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ORIGINAL ARTICLE

Continuous Probabilistic Analysis to Evolutionary Game Dynamics in Finite Populations

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Abstract Evolutionary game dynamics of two strategies in finite population is studied by continuous probabilistic approach. Besides frequency dependent selection, mutation was also included in this study. The equilibrium probability density functions of abundance, expected time to extinction or fixation were derived and their numerical solutions are calculated as illustrations. Meanwhile, individual-based computer simulations are also done. A comparison reveals the consistency between theoretical analysis and simulations.

Keywords Evolutionary game · Mutation · Equilibrium probability density · Extinction · Fixation

1. Introduction

Cooperation is ubiquitous on many levels of biological organization in nature (Doebeli and Hauert, 2004; Nowak, 2006, and references therein). In a really long period, the question of how natural selection favors cooperation was a major theme in evolutionary biology and behavioral sciences. Game theory, in which only selfish behaviors will be rewarded, shares the common dilemma as the evolution of cooperation in nature. Therefore, during the last few decades, game theory has been a central tool for understanding the origin of cooperation (Maynard Smith, 1982; Weibull, 1995; Hofbauer and Sigmund, 1998; Nowak and Sigmund, 2004; Nowak, 2006). Actually, there are a variety of game-theoretic models used to analyze cooperative dilemma, such as Prisoner's dilemma (PD) game, snow-drift (SD) game (or Hawk-dove game), and public goods games. The objective of evolutionary game theory is to remove these dilemmas and develop a biologically feasible mechanism to cooperation. Over the past few decades, several mechanisms have been proposed to successfully overcome the dilemma. Nowak (2006) reviewed the related studies and categorized there mechanisms as five rules: kin selection, direct reciprocity, indirect reciprocity, network reciprocity, and group selection. Generally, any game-theoretic

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model of cooperative evolution will be related to the five rules. In the following, we will simply review some game-theoretic models and introduce the advance of evolutionary game theory in finite population.

Traditionally, evolutionary game dynamics are studied by deterministic replicator dynamics, in which the populations are assumed to be infinite, homogeneous, and wellmixed (Taylor and Jonker, 1978; Hofbauer et al., 1979; Hofbauer and Sigmund, 1998). Although replicator dynamics did not successfully solve the dilemma in general in 2-player 2-strategies games (PD and SD games), it leads to numerous insights to evolutionary game theory. In particular, in recent studies, the replicator dynamics indicate that cooperative dilemma can be removed in the multiplayer public goods game (Hauert et al., 2002; Brandt et al., 2006). However, the size of real populations are finite rather than infinite, and the resulting stochastic effect cannot be neglected (Traulsen et al., 2005a, 2006a, 2006b). Earlier game-theoretic models, which deal with finite populations either structured or unstructured, are based on individual-based computer simulations. Axelrod (1984) used computer simulations to investigate a iterated prisoner's dilemma game (IPD) in unstructured population, and recently Nowak et al. (2004) have argued that cooperation in the IPD may be enhanced by small population sizes. The effect of stochasticity in finite population has been verified again. For structured population, the seminal work by Nowak and May (1992) spawned a large number of investigations of "games on grids." Although spatial structure does not always favor cooperation, it is considered to be of relevance to "kin selection" (Doebeli and Hauert, 2004, and references therein; Nowak, 2006). However, for finite populations, one inevitable problem in analysis of evolutionary game dynamics is the analytical intractability. Thus, a stochastic approach is required in studying evolutionary game dynamics in finite populations (Nowak et al., 2004; Taylor et al., 2004; Imhof and Nowak, 2006; Traulsen et al. 2006a, 2006b).

Recently, Nowak and coworkers (Nowak et al., 2004; Taylor et al., 2004; Traulsen et al., 2006b) generalized Moran's classical population genetic model to study the evolutionary game dynamics. The framework starts from a two-players two-strategies game, and generate a frequency-dependent Moran process, then the fixation probabilities are calculated in order to determine if a given resident strategy is protected by natural selection. The analysis showed that apart from the payoff matrix, the population size also plays an important role in the evolutionary game dynamics; in particular, Traulsen et al. (2007a) also found that the intensity of selection will be reduced if stochasticity is introduced in the payoff matrix. However, as the stochastic process of evolutionary game dynamics is intricate, some analytical solutions cannot be derived explicitly, such as the time to fixation. In fact, the problem of extinction or fixation is very important in evolutionary game dynamics. Deriving the condition of extinction or fixation is merely the first step, and obtaining the time to extinction or fixation is the second step. Antal and Scheuring (2006) derived the average fixation time by analyzing the discrete population model approximately. Recently, Traulsen et al. (2005a) studied a evolutionary game dynamics for finite but large population, where the discrete state variables were treated as continuous ones. These two studies stimulate us to study evolutionary game dynamics in finite population using continuous probability approach, in which the fixation problem may be solved analytically.

