

Diversity of reproduction time scale promotes cooperation in spatial prisoner's dilemma gamesZhi-Xi Wu,^{1,*} Zhihai Rong,^{2,†} and Petter Holme^{1,‡}¹*Department of Physics, Umeå University, 901 87 Umeå, Sweden*²*Department of Automation, Donghua University, 200051 Shanghai, China*

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We study an evolutionary spatial prisoner's dilemma game where the fitness of the players is determined by both the payoffs from the current interaction and their history. We consider the situation where the selection time scale is slower than the interaction time scale. This is done by implementing probabilistic reproduction on an individual level. We observe that both too fast and too slow reproduction rates hamper the emergence of cooperation. In other words, there exists an intermediate selection time scale that maximizes cooperation. Another factor we find to promote cooperation is a diversity of reproduction time scales.

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I. INTRODUCTION

Many biological, social, and economic systems are built and sustained by cooperating individuals [1,2]. The issue of how cooperation emerges and persists among selfish individuals is the topic of game theory [3–5]. The simplest and most versatile framework for evolutionary game theory is perhaps the so-called symmetric 2×2 games [6–8]. In such games, agents can employ two behaviors or strategies—cooperative or defective—in their interaction with others to optimize their fitness. The goal of this branch of game theory is to establish the conditions for cooperation (or, equivalently, defection) to spread. An important 2×2 game is the prisoner's dilemma (PD) that describes the situation when cooperation gives the highest population-level payoff but, in a short time scale, defection maximizes the expected payoff of an individual. In well-mixed populations, cooperators cannot outperform defectors and are doomed to extinction [5]. There are, however, many arguably realistic factors that favor cooperation. For example, one such factor is space—if the players are embedded in space, allowed only to interact with their neighbors, cooperation can spread in the population [9–14]. The microscopic explanation for this phenomenon is that cooperators can form spatial clusters where the boundaries, although exploited by defectors, protect the cooperators within [9–11]. On complex networks—scale-free networks in particular—cooperators have a tendency to occupy high degree nodes, which stabilizes cooperation [12–14]. For detailed surveys of this field, we refer to Refs. [15,16]. From these examples we learn that the spatial organization, the interaction patterns, are important elements behind the emergence of cooperation. This raises the question: are there also temporal patterns promoting cooperation? In a recent work [17], Chen and Wang investigated the effects of what they call “payoff aspiration” (roughly, the lower limit of the payoff before a player gets impatient and changes strategy). They found that intermediate aspiration levels maximize cooperation and argue that too high levels cause

too fast strategy changes, while too low levels make the agents not adaptive enough. These results suggest a more fundamental principle—to achieve cooperation, there might exist an optimal time scale for updating strategies. In the present paper, we address this hypothesis by studying evolutionary spatial PD games and by explicitly considering the time scales of interaction and selection.

One of our basic assumptions is that the selection time scale is slower than the interaction time scale. This means that even though each player has a finite lifetime, it can interact many times before selection occurs. During their lifetimes, agents do not change their strategies (or phenotype, in a more biological parlance).

How can we connect the payoff of the game to fitness? The meaning of payoff is more problem dependent than fitness—payoff is some result of the interaction that is correlated with reproduction ability [11,18] and often equated, mathematically, with fitness [5,11,15]. Some works using nonstandard relationships between payoff and fitness are Refs. [19] (where a background noise is added to the payoff to obtain fitness) and [20] (studying nonlinear fitness dependence on payoff). Though there are many possible ways to characterize the relationship between payoff and fitness, in our model, we assume the two quantities are positively correlated (such as in natural selection) and also including an inheritable fitness component (so called maternal effect [21]), which can appear due to social, environmental, or epigenetic mechanisms.

In the rest of the paper, we first introduce our model, defining the fitness and reproduction time scale. Then we present our numerical and analytic results in detail and relate these to other studies.

