



Dynamics of social interactions, in the flow of information and disease spreading in social insects colonies: Effects of environmental events and spatial heterogeneity

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ABSTRACT

The relationship between division of labor and individuals' spatial behavior in social insect colonies provides a useful context to study how social interactions influence the spreading of elements (which could be information, virus or food) across distributed agent systems. In social insect colonies, spatial heterogeneity associated with variations of individual task roles, affects social contacts, and thus the way in which agent moves through social contact networks. We used an Agent Based Model (ABM) to mimic three realistic scenarios of elements' transmission, such as information, food or pathogens, via physical contact in social insect colonies. Our model suggests that individuals within a specific task interact more with consequences that elements could potentially spread rapidly within that group, while elements spread slower between task groups. Our simulations show a strong linear relationship between the degree of spatial heterogeneity and social contact rates, and that the spreading dynamics of elements follow a modified nonlinear logistic growth model with varied transmission rates for different scenarios. Our work provides important insights on the dual-functionality of physical contacts. This dual-functionality is often driven via variations of individual spatial behavior, and can have both inhibiting and facilitating effects on elements' transmission rates depending on environment. The results from our proposed model not only provide important insights on mechanisms that generate spatial heterogeneity, but also deepen our understanding of how social insect colonies balance the benefit and cost of physical contacts on the elements' transmission under varied environmental conditions.

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1. Introduction

Social insect colonies provide one of the most fascinating and tractable contexts for theoretical and empirical explorations of biological complex adaptive systems (Wilson, 1978). The colonies function as decentralized systems for communications and collective actions (Fewell, 2003; Gordon, 1996). Lacking a central or hierarchical controller, group-level decisions in the colony are attained primarily via the spread and amplification of information communicated at a local level. Colonies use these self-organizational processes to respond and adapt to variable environment, to reach consensus when a single decision is required, and to distribute individuals across different roles, as in colony task organization

(Pratt, 2005). In social insect colonies, the role of interactions between nestmates in coordinating group level behavior have been investigated through a diversity of behaviors, including food distribution (Cassill and Tschinkel, 1999; Nixon and Ribbands, 1952), social defense (Hermann, 1984), social immunity (Cremer et al., 2007), and nest site selection (Pratt, 2005), as well as more generally in the recruitment of individuals across tasks (Gordon and Mehdiabadi, 1999; Greene and Gordon, 2003).

In this study we provide a rigorous agent-based modeling approach to explore how division of labor, and associated spatial heterogeneity, may impact the movement of elements, including information, food and disease, through a colony. Our model uses harvester ants (see Fig. 1) as a focal system to consider how individual task fidelity and colony division of labor influences movement patterns and associated information and/or disease transmission. The attributes of our proposed model are used widely

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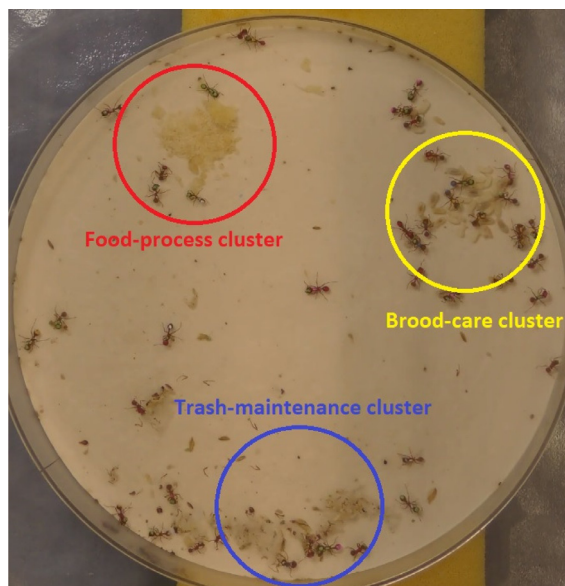


Fig. 1. Workers with three different task zones are clustered in their task SFZ as food-processing cluster, brood-care cluster and trash-maintenance cluster.

in network regulation, by social insect colonies and by other distributed communication systems in which spatial heterogeneity influences inter-individual contact patterns. Despite their multiple evolutionary histories, eusocial insect colonies generally share the features of distributed communication systems coupled with allocation of workers across different task roles (Tschinkel and Hanley, 2017; Crall et al., 2018; Jandt and Dornhaus, 2009; Baracchi and Cini, 2014; Sendova-Franks and Franks, 1995; Mersch et al., 2013; Baracchi et al., 2007). A large subset of (although not all) tasks occur in specific locations within the nest, creating Spatial Fidelity Zones (SFZs) for the workers performing those tasks (Fig. 1). This spatial structure should contribute to the regulation of local contact rates (Gordon et al. (1993)), shaping the structure of colony information networks (Mersch et al. (2013)), and potentially enhancing communication transmission for tasks (Sendova-Franks and Franks, 1994; Baracchi and Cini, 2014). Worker task assignments and associated zones of movement are not fixed however (Charbonneau et al., 2015), and changes in individual movement patterns can enhance or reduce SFZs, providing a much more complex and nuanced system for regulating information flow than would simple assignment of individuals to specific zones. This variation in individual movement patterns has a large potential effect on information flow. Differential worker movement patterns have been shown to influence multiple behavioral contexts, including alarm signal transmission (Regnier and Wilson (1968); Wilson and Regnier Jr (1971)), food distribution (Sendova-Franks et al. (2010); Feigenbaum and Naug (2010)), and pathogen transmission (Naug (2008); Feigenbaum and Naug (2010); Quevillon et al. (2015)).

Network models of information flow in social insects have focused primarily on the spread of three main classes of elements: information, food, and pathogens. Although information, food and contagious disease have both been shown to spread through the colony via physical contacts (Otterstatter and Thomson, 2007; Naug and Camazine, 2002; Charbonneau et al., 2013; Blonder and Dornhaus, 2011; Feigenbaum and Naug, 2010; Greenwald et al., 2015), they provide the network with oppositional goals. In the context of information flow, colonies should theoretically be organized in a way that allows individuals to transmit relevant information as quickly and accurately as possible (Franks, 1999; Richardson and Gorochofski, 2015). On the other hand, the rapid

development of network contacts is problematic to the control and regulation of pathogen spreading through contagious interactions (Schmid-Hempel, 1998; Hart and Ratnieks, 2001). Colonies must rely on social interactions to balance the demand for distribution of useful sources and the need to minimize the threat of pathogen spreading by contagious infection through interactions. Kappeler et al. (2015) showed that the division of a network into subgroups with higher connectivity can inhibit the initial spreading of contagion through social networks, while may rapidly increase spreading within network subgroups or clusters. Task fidelity could contribute to this network structure, if it provides a stable pattern of spatial occupancy and associated network contacts for the time that a worker is engaged in a specific task (Mersch et al. (2013)).

