Stochastic sexual interaction facilitates the evolution of asexual cooperation in the social amoeba

Shota Shibasaki and Masakazu Shimada

Department of General System Studies, The University of Tokyo, Tokyo, Japan
shibasaki.sh@gmail.com

Abstract

The evolution of cooperation is one of the most important problems in biology. The evolutionary game theory is a useful approach for investing this problem, and some researchers have recently improved it by adding another game to the dynamics. This framework is known as "multi-games". In this paper, we investigate the effect of the stochastic sexual interaction on the evolution of asexual cooperation. Our scenario is based on the life cycle of *Dictyostelium discoideum*, which has two cooperative phases: asexual fruiting body formation and sexual macrocyst formation. We assume that fruiting body formation is represented by the Prisoner's Dilemma game, while macrocyst formation provides the constant benefits; we focus on the evolution of cooperation in fruiting body formation. Our model shows that cooperators can eliminate different mating type defectors. This occurs only if the benefit from the stochastic sexual interaction is less than from asexual cooperation. This result suggests that macrocyst formation stabilizes the evolution of cooperation in fruiting body formation to some degree. Next, we investigate the metapopulation dynamics because cooperators are eliminated by the same mating type defectors in our model. The fixation time of defectors slows down due to the stochastic sexual interaction but cooperators finally become extinct. These results suggest that a mating type works as a tag and that *D. discoideum* avoids the exploitation from defectors by sexual interaction.

Introduction

The evolution of cooperation has been a challenging concept in biology. Although cooperation exists from human societies (Raihani and Bshary, 2015) to microbial commnities (Popat et al., 2012; Strassmann and Queller, 2011), studies based on the evolutionary game theory have shown that cooperators, which altruistically pay a cost for another individual to receive a benefit, are vulnerable to defectors, which pay no costs and produce no benefits for others (Nowak, 2006b). Some mechanisms, including tag-based cooperation (Antal et al., 2009; Traulsen and Nowak, 2007) and structured populations (Nowak et al., 2010), have been considered to resolve this contradiction. Tag-based cooperation enables cooperators to change their behaviors by measuring the similarities of another trait, or a tag, between the partners and themselves. If the tags of a cooperator and a partner are similar, the cooperator will cooperate; otherwise, it

will stop the cooperation and plays as a defector. On the other hand, structured populations decrease the frequency that cooperators interact with defectors. Many theoretical studies have reported the conditions under which cooperation can evolve in a single game by using ordinary differential equations (Hofbauer et al., 1979), the lattice models (Nakamaru et al., 1997), and the evolutionary graph theory (Ohtsuki et al., 2006).

Recently, researchers have developed the evolutionary game theory by coupling several games with a dynamic scenario. This framework is known as multi-games (Hashimoto, 2006; Wang et al., 2014) or mixed games (Wardil and da Silva, 2013); we call it "multi-games" here. In multi-games, individuals play two or more games whose payoff matrices are different. In addition, there can be numerous strategies for each game. The most important aspects of multi-games are unpredictability and complexity of the dynamics. Hashimoto (2006) shows with multi-games that it is possible that an orbit does not converge to a point that is a global attracter if the dynamics has only one game. In other words, cooperation can evolve under the multi-game dynamics, even if it does not evolve under the single game dynamics.

The framework of multi-games can be adapted to the species that use two cooperative systems simultaneously. Although the previous studies of multi-games do not mention to which species one can adapt this framework, we consider that one example of such a species is *Dictyostelium discoideum*. *D. discoideum*, also known as the social amoeba or slime mold, has two cooperative dormant phases in starvation: fruiting body formation and macrocyst formation. The amoebas aggregate together because of the chemoattractant cyclic AMP (cAMP) in both cases (Tyson and Murray, 1989; Abe et al., 1984), but fruiting body formation is the asexual interaction while macrocyst formation is the sexual version. In fruiting body formation, aggregated cells differentiate into spore cells (about 80%) or deadly stalk cells (Strassmann and Queller, 2011). Although stalk cells die, they can help the dispersal of spore cells (Smith et al., 2014), which is the reason that fruiting body formation is regarded as co-

operation. Some mutants, however, differentiate only into spore cells (Gilbert et al., 2007), and they receive the benefits from stalk cells by forming chimeric fruiting bodies with other strains. In macrocyst formation, on the other hand, some cells become gamete cells in the dark and moist environment before they aggregate (Erdos et al., 1976; O'Day and Keszei, 2012). Three mating types exist for *D. discoideum* (Bloomfield et al., 2010), and the gamete cells fuse with either of the two different mating types, after which they become a zygote and secrete cAMP to collect around ~ 200 cells (O'Day and Keszei, 2012). Zygotes receive energy from surrounding cells by cannibalism and they mature into macrocysts, where 105 amoebas germinate from each at most (Wallace and Raper, 1979).