II. MODEL**A. Payoff and fitness**

In the present study, we consider evolutionary games where individuals, located on a two-dimensional square lattice, play PD games with their closest neighbors. Following common practice [9,10], we consider pure strategies without self-interaction (where one player also plays with oneself [9]) and use the following parametrization of the PD: if two

*zhi-xi.wu@physics.umu.se

†rongzh@github.com

‡petter.holme@physics.umu.se

players both cooperate (C) then both get a “reward” of 1, two defectors (D) both obtain the “punishment” 0, a C meeting a D receives “the sucker’s payoff” 0, while D acquires “the temptation to defect,” $b \in [1, 2]$. For each site i , we define its fitness at generation t as $f_i(t) = af_i(t-1) + g_i - ag_i$, where $t > 0$ is the generation of i . g_i is the instantaneous payoff from the game and the parameter $a \in (0, 1)$, the *heritability*, sets the balance between the present and past payoff gains—the relative importance of a previous generations or strength of maternal effects [21] decays with a factor a per time step.

B. Reproduction

Since our main focus is to evaluate how the diversity of reproduction time scale affects the evolution of cooperation, we discard the normal setup that strategy updating of the players is implemented immediately after a round of game [15]. Instead, we follow the approach of Ref. [22] and assume that the time scale of selection is slower than that of the interaction. In particular, we update the population by using probabilistic dynamics: for each focal site i , a reproduction event occurs with probability p , whose magnitude therefore characterizes the time scale of selection. When p is close to unity, selection is frequent, while for small values of p , the reproduction event is rare and natural selection is slow. It is easy to see that the average time of selection on each site is $1/p$. By this simple way, we are also able to introduce diversity of reproduction time scales.

When strategies are updated, the focal player i and one randomly selected neighbor, say j , compete for creating an offspring at i . The focal site will, depending on their fitnesses, be occupied by either the offspring of i or j . To be specific, the neighbor j places a new offspring with the same strategy on the focal site i with a probability

$$W_{j \rightarrow i} = \frac{1}{1 + \exp[(f_i - f_j)/\kappa]}, \tag{1}$$

where κ measures the probabilistic selection intensity (or noise or temperature); otherwise i is replaced with an offspring of the previous individual at i . A newborn is assigned the initial fitness $f_i(0) = 1$ [the precise value of $f_i(0)$ does not affect our conclusions]. An alternative interpretation is that the individuals sometimes can start with new strategies taken from a neighbor with higher fitness than the individual.

C. Effects of noise

The noise parameter κ is known to have a nontrivial effect on the evolutionary trajectories [23–25]. More specifically, the highest cooperation levels appear in moderate amounts of noise. (Here we want to point out such optimal behavior of noise in promoting cooperation is not universal, but dependent on the topology of the connectivity structure.) Furthermore, in a very recent paper [26], Szabó *et al.* reported an interesting result that the Darwinian selection of “temperature” favors values of κ close to 0.1 which is related to the optimum providing the highest level of cooperation. In this paper, we will not investigate the effects of κ further, but set

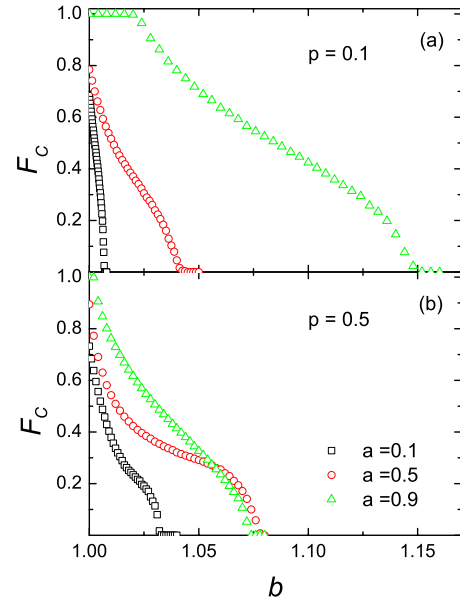


FIG. 1. (Color online) Average fraction F_c of cooperation as a function of b for different values of a . In (a) and (b), the individuals have reproduction rates $p=0.1$ and 0.5 , respectively.