Mathematical models have been an important tool to understand spatial and environmental effects on social contact dynamics and the spread of information and disease (Mollison et al., 1985; Barlow, 1991; 2000; Hassell et al., 1991; Myers, 1978; Onnela et al., 2007; Romano et al., 2010). Information flow has been studied under the framework of innovation diffusion (Coleman et al. (1966)) and epidemic infection (Daley and Kendall (1964)). Gernat et al. (2018) simulated spreading elements via an SI model in an empirical trophallaxis network and explored general similarities between human and social insect communication networks, although they have very different speeds in their spreading dynamics. Richardson et al. (2017) used a SIS-structured model for the spread of information was to investigate the influence of activity cycles on information spread through social insect colonies. Through simulations, they found out that short-term activity cycles on dynamic time-ordered contact networks inhibit transmission of information. However, we still have little understandings of mechanisms that generate spatial heterogeneity and how individual moving preferences affects social contact dynamics and elements' spreading in different environments.

In this article, we propose and study a discrete-time Markov chain model in *Netlogo* to explore spatial and environmental effects on social contact dynamics and spreading dynamics of transmissible elements in social insect colonies. We use variations in movement patterns associated with different tasks to build and study an agent-based model of social contact dynamics and the related elements' spreading dynamics. Our proposed model incorporates the following three components that generate spatial heterogeneity: 1) three task groups, each assigned a general spatial zone in which the task is preferentially conducted; 2) variations in initial distributions of individuals, from general (random) mixing to aggregated one; 3) variation in movement patterns associated with specific task roles, modeled either as a random walk, or via bias in turning radius towards the task zone. To mimic the realistic transition of elements initial spatial distributions corresponding to three different environmental events, we vary agents initial spatial distribution from random-mixing to aggregated one. We then quantify the process of elements' propagation under different initial spatial distributions of social insects workers. In our model simulations, we monitor dynamical interactive behavior of workers and information transmission in multiple scenarios. We further estimated the elements' propagation rate over the colony from the first seed in the modified logistic regression model. We also apply an estimator of clumping to quantify social insects heterogeneous distribution, and examine the relations among spatial heterogeneity, interaction and information spread at the colony level.

2. Method

We use an agent-based discrete-time Markov chain model in *Netlogo* to model a $K \times K$ grid colony of $N (\leq K^2)$ workers of social insect colonies as set of anonymous agents in *Netlogo*. Each

grid, occupied by at most one worker, captures spatio-temporal dynamics resembling the real system. At any given time t worker $\mathbf{A}$ is characterized by its attribute $\eta_t(\mathbf{A}) = (l_t(\mathbf{A}), p_t(\mathbf{A}), w_t(\mathbf{A}), f_t(\mathbf{A}))$, where $l_t(\mathbf{A})$ is the location of worker $\mathbf{A}$, $p_t(\mathbf{A})$ is its task, $w_t(\mathbf{A})$ is its walking style, and $f_t(\mathbf{A})$ is its information -or pathogen, here we use information as one of cases of spreading elements status at time t . The grid space in Netlogo provided a simple way to simulate agents spatial behavior, giving them four choices of direction of movement, and an applicable technique to quantify the spatial distribution of agents, e.g. grid-based sampling survey. The grid structure of the simulation nest also matches the nest box design housing the actual harvester ant colonies from which we obtained appropriate parameters. Now we explain each component of the attribute η separately:

Location and neighboring : Worker $\mathbf{A}$ at time t takes at most one of the grid cells in the colony $X = \{(i, j) : 1 \leq i \leq K, 1 \leq j \leq K\}$, that is, $l_t(\mathbf{A}) = l = (i, j)$ such that $1 \leq i \leq K, 1 \leq j \leq K$. Workers do not necessarily know their own inner state. Naturally, workers sensing mainly depends on antennation and tactile sensation. The use of visual signals in workers is very minor (Hölldobler and Wilson, 1990), and it is unlikely for them to perceive neighbors more than 1.2cm away (Gordon et al., 1993). With the assumption that workers can sense and interact with their neighbors locating in the neighboring lattice within the length of antenna (2mm), we define the set of neighboring cells of ant $\mathbf{A}$ as $NC_t(\mathbf{A})$. We also assume the colony is a grid system with a hard (non-periodic) border, thus, for the workers on the edge or in the corner of colony, the size of this neighboring cells will reduce to three and two. Similarly, set of its neighbors at time t is defined as

$$N_t(\mathbf{A}) = \{\mathbf{B} : l_t(\mathbf{B}) \in NC_t(\mathbf{A})\}.$$

Therefore, for any worker $\mathbf{A}$ at any time t we have $|N_t(\mathbf{A})| \leq 4$, and if the worker is on edge of colony or at the corner this maximum number of neighbors will reduce to three or two.

Task group : Based on the laboratory observations on the social insects colonies (*P. californicus*), three major task zones that workers aggregated around are usually formulated in the colony: brood-care cluster, trash-maintenance cluster, and food-processing cluster Fig. 1. There is P different task group that each worker takes exactly one of them at a time. For each task $p \in \{1, 2, \dots, P\}$ we allocate one central location- called SFZ- in the colony called $S_p \in X$. This SFZ for each task is disjoint from other task, that is, $S_p \neq S_q$ if $p \neq q$. The Fig. 1 shows how workers with different tasks are clustered in locations related to their task, SFZs.

We also assume there is no task switching in the model, that is, worker $\mathbf{A}$ keeps its initial task for all the time, $p_t(\mathbf{A}) = p_0(\mathbf{A})$ for all ts . With that assumption, we can partition N workers to sum of N_p s where N_p is the number of workers with task p :

$$N = \sum_{p=1}^P N_p = \sum_{p=1}^P |\{\mathbf{A} : p_0(\mathbf{A}) = p\}|.$$

Walking style : We have two different walking style for social insects colonies: Random (R), in which worker $\mathbf{A}$ randomly selects one of the neighboring cells and move toward that, or Drifted (D) in which worker $\mathbf{A}$ has some preferential direction toward its task SFZ, that is, if $p_t(\mathbf{A}) = p$ and $w_t(\mathbf{A}) = D$ then $\mathbf{A}$ moves to one of the neighboring cells closest to S_p . Similar to task, walking style for each worker is predetermined at time $t = 0$ and is fixed for all future time $t > 0$. Therefore, each task group N_p can be divided into two sets: a set of workers with task p who perform random walking and the set of workers with the same task who perform drifted walking style. Based on that we define the *spatial fidelity* (SF) of the task group p :

$$SF(p) = \frac{|\{\mathbf{A} : p_t(\mathbf{A}) = p \text{ and } w_t(\mathbf{A}) = D\}|}{N_p}, \quad (1)$$

that is the fraction of workers with task p having drifted walking style.

Information : Information with a property that can initiate a change in the state of the receiver advertently (a signal) or inadvertently (a cue), could be transmitted in the colony to complement individual decision-making capability on task performances. At time t we categorize worker $\mathbf{A}$ as informed $f_t(\mathbf{A}) = 1$, or not informed $f_t(\mathbf{A}) = 0$. An informed worker can spread information to other not informed neighbor workers with some probability β_i .

