Physics 569 Term Paper

Emergent Cooperation in Evolutionary Game Theory Coupled with Environment

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Abstract:

How cooperation happens in evolutionary is a long-standing puzzle and has been investigated by various models based on game theory. In nature, since interacting species evolve in a changing environment, the population size should also depend on the environmental influence. Here we introduce a stochastic model whose population-growing dynamics are coupled with the internal prisoners dilemma game. As a result, a transient but robust increase of cooperation emerges, which indicates that cooperators may overcome the desperate dilemma in a genuinely stochastic evolution.

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1 The Puzzle about Cooperation

Evolution is driven by competition between individuals and their interactions with environment. It is quite a discrepancy that cooperation behaviors happen in biology and also in human society and its abundance contributes the diversity. The problem can be investigated by considering two conflicting traits of species, the benefit producers(cooperators) and receivers who do not pay the cost of production(defectors, or free-riders). The interaction of the strains with two conflict strategies can be illustrated by the example in Fig.(1a) [1]. The benefit producers(blue oblongs) release public goods(purple circles), while the receivers(white oblongs) get free benefits. It is straightforwoard to conclude that the defectors will privilege since they get advantage to survive and reproduce without paying efforts. On the other hand, the benefit producers who pay costs to benefit others and cooperate are less competitive and should be eliminated in the long run.

Then how a cooperator can survive? One might guess that the real mechanism can be compensated by the third strains who depress the defectors and sooth the cooperators at the same time. It is true that the cyclic relations(like the rock-paper-scissors game) are observed in nature[2]. The male side-blotched lizards in the inner Coast Range of California have three morphs with distinct territory defense behaviors which correspond to different mating rates with females. The succession of these three morphs in this field research is also seen in the prey-predator cycles. Another example is the experiment on three strains of bacterium E. coli[3]. The toxin-producing strain kills the sensitive one. The resistant strain defeats the toxin-producing one due to no cost of production. The sensitive strain out-competes resistant one because it does not pay to produce immunity proteins. Therefore, the cyclic relation in nature explains the succession of the three species(phenotypes), which may assume the (bio)diversity though there are conflicting strategies. However, the puzzle still remains since there are cases like Fig.(1b) which describes another kind of benefit producers behaviors, altruistic sacrifice. The

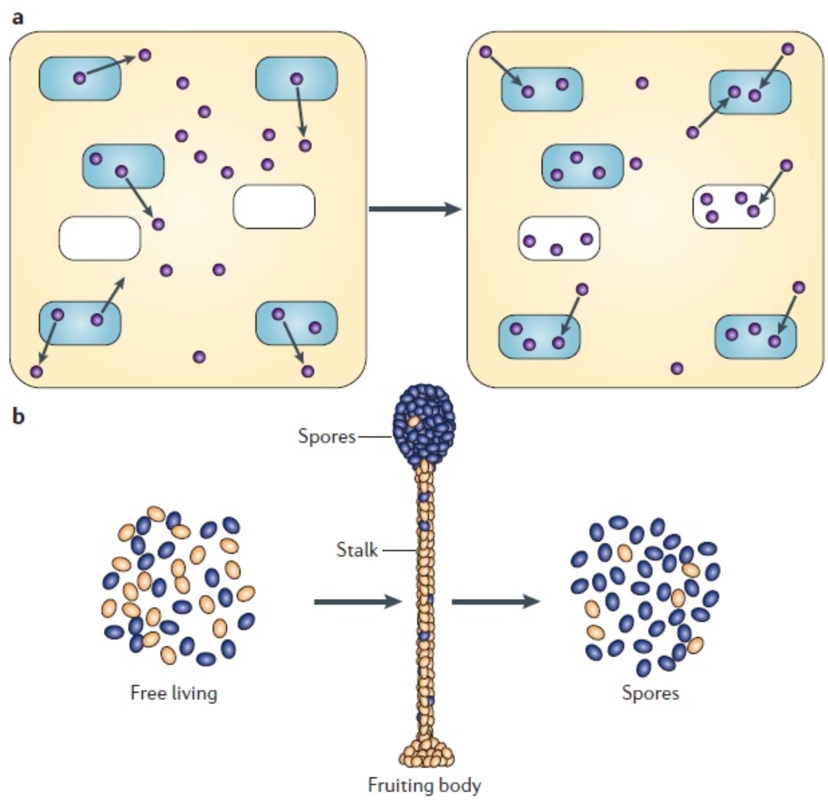

Figure 1:

fruiting body is composed of two kinds of lineages. The blue lineages tend to occupy more on the spores for larger reproduction possibility but less on the stalk, behaving as cheaters. The orange lineages contribute the whole fruiting bodys function by forming mainly on the stalk. Next we try to review the concept of evolutionary game theory to discuss the emergence of cooperation, which has been one of the most interesting puzzles in evolutionary theory.