κ to a value, 0.01, that is low enough for the effects of the game to dominate the effects of noise and high enough for selection to occur.

D. Parameter values and simulation technicalities

We investigate our model with Monte Carlo (MC) simulations. All runs are on a 100×100 square lattice with periodic boundary conditions. Initially, either a cooperator or a defector, randomly chosen with equal probability, occupies each site. During one MC sweep, we go through all players once in a random order. The key observable is the average fraction F_c of cooperators in the population in the stationary state, which is measured for the last 10 000 sweeps of the total simulation time 6×10^4 . The results presented below are averages over 20 realizations from independent initial configurations.

III. RESULTS AND ANALYSIS

A. Monomorphic populations

We start by investigating how the heritability a affects the evolution of cooperation. The simulation results for F_c as a function of b for three values of a and two values of p are shown in Fig. 1. In general, we can observe that with an increasing a , the average fraction of cooperation grows. For sufficiently large a , the system can even, for the weakest temptations to defect, reach the absorbing state of full cooperation. This means that the ability of inheritance of fitness from previous generations has a positive impact on the emergence of cooperation. The larger the a is, the greater is the cooperation level. This result is somewhat expected since other studies have shown that the average payoff of C in the equilibrium is greater than that of D [27].

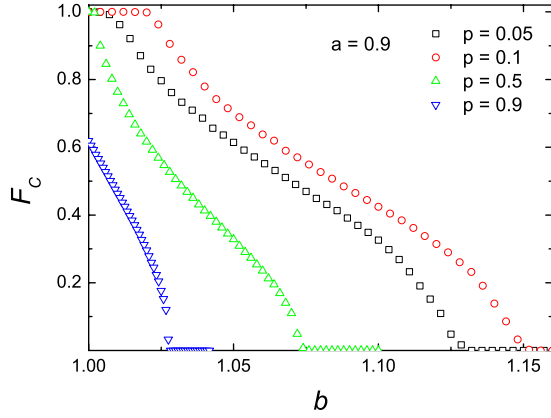


FIG. 2. (Color online) Average fraction F_C of cooperators as a function of b for different values of p . The parameter a is fixed to 0.9.

Even if the a dependence of F_C is qualitatively expected, it is rather different for the two p values of Figs. 1(a) and 1(b). In Fig. 2, we fix $a=0.9$ and study how the average fraction of cooperation evolves as p changes. For large ($p=0.9$) and small ($p=0.05$), values F_C is smaller than for $p=0.1$. This result suggests that a moderate reproduction rate promotes the spread of cooperation. To make this point clearer, in Fig. 3, we summarize the results of F_C as a function of p for different values of a . As surmised, the highest cooperation level is achieved in a region where p is moderate, resembling coherence resonance phenomenon, that p alone (without, e.g., any weak periodic force) can promote cooperation, as has been found frequently in recent literatures [24,25]. For example, by introducing additive noise to the payoff matrix of the PD game, Perc found that cooperation is maximized at a moderate variance of payoff variations [24]. Along a different research line, Ren *et al.* studied PD game on random regular graphs and found that there exists an optimal amount of topological randomness, leading to the highest level of cooperation [25]. Going back to our study, note that the optimal value p_o , where F_C is maximized, depends on the value a . Increasing a will shift p_o toward smaller values (smaller reproduction rates). For instance, for

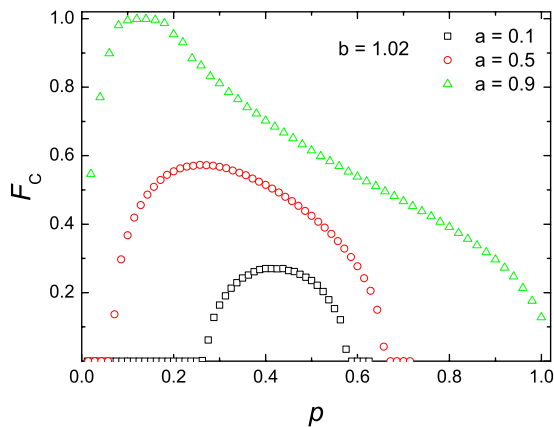


FIG. 3. (Color online) Average fraction of cooperation F_C as a function of reproduction rate p for $b=1.02$. The squares, circles, and triangles correspond to $a=0.1$, 0.5, and 0.9, respectively.