Now we explain the dynamic of movement and information spreading across social insect colonies through time. We assume each update, i.e., one-time tick, is consistent with Δt . We also assume that the basic speed of workers is one cell per time step. Workers cannot cross the reflecting walls and borders, instead when they reach the borders and walls, they will redirect randomly. At any time t we select a worker with attribute $\eta_t(\mathbf{A}) = (l_t(\mathbf{A}), p_t(\mathbf{A}), w_t(\mathbf{A}), f_t(\mathbf{A})) = (l, p, w, f)$ from the total population of N workers randomly to move to one of the cells $\in NC_t(\mathbf{A})$ randomly. If the selected cell is occupied with one of the neighbor worker $\mathbf{B}$ we say $\mathbf{A}$ and $\mathbf{B}$ have contacts, otherwise $\mathbf{A}$ performs walk. At any given time t , each worker $\mathbf{A}$ can change one or all of its attributes through the following procedure:

Randomly select $\mathbf{A}$ with attribute $\eta_t(\mathbf{A}) = (l_t(\mathbf{A}), p_t(\mathbf{A}), w_t(\mathbf{A}), f_t(\mathbf{A})) = (l, p, w, f)$.

1. The selected worker has $|NC_t(\mathbf{A})|$ neighboring cells and $|N_t(\mathbf{A})|$ neighbors, therefore with the probability of $1 - \frac{|N_t(\mathbf{A})|}{|NC_t(\mathbf{A})|}$, $\mathbf{A}$ walks into an empty location with the following rules:

- (a) If $w = R$, the chosen worker has a random walking style, the worker randomly walks into one of the empty locations $l' \in NC_t(\mathbf{A})$ with probability

$$\begin{aligned} P(l_{t+\Delta t}(\mathbf{A}) = l' \mid l' \text{ is empty \& } w_t(\mathbf{A}) = R) \\ &= \frac{1}{|NC_t(\mathbf{A})| - |N_t(\mathbf{A})|} \times \frac{|NC_t(\mathbf{A})| - |N_t(\mathbf{A})|}{|NC_t(\mathbf{A})|} \\ &= \frac{1}{|NC_t(\mathbf{A})|}. \end{aligned}$$

- (b) If $w = D$, the chosen worker has a preferential walking style, the worker walks into one of its empty neighborhood cell $l' \in NC_t(\mathbf{A})$ closest to its task SFZ S_p (SFZs) with probability

$$\begin{aligned} P(l_{t+\Delta t}(\mathbf{A}) = l' \mid l' \text{ is empty \& } w_t(\mathbf{A}) = D) \\ &= \frac{|NC_t(\mathbf{A})| - |N_t(\mathbf{A})|}{|NC_t(\mathbf{A})|}. \end{aligned}$$

2. The selected worker has $N_t(\mathbf{A})$ neighbors and therefore, it has a contact with one of its neighbors with probability $\frac{|N_t(\mathbf{A})|}{|NC_t(\mathbf{A})|}$.

Assume that the chosen neighbor $\mathbf{B}$ has attribute $\eta_t(\mathbf{B}) = (l_t(\mathbf{B}), p_t(\mathbf{B}), w_t(\mathbf{B}), f_t(\mathbf{B})) = (l', p', w', f')$. We have two cases:

- (a) If $f = f'$ then the two workers switches their location with the following probability:

$$\begin{aligned} P(l_{t+\Delta t}(\mathbf{A}) = l' \& l_{t+\Delta t}(\mathbf{B}) = l \mid l_t(\mathbf{A}) = l \& l_t(\mathbf{B}) = l') \\ &= \frac{|N_t(\mathbf{A})|}{|NC_t(\mathbf{A})|}. \end{aligned}$$

- (b) If $f \neq f'$ and without loss of generality we assume $f = 1$, that is $\mathbf{A}$ is informed, then the informed worker spreads information to the other one with probability

$$\begin{aligned} P(f_{t+\Delta t}(\mathbf{A}) = 1 \& f_{t+\Delta t}(\mathbf{B}) = 1 \mid f_t(\mathbf{A}) = 1 \& f_t(\mathbf{B}) = 0) \\ &= \frac{\beta_i |N_t(\mathbf{A})|}{|NC_t(\mathbf{A})|}. \end{aligned}$$

The schematic diagram of our dynamical model and the related variables are shown in the Fig. 2 and Table 1, respectively. To further study how environment and spatial components affect the dynamics of social interactions and information spread in social in-

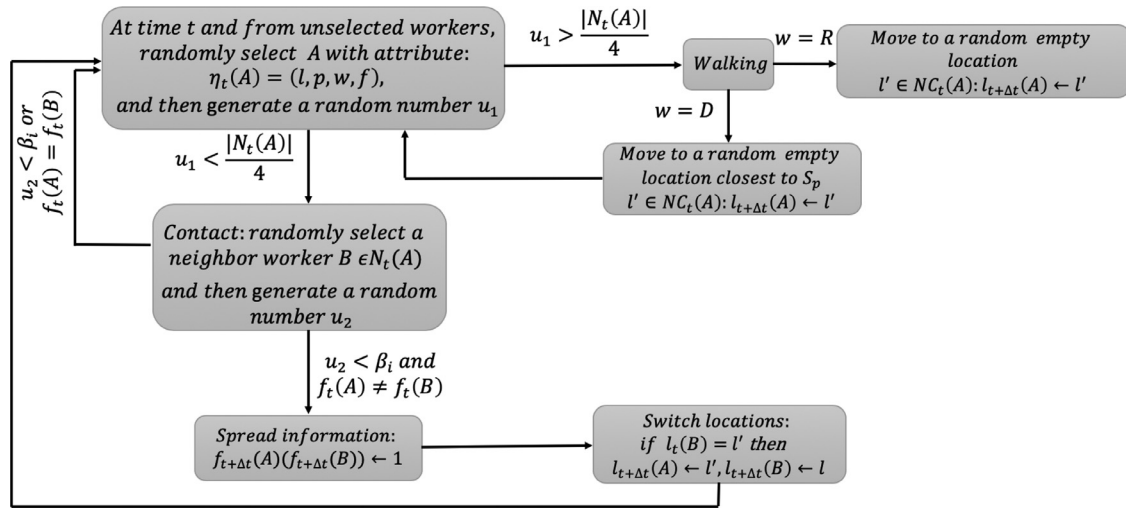


Fig. 2. Modeling schematic diagram of our social network model.

Table 1
Parameters, Variables and their definition.

