inactive as the number of total inactivity observed in the 24 observations. In three colonies, the proportion of inactive was significantly negatively related with age (a: slope = -0.0002, $R^2 = 0.12$; b: slope = -0.003, $R^2 = 0.03$; c: slope = -0.0005, $R^2 = 0.08$; figure 5*c*), suggesting that the young workers tended to be inactive.

4. Discussion

To understand the complex task allocation patterns in insect societies, network analysis is helpful to quantify the characteristics of task allocation. In this study, we recorded the behaviours of all individuals and investigated the individual-behaviour networks in five ant colonies using bipartite network analysis, in particular, the community detection method. The individual-behaviour networks strongly affected by age (figure 2). The modularity maximisation method quantified the patterns at the network, sub-network, and individual level. We detected consistent module structures classifying task groups throughout a day (i.e. no daily cycle) and three consecutive days (i.e. no daily changes). Furthermore, we compared individual-level properties ~~them~~ between the modules (figure 4).

Network analysis can summarise the complex interaction patterns as various values of a network level index. We used four network level properties: connectance, modularity, number of modules, and nestedness. We found no significant nested structures in most colonies (table 1), suggesting that a specific individual did not cover the tasks which others executed. In contrast, the fact that the modularities in all colonies were significantly large suggests the presence of the module structures, which were comprised of some individuals and a few behaviours. However, the normalised modularity largely deviated from 1 suggesting that there were no complete individual-task specialisations, and individuals were loosely linked to each behavior. As previously mentioned, the number of tasks within the colony is one of the fundamental factors in task allocation research. While many studies focused on just a few prominent tasks such as foraging, building, and brood care (e.g. [11, 13, 48]), many other studies also conducted the detailed behavioural observation (e.g. [34, 49-54]). High specialisation has been observed in other tasks such as guards [33, 55], glooming [51, 56], and inactive [57]. At this point, how many tasks exist in insect societies is still not completely understood. This, seemingly simple question, is not easy to answer because the demand of tasks can change depending on the context. In fact, the number of task groups as modules was different between colonies (figure 3). Detecting modules can tell us how many task groups (i.e. modules) exist in the network and which individual belongs to the specific task group. In this study, we found not only the module of forage and brood-care but also the module of walk and inactive. It suggested that inactive was one of the task groups, which is consistent with the previous study [57]. In our definition, walk included several behaviours, such as grooming, trophallaxis, and dominance behaviours. Therefore, it is possible that there were several task groups in the “walk” module. A more detailed observation should be incorporated in future studies.

Other clustering methods such as hierarchical clustering analysis can also classify workers into separate groups (e.g. [57]). However, there are at least two advantages of bipartite network (i.e. maximising modularity) instead of other methods. First, we could determine the number of modules based on the modularity criteria. Second, comparing empirical networks with null models, which are constructed from a randomly shuffled adjacency matrix, made it possible to infer the behavioural rules underlying the empirical task allocation patterns. In our analysis, we used the null model that the behaviour of each individual is executed as a proportion of the total number of executed behaviours (see method 2.5). In other words, each individual chooses the behaviour depending only on the demands. The results showed the significant differences between empirical and null networks (Table 1, modularity). Therefore, we confirmed that the individual ants determined the behaviour depending not only on the task demands but also on other factors including internal states, experiences, or interactions with other individuals.

Previous studies analysed the degree of specialisation at the network level and the individual level (e.g. *DOL* [58]). In contrast, in the present study, we also analysed the degree of specialisation at the sub-network level. Using this approach, we visualised the relationship between task groups as a module network, that is, how task groups (modules) are connected

with each other (figure 3). The module of walk strongly connected with other modules and the links were one-sided toward the walk module. It is not surprising because walk module is a certain state to shift a behaviour (task). These results also suggest that the module of walk could be a hub in this network.

At the individual level, we evaluated their roles with respect to their position within and among modules. We used a metric, *c*-score which is among-module connectivity, (i.e. degree of specialisation) [59]. This individual-level analysis takes account of module structures, characterised the role of each individual in the module networks, unlike previous metrics which characterised the role of an individual in the whole network. Individual-level metrics made it possible to answer further questions such as what kind of individuals belong to the module by comparing the scores between modules (figure 4), and what is the relationship with other individual's traits, such as age. Additionally, this method enabled us to perform the inter-species as well as inter-colony comparisons. As shown in figure 2, since task allocation patterns were complex, it would be difficult to compare them without such metrics.