$a=0.1$ we have $p_o \approx 0.41$, while for $a=0.9$, p_o is about 0.12. This point is also reflected by Figs. 1 and 2, where given $a=0.9$, the curves for $p=0.1$ take the rightmost position.

The nontrivial behavior of F_C in Figs. 1–3 can be qualitatively understood as follows. As $p \rightarrow 1$, selection happens frequently; the average fitness of C should be lower than that of D (due to the frequent exploitation on C by D), so F_C will decrease. On the other hand, in case of $p \rightarrow 0$, selection is very slow; defectors around the boundary have enough time to obtain a fitness high enough to out-compete the cooperators. This is reminiscent of the observation that the formation of C clusters can protect cooperation in the spatial PD, whereas the clusters of D would deteriorate their own environment [10,23,27]. In the light of this, the maximal cooperation levels are reached for p values that are neither too large nor too small, so that C has a larger chance than D to obtain high fitness. In order to investigate this hypothesis further, we will first check what will happen if the population is well mixed rather than two-dimensionally extended. Though mean-field treatment is not appropriate for spatial case, it is a fair first-order approximation of the well-mixed case.

For simplicity, we assume that the average coordination number (number of interactions per site per MC sweep) is z . In the mean-field approximation, we can write the following equation for the evolution of the average fraction of cooperation:

$$\begin{aligned} \frac{\partial F_C}{\partial t} &= (1 - F_C)F_C W_{D \rightarrow C} - F_C(1 - F_C)W_{C \rightarrow D} \\ &= F_C(1 - F_C) \left(\frac{1}{1 + \exp[(\bar{f}_D - \bar{f}_C)/\kappa]} - \frac{1}{1 + \exp[(\bar{f}_C - \bar{f}_D)/\kappa]} \right) \\ &= -F_C(1 - F_C) \tanh\left(\frac{\bar{f}_D - \bar{f}_C}{2\kappa}\right), \end{aligned} \quad (2)$$

where $\bar{f}_{C,D}$ denote the average fitness of C and D . The sign of $\bar{f}_D - \bar{f}_C$ determines whether F_C converges to 1, 0, or remains unchanged. Since each individual reproduces with probability p , the average reproduction period is $T = \lceil 1/p \rceil$ where $\lceil \cdot \rceil$ represent the smallest integer larger than the argument. The average fitness of D at age t can be written as $\bar{f}_D(t) = a\bar{f}_D(t-1) + zbF_C$. Assuming the age of the individuals are equally distributed in the region $t \in [1, T]$ using the boundary condition $\bar{f}_D(0) = 1$, we obtain the average expected fitness of D : $\bar{f}_D = \sum_{i=0}^{T-1} \bar{f}_D(t)$. After some algebra, we get

$$\bar{f}_D = p \left(\sum_{i=1}^{T-1} a^i + zbF_C \sum_{i=0}^{T-1} \sum_{j=0}^i a^j \right), \quad (3a)$$

$$\bar{f}_C = p \left(\sum_{i=1}^{T-1} a^i + zbF_C \sum_{i=0}^{T-1} \sum_{j=0}^i a^j \right). \quad (3b)$$

We can see that for any $b > 1$, because $\bar{f}_D - \bar{f}_C > 0$, F_C will go to zero. The incorporation of spatial effects or diversity of