The organization of this paper as follows: In the next section, we introduce the frequency-dependent Moran process and develop the continuous probability model. Then the analytically explicit solution of equilibrium abundance distribution and mean time to extinction or fixation will be derived. In Section 3, we show how the population size, payoff matrix, initial abundance, and mutation rate affect the evolutionary game dynamics. Finally, we give a short conclusion and discussion in the last section.

2. Model and method

2.1. Continuous probabilistic model

A frequency dependent Moran process for evolutionary game dynamics can be described as follows. The total number of the finite population is J, and J remains constant. A player can follow either A or B strategies defined by payoff matrix

$$\begin{array}{c|cc} & A & B \\ \hline A & a_{11} & a_{12} \\ B & a_{21} & a_{22} \end{array} \tag{1}$$

If there are N individuals playing strategy A and $J-N$ individuals playing strategy B, the expected payoff of an individual playing strategy A or B are respectively

$$f_N = \frac{a_{11}(N-1) + a_{12}(J-N)}{J-1}, \qquad g_N = \frac{a_{21}N + a_{22}(J-N-1)}{J-1}. \tag{2}$$

Now, as an important component in present evolutionary theory, mutation is also included in this study. At each time step, either an individual is chosen to reproduce a offspring of the same strategy proportional to its fitness (payoff), or changes its strategy to another strategy with probability m. Consequently, at each time step, N can change at most by one according to the following transition probabilities.

$$\begin{aligned} W[N-1|N] &= \frac{N}{J}\left[(1-m)\frac{(J-N)g_N}{Nf_N + (J-N)g_N} + m\right], \\ W[N+1|N] &= \frac{J-N}{J}\left[(1-m)\frac{Nf_N}{Nf_N + (J-N)g_N} + m\right], \\ W[N|N] &= 1 - W[N-1|N] - W[N+1|N]. \end{aligned} \tag{3}$$

This is, in fact, a discrete time Markov process or random walk process. Generally, the model can be analyzed within the framework of Moran process. However, in this study, we will analyze the model using continuous probability approach.

The formulation of continuous probability approach is as follows: In a small time interval Δt, the transition probabilities for the change ΔN of the number of individuals N of strategy A as

$$\begin{aligned} P[\Delta N = -1|N] &= \mu \Delta t W[N-1|N], \\ P[\Delta N = 1|N] &= \mu \Delta t W[N+1|N], \\ P[\Delta N = 0|N] &= 1 - \mu \Delta t \big(W[N+1|N] + W[N-1|N]\big), \end{aligned} \tag{4}$$

where $\Delta N = N(t+\Delta t) - N(t)$, and μ is the number of death events per unit time interval. In infinitely small time interval Δt, the first and second moments can be defined for the random variable ΔN ($\Delta N = -1, 0, 1$) and calculated as

$$V[N] = \lim_{\Delta t \to 0} \frac{E[\Delta N | N]}{\Delta t}, \tag{5}$$

$$D[N] = \lim_{\Delta t \to 0} \frac{E[\Delta N^2 | N]}{\Delta t}, \tag{6}$$

where $E[\Delta N|N] = P[\Delta N = 1|N] - P[\Delta N = -1|N]$ and $E[\Delta N^2|N] = P[\Delta N = 1|N] + P[\Delta N = -1|N]$.