In this paper, we investigate the effect of the stochastic sexual interactions on the evolution of cooperation in the asexual interactions by using the multi-games framework and the lattice model. The scenario is based on the simplified life cycle of *D. discoideum*; each colony plays either of two games with its neighbors. One game corresponds to macrocyst formation and is played only when the mating types of the two colonies are different, but this game is not played with some probability, as macrocyst formation requires certain environmental conditions. We ignore the evolution of cooperation in this sexual interaction and assume that players receive constant benefits. The other game corresponds to fruiting body formation and is played regardless of the mating types of the two colonies. We represent the payoff matrix of this game as the Prisoner's Dilemma (PD) game and each colony behaves as a cooperator or a defector. As a result, under some conditions, the stochastic sexual interaction enables cooperators to eliminate the defectors from the population if the mating types of the defectors are different from those of cooperators. Cooperators are, however, still vulnerable to the invasion of defectors of the same mating type. Of course, the other mating type cooperators can again invade the population once the defectors succeed in the invasion. If the sex ratio is biased, however, it seems difficult for cooperators to continue eliminating defectors. We, therefore, investigate the metapopulation dynamics to see whether cooperation eventually can be eventually maintained or not. Basically, the fixation times of defectors on the metapopulation scale become much longer due to the stochastic sexual interactions, but it is impossible for cooperators to continue eliminating the defectors indefinitely.

Model

Population dynamics

We investigated the effect of the stochastic sexual interactions on a spatial PD game in a population divided into 300×300 lattice points. The framework of the model is based on Nowak (2006a), although each agent represents a colony of *D. discoideum*; each agent has a pure strategy for the PD game (a cooperator or a defector), the lattice model

is torus, the agents interact with their eight neighbors, they change the strategies to that of an agent whose payoff is the highest in the neighborhood including itself, and all agents update their strategies at the same time.

In addition, we assign either of two mating types, type I or type II, to each agent. In our model, two kinds of interactions exist; one is an asexual interaction that occurs within and between mating types, and the other is a sexual interaction that is stochastically performed only between different mating type colonies. We assume that the asexual interaction is based on the PD game and that each agent behaves as a cooperator or a defector. On the other hand, agents receive the constant benefits from the sexual interaction. The payoff matrices are represented as follows:

$$A = \begin{pmatrix} 1 & 0 \\ b_A & \epsilon \end{pmatrix}, \quad B = \begin{pmatrix} b_B & b_B \\ b_B & b_B \end{pmatrix} \quad (1)$$

where A and B are payoff matrices of an asexual and a sexual interaction, respectively. In the asexual interaction, a cooperator receives a payoff 1 by interacting with another cooperator, while it receives no payoff from an interaction with a defector. On the other hand, a defector receives b_A by exploiting a cooperator, while it gains ϵ by interacting with another defector. Assuming that the asexual interaction is based on the PD game, the temptation to defect is larger than the benefit from the interaction between cooperators ($b_A > 1$), and the benefit from the interaction between defectors is very small ($0 < \epsilon \ll 1$). It is already known that cooperators cannot be maintained in a spatial PD game if $b_A > 8/3$ (Nowak, 2006a). We, therefore, assume that $b_A = 2.7$ in an effort to see clearly the effect of the stochastic sexual interaction. On the other hand, it is assumed that agents gain constant benefit, b_B, from a sexual interaction, regardless of their strategies for an asexual interaction.

By coupling mating types with the strategies for an asexual interaction, we achieve four strategies: type I cooperator (CI), type I defector (DI), type II cooperator (CII), and type II defector (DII). We denote the probability that a sexual interaction occurs between two agents of different mating types is θ while the probability that an asexual interaction occurs between two agents of different mating types is $1 - \theta$. It should be noted that $\theta = 0$ represents the original spatial PD game. This kind of sexual interaction must be valid, at least for *D. discoideum*, where darkness and humidity are necessary for sexual reproduction (Erdos et al., 1976; O'Day and Keszei, 2012). Within the same mating types, on the other hand, an asexual interaction always occurs (Fig. 1 a). The 4×4 expected payoff matrix E is written as below:

$$E = \begin{pmatrix} A & (1-\theta)A + \theta B \\ (1-\theta)A + \theta B & A \end{pmatrix}. \quad (2)$$

Notice that the expected payoff matrix E contains 2×2 matrices, A and B. Matrix A represents the payoff matrix when
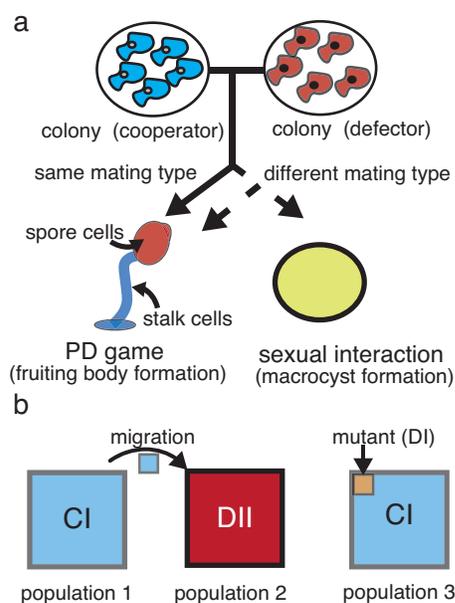
a

b

Figure 1: The diagram of the model. (a) Each agent represents the colony of *D. discoideum* and has a strategy for fruiting body formation. If the mating types of the two agents are same (solid arrow), they play the PD game, which represents fruiting body formation. If the mating types are different (dashed arrow), they form macrocysts with some probability θ and share the benefit; they, however, play the PD game with the probability of $1 - \theta$. (b) In metapopulation dynamics, migration and mutation can occur. A small number of agents migrate from one population to another with the probability of m, while mutation changes the strategies of a small number of agents in each population with the probability of μ.