2 Evolutionary game theory

The problem and many other issues in the related areas, have been developed for decades with the mathematical model, game theory. The mathematical description for fundamental concepts of evolution such as natural selection and mutation was first by R. A. Fisher and J. B. S. Haldane in 1930s. In 1950s, M. Kimura developed the neutral theory of evolution and the idea of random genetic drift for mutation. The game theory concepts were first applied to evolution by Lewontin in 1961. Further in 1964 W. Hamilton proposed the idea of connecting the close genetic relationship to the social altruistic behavior, which shed lights on the problem of cooperation. The evolutionary game theory was established by J. M. Smith in 1973.

The Hawk-Dove game was introduced by M. Smith[4] to describe the conflicts of two strains. If the injury caused from fighting between hawk behaviors is larger than the benefit of winning, one may better choose to play dove to avoid fighting. Therefore the two strains can coexist together.

The similar game called Prisoners dilemma studied by Axelrod and Hamilton in 1981[5] proposes the problem of cooperation. In this game two players considering two strategies, cooperation or defection. If more benefits get from defection rather than cooperation when the opponent plays defect, one will choose to defect. This describes the puzzle about the cooperation in the fruiting body.

To understand the complicated mechanism of real-world evolution, we should examine the beautiful, simplified models and consider more details about the realistic interactions of individuals, structure of the system and the environmental factors. For example, the population of species should be finite and even may be small in the evolutionary events, which leads the dynamics to be stochastic(probabilistic). Thus the fluctuations are intrinsic in the process.

In the standard game theory, the reproduction is also assumed to be asexual. In real case of evolution, most species behaviors are sexual and diploid[4]. Thus there should be some strategies set for choosing during reproduction. The strategies of individuals correspond to the phenotype of the strains. It could be sensible for some phenotypes the offspring can directly inherit or learn them from the ancestors. The question of replication suggests the assumption that the difference of adopting of individuals strategies is genetic[4]. In other words, it is more straightforward that the phenotypes chosen in reproduction are based on genetic information.

Moreover, in the game the individuals should be myopic[8], so they do not think too much and too far to decide the strategies. The instant decision-making should also imply that the interaction between individuals is space-dependent; they interact with near ones. In real life, if the interaction happen within short range, individuals are likely to meet same people repeatedly. This will stimulate individuals memorizing and learning from experiences in the evolutionary process and probably change their strategies(traits). The individuals would also consider the relatedness of opponents[4]. It is also reasonable that the individuals may just have mixed strategies. The strategies would be continuous, and there are infinite choices. Thus the performance of phenotype will be probabilistic.

Different interesting models considering various strategies and payoff structures and based on options mentioned above, have been investigated for decades on evolutionary dynamics[4, 6, 7, 8], and so far the emergence of cooperation is still the promising and exciting problem in the field.

3 Evolutionary game interacting with environment

It has also been considered that the community composed of individuals is not isolated; the interacting species evolve with the outside environment. In nature, since interacting species evolve in a changing environment, the population size should also depend on the environmental influence. The climate, seasonal variation, limited resources and other ecological factors all affect the internal evolution and its population size mutually.

The environment influences and interaction in microbial world have been studied prosperously these years[1]. For example, many regulation and communication between bacteria cells are processed through quorum sensing molecules. The signaling molecules regulate the production and the secretion of exoproducts, such as the ingredients for biofilm formation, virulence to damage the host. Therefore, it has been supposed that the mechanism of quorum sensing leads to cooperation between bacteria[11].

Another example is the bacteria experiment on Simpsons paradox. Simpsons paradox provides a condition for cooperators growth in a two-strain system. It supposes that the global population of public good producers may increase despite of their subpopulations are depressed by the nonproducers in the subsystems [10]. In experiment depicted by Fig. (2), the producers generate the public goods rhamnolipid (Rhl) autoinducer, which is rewised to activate the resistance gene called catLVA for the two strains. The producers grow rate slows down in each subsystem due to the cost, but their overall proportion increases.

3.1 A Model with environment coupling

Here a study provides a model to discuss the cooperation emergence through the evolutionary game theory with growing populations due to the environmental influence.