2.1.1. Equilibrium abundance distribution

Since the game defined by (1) is symmetric, without loss of generality, we only calculate the equilibrium abundance distribution of player A. Denote n, the number of individuals (abundance) playing strategy A, as a continuous variable allowing any real values in the interval $[0, J]$. Then the probability density, $p(n,t)$, and that the number of individuals playing strategy A has abundance n at time t, satisfies the Kolmogorov–Fokker–Planck forward equation

$$\frac{\partial p(n,t)}{\partial t} = -\frac{\partial (V(n)p(n,t))}{\partial n} + \frac{1}{2}\frac{\partial^2 (D(n)p(n,t))}{\partial n^2}, \tag{7}$$

where $n \in (0, J)$, and $t > 0$. The initial condition for Eq. (7) is $p(n,0) = p_0(n)$, $n \in [0, J]$. Moreover, Eq. (7) also has a natural boundary condition

$$\left.\frac{1}{2}\frac{\partial (D(n)p(n,t))}{\partial n} - V(n)p(n,t)\right|_{n=0,J} = 0. \tag{8}$$

Of course, $p(n,t)$ also satisfies the conservation condition

$$\int_0^J p(n,t)\, dn = 1, \quad \text{for all } t > 0. \tag{9}$$

The equilibrium distribution (or stationary distribution) $p^*(n)$ of $p(n,t)$ can be obtained by solving the second order ordinary differential equation

$$\frac{1}{2}\frac{d^2(D(n)p^*(n))}{dn^2} - \frac{d(V(n)p^*(n))}{dn} = 0, \quad n \in (0, J). \tag{10}$$

Equation (10) can be easily transformed into first order differential equation

$$\frac{1}{2}\frac{d(D(n)p^*(n))}{dn} - V(n)p^*(n) = 0, \quad n \in (0, J). \tag{11}$$

The solution of Eq. (11) with conservation condition (9) can be given

$$p^*(n) = C \exp\left[\int_0^n F(y)\, dy\right], \tag{12}$$

where $F(y) = [2V(y) - D'(y)]/D(y)$, $D'(y) = \frac{dD(y)}{dy}$, $C = [\int_0^J \exp[\int_0^x F(y) dy]\, dx]^{-1}$. Equation (12) is the equilibrium probability density function of the number of A-players.

2.1.2. Expected time to extinction and fixation

Define the probability that strategy A players do not go extinct by time t with n players initially at time 0 as

$$G(t,n) = P(T \geq t) = \int_0^J p(y,t|n,0)\,dy. \tag{13}$$

This probability fulfills the Kolmogorov–Fokker–Plank equation (Gardiner, 1983)

$$\frac{\partial G}{\partial t} = \frac{1}{2}D(n)\frac{\partial^2 G}{\partial n^2} + V(n)\frac{\partial G}{\partial n}, \quad n \in (0, J),\ t > 0, \tag{14}$$

where the initial condition is $G(n,0) = 1$, $n \in [0, J]$, and $V(n)$ and $D(n)$ are defined in Eqs. (5) and (6).

The expected time to absorbing state $N = 0$ (extinction) in the J community is

$$T(n) = \int_0^\infty G(t,n)\,dt \tag{15}$$

which can be derived from the following second order ordinary differential equation

$$\frac{1}{2}D(n)\frac{d^2 G}{dn^2} + V(n)\frac{dG}{dn} = -1, \quad n \in (0, J). \tag{16}$$

$T(n)$ can be solved explicitly supplemented with the absorbing boundary condition and the reflecting boundary condition

$$T(0) = 0, \qquad dT(n)/dn|_{n=J} = 0. \tag{17}$$

Gardiner (1983) gave the explicit solution of $T(n)$

$$T(n) = 2\int_0^n \frac{dy}{D(y)p^*(y)}\int_y^J p^*(z)\,dz, \tag{18}$$

where $p^*(z)$ is the equilibrium probability density defined in Eq. (12).

The expected time to fixation can also be obtained similarly from Eq. (16) if the boundary conditions are both absorbed at $n = 0$ and $n = J$. The explicit solution is in the following form (Gardiner, 1983)

$$T_{fix}(n) = 2\frac{[(\int_0^n \frac{dy}{\psi(y)})\int_n^J \frac{dx}{\psi(x)}\int_0^x \frac{\psi(z)\,dz}{D(z)} - (\int_n^J \frac{dy}{\psi(y)})\int_0^n \frac{dx}{\psi(x)}\int_0^x \frac{\psi(z)\,dz}{D(z)}]}{\int_0^J \frac{dy}{\psi(y)}}, \tag{19}$$

where $\psi(x) = \exp\{\int_0^x [2V(x)/D(x)]\,dx\}$.

Now, the equilibrium abundance distribution, expected time to extinction and fixation have been obtained. Given the payoff matrix and other parameters, such as community size and mutation rate, Eqs. (12), (18), (19) can be calculated numerically. In order to verify the utility of continuous probability approach, a individual-based computer simulation is also needed.