the mating types of the agents are same. On the other hand, $(1 - \theta)A + \theta B$ represents the expected payoff matrix when the mating types are different.

To see the effect of the stochastic sexual interactions, the evolutionary dynamics in a population consisting of CI and DII strategies were examined. We assumed that the initial frequencies of them were equal, and we changed the values for the benefit from the stochastic sexual interaction, b_B, and the probability of the sexual interaction, θ. Under the initial conditions, the position of each agent was randomly determined. To exclude the effect of initial position effect and the stochasticity of the sexual interaction, this simulation was repeated until 1000 time steps, and then repeated 50 times for each parameter value.

State transition

As CI eliminates DII from the population in some values for b_B and θ (see Results and Fig. 2), it is necessary to investigate the effect of the stochastic sexual interaction on

the metapopulation scale. Simulating the lattice model on the metapopulation scale is, however, wasteful. We avoided this problem by investigating all possible stable states in one population and their transitions. First, we simulated the cases where all agents had the same strategies for asexual interactions, but their mating types were different (*i.e.*, CI and CII, or DI and DII). Then, we performed the invasion analysis. We assumed that the initial frequency of each invader is very small, 0.01. Next, we simulated the cases where residents, or majorities, of a population are only CI, only DI, both CI and CII, and both DI and DII while invaders, or minorities, are either two or three other strategies.

Metapopulation dynamics

Next, we examined whether cooperators eventually became extinct from all populations or not, and how long it would take for that to occur if possible. We denoted the number of populations as n. Each population remained in one of the possible stable states; their states were changed by mutation or migration (Fig. 1 b). For simplicity, sexual transformation was ignored; mutations change only the strategies for asexual interaction, from cooperator to defector. It should be noted that mutation from a defector to a cooperator was ignored because such a mutant would never survive (see Results). We have denoted the mutation ratio in one population as μ, and the migration rate from one population to another as m. When a mutation occurs in a population, a small number of agents in the population change their strategies for asexual interaction. If migration occurs, on the other hand, a small number of immigrant agents replace those in a new population. In each time step, the mutation occurs with the probability of μ and the state of the population where mutation occurs is changed; then, the migration occurs with the probability of m and the states of the populations are updated.

In the simulation, the values for the number of population, n, and the mutation rate, μ, were fixed as $n = 10$, and $\mu = 10^{-4}$; the simulation was repeated for the various values of migration rate, m. We used the two initial conditions: (1) four CI populations, five CII populations and one DI population, or (2) five CI populations, four CII populations, and one DII populations. In each simulation, the initial condition was determined at random. The simulation was repeated $1,000$ times under each value of m to estimate the distribution of the fixation times of defectors in all populations.

Results

Population scale

To investigate the effect of the stochastic sexual interaction, population dynamics were simulated where CI coexisted with DII in the equal frequencies at the initial condition. The sexual interaction enabled CI to eliminate DII from the
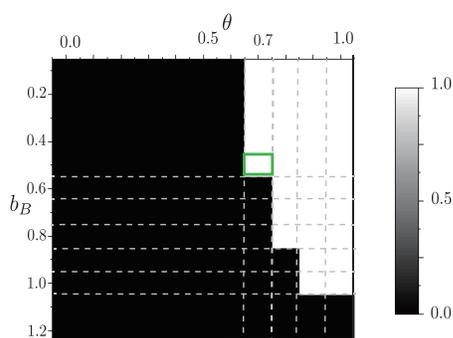
Figure 2: Probability that the frequency of CI at the end of the simulation is more than 0.99. Under each condition, the probability is either 0 (black) or 1 (white). The green area represents $(b_B, \theta) = (0.5, 0.7)$.

Figure 3: Invasion of CI (cyan) into DII (red). Initial frequencies CI : DII = 1 : 99 and the values of the parameters $(b_B, \theta) = (0.5, 0.7)$.

population under some parameter values (Fig. 2). This result occurred if $b_B \leq 1$ and $\theta \geq 0.7$, but the threshold of θ increased as the value of b_B increased. If θ was small, the sexual interaction did not frequently occur and the fate of the dynamics was the same as the original spatial PD game. If, on the other hand, b_B was larger than the payoff of the cooperation in the PD game, both cooperators and defectors gained larger payoffs from a sexual interaction than interacting among themselves, which then led their coexistence. The small benefit of a sexual interaction and relatively large probability of it are, therefore, necessary for cooperators to eliminate the other mating type defectors.