Behaviour can change with time such as daily rhythms. Our data on task allocation pattern included temporal data. We analysed these data by dividing daytime and night-time. We found that there was no daytime and night-time module structure, suggesting that the task allocation pattern is consistent throughout the day. Interestingly, individual ants show circadian activity rhythms even under the constant light conditions [45-47]. This unexpected result could be attributed to the social context, including interactions among workers or with brood. It is considered that nurses need to take care of brood all day long. In fact, the interaction with brood induced arrhythmic state on nurses in social insects [45, 60]. Moreover, the *Diacamma* sp. is known to occasionally forage at night by the field observation [61]. Foragers might be active during night as long as the temperature is suitable for foragers. For these reasons, their task allocation pattern did not have daily rhythms. Besides the daily cycle, temporal information such as their experience and previous state might affect decision makings in individuals. This assumption might be addressed in future studies, exploring the temporal network analysis which has ordered-data of time.

In social insect colonies, increasing number of studies indicate that worker inactivity is common (reviewed in [62]). In our focal *Diacamma* sp., some individuals are also specialised in inactivity, which is consistent with the previous study [57]. Although the existence of inactive individuals has been documented across many social insect species, we know very little about variations between individuals. The simplest hypothesis for inactive (lazy) ants is immaturity or senescence (proposed by [63, 64]). Young workers may be less active due to a still-developing physiology, on the other hand, older, senescing workers may be less active due to degraded physiology. Here, we tested this hypothesis. Our data showed that young workers tended to be inactive, however, there were differences between colonies. Although age could be related to inactivity, our results suggest that immaturity was related to inactivity however, the ant inactivity was also colony dependent.

How the quantified patterns emerge based on decision making in individuals is crucial for the understanding of task allocation. The interaction between individuals, stimuli from task demand such as signals from larva in nursing, and ageing may be candidates for regulating behaviour choice. To examine how these factors affect individual decision making and furthermore colony-level patterns, intervention and analysis by mathematical models for constructing the patterns of the networks from rules at individual levels are crucial [5, 65]. The network perspective can capture complex phenomena composed of many elements, and extract the important information at multiple levels. The task-individual relationships in mammal and even human societies [66] are crucial for understanding division of labour in complex societies. The methodology we introduced here may be applied to a wide range of individual-behaviour networks.

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Table 1. Colony information and the properties of network structure.

Colony ID	Num. of ants	Num. of behaviours × days	Sum of weights	Num. of links	Num. of modules	Connectance	Modularity	Normalised modularity	Nestedness
a	33	18	736	300	3	0.505	0.294*	0.333	24.03*
b	41	12	881	325	4	0.660	0.264*	0.283	20.05
c	78	9	1609	524	3	0.746	0.245*	0.333	21.71
d	104	15	2304	788	4	0.505	0.227*	0.302	18.10
e	122	12	1999	791	3	0.540	0.293*	0.262	20.62

