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ORIGINAL ARTICLE

Dynamics of Information Flow and Task Allocation of Social Insect Colonies: Impacts of Spatial Interactions and Task Switching

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Abstract

Models of social interaction dynamics have been powerful tools for understanding the efficiency of information spread and the robustness of task allocation in social insect colonies. How workers spatially distribute within the colony, or spatial heterogeneity degree (SHD), plays a vital role in contact dynamics, influencing information spread and task allocation. We used agent-based models to explore factors affecting spatial heterogeneity and information flow, including the number of task groups, variation in spatial arrangements, and levels of task switching, to study: (1) the impact of multiple task groups on SHD, contact dynamics, and information spread, and (2)

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the impact of task switching on SHD and contact dynamics. Both models show a strong linear relationship between the dynamics of SHD and contact dynamics, which exists for different initial conditions. The multiple-task-group model without task switching reveals the impacts of the number and spatial arrangements of task locations on information transmission. The task-switching model allows task-switching with a probability through contact between individuals. The model indicates that the task-switching mechanism enables a dynamical state of task-related spatial fidelity at the individual level. This spatial fidelity can assist the colony in redistributing their workforce, with consequent effects on the dynamics of spatial heterogeneity degree. The spatial fidelity of a task group is the proportion of workers who perform that task and have preferential walking styles toward their task location. Our analysis shows that the task switching rate between two tasks is an exponentially decreasing function of the spatial fidelity and contact rate. Higher spatial fidelity leads to more agents aggregating to task location, reducing contact between groups, thus making task switching more difficult. Our results provide important insights into the mechanisms that generate spatial heterogeneity and deepen our understanding of how spatial heterogeneity impacts task allocation, social interaction, and information spread.

Keywords Social insects · Task switching · Spatial fidelity · Social network

1 Introduction

Eusocial insects live in highly cooperative and cohesive societies with complex organizational structures (Class 2000). These societies are organized around the work of raising new individuals for colony growth and reproduction and maintaining conditions for colony function. These goals involve a series of differentiable tasks. Their systems of task allocation and division of labor allow the diverse members of these societies to perform multiple different tasks in parallel. At the same time, the colony as a whole regulates the allocation of effort to different tasks as needs and opportunities change. In fact, task allocation is a problem across most complex systems, such as multicellular organisms (Navlakha and Bar-Joseph 2014; Yanni et al. 2020), collective robotics (Gerkey and Matarić 2004). The distributed information systems provided by their social networks allow colonies to regulate work homeostatically and dynamically around current needs (Robinson et al. 2009; Charbonneau et al. 2017; Leitner and Dornhaus 2019; Beshers and Fewell 2001; Gordon 1996).

Many, although not all, tasks take place in specific locations in the nest of social insects, and workers performing the same task tend to aggregate around those locations, which are described as spatial fidelity zones (SFZ) (Mersch et al. 2013). Spatial fidelity adds an important spatial component to task regulation that likely influences task communication networks. The locations in which workers perform tasks, or spatial fidelity zones (SFZ), can reinforce communication among individuals within the corresponding task group and, in so doing, potentially enhance communication efficiency for elongating their fidelities toward that task location (Sendova-Franks and Franks 1994, 1995). Conversely, communication between task groups across SFZs may be less frequent, potentially limiting coordinating tasks across the colony. Cross-colony communication is necessary for the function of these distributed systems. Thus, we would expect more flexibility in task choice, spatial preferences, and communication strategies than would be provided with strictly delineated task zones. Flexible spatial strategies can provide multiple functionalities beyond task regulation, including facilitating information transmission or inhibiting the spread of pathogens (Sendova-Franks et al. 2010; Feigenbaum and Naug 2010; Naug 2008; Quevillon et al. 2015; Regnier and Wilson 1968; Wilson and Regnier 1971). These make it critical to understand the inter-dependency between social communication among individuals in the same or different task groups and the formulation or decomposition of task groups.

As decentralized distributed systems, social insect colonies rely heavily on the capability of individual workers to acquire information from the environment independently and on the ability to receive or send information via local inter-individual communications (Feinerman and Korman 2017). The specific information and resources acquired by workers can, in turn, influence individual spatial preferences and, in doing so, assist the whole colony to re-establish the spatial distribution of workers to cope with various challenges (Theraulaz et al. 2003). This interplay between information acquisition and worker spatial movement patterns has been widely studied in various ant species, for example, nest-site choice and famine relief of *T. albipennis* (Pratt et al. 2002a; Sendova-Franks et al. 2010), alarm propagation of *P. californicus* (Guo et al. 2022), social immunity of *L. niger* (Stroeymeyt et al. 2018) and nutritional balance of *C. sanctus* (Baltiansky et al. 2021). Although an ideal model for studying this interplay, the processes and mechanisms by which task-related information and social contact mediate workforce re-allocation within colonies are still understudied.

One way to study the dynamics of task regulation within a colony is to examine how internal factors, such as genotype (Oldroyd and Fewell 2007), physiological states (Robinson 1987), and environmental stimulus (Page and Mitchell 1998), induce workers to switch their tasks from one to another. Alternatively, it is worth considering the task allocation as a product of task recruitment via social interactions (Pacala et al. 1996). The task-related cuticular hydrocarbons of red harvester ant (*Pogonomyrmex barbatus*) have been found to assist workers' decision on task performances (Gordon 1989), and their encounter rate informs the possibility of task switching (Gordon and Mehdiabadi 1999). Models incorporating components of tasks, social interactions, and spatial behavior of individual workers are needed to better understand the dynamic task allocation in social insect colonies.

Previous models incorporating subsets of these components have revealed several potential mechanisms of how individuals acquire local information by spatial coincidence (Richardson and Gorochowski 2015), how task allocation is mediated by individual movement (Johnson 2009), and how the encounter rate of individuals contributes to collective patterns of task allocation (Pacala et al. 1996; Chen et al. 2020). However, these models do not provide an integrative view of task re-allocation as individual spatial behavior associated with task-related interactions changes dynamically. For example, the algorithm proposed by Johnson (2009) relying on a self-organizing model of task-quitting, patrolling, task-searching, and task-working, serves the random location of individuals throughout the colony without considering task demand. This model showed the dynamics of workers switching between tasks and locations. Pacala et al. (1996) demonstrated that responses to demand a task could arise from the interactions among individuals, environmental stimuli, and local densities. Therefore, a model that simultaneously integrates task fidelity, the spatial distribution of individuals, and task-related interactions would facilitate our understanding of relations among those three components in social insect colonies and further our understanding of mechanisms of adaptive task allocations.

In recent modeling work (Guo et al. 2020), we investigated the information transmission through physical contact in several realistic scenarios involving three task groups of ants. We assumed that the performance of each task group is tied to pre-defined spatial fidelities, which reflect the proportion of ants that prefer to drift back to the task location compared to those that move randomly. With this assumption in place, we revealed the contributions of ants with different spatial fidelities, e.g., random-walking and drifted-walking, to the information transmission. To explore further, in this study, we focused on how the number of task groups (ranging from 2 to 5) and the spatial distribution of task locations impact information transmission. Additionally, we investigate how the task switching associated with the spatial coincidence of ants is formulated by ants' spatial distribution and, in turn, affects task allocations, physical contact, and information transmission. Therefore, we propose two discrete-time Markov chain models: 1. Multiple-task-group model, which assumes that each task group (consisting of 2–5 tasks) has a fixed and pre-defined spatial fidelity (i.e., the proportion of drifted-walker within each task group); 2. Task-switching model assumes that individuals can be recruited to another task that is different from their original tasks by their neighboring ants via physical interactions, and after switching the task, they may change their task spatial fidelities with a certain probability. Our models address the following: (1) How do multiple task groups and related spatial distribution of workers affect social contact dynamics and information transmission; (2) How may task-switching lead to changes in spatial fidelity and therefore impact task allocation.; and (3) How may spatial fidelity dynamics affect contact and information dynamics after task switching.

The models and discussion are organized as follows. In Sect. 2, we derive our agent-based model with associated information and task-switching scenarios. We introduce two different modeling approaches: The multiple-task-group model, which includes various task groups while keeping spatial fidelity constant, and the Task-switching model, which provides for only a two-task group but dynamic spatial fidelity. In Sect. 3, we perform our simulations and analysis for those two models and compare their dynamics. In Sect. 4, we discuss the finding and conclude our study.

2 Model Derivation

Our model extends the agent-based discrete-time Markov chain model developed in Guo et al. (2020) by including various task groups and task-switching procedures. Unlike conducting experiments in such contexts that can be very challenging, our model is an easy while effective tool that can shed some light on dynamics in real social insect colonies.