Of course, as θ increases, the temptation to defect decreases and the expected payoff matrix does not represent the PD game if

$$(1 - \theta)b_A + \theta b_B < 1. \tag{3}$$

It is obvious that the cooperators always gain higher payoffs than the defectors of the other mating type if Eq (3) holds.

For some parameter values (*e.g.*, $(b_B, \theta) = (0.5, 0.7)$), however, CI eliminated DII, although the expected payoff matrix still represented the PD game. Moreover, CI invaded the population of DII when $(b_B, \theta) = (0.5, 0.7)$ and the initial frequency of CI was 0.01 (Fig. 3). Our model shows, therefore, that the stochastic sexual interaction enables cooperators to invade and to eliminate defectors of the other mating types. In addition, the fate of the stochastic dynamics cannot be predicted from the expected payoff matrix.

Stable states and the transition

While cooperators could eliminate the other mating type defectors, they were still invaded by the same mating type defectors because the expected payoff matrix was the same as that of the original spatial PD game. To see the fate of the evolution of cooperation, it was necessary to investigate whether cooperators continued eliminating defectors on the
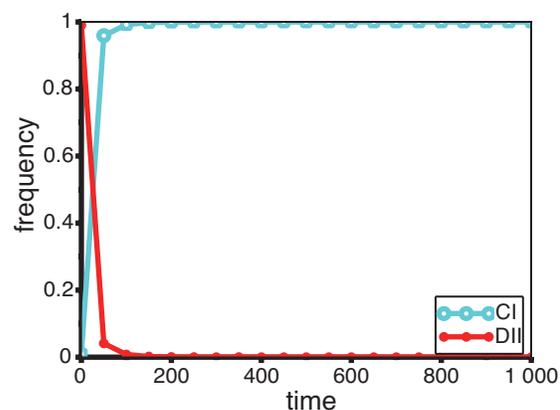
metapopulation scale or not; however, metapopulation dynamics using the lattice model takes too much time to calculate. We, therefore, simulated the population dynamics where the initial condition did not include the coexistence of CI and DII.

We first investigated the evolutionary dynamics on one population level, where all agents had the same strategies for asexual interactions, but their mating types were different. It should be noted that the fixed strategies are the same in 50 out of 50 simulations for each case below. When the population consisted of CI and CII, the positive frequency-dependent selection worked. Only if the initial frequencies were nearly equal, did the two mating types of cooperators coexist (Fig. 4 a); otherwise, only either of the two strategies, CI or CII, was maintained (Fig. 4 b). In contrast, the negative frequency-dependent selection worked if the population consisted of DI and DII. Regardless of the initial frequencies, DI and DII coexisted in the same frequencies at the end of the simulation (Fig. 4 c and d). This is because the benefit from an asexual interaction ϵ was much smaller than that from a sexual interaction when DI and DII coexisted ($\epsilon < b_B$), while the benefit from an asexual interaction was larger than that from a sexual interaction for the two mating type cooperators ($b_B < 1$). These results indicate that cooperators cannot invade the population of different mating type cooperators, while defectors can invade the population of different mating type defectors, and coexist with them.

Next, we instigated the cases where two or three strategies invaded at the same time, while one or two strategies existed as residents. The strategies maintained at the end of the simulation was always the same in 50 out of 50 simulations. We assumed that the initial frequencies of the invaders were 0.01. First, we investigated the cases where one coop-
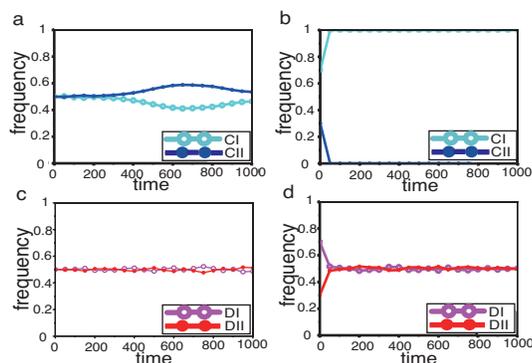
Figure 4: Examples of population dynamics. Initial frequencies are (a) CI (cyan) : CII (blue) = 5 : 5, (b) CI : CII = 7 : 3, (c) DI (purple) : DII (red) = 5 : 5, and (d) DI : DII = 7 : 3. In all cases, the values of the parameters are $(b_B, \theta) = (0.5, 0.7)$.