	Parameter	Description	Baseline value	Ref.
Colony Parameters and Variables	$K \times K$	Nest size	69×69	Assumed
	P	Number of different task	3	Assumed
	$SF(p)$	Spatial fidelity for task p	–	–
	S_p	SFZ for task p	–	–
	SHD	Spacial heterogeneity degree of colony	–	–
	m	The conversion ratio of space	3	Assumed
	t	The time unit of one tick	0.001 s	Hurlbert et al. (2008)
Worker Parameters and Variables	$lattice$	The detection distance of two neighboring ants	0.2cm	Measured
	N	The total number of workers in social insects colony	180	Assumed
	N_p	The total number of workers with task p	60	Assumed
	$l_t(\mathbf{A})$	Location of worker $\mathbf{A}$ at time t	–	–
	$p_t(\mathbf{A})$	Task of worker $\mathbf{A}$ at time t	–	–
	$w_t(\mathbf{A})$	Walking style of worker $\mathbf{A}$ at time t	–	–
	$f_t(\mathbf{A})$	Information status of worker $\mathbf{A}$ at time t	–	–
	$NC_t(\mathbf{A})$	Set of neighboring cells of worker $\mathbf{A}$ at time t	–	–
	$N_t(\mathbf{A})$	Set of neighbors of worker $\mathbf{A}$ at time t	–	–
	$C(t)$	Total number of contacts between workers at time interval $(0, t)$	–	–
	$R(t)$	Contact rate at time t	–	–
	$\bar{R}_w(t)$	Average within group contact rate at time t	–	–
	$\bar{R}_b(t)$	Average between groups contact rate at time t	–	–
	$f_t(\mathbf{A})$	Information status of worker $\mathbf{A}$ at time t	–	–
			{0(Informed), 1(Not informed)}	–
	$l(t)$	Fraction of informed workers at time t	–	–
	β_i	Probability of information spread	1	Assumed

sects colonies, we first define some concepts. Let $C(t)$ be the total number of contacts occurred between workers of social insects colony in the time interval $(0, t)$, then the contact rate $R(t) = \frac{dC}{dt}$ is approximated by the number of contacts during the small time interval Δt :

$$R(t) \approx \frac{C(t + \Delta t) - C(t)}{\Delta t}. \quad (2)$$

Similarly, we define $R_{pq}(t)$ as the contact rate between workers with tasks p and q . If $p = q$ then $R_{pp}(t)$ is the contact rate within a task group p . We also define $\bar{R}_w(t) = \frac{\sum_{p=1}^P R_{pp}(t)}{P}$ as the average contact rate within same task group, and $\bar{R}_b(t) = \frac{\sum_{p,q=1}^P R_{pq}(t)}{\binom{P}{2}}$ as the average contact rate between different task groups.

Let P_l be the probability that cell location l being occupied by a worker, then we define *spatial heterogeneity degree* (SHD) of the

colony as

$$SHD(t) = \frac{\sum_{l=1}^{K^2} (P_l - \frac{N}{K^2})^2}{K^2}, \quad (3)$$

where $\frac{N}{K^2}$ is the probability that a typical cell l is occupied by a worker when all workers have a random walk, that is, when $w(\mathbf{A}) = R$ for all $\mathbf{A}$ s. This definition indicates that the smallest value of SHD is the case when all workers do symmetric random walk ($SHD_{\min} = 0$), and the largest value of SHD is the case when workers do not move, that is, $P_l = 1$ for all N occupied l locations by N workers, and $P_{l'} = 0$ of the remaining $K^2 - N$ empty locations l' :

$$SHD_{\max} = \frac{N(1 - \frac{N}{K^2})^2 + (K^2 - N)(0 - \frac{N}{K^2})^2}{K^2} = \frac{N(K^2 - N)}{K^4}.$$

For simplicity, we rescale SHD by converting $K \times K$ grid colony to the $\frac{K}{m} \times \frac{K}{m}$ patches where each patch has $m \times m$ grids. The parameter m is a conversion parameter, for example, if we have a 300×300

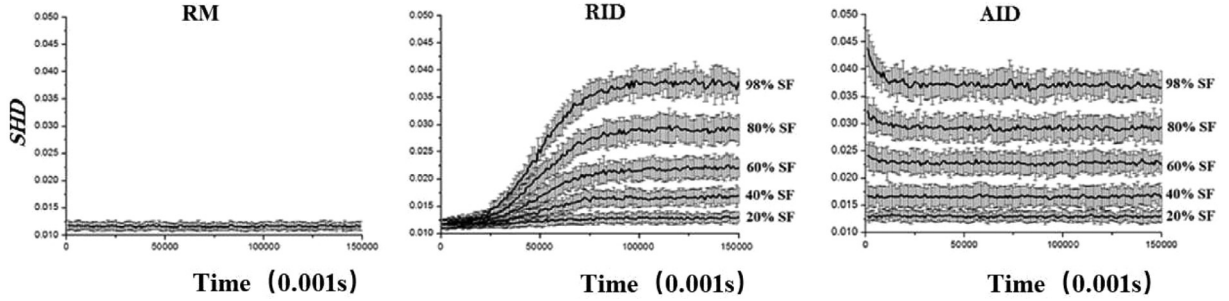


Fig. 3. Spatial heterogeneity degree and the average contact rate over time for RM, RID, and AID scenarios: Solid black lines represent the average of 40 replicates on each update and error bar are 95% confidence intervals. In all scenarios $SHD(t)$ and $R(t)$ share the same trend. SHD synchronizes with the average contact rate of workers in all of the scenarios with various spatial fidelity values. Biologically, when more workers perform preferential movement the SHD of workers distribution and their interactive behavior will escalate.

colony, we re-scale it by choosing $m = 10$ and the number of patches $\frac{300}{10} \times \frac{300}{10}$, that is, each new patch includes 10×10 cells. Let $P_l(\tau)$ be the ratio of occupied grids by workers to all $m \times m$ grids at patch l , then we have $SHD(\tau)$ calculated as follows

$$SHD(\tau) = \frac{\sum_{l=1}^m (P_l(\tau) - \frac{N}{K^2})^2}{K^2}. \quad (4)$$

We define $I(t)$ as the number of informed workers at time t :

$$I(t) = |\{A : f_t(A) = 1\}|,$$

The rate $\frac{dI}{dt}$ is approximated by the number of information received during the small time interval Δt :

$$\frac{dI}{dt} \approx \frac{I(t + \Delta t) - I(t)}{\Delta t}.$$

We use our model to explore how spatial fidelity affects the different average contact rates, spatial heterogeneity degree, and information spread in three different environmental scenarios of social insects colony. Each environmental scenario is characterized by the initial configuration of workers and the spatial fidelity as follows:

1. **Random-Mixing (RM)**: in which all workers are randomly distributed in the colony and all of them are assigned with random walking style, that is $SF(p) = 0$ for $p \in \{1, \dots, P\}$. Workers random walking corresponds to random-mixing in *Temnothorax albipennis* after famine emergency (Sendova-Franks et al., 2010).
2. **Random-Initial-Distribution (RID)**: in which all workers are initially distributed in a random location in the colony but a fraction f follow drifted walking style, that is $SF(p) = f$ for all $p \in \{1, \dots, P\}$.
3. **Aggregated-Initial-Distribution (AID)**: in which workers tend to segregate in their task SFZs Sendova-Franks and Franks (1993), we assign f_p fraction of workers with task p having drifted walking style, that is, that is $SF(p) = f_p$.