Figures

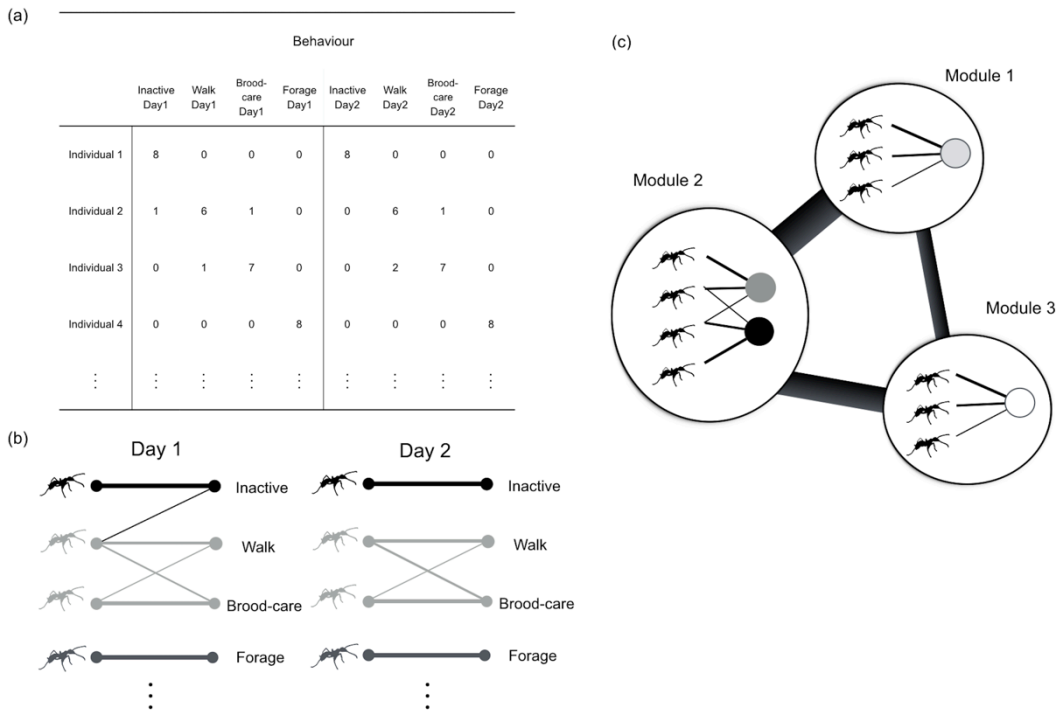

Figure 1. Individual-behaviour relationship as a bipartite network. An adjacency matrix for individual-behaviour (a) can be described as a bipartite network with weights and information of day (b). The thickness of the links represents weight of interactions. Module structures can be detected by maximising modularity (c). There were specialised individual-behaviour relationships in each module. The links between the modules represent the extent to which individuals within a module exhibit behaviour in the other modules.