Case	CI	CII	DI	DII	Winner
1	○	★	★		DI
2	○	★		★	CI
3	○		★	★	DI & DII
4	○	★	★	★	DI & DII
5	○	○	★		CII
6	○	○	★	★	DI & DII
7	★	★	○		CII
8	★		○	★	DI & DII
9		★	○	★	DI & DII
10	★	★	○	★	DI & DII
11	★		○	○	DI & DII
12	★	★	○	○	DI & DII

Table 1: Invasion analysis when two or three invaders existed. Each row represents each situation. Red circles represent the resident strategies, while blue starts represent invaders. Blank cells represent the absence of the strategies. The strategies that are fixed at the end of the simulations are shown in the column of Winner. The values of the parameters are $(b_B, \theta) = (0.5, 0.7)$.

erator (*e.g.*, CI) was invaded by two or three other strategies at the same time. When the invaders were the other mating type cooperator (CII) and the same meting type defector (DI), only the same mating type defector was maintained (case 1 in Table 1). When the invaders were the other mating type cooperator and the other mating type defector (DII), on the other hand, the resident cooperator survived (case 2 in Table 1). If the two mating type defectors invaded at the same time, however, these two defectors coexisted and cooperators became extinct, regardless of the invasion of the other mating type cooperator (cases 3 and 4 in Table 1).

As the two mating type cooperators could coexist, we investigated the cases where the two cooperators were the residents. If one mating type defector (*e.g.*, DI) invaded, only the other mating type cooperator (CII) was maintained (case 5 in Table 1). If the two mating type defectors invaded at the same time, however, the two cooperators were extinct and the two mating type defectors coexisted (case 6 in Table 1).

When one mating type defector (*e.g.*, DI) was the resident, it was replaced by the other mating type cooperator (CII) if the two cooperators invaded at the same time (case 7 in Table 1). If the other mating type defector (DII) also invaded at the same time (cases 8, 9, and 10 in Table 1) or coexisted as the resident (cases 11 and 12 in Table 1), the two mating type defectors coexisted and the cooperators became extinct.

The summary of the state transition is shown in Fig. 5. Coexistence of CI and CII is a stable state, but this state is broken if one mating type of defectors invade or the frequencies of the two cooperators are biased. The population where only cooperators of one mating type exist is invaded by defectors of the same mating type. When the population consists of defectors on one mating type, however, the defectors can be replaced by the other mating type cooperators. If the two different mating types of defectors exist in one population, they coexist in the equal frequencies and this is the only evolutionary stable state of the population.

Metapopulation scale

As the state transition was revealed (Fig. 5), we simulated the metapopulation dynamics, where 10 populations existed. The results of population dynamics depend on the mating types of the residents and the invaders, and therefore, it was necessary to investigate the maintenance of cooperators on the metapopulation scale. Under this scenario, mutation occurred in each population with the probability of μ and some agents migrated from one population to another with the probability of m. It was assumed that the dynamics within each population changed much faster than the occurrence of a new mutation of migration, and that the condition of each population would converge to one of the stable states. In addition, we ignored the sexual transformation; a mutation changed only the strategies for asexual interactions. Moreover, we only considered the mutations occurring from a cooperator to a defector because a mutant which changed its strategy from a defector to a cooperator would soon disappear, even if such mutations were to occurs (Fig. 5). As defectors were invaded by cooperators of the other mating types, we investigated whether it would be possible for defectors to be fixed in all populations and how long that would takes, if possible.

The fixation time distributions for the defectors are shown in Fig. 6. In the test cases (Fig. 6, right), the cooperators were able to invade the population consisting of the other mating type defectors due to the stochastic sexual interactions. In contrast, the sexual interactions never occurred in
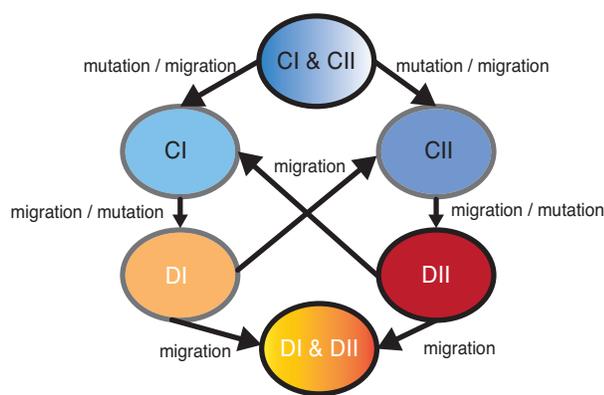
Figure 5: Graphical summary of the state transition. Invasion by two strategies is ignored in this figure.

Figure 6: Distributions of the fixation times of defectors in all populations. Test cases (right): cooperators can invade the population of the other mating defectors. Control cases (left): cooperators never invade the population of defectors.

the control cases, and therefore cooperators could not invade the population, regardless of the mating types (Fig.6, left). Obviously, the fixation time in the test cases was longer than in the control cases. When $m = 0$, the distributions of the fixation times were equal in the test and control cases because the spread of defectors was caused only by mutation. As m increased, however, the fixation times in the control cases became shorter because defectors were more likely to invade the population, while fixation times in the test cases were not very different because cooperators also invaded populations of the other mating type defectors.

However, cooperators still became extinct on the metapopulation scale. To investigate whether it is possible for cooperators to be maintained or not, we analyzed the possibility that the newly appeared defectors are eliminated in the next time step. As shown in Fig. 5, the coexistence of DI and DII was the only evolutionarily stable state and cooperators finally become extinct once this coexistence occurs. The coexistence, however, requires at least two mutations and one migration. If cooperators always eliminate the newly appeared defectors in the next time step, the coexistence does not occur unless mutations produce the two mating type defectors at the same time. If the new defectors remain, however, there exists a risk that the other mating type defectors would appear and the two mating type defectors coexist. Thus, we calculated the probability, P, that the newly appeared defector's population is eliminated in the next time step. If this probability is as large as $(1-\mu)^{n-1}$, the probability of the coexistence of DI and DII is very small because the coexistence does not occur unless the two mating type defectors appear at the same time. This probability, P, is written as follows:

$$P = (1-\mu)^{n-1} \times \frac{(n-(k+1))m_C}{n-1} \times \left(1 - \frac{km_D}{n-1}\right) \quad (4)$$

where k is the number of populations consisting of the cooperators whose mating type is the same as the newly appeared
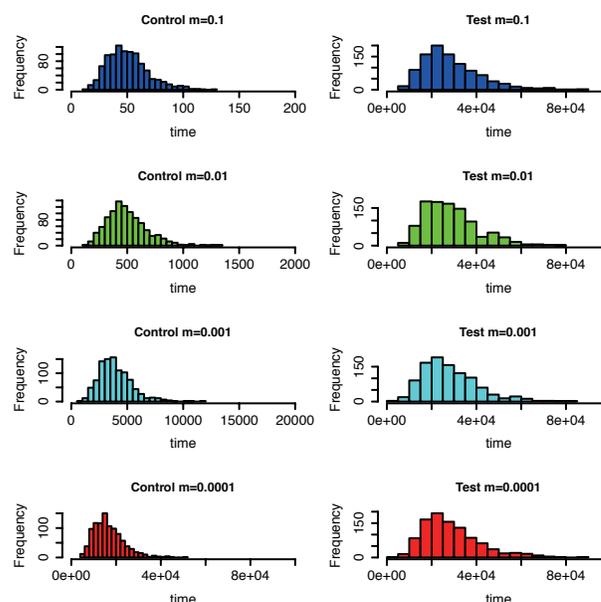
defectors, m_C is the migration rate for cooperators, and m_D is that for defectors. P is the product of the probability that a new mutation does not occur, that cooperators of the different mating type migrate to the population of defectors, and that the defectors do not migrate the population consisted of the same mating type cooperators. As P is an increasing function of m_C and a decreasing function of m_D, the maximum of P, P_M, is calculated by substituting $m_C = 1$ and $m_D = 0$:

$$P_M(k) = (1-\mu)^{n-1}\left(1 - \frac{k}{n-1}\right). \quad (5)$$

To evaluate the probability of eliminating defectors in the next time step, the probability is weighted by the sex ratio just before defectors invade:

$$\begin{aligned}
\tilde{P}_M(k) &\equiv \frac{k+1}{n}P_M(k) + \frac{n-k-1}{n}P_M(n-k-2) \\
&= (1-\mu)^{n-1}\frac{2(k+1)(n-(k+1))}{n(n-1)} \\
&\leq (1-\mu)^{n-1}\frac{n}{2(n-1)}. \quad (6)
\end{aligned}$$

The equality is attained if and only if $k = (n-2)/2$. If the sex ratio in the metapopulation scale is biased, it is difficult to eliminate the defectors whose mating types are dominant. The probability $\tilde{P}_M$ is, therefore, the largest when the sex ratio is balanced. Eq (6) indicates that the maximum average probability, $\tilde{P}_M$, that defectors are eliminated in the next

population is smaller than $(1-\mu)^{n-1}$ if $n > 2$. If $n = 2$, the value of $\tilde{P}_M$ is as large as $(1-\mu)^{n-1}$. In this case, however, $\tilde{P}_M$ is the maximum if and only if $k = 0$. This means that one of the two populations is consisted of one mating type cooperators while the other population is consisted of the other mating type defectors. In the next time step, the cooperators can eliminate the defectors by migration. However, the cooperators will become extinct once mutation occurs again; the remaining cooperators cannot eliminate the defectors as their mating types are the same. Thus, it is impossible for cooperators to continue eliminating defectors.

Discussion

In this paper, we show that the stochastic sexual interaction affects the evolution of asexual cooperation. Although the framework of the model was inspired by Nowak (2006a), we introduced the mating types of the agents and the stochastic sexual interactions in the model. Our model is, therefore, regarded as a "multi-games" and represents the simplified life cycle of *D. discoideum*. When the mating types of the two agents are the same, they play the PD game. When their mating types are different, on the other hand, the sexual interaction occurs with the probability of θ, while they play the PD game with the probability of $1 - \theta$. In the original spatial PD game (Nowak, 2006a), cooperators become extinct when $b_A > 8/3$, while our model shows that cooperators can eliminate the defectors of the other mating type.

Interestingly, this occurs if the benefit from the stochastic sexual interaction is smaller than that of asexual cooperation. In the case of *D. discoideum*, the benefit from fruiting body formation seems higher than that from macrocyst formation; about 80% of cells survive in fruiting body formation (Strassmann and Queller, 2011) while the number of cells produced by a macrocyst is about 50% of the number of cannibalized cells (O'Day and Keszei, 2012; Wallace and Raper, 1979). Our model, therefore, suggests that macrocyst formation facilitates the evolution of cooperation in fruiting body formation.

The reason that cooperators can invade and be maintained is regarded as follows. If one cooperative agent invades the population of the other mating type defectors (Fig.7, left), the eight neighbors of the cooperator will become cooperative with some probability in the next time step (Fig. 7, right). Once 3×3 or larger clusters of cooperators form, cooperators rarely become extinct; CI in the center of the cluster will never be defeated in the next time step and the cluster grows larger unless DIIs play the PD game twice (Fig. 7 right, (a) or (b)). It should be noted that we simulated the case which facilitated the maintenance of CIs as they could easily form the clusters due to their initial frequency.

In our model, a mating type is regarded as a type of tags in the models of tag-based cooperation. When a cooperator interacts with a defector of the other mating type, the cooperators can avoid the exploitation from the defectors by
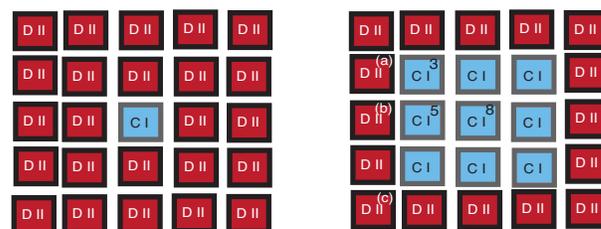

Figure 7: Images of the invasion of cooperators. CI invades the population of DII (left). CI can form a 3×3 cluster if the invasion succeeds (right). In the right figure, CIs receive at least 3, 5, or 8 benefits according to their positions. The maximum benefit of DIIs is dependent on their positions: (a) $2b_A + 6\epsilon$, (b) $3b_A + 5\epsilon$, and (c) $b_A + 7\epsilon$.

initiating a sexual interaction. In the previous models of tag-based cooperation (*e.g.*, Antal et al. (2009)), cooperators change their strategies and stop cooperative behaviors when they interact with those who have different tags. In our model, on the other hand, cooperators change the game rather than the strategy if the mating types, or the tags, of the two agents are different. By changing the game, cooperators can avoid the exploitation from defectors of the other mating type. The function of the mating types as tags is, therefore, the key to the evolution of asexual cooperation.

Of course, the mating types of *D. discoideum* serve as more than a type of tags. Homologous recombination is considered to occur during macrocyst formation (Flowers et al., 2010) and there may be some benefits from sex, such as the Fisher-Muller's effect (reviewed in Otto and Lenormand (2002)). The strength of these effects is, however, unclear because *D, discoideum* does not always form macrocysts in starvation. This issue should be analyzed in future works based on a population genetics rather than on an evolutionary game.

The cooperative agents in our model became extinct once the defectors of the same mating type appeared. Likewise, cooperators cannot be maintained in the tag-based cooperation models once a defector obtains the same tags of cooperators (Traulsen and Nowak, 2007). Of course, defectors in our model were again invaded by the cooperators of the other mating type. In metapopulation dynamics, however, cooperators cannot continue eliminating defectors. If cooperators invade a population consisting of the other mating type defectors, the sex ratio becomes biased. As the sex ratio is more biased, it is more difficult to eliminate the defectors of the dominant mating type. When either of the two mating type cooperators are extinct, it is impossible to eliminate the other mating type defectors once they have appeared. Cooperation is, therefore, evolutionarily unstable in our model.

This problem would be solved potentially if the two mating type cooperators could coexist in a population. Although our present model shows the difficulty of this coexistence

(Fig. 4 a, b, and Fig. 5), it would be eased by revising the model. For example, future models will contain a dynamic environment as well. Under water, *D. discoideum* cannot produce fruiting bodies but can produce macrocysts (Bonner, 1947). This means that *D. discoideum* produces neither fruiting bodies nor macrocysts without the other mating type strains in this environment. The dynamic environment would potentially show an increase in the benefit from the sexual interaction and enable cooperators of the two mating types to coexist.

In conclusion, our model shows that the stochastic sexual interaction stabilizes evolution of cooperation. We simplified the two games of *D. discoideum* (fruiting body and macrocyst formation) by using a multi-game dynamics. Our model shows that the stochastic sexual interaction enables cooperators to eliminate the other mating type defectors from one population under some parameter values. This result was unpredictable from the expected payoff matrix. Moreover, the stochastic sexual interaction slowed down the spread of defectors in the metapopulation scale. These results suggest that macrocyst formation stabilizes the evolution of cooperation in fruiting bodies, although cooperation is not evolutionarily stable in the metapopulation scale.