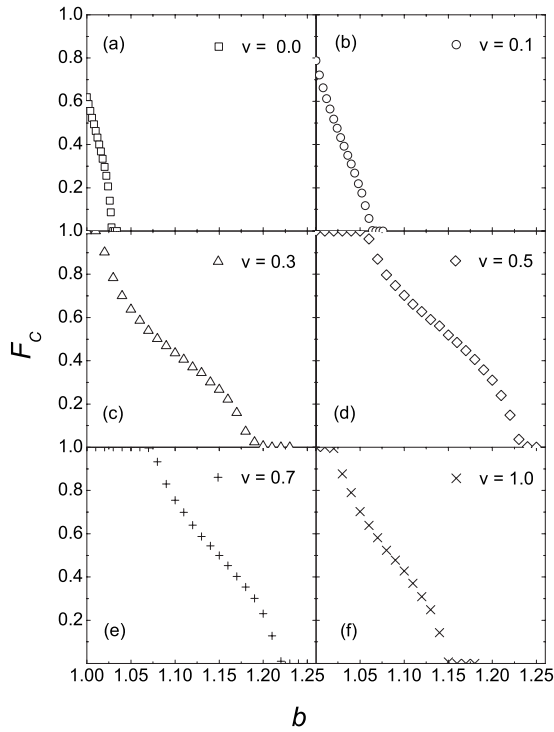


FIG. 4. Average fraction of cooperation F_c as a function of b for different systems where fraction v of population has reproduction rate 0.1 and the others have $p=0.9$. The parameter a is set to 0.9.

reproduction times will change this picture. The permission of only nearest-neighbor interaction and nonsynchronous reproduction also assures the possibility of $\bar{f}_D - \bar{f}_C < 0$ at a local spatial scale. Another factor is that D clusters “defeat themselves” [10,23,27]. In combination with these observations, the intrinsic stochasticity of probabilistic reproduction gives C a chance to out-compete D for dispersion, given that p is appropriately selected. As a consequence, cooperators are favored by diversity of reproduction and can even dominate the whole population provided that b is sufficiently small.

B. Polymorphic populations

In reality, there is a spread in reproduction times. We proceed to investigate the effects of diversity on our PD model. For simplicity, we restrict ourselves to a bimodal distribution of p values: we assign $p=0.1$ to a fraction v of the players and $p=0.9$ to the rest.

In Fig. 4, we show the dependence of F_c on b for $a=0.9$ and different values of v . We find that for appropriate mixing of the two types of individuals, for instance $v=0.5$ and 0.7 , the final cooperative level is further enhanced as compared to a monomorphic population ($v=0$ or 1). To investigate this further, in Fig. 5 we graph $F_c(b)$ for three systems: one with a polymorphic population where half of the population has $p=0.1$ and the other has $p=0.9$, another with a monomorphic population of the same average reproduction rate $p=0.5$ as the polymorphic population, and a third monomorphic population with the same average lifetime as the polymorphic population (giving $p=0.18$). In this comparison, the poly-

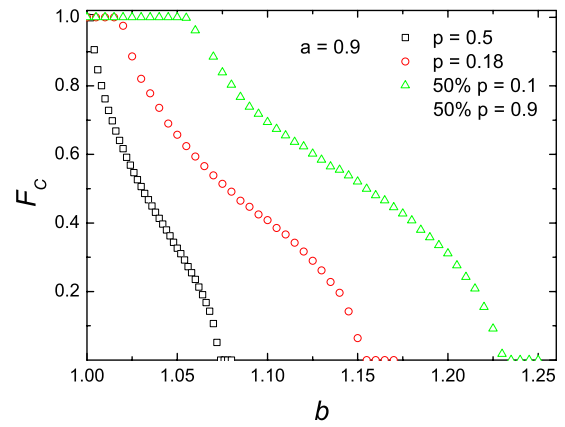


FIG. 5. (Color online) Average fraction F_c of cooperators as a function of b for three special cases where all players have a reproduction rate $p=0.5$ (squares), $p=0.18$ (circles), and 50% individuals with $p=0.1$ and the remaining with $p=0.9$ (triangles). Note that the population with half $p=0.1$ and half $p=0.9$ has the same average reproduction rate as the population with $p=0.5$ and the same average life span as the population with $p=0.18$.

morphic population has a higher cooperation level than both the monomorphic reference populations.