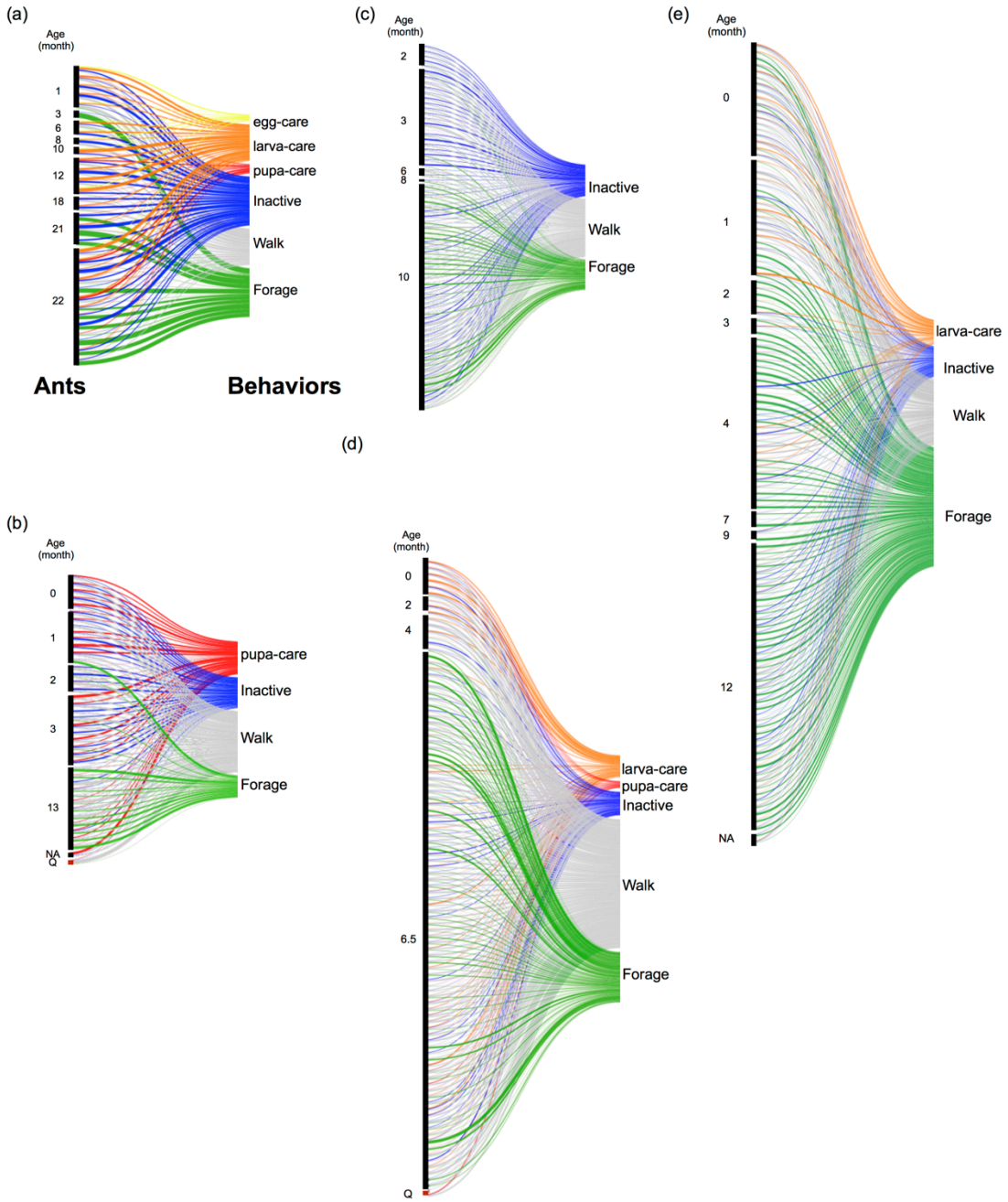

Figure 2. Task-individual networks of *Diacamma* sp. in 5 colonies (a to e). The left blocks are clusters of individual nodes depending on their age. The right blocks are nodes of behaviour. The flows represent the links between individuals and behaviour. The numbers next to left blocks represent age (month). The colours indicate behaviour. Each network was constructed from 3 day observation data, and the maximum weight of a link is 24. The width of each link is the number of executions of the behaviour. Nodes representing ant individuals are sorted by age (months), from youngest (top) to oldest (bottom). Q indicates queen (reproductive individual).