We assume that the colony has N workers living on $X = K \times K = \{(i, j) : 1 \leq i \leq K, 1 \leq j \leq K\}$ grids for some $K \in \mathbb{Z}$. We also assume that

$N \leq K^2$. At any given time t, a worker $\mathbf{A}$ is characterized by $\eta_{\mathbf{A}}(t) = (l_{\mathbf{A}}(t), p_{\mathbf{A}}(t), w_{\mathbf{A}}(t), f_{\mathbf{A}}(t))$ with four attributes explained below. The $l_{\mathbf{A}} \in X$ is the location of worker, and $p_{\mathbf{A}} \in \{1, 2, \dots, P\}$ is its task group. The walking style of the worker is represented by $w_{\mathbf{A}} \in \{\text{Random (R)}, \text{Drifted (D)}\}$. Based on previous work and literature (Charbonneau and Dornhaus 2015a; Mersch et al. 2013; Guo et al. 2020), we set two walking styles for Worker $\mathbf{A}$: Some workers do not wander inside during each task; they randomly select one of the neighboring cells and moves toward that Charbonneau and Dornhaus (2015a). We set the walking style of such an ant to be $w_A = R$. This random walking behavior provides the chance of task switching. In the drifted walking style, when $w_A = D$, the worker has a preferential direction toward its task location (S_p) (Mersch et al. 2013). Finally, $f_{\mathbf{A}} \in \{0 \text{ (not informed)}, 1 \text{ (informed)}\}$ represents its information state. Informed workers have the ability to disseminate information to their uninformed workers.

Let $N_p(t)$ be the number of workers performing task p at time t, then we have $N = \sum_{p=1}^{P} N_p(t) \leq K^2$. The notation $SF_p(t)$ is dynamical spatial fidelity (SF) of task p at time t, and it is calculated by the fraction of workers performing task p at time t who have drifted walking style (D). That is,

$$SF_p(t) = \frac{|\{\mathbf{A} : p_{\mathbf{A}}(t) = p \& w_{\mathbf{A}} = D\}|}{N_p(t)}. \tag{1}$$

We adopt notations in Guo et al. (2020). Each worker A with $l_{\mathbf{A}}(t) = (i, j)$ has up to four neighbors that are located at $\{(i \pm 1, j), (i, j \pm 1)\}$. If workers are on the edge or in the corner of the colony, the size of these neighboring cells will reduce to three and two, respectively. For convenience, we use $NC_{\mathbf{A}}(t)$ to denote its neighbor sites which could have four, three, or two depending on its location $l_{\mathbf{A}}(t) = (i, j)$. We define $|N_A(t)|$ as the number of nonempty neighbors of worker A.

We develop models to address two questions: (1) How do multiple task groups with associated spatial fidelity affect social contact dynamics and information spread through a colony when tasks are located in different zones? and (2) How does task switching affect dynamical spatial fidelity and social interactions? We use a multiple-task model to explore the first question by allowing information to spread over the whole colony with different numbers of tasks, and we use the task-switching model to explore the second question.

Initially, workers are located randomly in the colony, and the population of task groups and initial spatial fidelity are the same (i.e., $N_1(0) = N_2(0) = \cdots = N_P(0)$ & $SF_1(0) = SF_2(0) = \cdots = SF_P(0)$). We set the population of drifted walking workers in each task group by $N_p(0) * SF_p(0)$, and other workers are random walking. Then, we randomly choose one worker $\mathbf{A}$ in the multiple-task-group model, make it informed ant, $f_{\mathbf{A}}(0) = 1$, and set its location at the center of the colony, $l_A(0) = (\frac{K-1}{2}, \frac{K-1}{2})$ with K is odd number.

For each update $\Delta t = 1$ (each update corresponding to 0.001s in real colonies) (Guo et al. 2020; Hurlbert et al. 2008), we randomly select a worker $\mathbf{A}$ to do the following steps:

1. Based on the neighbors of worker **A**, it has a probability of $\frac{|N_{\mathbf{A}}(t)|}{|NC_{\mathbf{A}}(t)|}$ to make a contact with one of its neighbors and then switch its location with the neighbor. And it has a probability of $1 - \frac{|N_{\mathbf{A}}(t)|}{|NC_{\mathbf{A}}(t)|}$ to move into its neighborhood sites in next step 2 based on its walking style:
2. (a) If the walking style of **A** is random ($w_{\mathbf{A}}(t) = R$), **A** randomly selects an empty neighboring cell $l_{\bar{\mathbf{A}}} \in NC_{\mathbf{A}}(t)$ to move in the new location $l_{\bar{\mathbf{A}}}$: $l_{\mathbf{A}}(t+1) = l_{\bar{\mathbf{A}}}$,
   (b) If the walking style of **A** is drifted ($w_{\mathbf{A}}(t) = D$), **A** selects an empty neighboring cell $l_{\bar{\mathbf{A}}} \in NC_{\mathbf{A}}(t)$ closest to SFZ (S_p) to move in new location $l_{\bar{\mathbf{A}}}$: $l_{\mathbf{A}}(t+1) = l_{\bar{\mathbf{A}}}$. To determine the distance between task SFZ and all neighboring empty lattices, we utilized Euclidean distance. In the event that two empty lattices are equidistant from SFZ, the worker will randomly select one to move to.

   We repeat the process for the next randomly selected worker.
3. Makes contact with one of its neighbors by randomly selecting a neighbor worker $\mathbf{B} \in N_{\mathbf{A}}(t)$ and switches its location with this neighbor worker **B**, and $l_{\mathbf{A}}(t+1) = l_{\mathbf{B}}(t)$ and $l_{\mathbf{B}}(t+1) = l_{\mathbf{A}}(t)$.
   Workers can sense and communicate with neighbors located in adjacent grids within the length of the antenna (2 mm) (Guo et al. 2020). Each grid can occupy at most one worker; therefore, the physical contact of two workers results in their movement. Because of their proximity, these motions cause them to switch locations, which is biologically and mathematically reasonable. Now we have the following two scenarios:

   (a) In multiple-task-group model: if two contact agents have different statuses in information, i.e., $f_{\mathbf{A}}(t) \neq f_{\mathbf{B}}(t)$, we define $f_{\mathbf{A}}(t+1) = f_{\mathbf{B}}(t+1) = 1$,
   (b) In the task-switching model: worker **A** is randomly chosen from population, without loss of generality, we assume that neighbor **B** will switch its task to worker **A**'s with probability β_A when worker **A** and **B** have different tasks (i.e., $p_{\mathbf{A}}(t) \neq p_{\mathbf{B}}(t)$), thus the task of **B** at time $t+1$ is $p_{\mathbf{B}}(t+1) = p_{\mathbf{A}}(t)$. Based on task-switching mechanisms in ant colonies (Wilson 1985; Robinson 1992), individuals in our model are assumed to update their walking style in a negative feedback manner via sensing the demand/supply of task activities.After task switching, the worker **B** updates its walking style ($w_{\mathbf{B}}$) to be drifted (D), i.e., $w_{\mathbf{B}}(t+1) = D$, with probability $1 - SF_{p_A}(t)$; and to be random with probability $SF_{p_A}(t)$. The assumptions of how the worker **B** updating its walking style follow from the “balancing," which means if more workers stay at the task location, then the new workers who join this task group will be more inclined to do a random walk.

   We repeat the process for the next randomly selected worker.

The model flowchart for a single time-step is shown in Fig. 1, and the left of Fig. 2 shows the walking style of a typical worker, and the right of the Fig. 2 shows the location of the different number of groups, and the right bottom of the Fig. 2 shows different spatial arrangement of four task-groups.