First, to describe the dynamics of the cooperators populations, the standard differential replicator equation for the density of the strain is introduced. Another replicator equation for the total populations, which is a non-linear function including the effect of the environmental-internal couplings, is also considered. The dynamical processes are discussed stochastically, driven by replication and death rates. Here, the reproduction and death rate are assumed to be separable into a global and relative part. The relative part is the internal fitness of the species in the standard game theory. The global fitness should depend on the density of strains abundance, but it is the same for both traits since it usually refers to the effect of public goods shared by all.

The internal evolutionary dynamics is modeled by the standard prisoners dilemma game with a selective intensity parameter, s. The selection describes the contribution of the internal game to the fitness. Thus there are continuous choices of strategies. For the environmental influence part, the global fitness is assumed to increase with cooperators density, while the global death rate is set to be proportional to the total populations, which indicates the limited resources.

3.2 Results and Discussion

The model is tested by simulations of the stochastic replicator equations. The stochastic process leads to the intrinsic fluctuations. The global population rates are taken from the bacteria experiment[10]. In Fig.(3a), it is found that for weak selection(s¡¡1), which corresponds to the near neutral evolution, the total population size grows quickly at the beginning due to the global fitness which increases with the cooperators fraction. Moreover, the cooperation fraction is also driven to grow exponentially, and a transient increase is maintained robust until a cooperation time as in Fig.(3b). When compare to the result of deterministic equation shown as the black line, there still exist quickly ascending total populations in a regime, but the cooperation ratio always decays. Therefore, it can be concluded that here the robust emergence of the transient increase of cooperation comes from the intrinsic fluctuations in the stochastic process.

The phase diagram is plot with the selection strength and the initial populations as Fig.(4), which indicates two distinct phases. The transient increase of cooperation emerges under weak selection and with small initial populations. While for strong selection and initial populations, which refers to the dominance of the prisoners dilemma game, the cooperators-dependent global fitness is outcompeted, leading to no transient increase of cooperation. The inset shows that the transient increase cooperation time which characterizes the phases is discontinuous as to the selection strength. Thus tc plays the role of order parameter in the special system here.

The robustness of emergence of the transient increase of cooperation in the stochastic process is contributed by the asymmetric favoring of cooperation in the global growing rate and eases the prisoners dilemma. It is particularly pointed out that the primary transient increase might have large importance for microorganisms whose life cycle is short and with changing phases.

The selection disadvantage for cooperators comes from the prisoners dilemma. The dilemma still leads to the final extinction of the cooperation here in both phases. It has been suggested that the snowdrift game would be more suitable to describe the social behaviors, which might be not necessarily lead to the inevitable extinction of the cooperation[14]. In real life, the interaction structure in real life is space-dependent, and the dynamics may contain mobility of individuals, even for microorganisms. In real life the social behaviors of individuals might be affected by others, such as the tendency to the (near) majority, the probability of infection or a dependence on relatedness as mentioned before. Their decisions may also be mutable. Thus the strength of selection could also depend on the strains population fraction.