In the next Section we will study the dynamics of the contact rate $R(t)$ and its average, the average spatial heterogeneity degree SHD and the elements spreading defined in this Section under the above environmental scenarios.

3. Result

In this Section, we perform our analyses and simulations on three different scenarios explained in the Section 2: RM for $SF = 0$, RID and AID for $SF = 20\% - 98\%$. We will provide results on the dynamics of the contact rate $R(t)$ and the averages $\bar{R}_w(t)$, the spatial heterogeneity degree $SHD(t)$ of the colony and the information spread for different environment scenarios. Each plot is the average of 40 different stochastic simulations seeding the same initial condition, with the model baseline parameters in Table 1, unless stated otherwise.

3.1. Dynamics of the average contact rates $R(t)$ and spatial heterogeneity degree $SHD(t)$

In this subsection we study the dynamic of spatial heterogeneity degree, $SHD(t)$ (see (3)), the contact rate dynamics $R(t)$ (see (2)) and its averages over different environmental scenarios. The main observation of this part is that the spatial heterogeneity degree dynamics follow the logistic growth patterns with different intrinsic growth rates and carrying capacities in the scenarios of RID, Fig. 3.

Spatial heterogeneity degree defined in Eq. 4 measures the level of deviation from the even distributions of workers of social insects colonies over the space. In Fig. 3 we observe that in the RM scenario $SHD(t)$ is almost constant over the time with the value of 0.0115, but in the RID and AID scenarios, the dynamics of $SHD(t)$ is not constant but grows logistically. We also find SHD synchronizes with the average contact rate of workers in all of the scenarios and for all spatial fidelity values. To further explore the correlation between $SHD(t)$ and $R(t)$ under different scenarios, we pooled them pairwise, and observed a linear trend. There is a linear correlation between $SHD(t)$ and $R(t)$ that is represented by Eq. 5.

$$R(t) = -0.1033 + 11.895SHD(t), \quad (5)$$

with $\text{adj-}R^2 = 0.9985$, $F\text{-value}(1, 1642) = 1.10029$, and $P\text{-value} < 0.001$. This result means that the social contact network (e.g., the average contact rate) could be formulated by spatial heterogeneity due to non-random walking styles. As consequences, RID could be the scenario interlinking the random distribution of workers initially (RM) and the segregation in their corresponding SFZ at the end (AID). Specifically, more workers perform preferential movement- the higher spatial fidelity SF - higher degree of SHD plateau for the colony and higher contact rates consequently.

Our spatial heterogeneity degree $SHD(t)$ reflects the "mean-crowding" concept introduced by Lloyd Lloyd (1967). Mean-crowding measures the spatial heterogeneity of the disease/host model, which is calculated by the total number of neighbors every organism has over the number of organism with at least one neighbor. To illustrate relationships among mean-crowding, $SHD(t)$ and the $R(t)$, we calculated them within the RID scenario for the spatial fidelity being $SF = 98\%$. Both SHD and mean-neighbors increase linearly as the average contact rate increases, Fig. 4. This result illustrates that SHD provides a quantified measure of spatial heterogeneity as the "mean-crowding" concept. Also, the overlapping between SHD and mean-neighbors offers an explanation for the synchronization of $SHD(t)$ and $R(t)$ that the larger value of SHD represents the more crowded neighboring space, as a consequence, ensures more opportunities to contact with nest-mates.

In both RID and AID scenarios, we also find as the spatial fidelity increases, the between-group average contact rate $\bar{R}_b$ de-

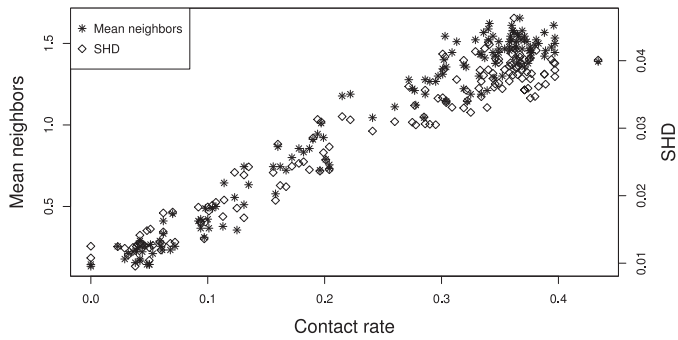


Fig. 4. Overlapping between mean-neighbor and SHD over contact rate in double y-axes for RID scenario and $SF = 98\%$: there is a synchronization between $SHD(t)$ and $R(t)$, that is, that the larger value of SHD , the more crowded neighboring space, therefore, more contact with nest-mates.

creases, and the within-group average contact rate $\bar{R}_w$ increases, Fig. 5.

3.2. Information spread dynamic $I(t)$

In order to understand how the spreading elements such as information or pathogen propagate over the contacting space, we track the fraction of informed workers $I(t)$ in colony under different spatial fidelity and environmental scenarios.

For the RM and RID scenarios, the quasi-stationary state for the average fraction of informed workers is almost 100%, but for AID scenario, an outstandingly varied fractional workers (12%–97%) being informed in the end suggests that the inhibition of elements' transmission is probably caused by the spatial segregation, Fig. 6.

Another important observation from the dynamic of $I(t)$ is that spreading elements follow a modified logistic growth pattern, Fig. 6. To identify how the dynamics of elements correlates to the traditional non-spatial logistic growth model, we estimated the in-

trinsic growth rate $\gamma(t)$ by using the following equation

$$\gamma(t) = \frac{I(t + \Delta t) - I(t)}{\Delta t \cdot I(t) \cdot (1 - I(t))},$$

where $I(t)$ is the fraction of informed workers at time t and $\Delta t = 10000$ is the time interval. The intrinsic growth rate $\gamma(t)$ decays over time in all scenarios, which is different from the constant rate in traditional non-spatial logistic model without space, Fig. 7. The work on the effects of spatial correlation between the susceptibles and infected by Keeling (1999) indicates that transmissibility of pathogens could be restricted by the identity of neighbor nodes in the network. Thus we speculated the intrinsic growth rate $\gamma(t)$ in our spatial model can be a function of e^{-I} to reflect the local saturation of transmission due to the restricted spatial connection between informed and non-informed workers. Therefore, we perform the nonlinear regression by using the following modified-logistic model

$$\frac{dI}{dt} = R_{RM} \cdot Q_p \cdot e^{-I(t)} \cdot I(t) \cdot (1 - I(t)), \quad (6)$$

where the carrying capacity of fractional informed workers equal to 100%, $R_{RM} = 0.035$ is parameter of contact rate without spatial effect, which is the same for all scenarios and is estimated from average of contact rate over time in RM scenario, and the parameter Q_p is the transmission rate of spreading elements estimated from Eq. 6, and $e^{-I(t)}$ is a encountering probability between informed and non-informed workers in the Poisson process. We estimated Q_p in different scenarios and different spatial fidelity SF to examine effects of SHD , Table 2. This estimation for Q_p shows that in RID scenarios the larger SF gives larger SHD and larger Q_p , but in AID scenarios larger SF gives smaller Q_p . Our regression model fits the sigmoid curves of elements' spread robustly for all scenarios, Fig. 6. We also observed that the larger value of Q_p , faster the fractional informed ants arrive to the plateau.