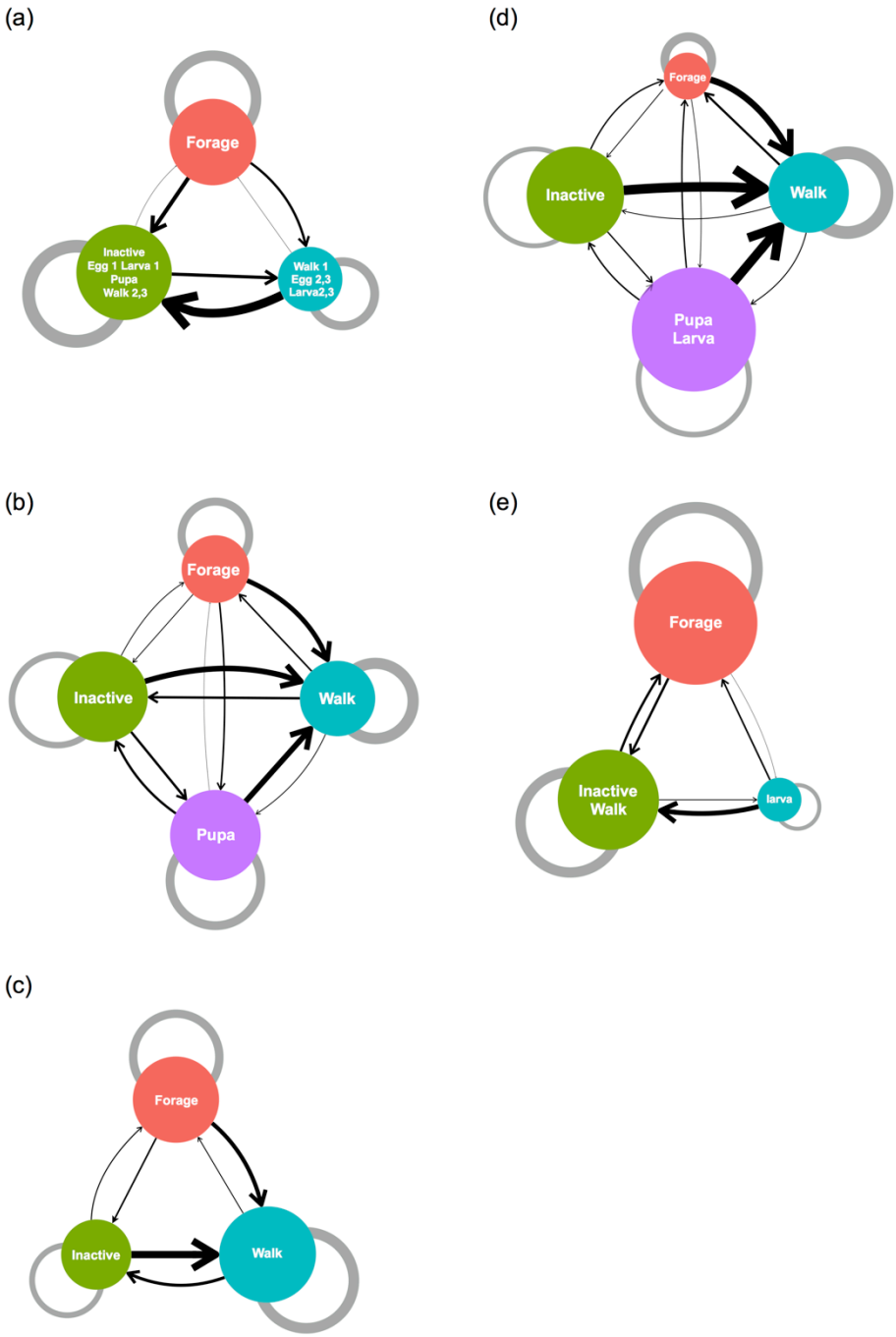

Figure 3. Networks of modules in 5 *Diacamma* sp. colonies (a to e). The node represents modules containing individuals and behaviour. The labels on the nodes indicate the behaviour contained in the module. The size of the nodes is weighted by the number of individuals belonging to the module. The links have a direction and width as the mean weight from ant individuals belonging to module *i* to behaviour belonging to module *j* (q_{ij}). The width of grey self-links indicates the mean weight from ant individuals belonging to module *i* to behaviour belonging to the same module *i* (q_{ii}) Day information was omitted when Day 1, 2, and 3 belonged to the same module.