2.2. *Individual-based simulation*

Assume a community has J players, and there are N players of strategy A. For facility of simulation and without loss of generality, J is assumed to be a even integer. At each time step, every player must choose a random opponent to play the 2×2-play, and the payoff is calculated by Eq. (1). Then an individual is chosen for reproduction proportional to its fitness. Meanwhile, to include mutation, we also assume that the offspring may be either of the same strategy as its ancestor or of the opposite type. The mutation probability is m. Next, this newborn individual replaces another randomly selected individual, hence the total number of the population J remains constant. The process continues until one type of players dominate the whole community. This process of the same configuration are repeated 100 times, the average persistence time are recorded. By varying the payoff matrix, we will mainly consider PD and SD game, where the payoff matrixes are

$$\begin{array}{c|cc} & A & B \\ \hline A & b-c & -c \\ B & b & 0 \end{array} \tag{20}$$

and

$$\begin{array}{c|cc} & A & B \\ \hline A & b-c/2 & b-c \\ B & b & 0 \end{array} \tag{21}$$

where strategies A and B represent cooperation and defection, and b and c represent defectors benefit and cooperator's cost.

3. Results

3.1. *Equilibrium abundance distribution*

From Eq. (12), it can be observed that initial configuration has no influence on equilibrium abundance distribution. Moreover, for different community size, the shape of equilibrium abundance distribution are also similar. Then we only focus our attention on mutation rate and payoff matrix.

For the PD game, from Eq. (20), we can see that strategy B is the evolutionary stable strategy. Strategy A will be fully excluded by strategy B, and A-players will become extinct. However, for finite population, as the influence of random drift, strategy A also has the opportunity to win the competition. That is to say, the equilibrium probability density function of strategy A abundance will both peak at $N = 0$ and $N = J$ when mutation probability m is small. But if mutation probability m increases slightly, the peak at $N = J$ will disappear. No doubt, when m further becomes larger, the peak at $N = 0$ will also disappear and the sole peak will appear at $N = J/2$. Then a reversed U-shaped probability function arises. We also give a numerical example for this case in Fig. 1. When payoff matrix varies, we find that the equilibrium abundance distribution nearly does not change.

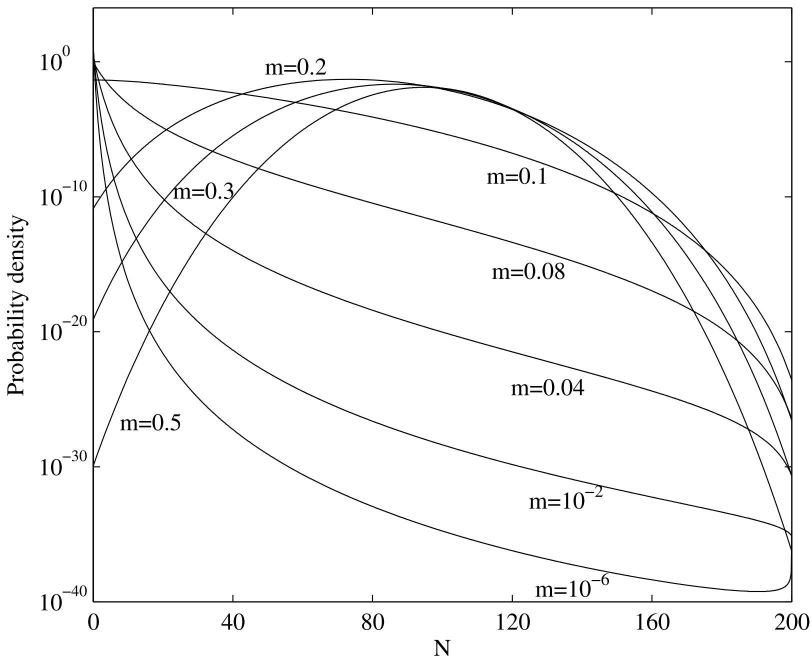

Fig. 1 Equilibrium probability density of abundance of A-players for prisoner's dilemma game (Eq. (12)), $J = 200$, $b = 1$, $c = 0.1$.

For the SD game, we know that strategies A and B will coexist at stable equilibrium $N^* = 2J\frac{b-c}{2b-c}$ if the population size is infinite. However, as the effect of random drift, especially for small benefit to defect c, cooperators are more prone to win in the finite population (see Fig. 2). The equilibrium probability density function peaks at $N = J$ for very small mutation probability. When mutation probability increases, the peaks of equilibrium probability density function will move left. In the inlet of Fig. 4, it is observed that the peaks of equilibrium probability density function also move left as c increases. That is consistent with the case of infinite population.