To further study the correlation between Q_p and SF values under different scenarios, we plot the spatial fidelity SF versus Q_p ,

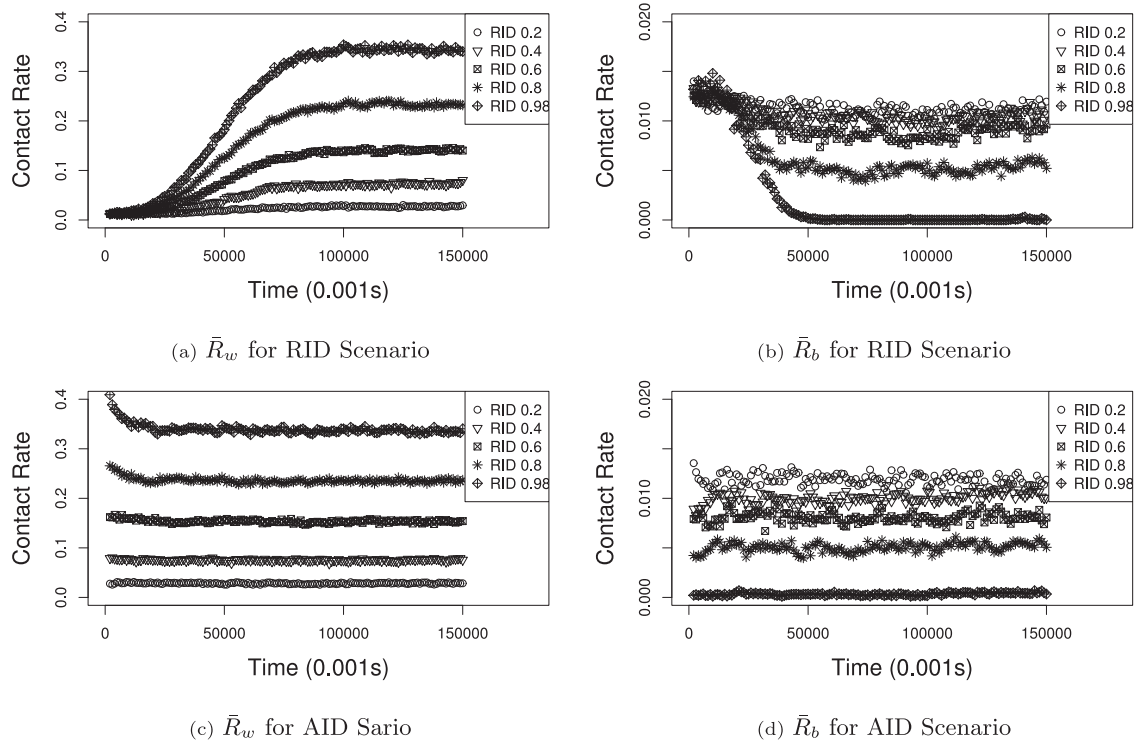


Fig. 5. Different average contact rates for RID and AID Scenarios: For both RID and AID scenarios the between-group average contact rate decreases, and the within-group average contact rate increases as spatial fidelity increases.

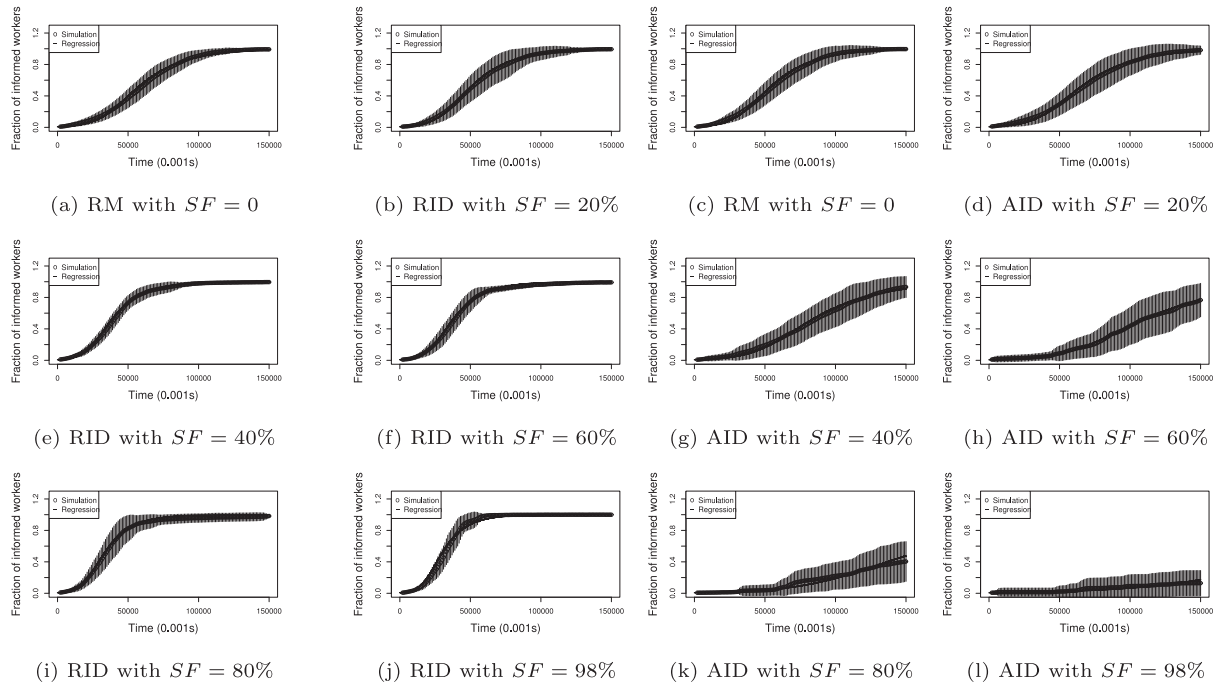


Fig. 6. Fraction of informed workers over time in RM, RID, and AID scenarios and different SF values: The points represent the dynamic of the average of 40 replicates and error bars are 95% confidence intervals. The black curves are predicted values from the fitting model Eq. 6. For RM and RID scenarios all the workers become informed at quasi-stationary state, however for AID scenario the quasi-stationary state value depends on spatial fidelity SF .

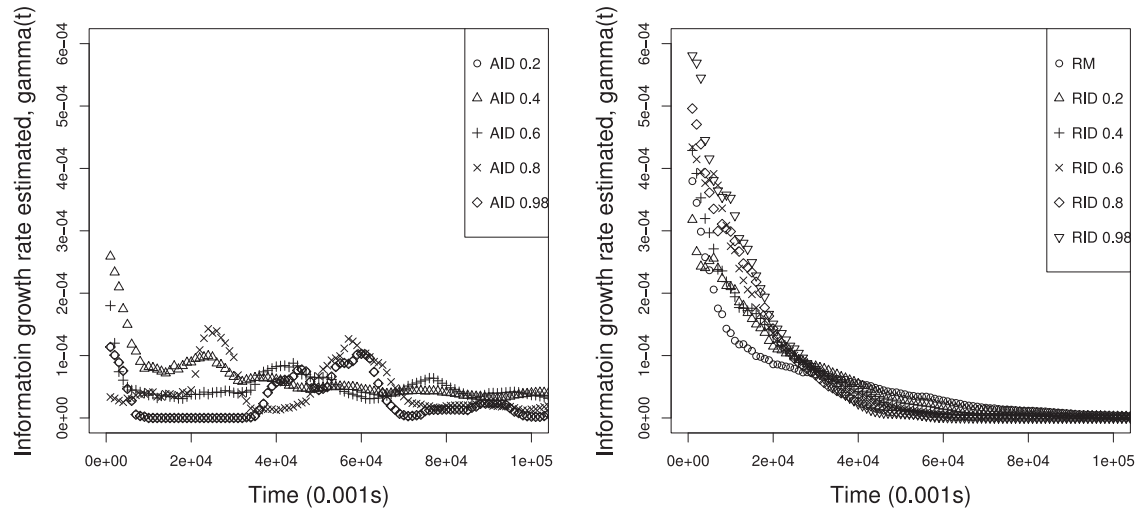


Fig. 7. Calculated $\gamma(t)$ over time in scenarios AID (left panel) and RM and RID (right panel): $\gamma(t)$ decays exponentially over time in all scenarios.

Table 2

Q_p estimation for Eq. 6, the asterisk indicates statistical significance ($t < -835$, d.f. = 148, P-value < 0.0001).

SF	Q_p for AID	Q_p for RID
20%	0.002457***	0.00331***
40%	0.002014***	0.00417***
60%	0.001526**	0.00443***
80%	0.001083***	0.00491***
98%	0.000691***	0.00563***

Fig. 8. The result provides a visual presentation: diamonds are RID scenarios, stars are for AID scenarios, and the square is the RM scenario. We observe that there is a bifurcating pattern of Q_p as a linear function of SF in RM, RID, and AID scenarios. The linear fits

for RID and AID are shown as follow:

$$\begin{cases} Q_p = 0.003 + 0.0025SF, & \text{RID scenario, (Adj-}R^2 = 0.99, F(1, 4) = 524.9, \text{P-value} < 0.001) \\ Q_p = 0.003 - 0.0024SF, & \text{AID scenario, (Adj-}R^2 = 0.99, F(1, 4) = 6497, \text{P-value} < 0.001) \end{cases}$$

4. Discussion

The flow of spreading elements within a biological social network is not random. Instead, heterogeneity among individuals in their communication clusters and in their spatial distributions influences spreading elements across groups. For a social insect colony, in which individual behavior depends on their task, both spatial and network heterogeneity are driven by individuals task roles at any given time. In this paper, we assigned task roles to in-

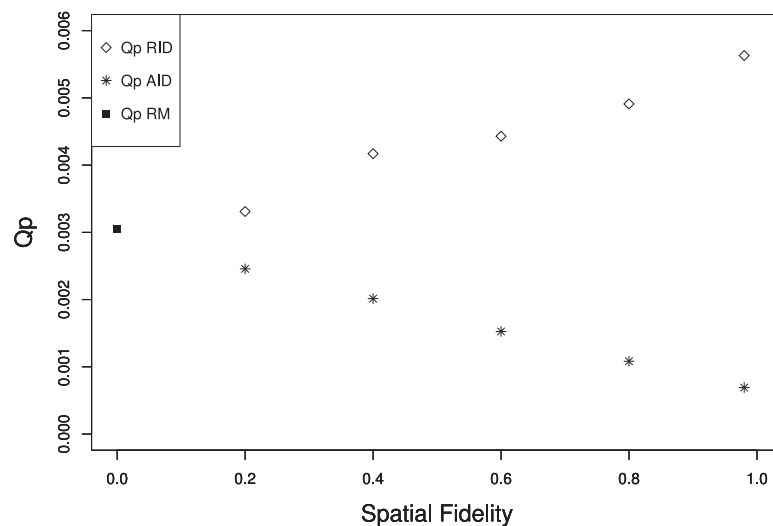


Fig. 8. Pairwise comparisons of transmission rate for RM, RID, and AID scenarios: There is a positive linear correlation between transmission rate Q_p and spatial fidelity SF for RID scenario indicating its transmission promotion effects, but the correlation between Q_p and SF for AID scenario is negative because of transmission inhibition effects.

dividual agents and manipulated individual spatial preferences and initial conditions to explore the impact of spatial behavior on social contacts and elements' transmission. Our dynamical model included three different task groups, with their corresponding SFZs. We additionally studied the impact of task on movement, by assigning workers in social insect colonies with different tasks to either random or preferential walking styles. We will discuss dynamical effects on the processes of social contacts and elements spreading in the following four different aspects:

Dynamics of social contacts: The individual interactions in social insects colony were the straightforward pathway to inseminate and transmit spreading elements such as information or pathogens in a contacting network (Pacala et al., 1996). Ant workers were found to change their contact rates flexibly over time to regulate local information capturing (Gordon, 1996; Gordon et al., 1993), e.g. restricting the flow rate of spreading elements through regulating the contact rate in a time-order network (Blonder and Dornhaus, 2011). In our model simulations, the probability of contact between workers depends on their neighboring space. Meanwhile, we observed that contact makes varied contributions on the spreading elements propagation. For example, for the scenarios with 40% spatial fidelity, the functional contacts contributing to elements' spread were only accounted for less than 1% of total contacts when initial aggregation of workers, but 7% when their initial distribution is random. It was suggested that the spatial correlation between the informed and non-informed workers in the local scale might interfere with an expected speed of transmission of spreading elements (Keeling, 1999). As the spatial fidelity escalates the spatial heterogeneity degree, information about tasks is more likely to be transmitted within groups in colonies, which may be a potential mechanism to maintain the task specialties (Naug, 2009). When the colony has extremely high spatial fidelity (e.g., 98%) with aggregated initial distribution (AID), the propagation of spreading elements highly relies on the contacts between groups through random walkers. One of the consequences is that the high spatial fidelity results in the slower transmission rate of elements, e.g. pathogens, which is probably one of mechanisms of social immunity in the social insects colonies (Cremer et al., 2007).

Spatial effects: The fraction of informed workers in our simulation shows an obvious logistic-pattern which corroborates the finding of previous studies on mobile encounter networks (Adler and Gordon, 1992; Arai et al., 1993; Korhonen and Kurhinen,

2007; Pratt, 2005), a food trophallaxis network in an ant colony (Greenwald et al., 2015; Sendova-Franks et al., 2010) and contagious pathogen model simulations for social insect colonies (Naug and Camazine, 2002). Comparing to the standard logistic growth model without spatial components, modifications in Eq. 6 imply that spatial effects, such as local spatial correlation, cluster distribution and preferential movement of workers may distort the linkage between physical contagion and mass action of spreading elements. The modified-logistic model in Eq. 6 uncovers two main spatial effects: local saturation of spreading elements and spatial segregation of workers. In the correlation model (Keeling, 1999), the local spatial correlation between the susceptible and the infected ones was found to lead the reproductive ratio of spreading elements to decay over time after the single infectious individual invades a cluster of susceptible individuals.

The other spatial effect that can be observed is the strong linear relation between agents' spatial fidelity and the transmission rate of spreading elements, Q_p in different scenarios, Fig. 8. In general, the estimates of transmission rate Q_p in Fig. 8 suggest the dual-functionalities of spatial fidelity on elements' transmission rate in scenarios. When the initial distribution of workers is aggregated, the structure of spatial clusters induced by workers preferential movement heterogenized the neighboring space of the non-informed/informed workers, and shielded workers from being exposed to external spreading elements. The inhibiting effects of spatial fidelities on spreading elements are similar as the clustering effects that restrict the potential further transmission across household (Grassly and Fraser, 2008). Specifically, the biological barriers in colonies arising from spatial aggregations are one of the mechanisms of organizational immunity (Feigenbaum and Naug, 2010; Naug and Smith, 2007). Meanwhile, we observed the promoting effect of spatial fidelities on spreading elements in random mixing and random initial distribution scenarios, Fig. 8. Intuitively, workers directional movements arising from the initial random positions would intensify the mixing effects and help elements being transmitted over the colony. Spreading elements, such as food have been observed to spread faster and more uniformly in the groups with better spatial mixing among individuals in the colonies of honeybee *Apis mellifera* Naug (2008) and the ant *Temnothorax al-bipennis* Sendova-Franks et al. (2010).

Environmental effects on spreading elements: The trade-off between beneficial and harmful spreading elements through social

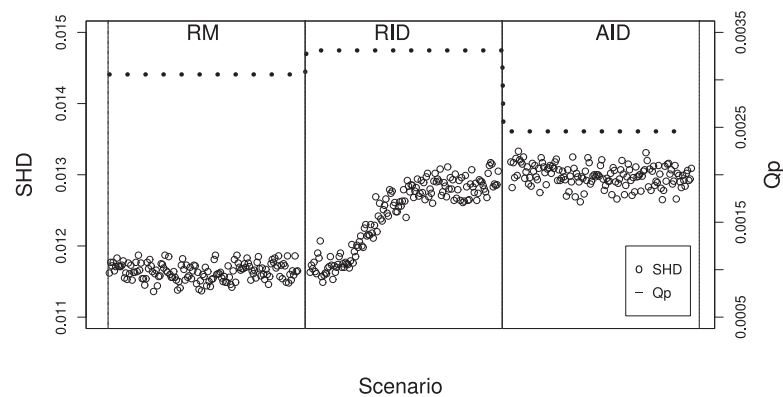


Fig. 9. Possible adaptive spatial strategies in three scenarios with $SF = 20\%$: Social insect colonies can regulate the cost and benefits arising from properties of spreading elements during the consecutive scenarios, $RM \rightarrow RID \rightarrow AID$.

insect colonies could be resolved by mechanisms of encountering networks and diffusion of chemical signals (Blonder and Dornhaus, 2011; Pinter-Wollman, 2015; Richardson and Gorochowski, 2015; Sendova-Franks et al., 2010). Our model simulation provides an alternative explanation for the trade-off through changes in individual spatial behavior induced by environmental events/scenarios. In social insects colonies, the spatial distribution of workers has been observed to change in response to environmental events instantly. For example, under threats, workers break down their spatial tendency and mix randomly as an effective strategy to relieve threats (Sendova-Franks et al., 2010; Wilson and Regnier Jr, 1971). Without immediate threats, it was found that spatial segregation provided colonies protection against pathogens exposure (Fefferman et al., 2007; Naug and Camazine, 2002; Pie et al., 2004; Stroeymeyt et al., 2014). Thus, the opposite effects of workers' spatial behavior on transmissions of spreading elements demonstrates the capability of social insect colonies to regulate cost and benefits arising from properties of spreading elements during the consecutive scenarios, $RM \rightarrow RID \rightarrow AID$, Fig. 9.

Significance of spatial behavior: Individual movement patterns heterogenize the probability of being exposed to spreading elements (Stroeymeyt et al., 2014). Pinter-Wollman (2015) suggested that workers' persistence in walking orientation may facilitate the information flow in a restricted space due to high interaction rates. We found the same effects of spatial fidelities in the RID scenarios: high spatial fidelity of workers on each task group leads high contact rate of workers, and as consequences, speeds up transmission of spreading elements when the proportion of the workers (i.e., ones with the preferential walking style) persist in orientation and walk to SFZs from initial random positions. High spatial fidelities could maximize the benefit of the elements' transmission rate Q_p in the environment with threat, and minimize the cost of Q_p in normal environments with pathogens. Nevertheless, workers in the colonies of *T. rugatulus* and *Leptothorax longispinosus* were found to spend non-negligible amounts of time on wandering in the nest (Charbonneau et al., 2015; Charbonneau and Dornhaus, 2015; Cole, 1986). We speculated it would be beneficial to maintain some proportion of random walkers as a way to ensure the instant responses to local threatening events in the transitional scenario from initial spatial segregation to random mixing ($AID \rightarrow RID$).

Our study provides important insights as represented above. But our proposed model does have its own limitations that we should work further more. In a real social insect colony, element itself, such as alarm signal, is a potential factor influencing individual spatial preference. For example, the informed individuals by alarm pheromone tend to walk randomly in order to recruitment nestmates as fast as possible Wilson (1958). This suggests that the

individual preference of movement could be linked to the status of individuals being informed or not. One limitation of our current model is that agents' spatial fidelity is independent on their information status. In addition, the transmission probability of elements via contact may be homogenized and overestimated in our model. Because in reality, this probability is expected to be varied across individuals. For simplification, we simulated the propagation process of one element in a social insect colony. In our future work, we should include varied elements, such as information, food and pathogens, to be transmitted simultaneously. And we should include task switching in RID scenario to study how the social insects employ their spatial behavior to regulate information flow with a limited transmissibility, e.g. task cues rather than alarm signal. We are building a model based on attenuation-networks with several mechanisms, e.g. individuals have spatial preferences based on spatial fidelity and mission location density, and individuals could switch their tasks based on the task cues captured from their neighbors. Also, those simulation results inspired us to conduct experiments to track how spatial clusters of social insects affect the information flows, e.g. alarm signal propagation in the colony.

CRediT authorship contribution statement

Xiaohui Guo: Conceptualization, Data curation, Formal analysis, Visualization, Writing - original draft. **Jun Chen:** Formal analysis, Visualization, Writing - review & editing. **Asma Azizi:** Formal analysis, Visualization, Writing - review & editing. **Jennifer Fewell:** Conceptualization, Writing - review & editing. **Yun Kang:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Project administration, Writing - original draft, Writing - review & editing.

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