To continue our study, we define the following measurements. Spatial heterogeneity degree (SHD) measures the distribution of workers in the colony (Myers 1978) and is defined as

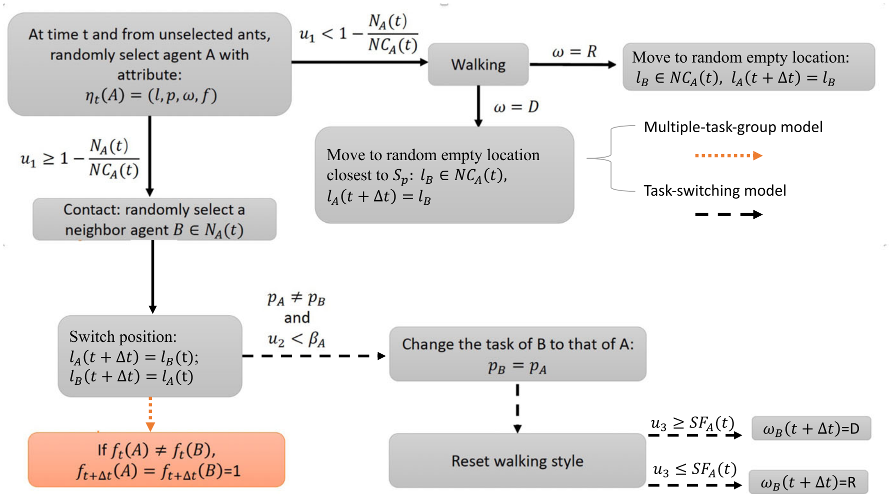


Fig. 1 (Color figure online) The dynamics process for each update Δt. u_i indicates random numbers in (0, 1) generated to compare with $SF_A(t)$, $i = 1, 2, 3$

$$SHD(t) = \frac{\sum_{l=1}^{K^2} \left(P_l(t) - \frac{N}{K^2}\right)^2}{K^2}, \tag{2}$$

where $P_l(t)$ indicates the probability that location l is occupied by a worker at time t, $\frac{N}{K^2}$ is the probability of location occupation when all workers do symmetric random walks. The function $SHD(t)$ is bounded from the above by its maximum $SHD_{max} = \frac{N(K^2-N)}{K^4}$. We assume one lattice has 1 or 0 workers at any given time t, and we calculate the approximation of SHD following the method in Guo et al. (2020).

Let $C_{pq}(t)$ be the total number of contacts that occurred between two different task workers of a social insects colony in the time interval $(0, t)$. If $p = q$, then $C_{pp}(t)$ is the total number of contacts within a task group p, and R_{pp} is the contact rate within a task group p; if $p \neq q$ then $C_{pq}(t)$ is the total number of contacts task group p and task group q over time $(0, t)$ and R_{pq} is the contact rate between task group p and task group q. Therefore,

$$R_{pq}(i) = \frac{C_{pq}(im) - C_{pq}(1 + (i-1)m)}{m}, i \in \mathbb{Z} \cap [1, \frac{\text{total time}}{m}] \tag{3}$$

Similarly, we define $R_{pp}(i)$ to be the contact rate within the task groups p. Then we set the total contact rate within the group across all task groups $p = 1, \ldots, P$ as $R_w = \sum_{p=1}^{P} R_{pp}(i)$, and the total contact rate between two different task groups as $R_{bt} = \sum_{p=1}^{P} \sum_{q=1}^{P} R_{pq}(i)$, where $p \neq q$.

The task switching rate per m updates shown by TS_{pq} is the total number of workers that change their task from task p to task q through contacts over $m-1$ updates divided by m updates (Guo et al. 2020):

$$TS_{pq}(i) = \frac{\text{The total number of workers who switch task p to q from time 1+(i-1)m to time im}}{m}. \quad (4)$$

Finally, let $I(t)$ as the total number of informed workers ($f_{\mathbf{A}}(t) = 1$) in the time interval $(0, t)$. We denote $I_{trans}(i)$ as the information transfer rate per m updates. This implies the following formulation:

$$I_{trans}(i) = \frac{I(im) - I(1 + (i-1)m)}{m}, \quad (5)$$

Those definitions above allow us to ask the following questions:

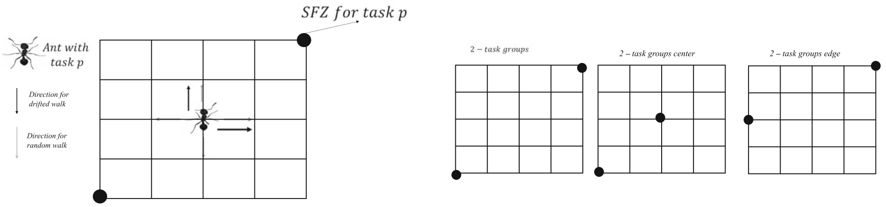
1. What are the main differences between the two models, multiple-task-group and task-switching, in effects on spatial heterogeneity degree (SHD) and contact dynamics?
2. How does the presence of multiple task groups with their associated spatial arrangement influence the dynamics of spatial heterogeneity degree (SHD) and contact dynamics, and how does this consequently impact information spread and/or task switching rates?
3. What are the relationships between spatial fidelity (SF), spatial heterogeneity degree (SHD), and contact dynamics in the task-switching model, and how do they affect the dynamics of task population for a task group of p workers ($N_p(t)$)?

In the following section, we implemented 2–5 groups in our simulations, given that social insects exhibit various task allocations in response to their environment (Guo et al. 2020; O'Donnell and Bulova 2007; Pinter-Wollman et al. 2012) with associated SFZs as shown in Fig. 2, because Charbonneau et al. (2015) observed that workers' tasks and associated movement areas are not fixed, to answer these three questions.

Agent-based model simulations, based on three major tasks (brood-caring, food-processing, and trash-maintaining) observed in *P. californicus* ant colonies (Holbrook et al. 2011), revealed the relation between individual spatial distribution and spreading agents transmission (Guo et al. 2020). To incorporate more possible scenarios, such as more than 3 tasks in the nest (Charbonneau and Dornhaus 2015a), and spatial arrangements of tasks beyond the triangular structure of task locations described in other species of social insects (Richardson et al. 2022), we simulate scenarios where colonies consist of 2–5 task groups in 6 different spatial arrangement of task locations.

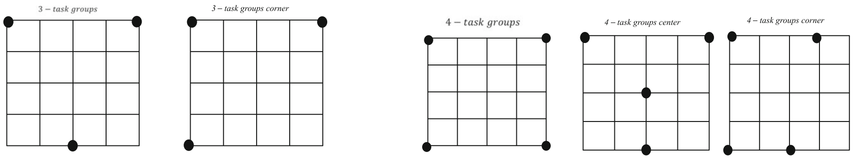
3 Results

In this Section, we perform our simulations and analyses on the two models provided in Sect. 2. Spatial fidelity (SF) of task group p denoted by $SF_p(t)$ is the fraction of workers performing task p that does preferential walking to their own task location at time t. Spatial heterogeneity degree ($SHD(t)$) defined as in Eqt. (2) measures how workers



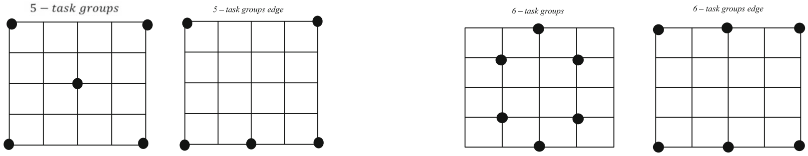
(a)

(b) two task groups



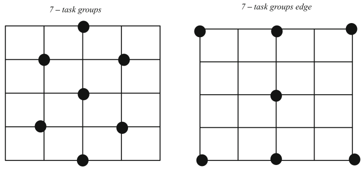
(c) three task groups

(d) four task groups



(e) five task groups

(f) six task groups



(g) seven task groups

Fig. 2 Schematic illustrations of walking style and the SFZ geometry when the colony has two, three, four, five, six and seven task groups: A worker performing task p moves to its random adjacent neighboring cell if its walking style is random ($w = R$) or moves to its adjacent neighboring cell that is the closest to its SFZ S_p if its walking style is drifted ($w = D$). The SFZ for two, three, four, five, six, and seven task groups are shown as the big solid dark dots in the grid worlds of the **b**–**g**

are distributed in the colony at time t. Our recent work (Guo et al. 2020) indicates that $SHD(t)$ can be affected by task-associated spatial fidelity SF_p in a significant way. We aim to use the multi-task-group model, we set different numbers of groups. Because there is no task switching in this model, spatial fidelity remains constant. Due to the different number of groups, the model has different spatial arrangements of these groups (see Fig. 2). After these settings, we aim to explore how the number

Table 1 Parameters used in the simulations for the multiple-task-group and task-switching models

Parameter	Description	Baseline
$K \times K$	Colony size	69×69
N	Total number of workers	180
p	Workers task	$p \in \{1, 2, 3, 4, 5, 6, 7\}$
β_p	Task switching probability	0.5
$SF_p(0)$	The initial spatial fidelity in task groups	0.4–0.8
m	Per m updates	1000
I	Initial informed workers	1

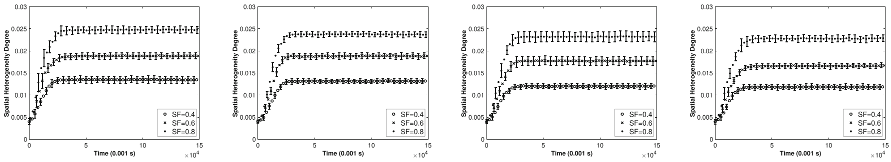
of task groups may impact their related spatial distribution (SHD) and thus influence social contact dynamics and information spread through a colony. In the task-switching model, workers can switch tasks. Due to task switching, spatial fidelity has changed. After these settings, we aim to study how the task-switching dynamics may impact spatial heterogeneity degree (SHD) and therefore impact social contact dynamics and task allocation.