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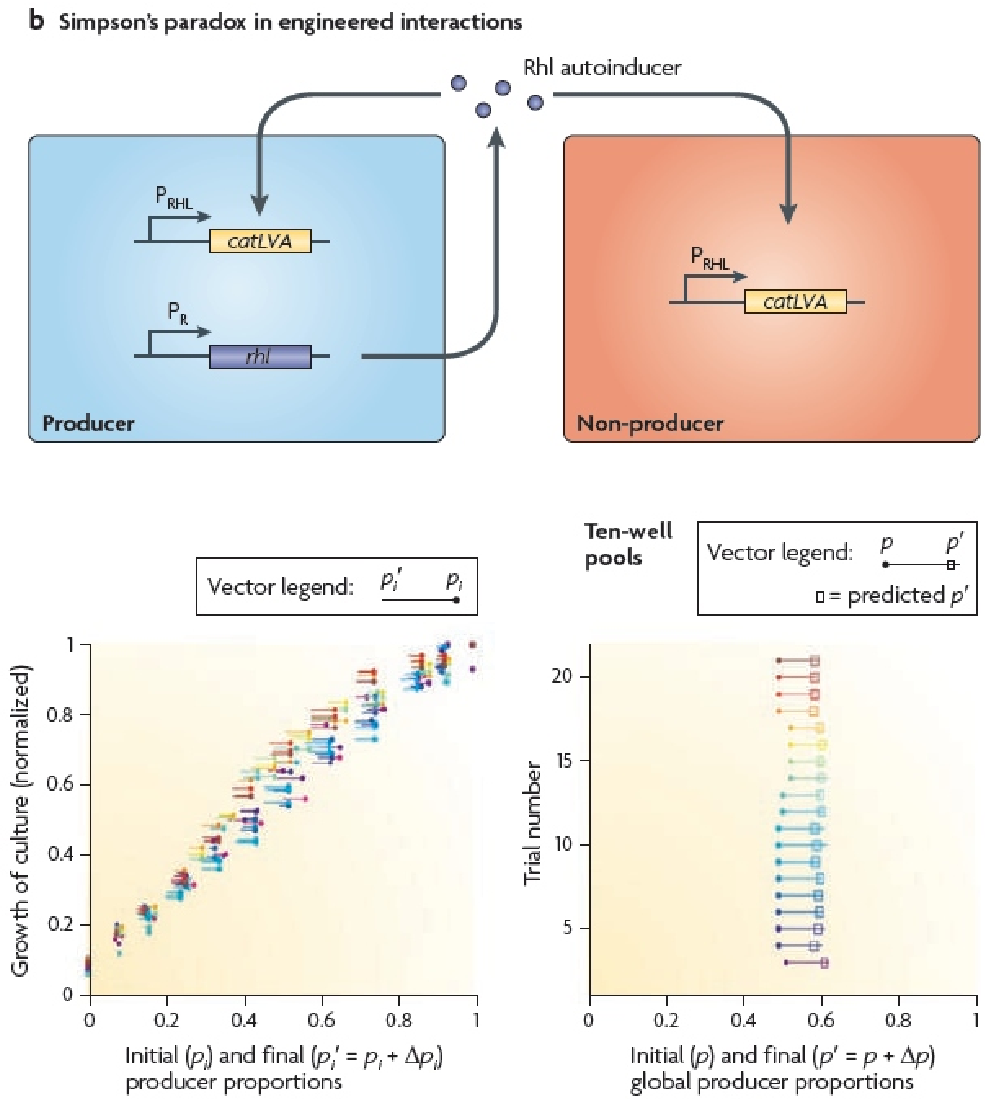

Figure 2: The bacteria experiment on Simpsons paradox illustrates the ecological influence and cooperators growth[12].

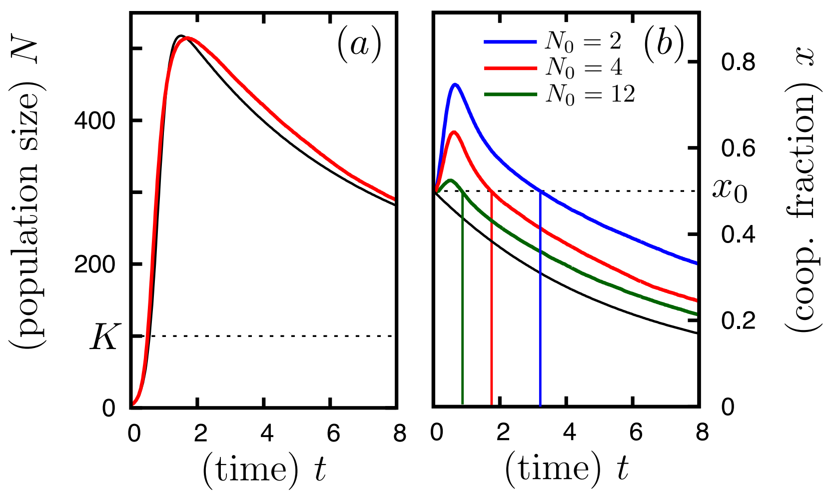

Figure 3:

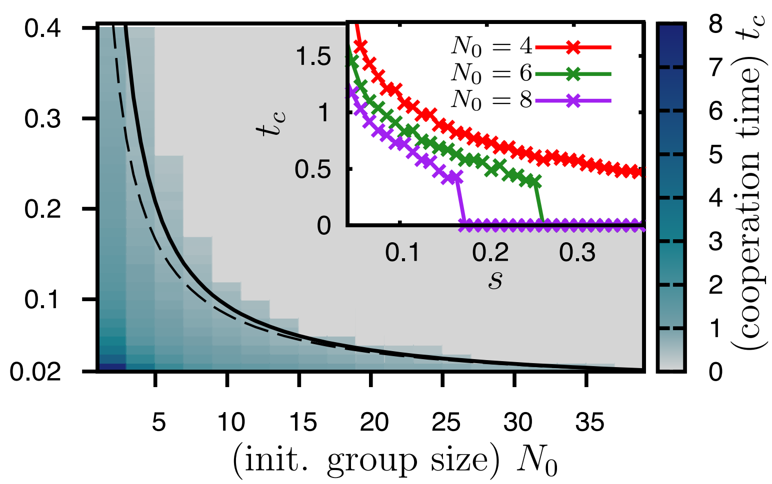

Figure 4: