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Simulation of evolutionisms for the double-membrane prokaryotes based on Parrondo's model

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ABSTRACT

Lake proposed a hypothesis that symbiosis between a clostridium and actinobacterium produced the double-membrane prokaryotes and endosymbiosis. On the basis of Lake's hypothesis, this paper explains the rationality from quantitative analysis by using game theory so as to show symbiosis is a successful direction of evolution. The paper devises a multi-agent Parrondo's model, which consists of game A and game B. Game A reflects the interaction relationship among individuals. Considering the symbiosis and endosymbiosis of actinobacteria and clostridia, we match them into the double-membrane prokaryotes by pairs. Complementary cooperation mechanism is adopted if the same type of individuals encounter, whereas competitive mechanism is adopted if the different types of individuals encounter. Game B reflects the environmental effect on individuals and is devised to be a negative-sum game, reflecting the harsh natural environment. It has two branches depend on the divisibility of a module M. One branch represents the unfavorable factors of environment, which has little probability to win; the other indicates the favorable conditions of environment with a large probability of winning. Besides, we set up a feedback mechanism to express the photosynthesis of the double-membrane prokaryotes. Through feedback of this mechanism, the structure of game B is improved. The improvement is mainly reflected in two aspects: quantitative and qualitative changes. Quantitative change means the winning probability of the favorable branch increases, while qualitative change indicates the module M becomes large. The simulation results show the endosymbiosis and the photosynthesis can make the double-membrane prokaryotes obtain a greater fitness and a higher survival percentage. © 2013 Trade Science Inc. - INDIA

KEYWORDS

Parrondo's paradox;
Evolutionary game;
Cooperation;
Double-membrane prokaryotes;
Endosymbiosis.

INTRODUCTION

Lake^[1] has provided a significant hypothesis regarding prokaryotes and the evolution of life in his latest

research. He pointed out that the double-membrane prokaryotes were formed through a symbiosis between two groups of prokaryotes, an actinobacterium and a clostridium. The symbiosis of the double-membrane

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prokaryotes generated mitochondria lying in the cell of body. The subgroup of the double-membrane prokaryotes—cyanobacteria directly led to the emergence of oxygen on the Earth through photosynthesis.

This paper explains the rationality from quantitative analysis by using Game Theory based on Lake's hypothesis, so as to clarify the symbiosis is a successful evolutionary direction. Game Theory is a mathematical theory concerning competition, cooperation and game rules. It is a very important research topic that provides a mathematical and physical basis for Darwin's natural selection process, by using game theory to analyze the behavioral strategies of biology^[2-3]. In order to simulate the competition and cooperation relationships among individuals in biological and social systems, game theory scholars have proposed a number of well-known models, such as the Prisoner's Dilemma model, the Snow model and the Minority Game model and so on. We establish a corresponding game model based on Parrondo's paradox to simulate the evolutionary mechanisms of the double-membrane prokaryotes. The following are the main mechanisms and corresponding details.

- (1) The effects of the environment on the prokaryotes. The main contents are: 1) The poor survival condition of the overall environment; 2) Not only the unfavorable influence factor exists in nature but also the favorable one (such as sunlight)
- (2) The interaction between prokaryotes. The detail needed to express is that the survival competition between individuals.
- (3) The differences between the double-membrane prokaryotes and the general prokaryotes, including: 1) the endosymbiosis of the double-membrane prokaryotes, 2) the photosynthesis of the double-membrane prokaryotes.

Parrondo's paradox is an apparent paradox in game theory and is named after its creator Parrondo, a Spanish physicist^[4]. Parrondo's paradox claims that two losing games, under random or periodic alternation of their dynamics, can result in a winning game. The seminal papers concerning Parrondo's Paradox were published by Abbott and Harmer^[5-6]. Already, Parrondo's paradox has been confirmed by means of computer simulation, the Brownian ratchet and discrete time Markov chain theory. Moreover, Parrondo's paradox has been

developed into many different versions^[7]. The original version of Parrondo's games involves two games^[6], A and B, each based on tossing biased coins: 1) Game A is a game of tossing biased coin 1 with the probability of winning p_1 . 2) Game B is a little more complex. If the present capital is a multiple of some integer M , a biased coin 2 is tossed with the probability of winning p_2 . If not, another biased coin 3 is tossed, with the probability of winning p_3 . Winning a game earns 1 unit and losing surrenders 1 unit. Playing game A or B is always a losing game, but when these two losing games are played under random or periodic alternation, the combination of the two games is, paradoxically, a winning game via an effective set of probability p_1, p_2, p_3 and modulus M , for instance, $p_1 = 0.5 - \varepsilon$, $p_2 = 0.1 - \varepsilon$, $p_3 = 0.75 - \varepsilon$, $M = 3$, ε has a small positive value and 0.005 can be chosen, for example. Observing the original version further, we can find that dependence on the capital limits its application in practice. Therefore, Parrondo^[8] modified game B in the original version and presented a new version which was related to the history of the games instead of the capital. This new history-dependent structure has enlarged the parameter space of Parrondo's paradox. Kay^[9] further studied the Parrondo's paradox effect where both game A and game B were history-dependent. Arena^[10] devised a new version which was constituted of three games. Game A and game B were the same as the original version while the rule of game C depended on the recent game history of winning or losing. By analyzing the above game versions, we find that Parrondo's paradox required some form of dependence, such as the dependence on capital and game history. Toral^[11] proposed a space-dependent "cooperative Parrondo's paradox" version. A remarkable difference was that there were $i(1, 2, \dots, N)$ players instead of only one player involved in the game. On each round, one player 'i' was randomly chosen from N persons to play game A or B according to some rules. Game A remained unchanged as was defined in the original Parrondo's games. Game B depended on the states of winning or losing of two neighbor players, $i-1$ and $i+1$. Mihailovic carried out theoretical analysis on cooperative Parrondo's paradox and provided cooperative game model based on one dimension^[12] and two dimensions^[13] respectively. Since the previous

versions have focused on how to modify game B, Toral^[14] proposed a modification of game A. There were N players involved in this version as well. Game A was devised that a player *i* paid for a unit to a player *j* that was also chosen randomly. Game B remained unchanged as was defined in the original Parrondo's games or history-dependent version.

Abbott pointed out that^[7], Parrondo's paradox now has connections in physics, biology and economics and other disciplines. In the area of biology, it has been proposed that Parrondo's paradox may relate to the dynamics of gene transcription in GCN4 protein and the dynamics of transcription errors in DNA^[17]. Parrondo's paradox has been studied in various interesting scenarios involving population genetics^[18-21].

MODEL

Abbott thought that Parrondo's paradox might help scientists find new methods for explaining the level of individual genes of the survival game. This paper designs a multi-agent game model of biology based on Parrondo's game version proposed by R. Toral^[14].

The model (Figure 1) is composed of two games: 1) Game A reflects the interactive relationship among individuals; 2) Game B reflects the environmental effect on individuals. There are N individuals of the population. The dynamic process of the model is as follows: Randomly choose one individual *i* (called the principal) to play game A with the probability of p_1 or game B with the probability of $1 - p_1$. When it comes to game A, we need to randomly choose individual *j* from the population (called the receptor). The specific forms of

game A are determined by the interaction between the principal *i* and receptor *j*.

Expression of the endosymbiosis - Game A

Game A is a zero-sum game to reflect the interaction between individuals. It does not have an effect on the total earnings of the population but only changes the income distribution in the population.

The basic mechanisms among individuals are competition and cooperation, and their corresponding forms in game A are as follows:

The competition mechanism: the winning probabilities of the principal *i* and receptor *j* are both 0.5. When *i* wins, *j* pays for an unit to *i*; otherwise, *i* pays for an unit to *j*.

The cooperation mechanism: symbioses and endosymbioses of the double-membrane prokaryotes^[1] show that, if two cells co-exist for a long enough time, they will exchange genes. However, they retain their own cell membranes in the course of symbioses. Sometimes they keep their own genome. Therefore, once actinobacteria and clostridia are in the state of symbioses, there is a selective information exchange (or retain) between them. Thus we design a complementary cooperation mechanism so as to express the symbioses. When $C_i(t) \geq C_j(t)$, the principal *i* pays for an unit to the receptor *j*; when $C_i(t) < C_j(t)$, the receptor *j* pays for an unit to the principal *i*. $C_i(t)$ and $C_j(t)$ are capital of principal *i* and receptor *j* at time *t* respectively.

The expression of environmental mechanism - Game B

When the two kinds of early prokaryotes, the actinobacteria and clostridia, evolve, the Earth's living environment is very bad. The environmental mechanism is devised to be a game B which is a negative game, reflecting the whole harsh natural environment. Game B has a special structure, which has different branches dependent on the divisibility of module *M*. The first branch (The total capital can be divided by *M*) describes the unfavorable factor of environment, which has a little probability p_2 to win; the second (The total capital cannot be divided by *M*) expresses the favorable condition of environment (e.g. sunlight), which has a large probability p_3 to win.