All simulations start with the same initial condition and use the same baseline parameters listed in Table 1 unless stated otherwise. Our initial setting values are from previous work (Guo et al. 2020). We can also roughly calculate the colony size and population of workers by some information from Waters et al. (2017) to be equivalent to our settings. However, our model is not only for this species. Our model serves more general species. The purpose of our model is to learn the dynamic changes of the internal space and information of the system. In this study, we did not incorporate the influence of the external environment into our model. To ensure the competition of two task switching is equal, we assigned an equal and unbiased probability of 50% for task switching between the two tasks we have set.

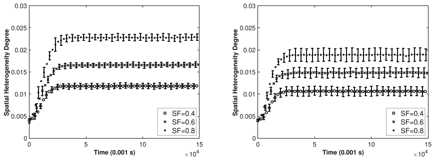
3.1 Dynamics of the Multiple-Task-Group Model

We adopted the modeling approach of Guo et al. (2020) to inform our multiple-task-group model. The number of task groups in our previous model (Guo et al. 2020) is three. This model expands to scenarios of 2, 3, 4, 5, 6, and 7 task groups while the total population of 180 is fixed for all cases, and we assume that the same population size of each task group in each case. Thus, for the two task groups model, each task group has 90 agents; for the three task groups model, each task group has 60 agents; for the four task groups model, each task group has 45 agents; for the five task groups model, each task group has 36 agents; for the six task groups model, each task group has 30 agents; and for the seven task groups model, each task group has 26 agents. We also assume that spatial fidelity (SF) for each task is the same for all cases, i.e., $SF_p(t) = SF_p(0) = SF$.

Dynamics of Spatial Heterogeneity Degree (SHD): Figures 3 and 4 provide us insights on how the number of task groups and spatial fidelity affect SHD. In Fig. 3, we varied spatial fidelity (SF) $SF = 0.4$ (circle), 0.6 (cross), and 0.8 (dot) for colonies

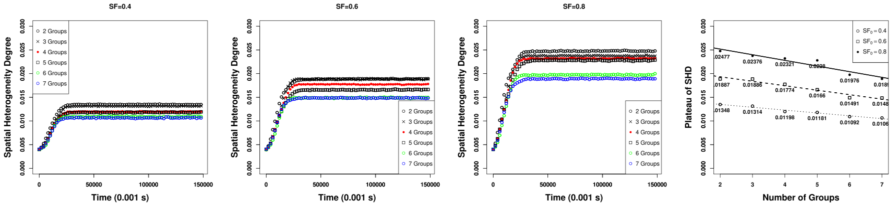


(a) Two groups (b) Three groups (c) Four groups (d) Five groups



(e) Six groups (f) Seven groups

Fig. 3 The impact of spatial fidelity (SF) on spatial heterogeneity degree (SHD) across 2, 3, 4, 5, 6 and 7 task groups: $SF = 0.4(circle), 0.6(cross), 0.8(dot)$. The position of each case are in Fig. 2. The plateau of SHD increases with its fixed SF $SF = SF_p(0)$. The curves represent the dynamic of the average of all replicates of all positions in each case. Each case has 40 replicates. The error bars show the standard deviation of the data



(a) $SF = 0.4$ (b) $SF = 0.6$ (c) $SF = 0.8$ (d) Plateau fitting

Fig. 4 (Color figure online) The impact of multiple task groups on spatial heterogeneity degree (SHD): Different numbers of task groups (2, 3, 4, 5, 6 and 7 task groups) for $SF = 0.4, 0.6, 0.8$ respectively. **d** is the plateau value of SHD and fitting by linear equation ($SHD = a * x + b$, x is the number of task groups). The curves represent the dynamic of the average of all replicates of all positions in each case. Each case has 40 replicates

with 2 task groups (see Fig. 3a), 3 task groups (see Fig. 3b), 4 task groups (see Fig. 3c), 5 task groups (see Fig. 3d), 6 task groups (see Fig. 3e), and 7 task groups (see Fig. 3f).We calculate the average for all cases with the same number of groups; for example, 2 task groups have 3 location cases, then we calculate the mean of these three cases, and the error bar (standard deviation) is calculated by all three cases data. Our results show that SHD increases with its SF for all numbers of task groups. This observation is in line with results observed in Guo et al. (2020), Lloyd (1967). The potential explanations are that with larger SF, more workers aggregate to their task location after large enough time, thus larger SHD, which measures the spatial distribution of workers in the colony. However, the increasing rate of SHD with respect to SF varies with multiple task groups.

Figure 4 reorganizes the presentation of results in Fig. 3, comparing how the number of task groups impacts spatial heterogeneity degree (SHD) when the spatial fidelity

Table 2 The first equation shows the plateau of SHD has a negative linear relationship with the number of task groups (x): $SHD = a * x + b$ (see Fig. 4d)

$SHD = a * x + b$		
SF	a ($\times 10^{-3}$)	b ($\times 10^{-3}$)
0.4	−0.601	14.7
0.6	−0.945	21.2
0.8	−1.19	27.6

Table 3 The mean of plateaus of the contact dynamics between groups and with-in group for colonies having two, three, four, and five task groups when the spatial fidelity is 0.6, i.e., $SF = 0.6$

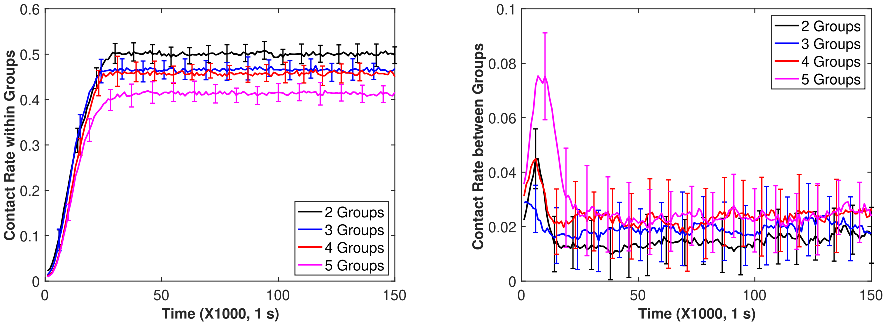
Groups	Between groups	With-in group
2	0.0155	0.500
3	0.0230	0.463
4	0.0234	0.457
5	0.0237	0.414

The plateau of contact dynamics within task groups decreases with the number of task groups, and the plateau of contact dynamics between task groups increases with the number of task groups, same with Fig. 11

(SF) is $SF = 0.4, 0.6, 0.8$ respectively. After analyzing the data (see Fig. 4d), the dynamics shown in Fig. 4 suggest that the plateau of SHD decreases as the number of task groups increases, but some plateau differences are very small. We performed linear fitting. The dynamics shown in Fig. 4 suggest that (1) the plateau of SHD decreases as the number of task groups increases and (2) The plateau of SHD drops faster as SF increases (see Fig. 4d and the value of a in Table 2). To determine the quantified relationship between SF, SHD, and multiple task groups, The best-fit outcomes are provided in Table 2.

Effects of the number of task groups on the contact dynamics: Figure 5 shows the contact dynamics within groups (Fig. 5a) and between groups (Fig. 5b) for a colony with two, three, four, and five task groups when the spatial fidelity (SF) is 0.6. The dynamics shown in Fig. 5b suggest that with a higher number of task groups within the colony, the plateau of the contact dynamics within task groups is lower. Through the Welch ANOVA test (Table 5 in “Appendix”), Fig. 5b and Table 3 observe the number of task groups impacts on the plateau of the contact dynamics between groups. Among them, the t-test shows that 2-group, 3-group, and 5-group have significant differences; the plateau of the contact dynamics between groups increases as the number of task groups increases. However, the t-test shows 3-group compared with the 4-group and the 4-group compared with the 5-group have no significant difference. In other words, when the number of groups increases, the difference between adjacent cases is not significant and shrinks as the number of groups increases.

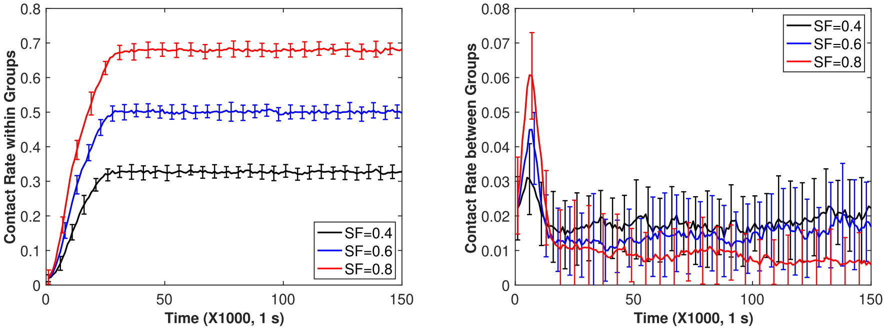
From Fig. 3, we find that higher spatial fidelity (SF) leads to a higher spatial heterogeneity degree (SHD) because of more agent clustering. We find the contact dynamics ($R = R_1 + R_2$) have a strong positive linear relationship with SHD, i.e., the more agents gathering, the more contact that occurs. For example, $R(t) = 63.46SHD(t) - 0.06$ when $SF = 0.6$ with two task groups in the colony. The contact dynamics includes contact rate between groups ($R_{12} + R_{21}$) and within group ($R_{11} + R_{22}$). Figure 3 shows



(a) Contact dynamics with-in task groups

(b) Contact dynamics between task groups

Fig. 5 (Color figure online) Impacts of multiple task groups on the contact dynamics: Colony has two, three, four, and five task groups when the spatial fidelity (SF) is 0.6. 4-task groups are four groups at the corner shown in the bottom left corner of Fig. 2b. **a** The plateau of contact dynamics within task groups seems to decrease with multiple task groups increasing. **b** The plateau of contact dynamics between task groups is increasing with multiple task groups increasing. The curves represent the dynamic of the average of 40 replicates



(a) Contact rate within a task, 2 task groups with different SF

(b) Contact rate between tasks, 2 task groups with different SF

Fig. 6 (Color figure online) Spatial fidelity affects the plateau of contact dynamics. The error bar shows standard deviation. The curves represent the dynamic of the average of 40 replicates

that the colony with more task groups has smaller SHD; then it leads to lower contact dynamics.

Effects of different SF on contact dynamics: Figure 6 shows that (1) the plateau of contact dynamics within the group increases with spatial fidelity (SF), (2) the plateau of contact dynamics between groups decreases as SF increases, and (3) the highest value of contact rate between groups is higher as SF increases.

When SF increases, more agents prefer walking to their task location. After a specific time, more agents aggregated in their task location, which led to the increased density for increased contacts within their task group. When SF reduces, more agents would prefer doing the random walk, and then they will move out of the task fidelity

Table 4 The equation shows the proportion of informed workers (y) has a positive linear relationship with time: $y = c * time + d$ (see Fig. 7 yellow lines)

SF	$y = c * time + d$	
	c	d
0.4	2.806×10^{-5}	5.933×10^{-2}
0.6	3.644×10^{-5}	7.13×10^{-2}
0.8	4.77×10^{-5}	8.602×10^{-2}

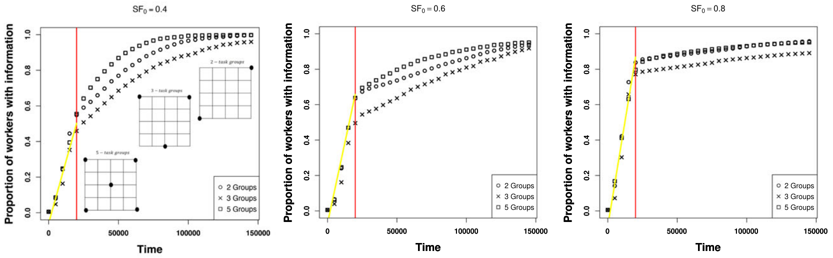
zone, which increases the density of the contact between task groups (higher contact between groups). In the beginning, a larger SF will cause more agents to walk toward their task zone location, and this movement will inevitably lead to more contact dynamics between and within groups during this process.

Effects of the number of task groups and task location on spreading information: Our model focuses on the case when information spreads through physical contact between workers, with higher contact rates leading to faster information spread. Figure 7 shows the dynamics of information spread in the colony for different values of spatial fidelity (SF) and the number of task groups. From this Figure, we observe that: (1) In Fig. 7a–f, there exists some special time (horizontal red line) before which all cases have similar trends. (2) Our fitting (equation in Table 4) explores that information spread speed rises when SF increases. (3) After the special time (horizontal red line), information continues to be transmitted at a slower speed. (4) In Fig. 7a–c, 3-group (asymmetric)' information transfer process is slower than 2-group and 5-group. We defined the spatial arrangement of 2 and 5 groups case as Symmetric". Therefore, symmetry may be a positive influence on information spreading. The greater number of groups may take less time to make all workers get the information. (5) Fig. 7d–f are all four groups of information transmission, and the difference is that the task locations are different (see Fig. 2). The corner case (green dots) has the largest average distance between locations, and information spreading is slowest, and the center case (blue dots) has the lowest average distance, then information spreading is fastest. Therefore, the lower average distance between locations may lead to the information spreading faster. And the larger the SF, has more significant the result. (6) In Fig. 7g–i, SF=0.8 is always lower than others, and 2 task groups case and 3 task groups case show that the number of task groups is the same but with lower SF, information is faster delivered to all workers. Therefore, the symmetrical distribution of task locations may help information transfer faster.

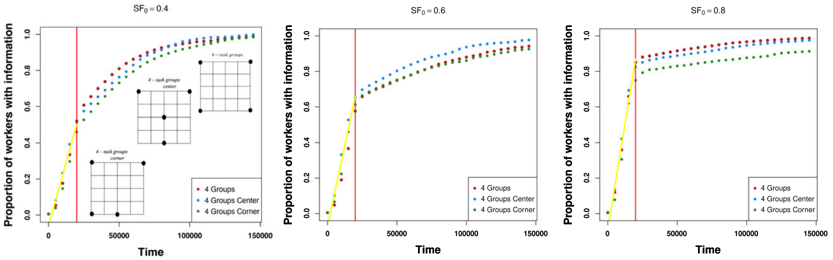
3.2 Dynamics of Task-Switching Model

The task-switching model has dynamical spatial fidelity (SF) shown by $SF_p(t)$. In this model, we assume that our simulations have only any two task groups that differ in the population and focus on task switching, in which the selected agent contacts its neighbor with a different task, and then this neighbor switches its task to that of the selected agent via some probability.

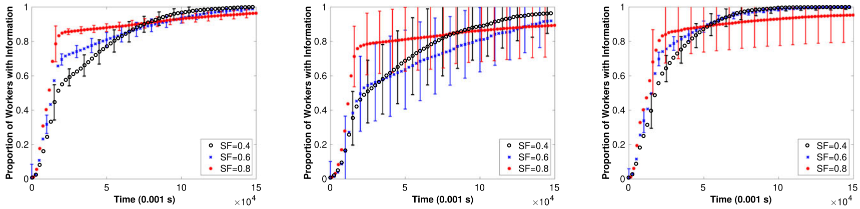
Spatial dynamics: Figure 8 shows the time-series of spatial heterogeneity degree (SHD) and spatial fidelity (SF) with varied initial SF. Figure 8 suggests that (1) dynamic



(a) $SF = 0.4$ with 2,3,5 groups (b) $SF = 0.6$ with 2,3,5 groups (c) $SF = 0.8$ with 2,3,5 groups

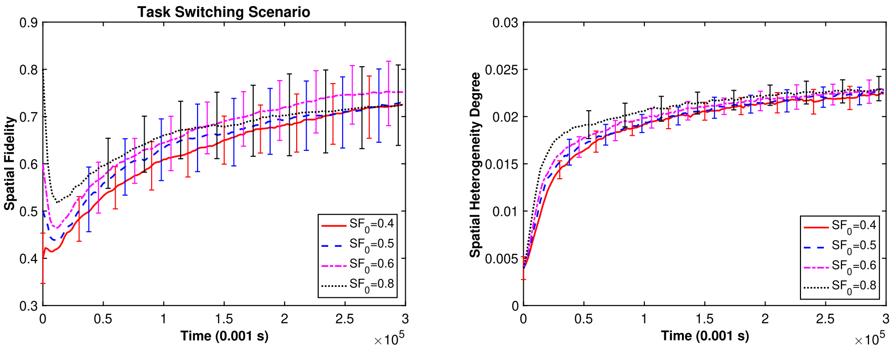


(d) $SF = 0.4$ with the different spatial arrangement of 4 groups (e) $SF = 0.6$ with the different spatial arrangement of 4 groups (f) $SF = 0.8$ with the different spatial arrangement of 4 groups