Acknowledgements

References

Abe, K., Orii, H., Okada, Y., Saga, Y., and Yanagisawa, K. (1984). A novel cyclic AMP metabolism exhibited by giant cells and its possible role in the sexual development of Dictyostelium discoideum. *Dev. Biol.*, 104(2):477–483.

Antal, T., Ohtsuki, H., Wakeley, J., Taylor, P. D., and Nowak, M. a. (2009). Evolution of cooperation by phenotypic similarity. *Proc. Natl. Acad. Sci.*, 106(21):8597–8600.

Bloomfield, G., Skelton, J., Ivens, A., Tanaka, Y., and Kay, R. R. (2010). Sex Determination in the Social Amoeba Dictyostelium discoideum. *Science.*, 330(6010):1533–1536.

Bonner, J. (1947). Evidence for the formation of cell aggregates by chemotaxis in the development of the slime mold Dictyostelium discoideum. *J. Exp. Zool.*, 106:1–26.

Erdos, G. W., Raper, K. B., and Vogen, L. K. (1976). Effects of light and temperature on macrocyst formation in paired mating types of Dictyostelium discoideum. *J. Bacteriol.*, 128(1):495–7.

Flowers, J. M., Li, S. I., Stathos, A., Saxer, G., Ostrowski, E. A., Queller, D. C., Strassmann, J. E., and Purugganan, M. D. (2010). Variation, Sex, and Social Cooperation: Molecular Population Genetics of the Social Amoeba Dictyostelium discoideum. *PLoS Genet.*, 6(7):e1001013.

Gilbert, O. M., Foster, K. R., Mehdiabadi, N. J., Strassmann, J. E., and Queller, D. C. (2007). High relatedness maintains multicellular cooperation in a social amoeba by controlling cheater mutants. *Proc. Natl. Acad. Sci.*, 104(21):8913–8917.

Hashimoto, K. (2006). Unpredictability induced by unfocused games in evolutionary game dynamics. *J. Theor. Biol.*, 241(3):669–675.

Hofbauer, J., Schuster, P., and Sigmund, K. (1979). A note on evolutionary stable strategies and game dynamics. *J. Theor. Biol.*, 81(3):609–612.

Nakamaru, M., Matsuda, H., and Iwasa, Y. (1997). The Evolution of Cooperation in a Lattice-Structured Population. *J. Theor. Biol.*, 184(1):65–81.

Nowak, M. A. (2006a). *Evolutionary dynamics exploring the equations of life*. Belknap Press of Harvard University Press, Cambridge.

Nowak, M. A. (2006b). Five Rules for the Evolution of Cooperation. *Science.*, 314(5805):1560–1563.

Nowak, M. A., Tarnita, C. E., and Antal, T. (2010). Evolutionary dynamics in structured populations. *Philos. Trans. R. Soc. B Biol. Sci.*, 365(1537):19–30.

O'Day, D. H. and Keszei, A. (2012). Signalling and sex in the social amoebozoans. *Biol. Rev.*, 87(2):313–329.

Ohtsuki, H., Hauert, C., Lieberman, E., and Nowak, M. A. (2006). A simple rule for the evolution of cooperation on graphs and social networks. *Nature*, 441(7092):502–505.

Otto, S. P. and Lenormand, T. (2002). Resolving the Paradox of Sex and Recombination. *Nat. Rev. Genet.*, 3(4):252–261.

Popat, R., Crusz, S. a., Messina, M., Williams, P., West, S. a., and Diggle, S. P. (2012). Quorum-sensing and cheating in bacterial biofilms. *Proc. R. Soc. B Biol. Sci.*, 279(1748):4765–4771.

Raihani, N. J. and Bshary, R. (2015). Why humans might help strangers. *Front. Behav. Neurosci.*, 9:39.

Smith, J., Queller, D. C., and Strassmann, J. E. (2014). Fruiting bodies of the social amoeba Dictyostelium discoideum increase spore transport by Drosophila. *BMC Evol. Biol.*, 14(1):105.

Strassmann, J. E. and Queller, D. C. (2011). Evolution of cooperation and control of cheating in a social microbe. *Proc. Natl. Acad. Sci.*, 108(Supplement_2):10855–10862.

Traulsen, A. and Nowak, M. A. (2007). Chromodynamics of cooperation in finite populations. *PLoS One*, 2(3):e270.

Tyson, J. J. and Murray, J. D. (1989). Cyclic AMP waves during aggregation of Dictyostelium amoebae. *Development*, 106:421–426.

Wallace, M. A. and Raper, K. B. (1979). Genetic exchanges in the macrocysts of Dictyostelium discoideum. *J. Gen. Microbiol.*, 113(2):327–37.

Wang, Z., Szolnoki, A., and Perc, M. (2014). Different perceptions of social dilemmas: Evolutionary multigames in structured populations. *Phys. Rev. E - Stat. Nonlinear, Soft Matter Phys.*, 90(3):1–7.

Wardil, L. and da Silva, J. K. (2013). The evolution of cooperation in mixed games. *Chaos, Solitons & Fractals*, 56:160–165.