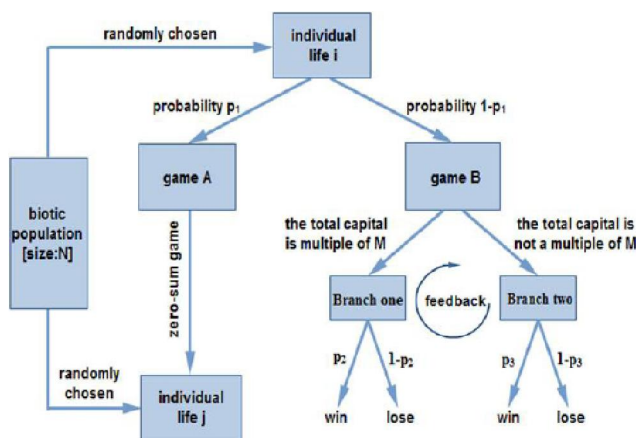


Figure 1 : The multi-agent Parrondo's model

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G. P. Harmer, et al.^[17,22] proved the following condition when game B was a negative game.

$$p_2 < \frac{(1 - p_3)^{M-1}}{p_3^{M-1} + (1 - p_3)^{M-1}} \quad (1)$$

Statistical methods

We define the fitness index d as follows

$$d(t) = \frac{W(t)}{K} \quad (2)$$

Where: $W(t) = C(t) - C_0$, let $W(t)$ be earnings and $C(t)$ be capital at time t , respectively. C_0 is the original capital; K is the average frequency for an individual game. $K = T/N$, where T is the total time of the game and N is the population size.

Therefore, the fitness of any i th individual at time t is:

$$d_i(t) = \frac{W_i(t)}{K} \quad (3)$$

The average fitness of the population at time t is

$$\bar{d}(t) = \frac{\left(\sum_{i=1}^N W_i(t)\right) / N}{K} \quad (4)$$

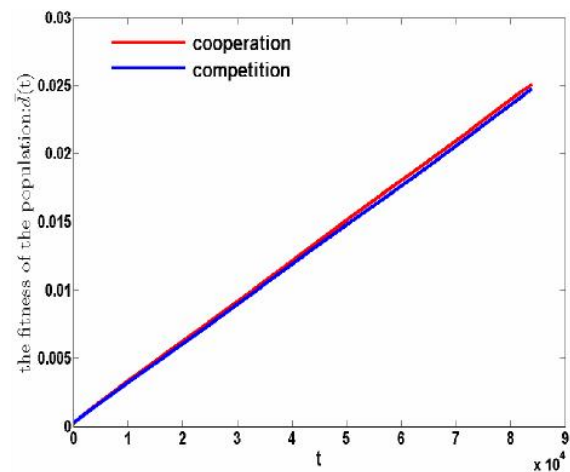
The initial capital is $C_0 = 10000$ and game time is $T = 84000$. We use different random numbers to play the game 100 times repeatedly, and draw figures according to the average results of the games played 100 times.

RESULTS

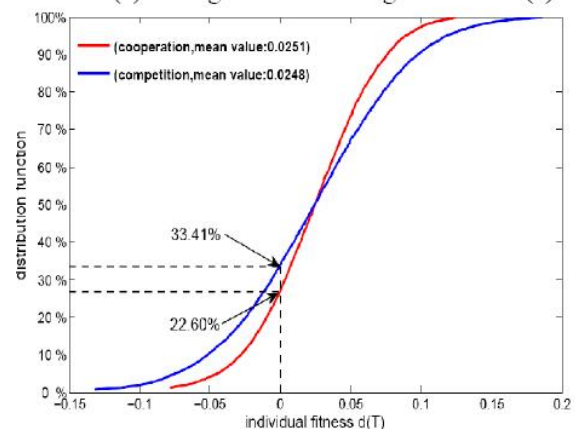
The fitness calculation of two populations

For the purpose of contrasting the survival adaptability between the double-membrane prokaryotes and the general prokaryotes, we calculate and analyze the fitness of two populations: 1) the population is composed of the general prokaryotes (competition pattern). The population consists of the general actinobacteria and clostridia in equal portions. When game A is played by individuals, competition pattern is adopted. 2) The population is composed of the double-membrane prokaryotes (cooperation pattern). The population totally consists of the double-membrane prokaryotes. For

symbioses and endosymbioses between the actinobacteria and clostridia, the double-membrane prokaryotes are matched in pairs. When the same pair encounter, complementary cooperation mechanism is adopted; while the different pair of individuals encounter, competition mechanism is used. Under the adverse living environment (negative game B), both competition and cooperation can promote the improvement of the average fitness of the populations and guarantee the survival and growth of the populations, as shown in Figure 2(a). More specifically, the average fitness of the double-membrane prokaryotes is slightly higher ($0.0251 > 0.0248$). We define the survival proportion of the population as the proportion of individuals whose fitness is positive in a population. Figure 2 (b) shows that the survival ratio of the population composed of



(a) Changes of the average fitness $\bar{d}(t)$



(b) The distribution of individual fitness $d(T)$

Figure 2 : Analysis of the fitness (Population size $N = 200$. Parameters are $p_1 = 0.5$, $M=3$, $p_2 = 0.1 - \varepsilon$, $p_3 = 0.75 - \varepsilon$, and $\varepsilon = 0.005$. The parameters satisfy formula (1) when game B was a negative game.)

the double-membrane prokaryotes is 73.4%, while the general population of the prokaryotes is 66.59%. Thus, the survival ratio of individuals in a population composed of the double-membrane prokaryotes is high, which indicates the symbiosis is a successful direction of evolution.

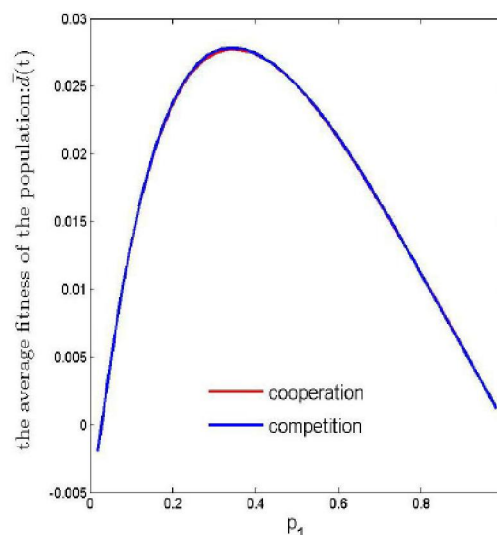
In addition, from a systematical perspective, game A is a zero-sum game and game B is a negative game for each individual in the population. However, the combination of the two losing games can produce a winning game. The increase of the average fitness of the population reflects Parrondo's Paradox counterintuitive nature. Abbott^[23] pointed out that life itself may be self-guided by means of a ratcheting effect. When some kind of evolutionary direction forms occasionally, environmental forces can easily destroy the initial order. Those factors that play a role as a ratchet can stop the destruction and help life form a higher complexity along the evolutionary path. The special structure of game B plays the analogous role that natural environment has on biological evolution in terms of a ratcheting effect, and competition and cooperation are the successful directions of evolution.

Effect of p_1

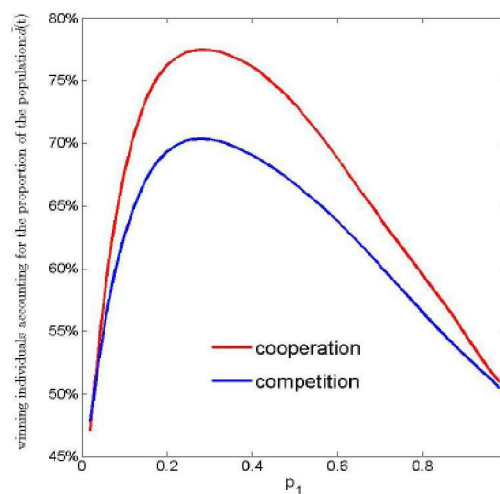
Figure 3 shows that, within the variation range of p_1 , the average fitness is basically the same between the double-membrane prokaryotic population using the cooperation pattern and the general prokaryotic population using the competition pattern. However, the survival ratio of the former is higher than that of the latter. Moreover, either the cooperation mode in pairs or the competition mode, the peak of the average fitness and the survival percentage generally happen at $p_1=1/3$. That is to say, when the probability of playing game A is 1/3, the population will achieve the best return. Here, we are willing to point out if game A is regarded as a manifestation of individual's social attribute and game B as a manifestation of individual's natural property, then game A whose optimum performance of the population happens to the probability of 1/3 may be a reasonable explanation for 8-hour work system of human society.

Impacts of P_2 and P_3

From Figure 4, even though the environmental mechanism (Game B) still remains to be a negative game,



(a) Change of the average fitness $\bar{d}(T)$



(b) Change of the survival ratio

Figure 3 : The effect of the probability p_1 ($0.02 \leq p_1 \leq 0.98$, Population size $N = 200$ and the game parameters are $M=3$, $p_2 = 0.1 - \varepsilon$, $p_3 = 0.75 - \varepsilon$, $\varepsilon = 0.005$.)

enhancement of the winning probability p_3 of the second branch can improve the average fitness of the population. Therefore, increasing the probability p_3 is the right direction for evolution. This may be the driving factor for the emergence of photosynthesis (efficient use of sunlight).

Analysis of the mixed population

When the double-membrane prokaryotes are mixed with the general prokaryotes, we divide the population into two subgroups, namely S class and D class, so as

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to investigate their survival conditions. S class consists of the general actinobacteria and clostridia and D class is formed by the double-membrane prokaryotes in pairs of actinobacteria and clostridia. When pairs of the individuals who are the double-membrane prokaryotes

encounter, cooperation mechanism is adopted; while the other individuals encounter, competition mechanism is used. According to Figure 5, for most of the population size (n), the average fitness of D class, formed by the double-membrane prokaryotes, is slightly better than that of S class, composed of the general prokaryotes. Besides, the survival ratio of D class is significantly higher than that of S class. Therefore, the double-membrane

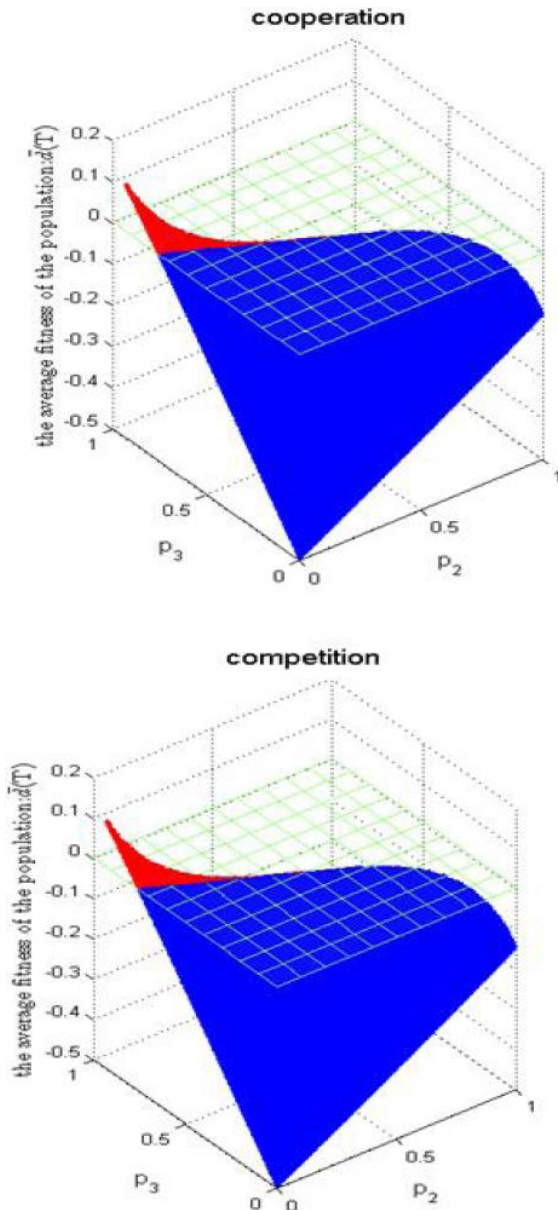
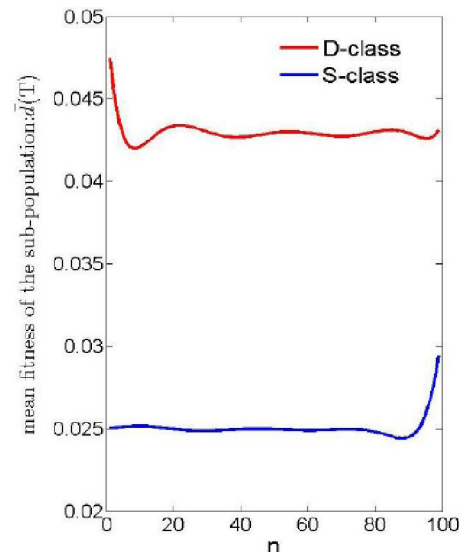


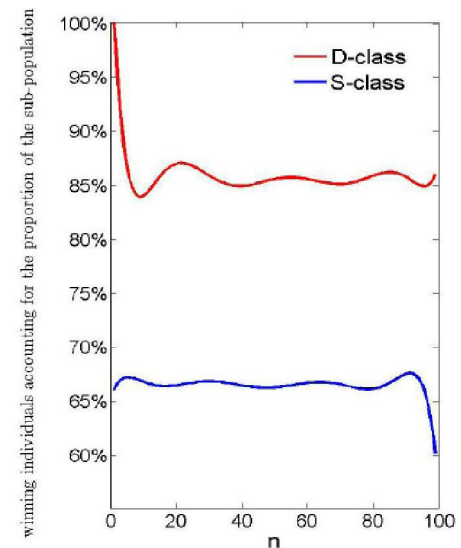
Figure 4 : The effects of the probabilities p_2 and p_3

$$(p_2 < \frac{(1 - p_3)^{M-1}}{p_3^{M-1} + (1 - p_3)^{M-1}} \cdot \text{Population size } N = 200 \text{ and}$$

the game parameters are $p_1 = 0.5$ and $M=3$. The values of the red part are positive and the corresponding p_2 and p_3 are the parameter space for the established Parrondo's paradox)



(a) Change of the fitness along with the size change of D class



(b) Change of the survival ratio along with size change of D class

Figure 5 : The survival conditions of the double-membrane prokaryotes mixed with the general prokaryotes (Population size $N = 200$, size n of D class is changed from 1 to 99 pairs and the game parameters are $p_1 = 0.5$, $M=3$, $p_2 = 0.1 - \epsilon$, $p_3 = 0.75 - \epsilon$, and $\epsilon = 0.005$.)

prokaryotes can obtain the primary footholds and survival among the prokaryote population, which is composed of the general clostridia and actinobacteria.

The expression of the photosynthesis - structural change of game B

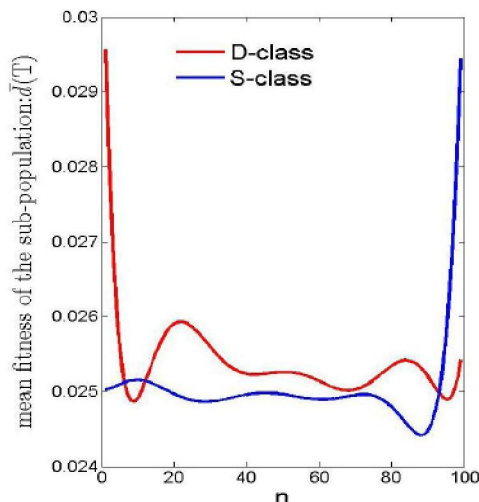
Comparing the double-membrane prokaryotes produced by symbiosis with the general prokaryote prokaryotes, we find that the biggest success results from the photosynthesis. The double-membrane prokaryotes (sub-group of D class) can make effective use of the sunlight environment through photosynthesis. For the purpose of expressing the photosynthesis, we set up a feedback mechanism in the model of game B. As shown in Figure 1, in contrast to the general prokaryotes (sub-group of S class), when the double-membrane prokaryotes plays the second branch of game B, they can improve the structure of game B through the feedback mechanism to enhance their own fitness. Improvement on the structure of game B through feedback mechanism can be expressed in two forms: 1) Quantitative change——increasing the probability p_3 . Effective use of sunlight for the double-membrane prokaryotes can be expressed as increasing winning probability p_3 of the second branch in game B. Game B is still defined to be a negative game because of the

quantitative change. That is $p_2 < \frac{(1 - p_3)^{M-1}}{p_3^{M-1} + (1 - p_3)^{M-1}}$.

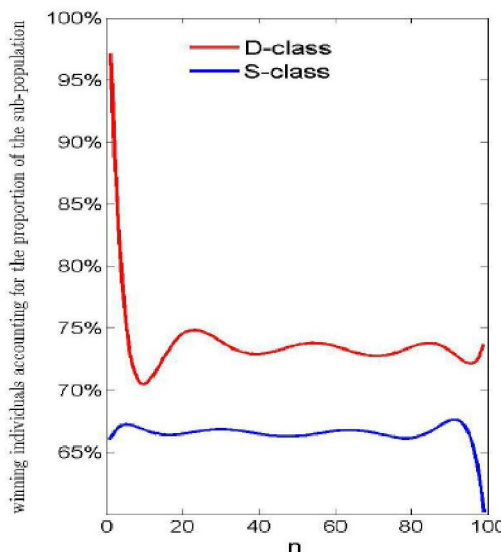
From Figure 6 and Figure 7, we can see even if the overall tough environment still exists (Game B is still a negative game), the accretion of p_3 can effectively raise the survival fitness and survival ratio of the double-membrane prokaryotes. Therefore, photosynthesis is the key to successful evolution for the double-membrane prokaryotes. 2) Qualitative change——increasing the modulus M . The accretion of modulus M leads to qualitative change. According to Fig.8, when the modulus M increases from 3 to 4 or 5, $p_2 = 0.1 - \epsilon$ and $p_3 = 0.75 - \epsilon$ ($\epsilon = 0.005$), the condition

$p_2 < \frac{(1 - p_3)^{M-1}}{p_3^{M-1} + (1 - p_3)^{M-1}}$ is violated. Game B becomes

a positive game. Thus, the survival fitness and survival proportion of the double-membrane prokaryotes are



(a) Change of the fitness along with the size change of D class

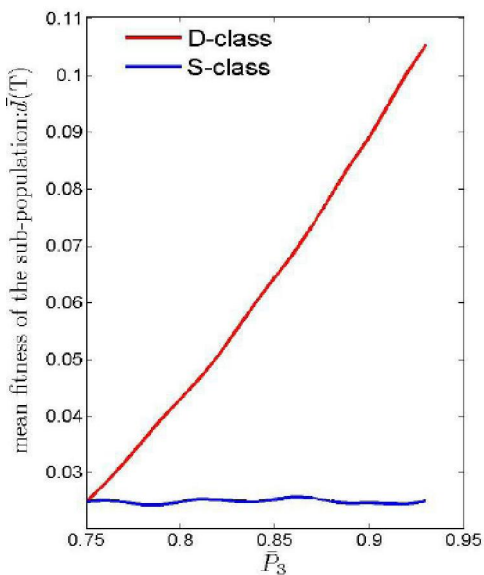


(b) Change of the survival ratio along with the size change of D class

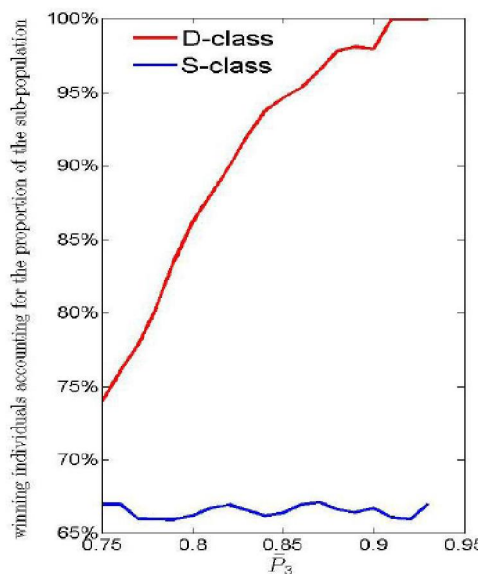
Figure 6 : Quantitative effect on the mixed populations. (Analysis of the survival conditions of the double-membrane prokaryotes mixed with the general prokaryotes. Population size $N = 200$. The probability p_1 of playing game A is 0.5. Size n of D class is chosen from 1 to 99 pairs. The game parameters of S class are: $M=3, p_2 = 0.1 - \epsilon, p_3 = 0.75 - \epsilon$ and $\epsilon = 0.005$. Considering the quantitative change along with the increase of p_3 resulted from photosynthesis and the condition that game B is a negative game, we choose $M=3 \nmid p_2 = 1/17 - \epsilon \nmid p_3 = 0.8 - \epsilon \nmid \epsilon = 0.005$ for D class.

We find the accretion of p_3 makes the survival fitness and survival ratio of D class much better than those of S class. The photosynthesis of the double-membrane prokaryotes improves their own adaptation to the survival.)