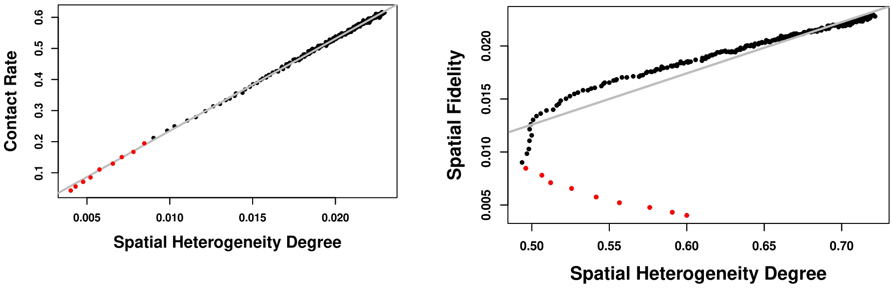
(g) 2 task groups with $SF = 0.4, 0.6$ and 0.8 (h) 3 task groups with $SF = 0.4, 0.6$ and 0.8 (i) 5 task groups with $SF = 0.4, 0.6$ and 0.8

Fig. 7 (Color figure online) Impacts of multiple task groups and task location on information spread with varied fixed spatial fidelity (SF): **a**–**f** are different numbers of task groups (2, 3, 4 and 5 task groups) for $SF = 0.4, 0.6, 0.8$. The task locations in the 2-task-group and 5-task-group are symmetric with respect to the colony's center, while the task locations in the 3-task-group are asymmetric with respect to the central location. Horizontal red lines (all lines are t = 20,000) are the special time value for speed change of information spreading. Before this time, the spatial arrangement of task location does not affect the information spread in the same SF case. The yellow lines are linear regression of the proportion of informed workers (y) with time before critical values: $y = c * time + d$. In $SF = 0.4$, $c = 2.806 \times 10^{-5}$ and $d = 5.933 \times 10^{-2}$; in $SF = 0.6$, $c = 3.644 \times 10^{-5}$ and $d = 7.13 \times 10^{-2}$; in $SF = 0.8$, $c = 4.77 \times 10^{-5}$ and $d = 8.602 \times 10^{-2}$. **g**–**i** are the same data from **a**–**c** and show same numbers of task groups with varied SF. The points represent the dynamic of the average of 40 replicates



(a) Dynamics of Spatial Fidelity (b) Spatial Heterogeneity Degree

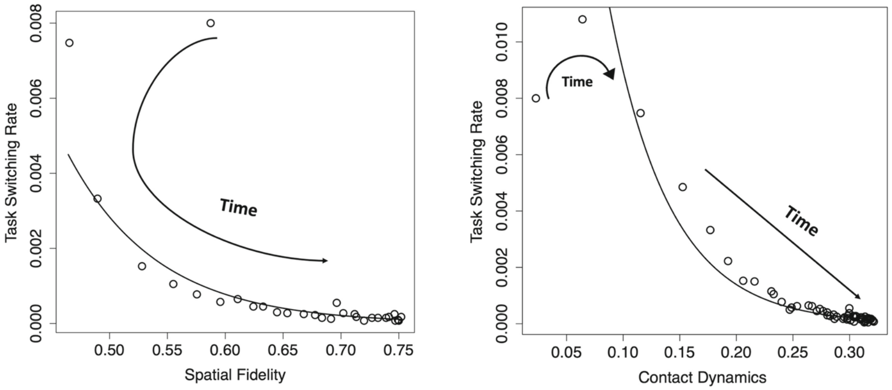
Fig. 8 (Color figure online) Dynamics of spatial fidelity (SF) and spatial heterogeneity degree (SHD) with varied initial spatial fidelity values: The curves represent the average of 40 replicates, and error bars are the standard deviation. In the task-switching model both $SHD(t)$ and $SF_p(t)$ are independent from its initial value $SF_p(0)$



(a) **Spatial heterogeneity degree versus contact rate**: task-switching model with initial spatial fidelity being 0.6 $SF_p(0) = 0.6$. Contact rate ($R = R_1 + R_2$) is the inclusion of between groups ($R_{12} + R_{21}$) and within groups ($R_{11} + R_{22}$). These two metrics have an strong positive linear relationship: $R(T) = 29.67SHD(T) - 0.06$.

(b) **Spatial heterogeneity degree versus task 1 spatial fidelity (SF)**: task-switching model with initial spatial fidelity being 0.6 $SF_p(0) = 0.6$. These two metrics have a strong positive linear relationship: $SHD(t) = 0.048SF_1(t) - 0.012$ (gray line). Figure 8a shows SF decreases with time series, in the beginning, these data are red dots in this figure.

Fig. 9 (Color figure online) Strong linear relationship in task-switching model: Spatial heterogeneity degree has a linear relationship with contact rates and spatial fidelity (SF) in the task-switching model. Thus, it can be deduced that contact rates and SF also have a linear relationship. Both figures use the same simulations. The red dots are the negative correlation between SF and SHD in **b**. We keep colors for both figures. The curves represent the dynamic of the average of 40 replicates



(a) **Task switching rate versus spatial fidelity**

(b) **Task switching rate versus contact rate**

Fig. 10 The relationship between contact rates and spatial fidelity: The task switching rate is non-linear decay with spatial fidelity (SF) and contact rate. Among them, contact rate (R_1) is the inclusion of between groups (R_{12}) and within groups (R_{11}), task switching rate is the rate of task 2 agents switch to task 1 (TS_{21}), and SF is SF in task 1 ($SF_1(t)$). **a** The function of the curve is $TS_{21}(t) = e^{0.60-12.94SF_1(t)}$; **b** The function of the curve is $TS_{21}(t) = e^{-2.85-18.64R_1(t)}$. The curves represent the dynamic of the average of 40 replicates

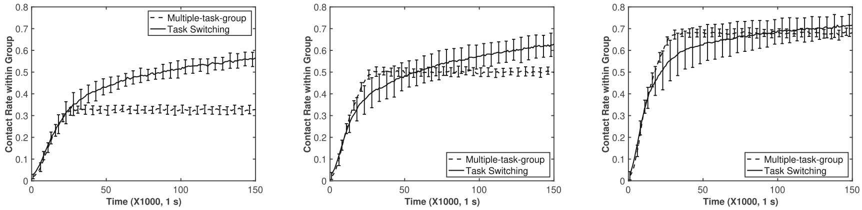
SF and SHD are not affected by initial spatial value, and 2) SF with varied initial values has a similar shape; the shapes of SHD are similar as well.

Figure 9a shows that contact rate positively correlates with spatial heterogeneity degree (SHD). Physical contact between groups leads to agents switching their tasks. As spatial fidelity (SF) increases, more agents aggregate at their task locations. Therefore, when spatial fidelity (SF) is higher, they will have more chance for within-group contact and less chance to contact other groups' agents with an increased probability of switching their tasks. The data fitting shows that the task switching rate has an exponential decay by SF (see Fig. 10a). Due to the positive linear relationship between contact rate and SF (see Fig. 9), task switching rate also has an exponential decay in relation to contact dynamics (see Fig. 10b). Figure 9b shows that red points are under the gray line of

$$SHD(t) = 0.048SF_1(t) - 0.012.$$

Those points occur at the initial time frame of [0, 10000] and suggest the negative correlation between spatial fidelity and the spatial heterogeneity degree (Fig. 8a).