3.2. Expected time to extinction and fixation

The theoretical expected time to extinction and fixation can be directly derived from Eqs. (18), (19). Meanwhile, we can see that apart from the payoff matrix, the expected time to extinction or fixation is also determined by the community size, mutation rate, and initial configuration. Not all scenarios are covered comprehensively in this study. Instead, some numerical results will be simply illustrated as figures here. Moreover, to verify the theoretical predications, results from individual-based computer simulations are also given.

First, the theoretical expected first time to extinction for PD game with the same parameters and payoff matrix as in previous subsection are calculated. It is clear that the expected time to extinction will be increasing when initial individual number of A-player

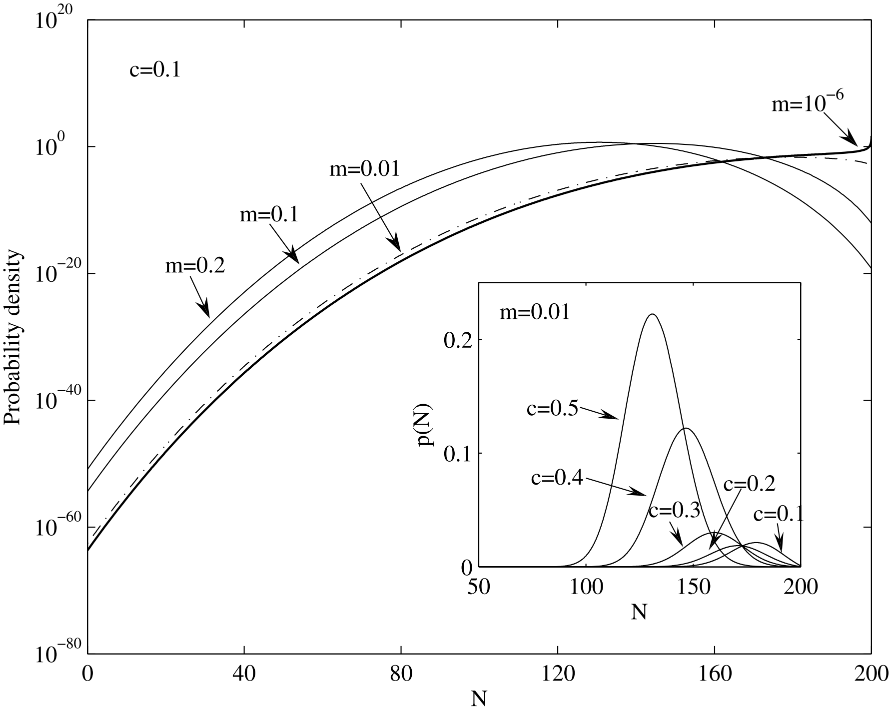

Fig. 2 Equilibrium probability density of abundance of players in strategy A for snow-drift game (Eq. (12)). Without indicated explicitly, the parameters are $J = 200$, $b = 1$, $c = 0.1$.

increases (Fig. 3a). Meanwhile, the effect of mutation cannot be neglected on the mean first time to extinction. Figure 3b illustrates the result. From Fig. 3b, we can see that the average first time to extinction will first decrease and then increase when the mutation probability is increased. That is to say, mutation does not always favor the persistence of the cooperators. As influence of community size, it is more intuitive: expected time to extinction will increase as community size increases. Figure 4 illustrates both the theoretical and simulation results for $J = 200$, 400, 600, 800, and 1,000 respectively. It can be easily observed that the theoretical and simulation results are consistent.

Second, we will consider the expected time to fixation for the PD game. We are only interested in the influence of mutation rate and initial abundance of A-players. As strategy A and B are not symmetric, the expected time to fixation is much more complicated. From Fig. 5, it is easily to be observed that expected time to fixation starts from zero, then increases and reaches its peak, and finally decreases to zero again. Particularly, we also find that there exists a threshold in initial abundance of cooperators near 50. Below the threshold, the expected fixation time will decrease when the mutation probability increases. While above the threshold, the expected fixation time will increase. This result can be explained as follows. There are two fixation states: strategy A go extinct or dominate. The model used in this study is a random walk where the abundance of A-players at time t is like the walker subjected to the influence of random drift, frequency

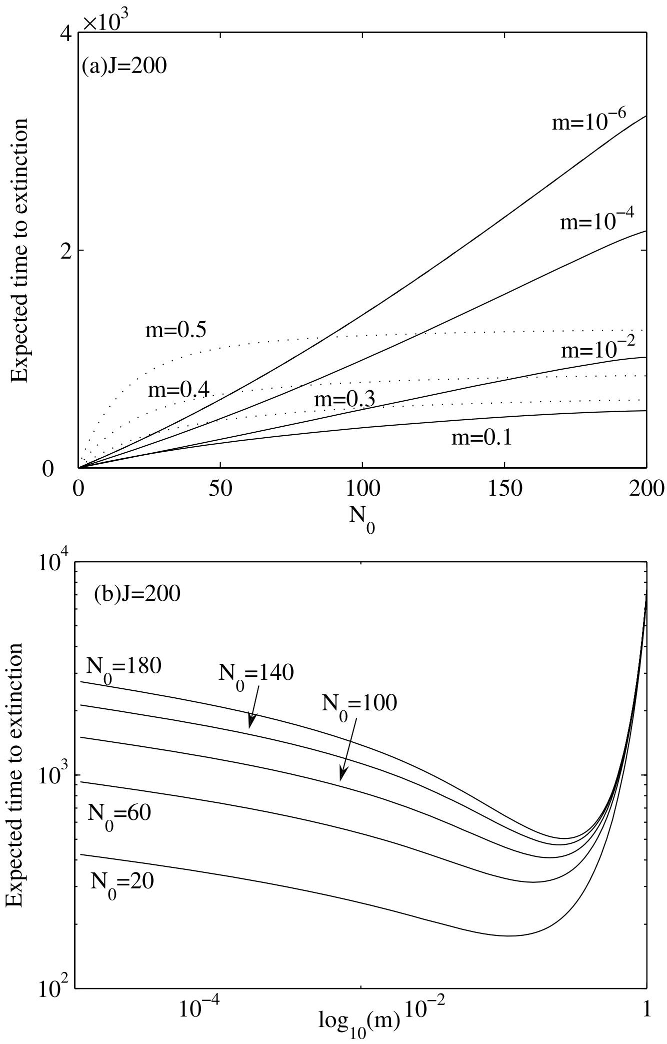

Fig. 3 Expected time to extinction of A-players for prisoner's dilemma game, N_0 is the initial abundance and parameters are: $J = 200$, $b = 1$, $c = 0.1$.

dependent selection, and mutation. For the prisoner's dilemma game, evolutionary games provide one-way and directed force to the states extinction of strategy A, which is inversely proportional to the abundance of strategy A players (the distance to the endpoint). Random drift provides a weak and two-way directed force to the two statuses extinction and dominance of strategy A. Another force, which can also be bidirectional, comes from mutation. And this force is just like gravitation, which is also inversely proportional to distance. When the initial abundance of strategy A is small, all the forces are leading to the state of extinction of strategy A, and fixation mainly refers to extinction of strategy

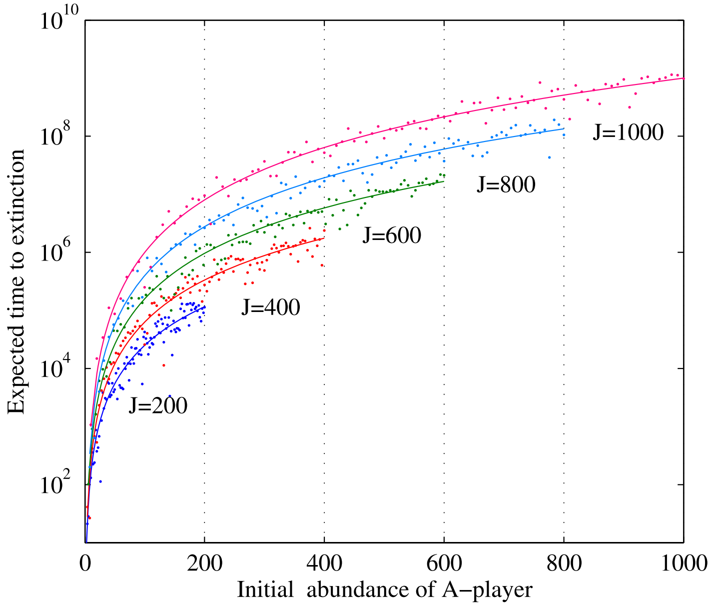

Fig. 4 Expected time to extinction of A-players for prisoner's dilemma game, $m = 10^{-3}$, $b = 1$, $c = 0.1$. Solid lines: theoretical predictions from Eq. (18); dots: individual-based computer simulations.