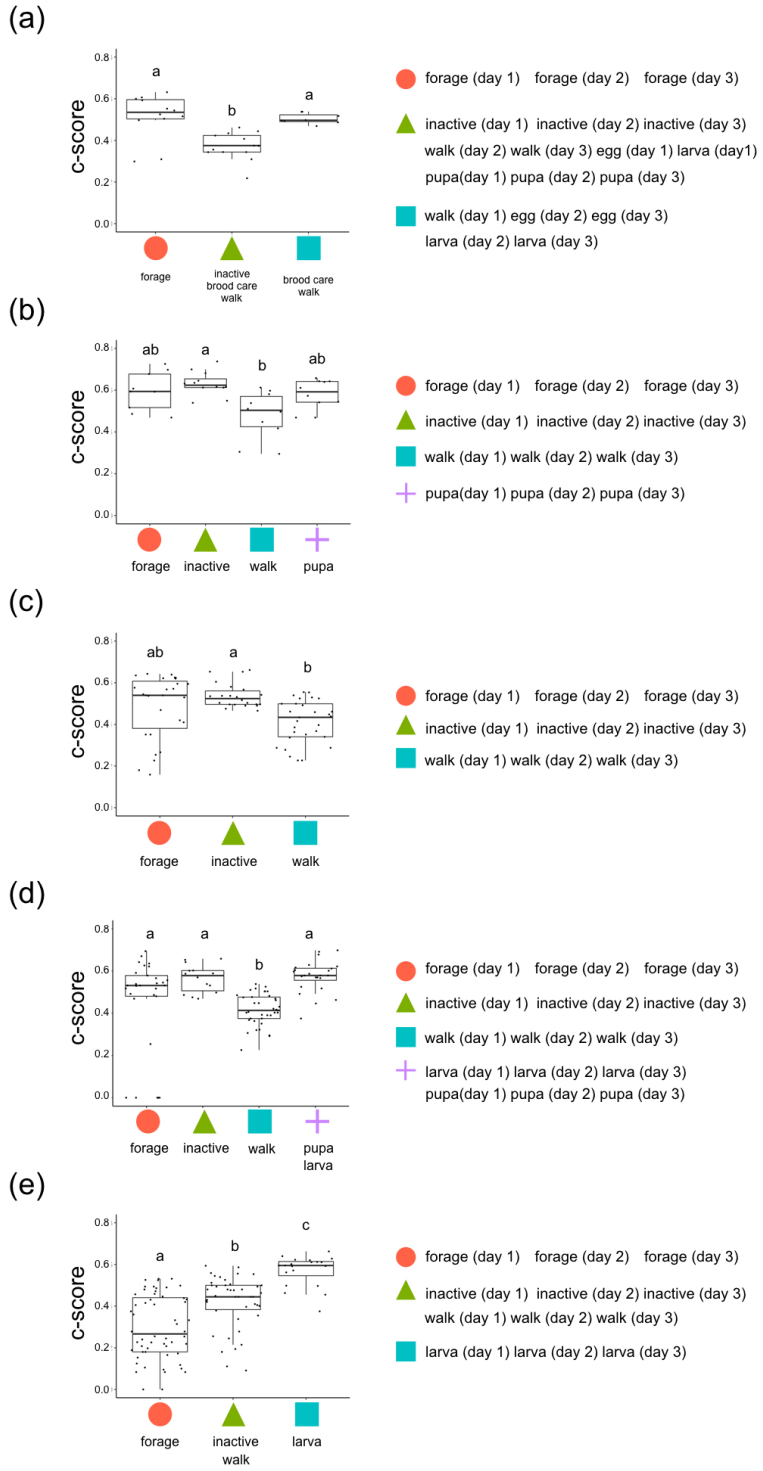

Figure 4. Relationship between modules and *c*-scores in 5 *Diacamma* sp. colonies (a to e). The *x* axis represents each module, and the *y* axis represents *c*-score. The low *c*-score indicates the strong specialisation, and vice versa. Right panels indicate behaviour (each day) that belong to each module. Different letters above the boxes indicate significant differences (by Steel-Dwass test, $p < 0.05$).

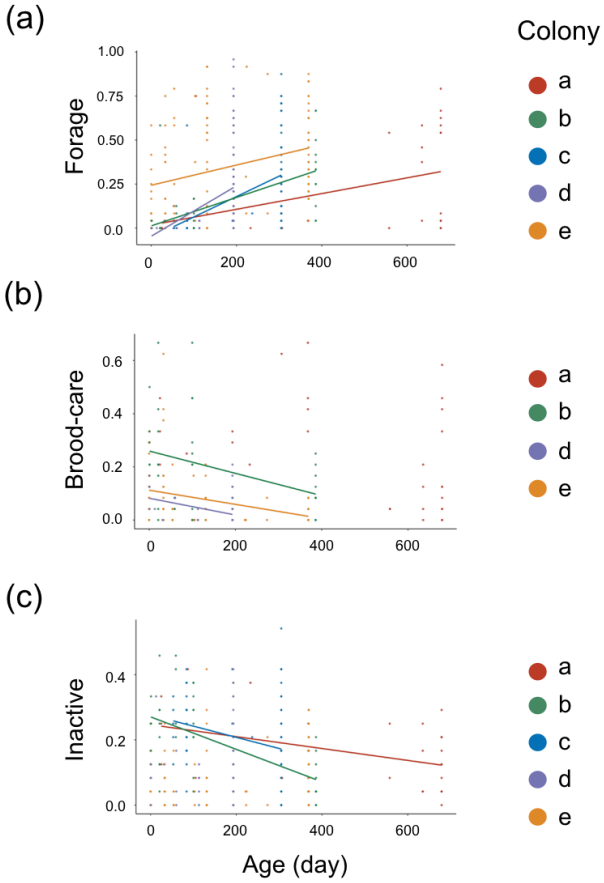

Figure 5. The proportion of *Diacamma* sp. behaviour (a) forage, (b) brood-care, and (c) inactive with respect to the age of an individual. Each point indicates an individual and the colour represents the colony. No data about broods is in colony c because the colony c did not have broods.