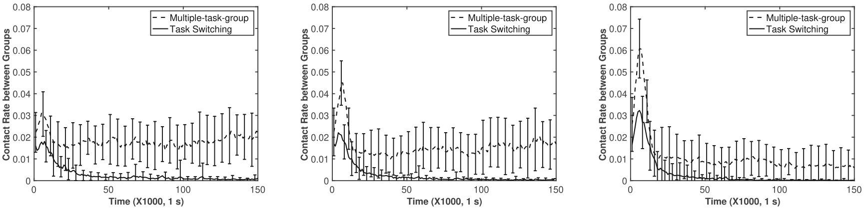
Comparison of contacts between the multiple-task-group model and task-switching model: Figure 11 compares the time-series of contacts when the colony has two task groups in multiple-task-group model and task-switching model. Notice that spatial fidelity (SF) in the multiple-task-group model is constant while SF in the task-switching model changes by time (see Fig. 8a). Figure 11 in the task-switching model suggests that (1) the plateau of contacts within and between groups are similar with different initial SF, (2) the initial increase in speed is faster with higher initial SF (see



(a) The contact rates within group R_{pp} when the initial spatial fidelity (SF) is 0.4 $SF = SF_p(0) = 0.4$

(b) The contact rates within group R_{pp} when the initial spatial fidelity (SF) is 0.6 $SF = SF_p(0) = 0.6$

(c) The contact rates within group R_{pp} when the initial spatial fidelity (SF) is 0.8 $SF = SF_p(0) = 0.8$



(d) The contact rates between groups R_{pq} when the initial spatial fidelity (SF) is 0.4 $SF = SF_p(0) = 0.4$

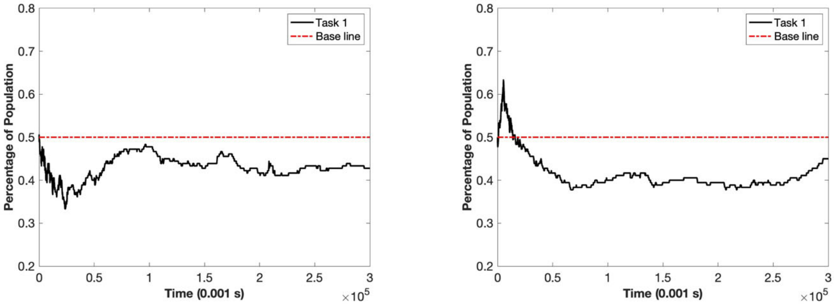
(e) The contact rates between groups R_{pq} when the initial spatial fidelity (SF) is 0.6 $SF = SF_p(0) = 0.6$

(f) The contact rates between groups R_{pq} when the initial spatial fidelity (SF) is 0.8 $SF = SF_p(0) = 0.8$

Fig. 11 Task switching leads to dynamic spatial fidelity. Impacts of task switching on contact rates for two task groups with varied initial spatial fidelity (SF) and fixed SF on contact dynamics for two task groups: For the model of multiple task groups, spatial fidelity is constant while task switching changes by time. **a**–**c** The plateau of the contact within group R_{pp} in the multiple-task-group model (dash curve) is increasing as SF increases, while in the task-switching model, they (solid curves) are similar. **d**–**f** The plateau of the contact between groups R_{pq} in the multiple-task-group model (dash curve) decreases as SF increases, while in the task-switching model, they (solid curves) are similar; and the peak of R_{pq} is higher as SF increasing in both model. The curves represent the dynamic of the average of 40 replicates

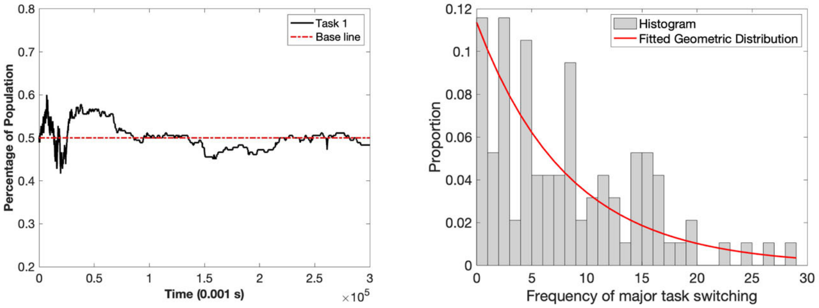
Fig. 11a–c), and (3) the largest value of contacts between groups is higher when initial SF is higher (see Fig. 11d–f). On the other hand, Fig. 11 suggests that (1) the plateau of within-group contacts group in the task-switching model is always higher than that of the multiple-task-group model, and (2) the plateau of contact between groups in the task-switching model is always lower than that of the multiple-task-group model when the final result stabilized.

Task groups: Figure 12 presents three different dynamics of task populations from our simulations. The replicate runs of the model with the same parameter values. We set two task groups with the same population at proportion values of 0.5 for each task (red baseline) initially. The black curves are the proportion of the task 1 population size in the colony. We use a histogram to show the frequency of population switching,



(a) Major-minor tasks non-rotated

(b) Major-minor tasks rotated less than 5 times



(c) Major-minor tasks rotated more than 5 times

(d) Proportion of varied frequency of major-minor task rotations

Fig. 12 (Color figure online) Different dynamics of two task group populations.**a**–**c**: Individual case for population changing in task 1 with initial spatial fidelity (SF) being 0.5 ($SF_p(0) = 0.5$). The baseline (red line) is set at 0.5 because both groups start with the same number of agents, with an associated proportion of task 1 and task 2 groups of 0.5 ($N_1(0) = N_2(0)$). **d**: Proportion of varied frequency of major-minor task rotation. There are 11 cases (11.58%) where one task has been the leading task. The total is 95 replications in $SF_0 = 0.5$. The geometrical distribution fitting probability is 0.1136, mean of the distribution is 7.8, and the median is 4.7

which is the major task change. The histogram of Fig. 12d shows the proportion of the major task changing less or equal to 6 is 49.47%, including 11 cases is no-changing. We used geometric distribution to fit the histogram (red curve) with a probability value of 0.1136. The median of the fitting distribution is 4.7. Half of the simulations changed the major task 5 times. For example, Fig. 12a has no switching (0 bar), which means one task is always a major task and needs more agents. Figure 12b has fewer switching (less than 5 times), which means the major task can switch to another one but not often. Figure 12c has fewer switching (more than 5 times), which means the major task often switches to another one, and both tasks have equal demand. The simulations can be classified into those categories that align with the observation of experiments in the lab and literature (Leighton et al. 2017).

4 Discussion

We used an agent-based model to explore the factors that generate spatial heterogeneity and explore how spatial heterogeneity affects contact dynamics, information spread, and task switching. We focused on two models based on the consequences of social contact inside the colony: (1) The first consequence of social contact is that contact leads to potential information spread. We developed the multiple-task-group model to understand how the number of task groups and associated constant SFZs and spatial distributions would affect contact dynamics and information spread. (2) The task-switching model studies the second consequence of social contacts; the contact between two workers can lead to a change in behavior by increasing the chance that one worker may decide to switch tasks with associated changes in walking style. These behavioral changes can generate spatial heterogeneity and dynamical changes in spatial fidelity and can affect the size of the task group if this leads to task switching.

When few workers are engaged in a task (low spatial fidelity), positive feedback draws more workers toward their task locations, while a disproportionately high density of workers at a task results in negative feedback that increases the likelihood of workers leaving to search for a new task (Page and Mitchell 1990; Gordon et al. 1992). Thus, spatial fidelity allows the colony to balance workers among tasks regardless of the initial spatial heterogeneity (see Fig. 8). Spatial fidelity influences physical interactions among ants, affecting task switching. The findings of this study should be considered with the following caveats: First, our results are simulation-based, and there are no experimental data to support the findings. Second, the model is a general case only. In the future, we could set specific tasks for each group relevant to colony task organization, for example, by introducing a food source to increase demand for the task of foraging. This would allow us to further study the impact of space on task switching in a more specific context. Below we review how insights gained from the models may be applied to the case of social insect task organizations by discussing the interaction between spatial effects and mechanisms of task allocation and the role of interactions in information transfer.

4.1 Group Effects

In the multiple-task-group model, we explored how the different numbers of groups in the colony influence information spread. We tested groups 2, 3, 4, 5, 6, and 7 in one colony with varied spatial fidelity (SF). Varied SF and task group location both affect the information spread speed (see Fig. 7). Different SF and task group locations influence the spatial heterogeneity degree (Fig. 4). When space is more heterogeneous, task-related information can be more quickly communicated within a task group (Naug 2009). In contrast, with lower spatial fidelity, information transmission speed may be slower locally, but information spreads through the colony more quickly. Spreading information or transmission elements (i.e., food) is easier between individuals within a colony (Naug 2008), and information spreads faster at beginning (Sendova-Franks et al. 2010). We observed from Fig. 7 that the number of task groups could affect information transmission speed and process. This suggests that geometry is a key to information transmission speed and process. This may also be why the organizational layout of tasks within social insect colonies is often similar. Although the specific locations and substrates for tasks vary considerably, the organizational relationships among tasks often follow similar rules (Mersch et al. 2013). Therefore, further exploring the task-switching model, we focus on the dynamics of spatial fidelity rather than on different numbers of tasks. Additionally, the plateau of within-group contact rates decreases as the number of task groups increases; there will be more contact between groups conversely. Therefore, more task groups will disperse the population, reduce the social interaction within the group, but increase the social interaction between the groups and create more opportunities for task switching.