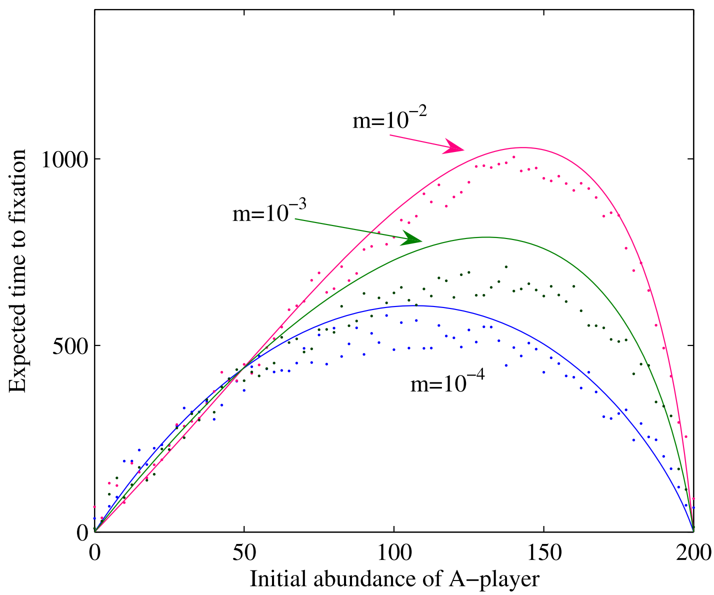

Fig. 5 Expected time to fixation of A-players for prisoner's dilemma game, $J = 200$, $b = 1$, $c = 0.1$. Solid lines: theoretical predictions from Eq. (19); dots: individual-based computer simulations.

A. When the initial abundance of strategy A increases, the force to state of strategy A player extinction becomes weak, so possibility becoming the dominance of strategy A also increase. As the swing between the states, the average first time to fixation also increase. When the forces leading to the two states are equal, then the average first time to fixation will reach its peak. In Fig. 5, we also see that show that the actual average time to fixation computed from individual-based computer simulations is a little smaller than the theoretical prediction. We note that it is because the community size is not large enough to totally approximated by continuous variable.

4. Conclusion

Since Nowak and coworkers (Nowak et al., 2004; Taylor et al., 2004) first use the Moran process as the tool to analyze the evolutionary game dynamics in finite population, there has been a lot of progress in this field. For example, Traulsen et al. (2005b) first considered a two level evolutionary game model, and discussed the selection on individual and group levels. In the following work, Traulsen and coworkers extended the standard Moran process and investigated the effect of selection temperature and stochasticity of payoff on fixation probability (Traulsen et al., 2007a, 2007b). However, the expected time to fixation cannot been easily obtained. Antal and Scheuring (2006) derived a approximation of the fixation time, when the population size is large. In this paper, we also started from the framework of the Moran process and incorporate mutation in the model, which is like the asymmetric random walk model on a line with two reflecting boundaries. Contrary to previous studies, we did not analyze the discrete state model directly, but introduced the continuous probabilistic approach to analyze the equilibrium probability density and the expected time to extinction and fixation. By applying to this approach to prisoner's dilemma and snowdrift games, we found that this approach is effective in giving an accurate approximation of expected time to fixation.

However, there are still two problems to be pointed out. First, we know that in the Moran process, all individuals are well mixed and spatial structure is not included. For the purpose of removing cooperative dilemma, however, spatial structure is a very important factor, such as the graph with finite vertices (Lieberman et al., 2005). Although the fixation probability can be derived explicitly, the expected time to fixation is not a easy task; maybe, deriving the expected time to fixation on graph structure might be more meaningful and useful. Second, the game-theoretic model in this paper and some previous studies are 2×2 games, in which the cooperative dilemma has not been removed. But recent studies revealed that cooperative dilemma will vanish when a third strategy is introduced (Imhof et al., 2005). It shows that the three strategies form cycle which is similar to the "rock-paper-scissors" game. As the dynamics of the multistrategy game model is very intricate, the framework used in this study will not be applicable. Therefore, it will be interesting if the continuous probability approach can be used to the multistrategy game model. These two questions deserve more attention in future studies.

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