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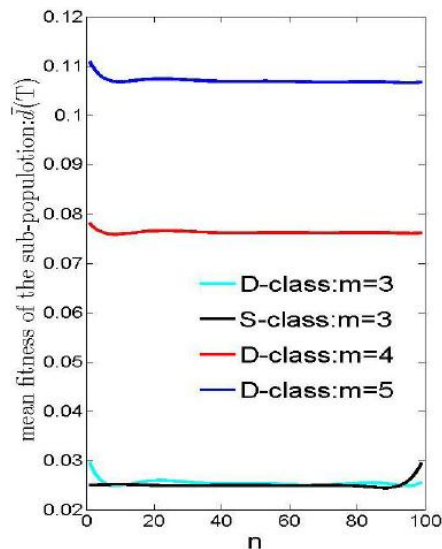


(a) Change of the fitness

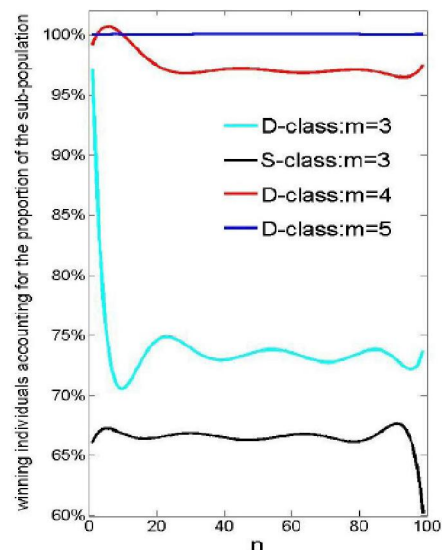


(b) Change of the survival ratio

Figure 7 : Impact by the change of \bar{p}_3 (photosynthesis quantitative) of D class. (Population size: $N = 200$. The probability p_1 of playing game A is 0.5. The size of S class is 100 and the game parameters are $M=3, p_2 = 0.1 - \epsilon, p_3 = 0.75 - \epsilon$ and $\epsilon = 0.005$. The size of D class is 50 pairs and the game parameters are $M=3, p_2 = \frac{(1 - \bar{p}_3)^2}{\bar{p}_3^2 + (1 - \bar{p}_3)^2} - \epsilon$ and $\epsilon = 0.005$, which satisfy with the requirements that game B is a negative game. With the increase of \bar{p}_3 , the fitness and the survival proportion of D class significantly increase.)



(a) Change of the fitness along with the size change of D class



(b) Change of the survival ratio along with the size change of D class

Figure 8 : The first type of qualitative effect. (Analysis of the survival conditions of the double-membrane prokaryotes mixed with the general prokaryotes. Population size $N = 200$. The probability p_1 of playing game A is 0.5. Size n of D class is chosen from 1 to 99 pairs. The game parameters of S class are: $M=3, p_2 = 0.1 - \epsilon, p_3 = 0.75 - \epsilon$ and $\epsilon = 0.005$. The game parameters of D class are: $M=3, 4$ and $5, p_2 = 0.1 - \epsilon, p_3 = 0.75 - \epsilon, \epsilon = 0.005$. For D class, when $M=4$ and $5, p_2 = 0.1 - \epsilon$ and $p_3 = 0.75 - \epsilon$ no longer satisfy with the condition $p_2 < \frac{(1 - p_3)^{M-1}}{p_3^{M-1} + (1 - p_3)^{M-1}}$. Thus, game B becomes a positive game.)

greatly enhanced.

DISCUSSION

Evolutionary process of the double-membrane prokaryotes and the corresponding driving mechanisms can be divided into four phases as follows: Individuals are produced (mutation) → The initial foothold and survival (endosymbioses mechanism caused by symbiosis) → The Population grow (the effect of photosynthesis) → The successful evolution (survival of the fittest). Detailed descriptions are: firstly, the accident mutation in the general prokaryotic population composed of the clostridia and actinobacteria generates the double membrane prokaryotes. Secondly, the cooperation mode caused by symbiosis makes the double-membrane prokaryotes obtain greater fitness and higher survival percentage; According to Figure 5, when n is very small, that is, $n = 1, 2, \dots$, the average fitness of the sub-group composed of the double-membrane prokaryotes is slightly better than that of the sub-group composed of the general prokaryotes. Besides, the survival ratio is significantly higher than that of sub-group of the general prokaryotes. Therefore, the double-membrane prokaryotes win the primary footholds and survivals among the general prokaryotic population composed of the clostridia and actinobacteria. Then, the double-membrane prokaryotes improve the structure of game B through photosynthesis, and hence the living environment of double-membrane prokaryotes is improved, which corresponds to the accretion of modulus M and the probability p_3 of game B in the model. So the double-membrane prokaryotes obtain better fitness and higher survival proportion. Finally, under the action of natural selection, survival is the fittest. The double-membrane prokaryotes obtain a successful evolution. Therefore, the evolution information provided by the double-membrane prokaryotes is that symbiosis is a successful evolutionary direction and cooperation is also a way of life ahead.

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