From Fig. 4, we also note that an intermediate mixing of reproduction rate of the population benefits the maintenance of cooperation. This finding is corroborated by Fig. 6 where $F_c(v)$ is displayed for various b values. For small b , F_c can reach unity even for moderate values of v . With an increasing temptation to defect, the region of v with nonzero cooperation vanishes. Despite this, the peak of F_c is located at intermediate p values.

The enhancement of cooperation at intermediate levels of mixing of two types of individuals can be explained in the same vein as Ref. [28], where Szolnoki and Szabó studied evolutionary PD game with a fraction v of players having higher influence to spread their strategies than the others. They found that highest level of cooperation is attained when v is around 0.5. Their interpretation was that the less influ-

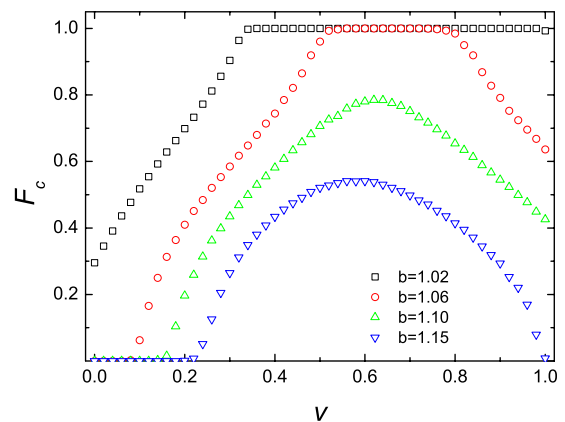


FIG. 6. (Color online) Average fraction of cooperators as a function of the balance between reproduction rates v for different values of b . $v=0$ or 1 represent monomorphic populations; diversity (measured in standard deviation) is largest for $v=1/2$. a is set to parameter 0.9.

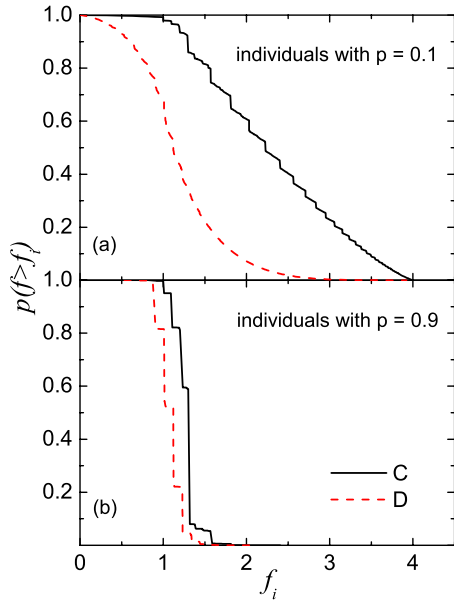


FIG. 7. (Color online) The cumulative distribution of the fitness of agents with different p values in a mix of half $p=0.1$ and half $p=0.9$. (a) shows the fitness for agents with $p=0.1$, (b) shows curves for agents with $p=0.9$. Solid and dashed lines are for C and D, respectively. Other parameters: $a=0.9$, $b=1.1$. Under such parametrization, the final fraction of C, with $p=0.1$ and $p=0.9$, is about 0.38(2) and 0.33(2); the corresponding D, with $p=0.1$ and $p=0.9$, is about 0.12(2), and 0.17(2), respectively.

entail individuals act as followers [28] which stabilizes cooperation. In our case, by analogy, we can assume individuals with high reproduction (large p) act as followers [28], since, on average, they always get lower fitness than those with slow reproduction rate. This point can be verified by the data presented in Fig. 7, where the cumulative distribution of the fitness of the population is shown. In this sense, even though the microscopic mechanisms are different, both our present model and that of Ref. [28] can be regarded as belonging to a generalized class that adjusts the temporal organization of the individuals in a way that maximizes cooperation.