4.2 Spatial Effects on Task Switching and Task Allocation

In the task-switching model, individuals use both social (shared task information) and contextual (density of workers at task location) cues to make decisions about task allocation. In contrast, in the multiple-task-group model, only contextual cues are used. Furthermore, the contextual cues in the task-switching model are dynamic, adjusting to the relative density of workers actively engaged in a task. As such, the task-switching model more closely resembles cases of flexible task allocation, such as the role of response thresholds in bee fanning behavior (Weidenmuller 2004; Jones et al. 2004). The multiple-task-group model better mimics cases in which tasks are more fixed, such as morphologically specialized workers (e.g., soldiers) or more intrinsically directed temporal polytheism (as in honey bee nursing vs. foraging) (See Charbonneau and Dornhaus 2015b; Johnson 2003 for a discussion on fixed vs. flexible task allocation mechanisms).

These two models have different spatial fidelity (SF) settings, one changes by time and one is constant. Comparison of the model's performance in SHD to explore how SF infects spatial heterogeneity. SHD shows faster reaching steady state in the multiple-task-group model than in the task-switching model, suggesting that fixed task allocation mechanisms may be more efficient (i.e., workers allocated to their tasks more quickly) than flexible task allocation mechanisms. On the other hand, SHD plateaus in the task-switching model converge on similar numbers regardless of the initial value of $SF_p(0)$. In contrast, the level of the SHD plateaus in the multiple-task-group model directly depends on the $SF_p(0)$ value. This suggests that flexible task allocation mechanisms may take longer to reach equilibrium but are more robust to perturbation. Indeed, if these systems suffered large losses of individuals in one task group, thereby changing the value of spatial fidelity ($SF_p(t)$), the task-switching model would return to the distribution of workers among tasks (i.e., SHD) comparable to pre-disturbance levels, while multiple-task-group model would be irreversibly changed and be unable to return to pre-disturbance SHD levels.

4.3 Social Interaction

We discuss how these elements influence contacts, including the information, in the following paragraphs. In both models, there are two main processes that influence behavior: allocation of workers among spatially segregated tasks and information transfer among workers. In the multiple-task-group model, task allocation, i.e. task group in which the population of each group is fixed, affects the contact rate among workers, which in turn affects the speed with which information is propagated among workers. However, information in the multiple-task-group model does not affect task allocation. For the task-switching model, task allocation affects information transfer via the same process as in the multiple-task-group model (task switching rates and likelihoods of information transfer), but in the task-switching model, information also affects task allocation. The result is a growth of informed individuals (vs. uninformed) in the multiple-task-group model, where propagation speed is determined by constant SF. In the task-switching model, both bits of information compete with each other, and no single task can eliminate the other within a certain time, though they may go through phases of fluctuation over time (Fig. 12). In our algorithm, we set the task switching rate (β_p) to 50%, which is $\beta_A = \beta_B$. Although this is not our purpose in this study, we tried different values of β_A and β_B during some test simulations. We found that the results were influenced by the comparing value of β_p. If $\beta_A = \beta_B$, the dynamics of SF and task switching rate have no significant difference, but if $\beta_A \neq \beta_B$, the situation becomes different. Therefore, task-switching probabilities will have different effects to some extent, as larger β_p leads to a higher number of this task (Fig. 13 in "Appendix"). Therefore, we believe that the random selection of the worker and our setting of task switching is a process without losing generality.

Interestingly, regardless of the mode of the consequence of social contact (i.e., task switching or information transfer), the contact dynamics are very similar. This suggests that the mechanisms allowing increased robustness in task allocation to disturbance (discussed above) are not necessarily dependent on transmission rate, but rather the dynamic nature of task allocation in the task-switching model, i.e., feedback between spatial fidelity and task information. This is particularly interesting because several behaviors in social insects have been shown to be dependent on interaction rate (e.g., foraging Gordon and Mehdiabadi 1999; Greene and Gordon 2007, emigration consensus (Pratt et al. 2002a; Mallon et al. 2001)). However, our model shows that spatially dependent individual feedback mechanisms, as opposed to interactions rates *per se*, can also result in collective flexibility.

In both models, contact rates between task groups initially peak at approximately the same moment, then decrease and stabilize. Their simultaneous peaking is likely caused by the initial random location of individuals. Though this may be an artifact of the initial model setup, it can provide insight into how colonies may react to disturbances that would relocate individuals (e.g., emigration or nest destruction) (Pratt et al. 2002a). The fact that the same pattern seems to occur in both models suggests that, regardless of whether task allocation mechanisms are flexible or rigid, both models are capable of adjusting to disturbances.

After the initial peak in contact rate during which the colony reorganizes, contact rates between task groups are lower in the task-switching model than in the multiple-task-group model. Additionally, contact rates within groups rise more slowly in the task-switching model than in the multiple-task-group model and reach a plateau more slowly (Fig. 11). This suggests that in the multiple-task-group model, workers can resume their set distribution among tasks more rapidly after disturbance than in the task-switching model. However, in the event of a disturbance where workers are lost (e.g., forager loss or nest defense) (Tschinkel and Hanley 2017), the task-switching model should be more robust, and with the colony re-equilibrating according to the relative densities of workers per tasks (i.e., reach similar plateaus of SHD), In contrast, in the multiple-task-group model, workers will attempt to reach there and thus may not reach optimal task allocation.

4.4 Future Works

Our previous models (Guo et al. 2020) have studied information transmission with three task groups and fixed spatial fidelity to indicate that information spreads faster within groups and slower between task groups, while our study provides important insights into the number of task groups and task switching. We build the network model constructed by social insect behavior to analyze the spatial heterogeneity, the number of task groups, and the process of information spreading and task switching from individual-level effects to group-level process. But our proposed model does have its limitations that we should work with. In an actual social insect colony, there are more complex reasons for workers to change their tasks, such as environmental stimulus (Page and Mitchell 1998) and task performances (Gordon 1989), not as straightforward as designed in our model, contact and switch with a fixed probability. In addition, the location of our task group zone is simply defined from geometry and is not combined with the task distribution of the social insect colony in reality. In our future work, we should include setting particular tasks and task-related response thresholds in our model. As a basis for future work, our current research is of great help to the understanding of social contact processes with spatial distribution.

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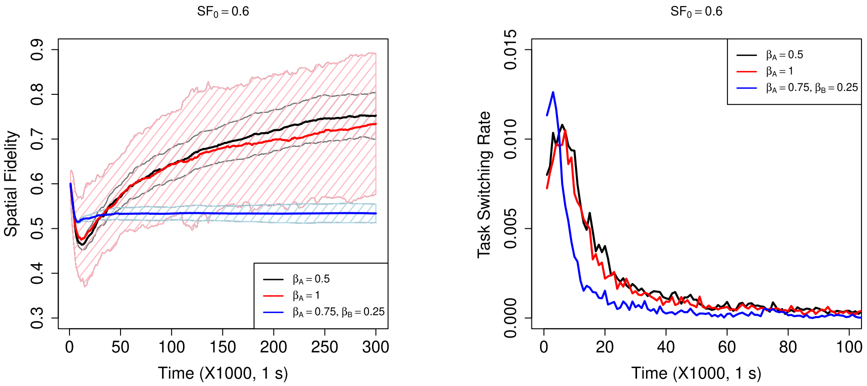
A Appendix

See Fig. 13 and Table 5.



(a) The time-series of spatial fidelity with different task switching probability.

(b) Task switching rate from task B to task A with different task switching probability.

Fig. 13 Black and red curves which are $\beta_A = \beta_B = 0.5$ and $\beta_A = \beta_B = 1$, separately. The blue curve is task switching probability to task A is $\beta_A = 0.75$; however, to task B is $\beta_A = 0.25$. **a**: Black, red, and blue shadows are standard deviations

Table 5 *P* values of the Welch ANOVA test and T-test

Test	*P* value	Test	*P* value
ANOVA for all groups *	$< 2.2e{-}16$	3 groups versus 4 groups *	0.1409
2 groups versus 3 groups *	$< 2.2e{-}16$	3 groups versus 5 groups	0.0051
2 groups versus 4 groups *	$< 2.2e{-}16$	4 groups versus 5 groups	0.2512
2 groups versus 5 groups *	$< 2.2e{-}16$		

Star * means they have different variances

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