To further investigate how the difference of reproduction rate affects the evolution of cooperation, we measure the v dependence of extinction threshold of b_D and b_C —the values of b that demarcate the region of coexisting cooperators and defectors. The simulation results are shown in Fig. 8. Between the upper and lower critical points, C and D can coexist. Above (below) this region, only defectors (cooperators) remain alive in the final stationary states. Note that, for the sake of comparison, we extend the b values to the region smaller than 1 where the game is a Stag-Hunt game rather than a PD [15]. From this figure, we observe that for intermediate v , both b_D and b_C attain their maximum values, though not at the same v .

IV. CONCLUSIONS AND DISCUSSION

To summarize, in the present work, we have proposed and analyzed an evolutionary, spatial prisoner’s dilemma game

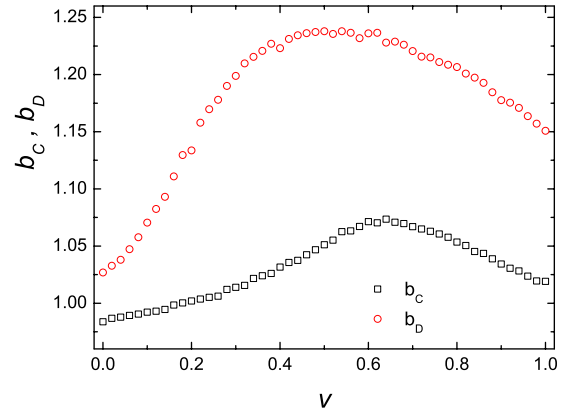


FIG. 8. (Color online) The extinction thresholds b_C and b_D of cooperators and defectors, respectively, as a function of v . The parameter $a=0.9$. Note that the range of b extends to values lower than 1, where the game is not a proper prisoner’s dilemma.

including a partial inheritance of fitness, a probabilistic reproduction, and a diversity of reproduction rates. The combination of these factors gives rise to rich dynamic behavior of the system. In particular, the stronger the ability of inheritance of fitness is, the more cooperation there is. The reproduction rate has a nontrivial effect on the evolution of cooperation. When the parameter a (characterizing the strength of inheritance of fitness) is fixed, the highest cooperation level is realized for moderate reproduction rates. Both too slow and too fast reproduction rates can harm cooperation. Moreover, we find that the presence of diversity of reproduction rate can enhance cooperation. The behavior of promoting cooperation is found to resemble coherence resonance. These findings suggest that the heterogeneity of individual traits might benefit cooperation in PD situation, giving another clue to the emergence of population in social and biological systems of selfish individuals.

In a recent work, Qin *et al.* [29] explored the effects of infinite memory in a spatial PD game (allowing self-interaction). They found that with a moderate memory effect, the extinction threshold b_D reaches a maximal value, but observed no such behavior for b_C . Their memory mechanism is similar to the maternal-effect fitness inheritance in our model. In another related work [22], Roca *et al.* considered independent interaction and selection time scales in evolutionary games. The authors studied all 12 nonequivalent symmetric 2×2 games and found that, depending on the type of the game, rapid selection may lead to changes of the asymptotic equilibria and changes in the basins of attraction [22]. Reference [22] differs from ours in the approach to strategy updates—they model updates as a Moran process, whereas we use a stochastic migration rule and in the interaction configuration they, in contrast to us, consider a nonspatial (or well-mixed) population.

One future problem is how cooperators vanish as the temptation to defect increases. For evolutionary PD with stochastic imitation rules, Szabó and Tóke [10] found a phase transition of the directed percolation universality class [10]. We expect a similar transition can occur in our model in the case of large value of p . However, this point needs to be confirmed in further studies. Moreover, how the p value

maximizing F_c depends on the parameter a is not addressed in the present work. The work in [12] suggests that large degree nodes are important for promoting cooperation. In a recent paper [30], middle degree nodes, on the other hand, are found to be crucial for stabilizing cooperation. Along these lines, we expect that the integration of inhomogeneous interaction pattern and reproductive diversity to our present model would be interesting.

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