RGB Algorithm for Spatial Evolutionary Game Theory with Finite Populations

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***Abstract*—Evolutionary dynamics is captured by replicator equations when populations are well mixed. However, in realistic ecosystems, competitions often occur between neighbors and the spatial structure of the system is of significant importance. In most evolutionary algorithms, the dynamics of local death/birth processes often relies on the effective fitness: a global knowledge of the whole ecosystem. To make the spatial game theory logically consistent, it is desirable to introduce an algorithm where only local information is necessary. Here we resolve the challenge by introducing the three-party Reference-Gamble-Birth (RGB) algorithm. For the well-mixed case, the RGB algorithm reproduces the replicator equations in the large population limit. We also apply the RGB algorithm on the rock-paper-scissor game to demonstrate how the ecological stability sensitively depends on the spatial structures. The proposed RGB algorithm is not limited to cyclically competing systems and can be applied to various spatial games with different network structures.**

I. Introduction

In evolutionary game theory, the deterministic population dynamics under frequency-dependent selection can be described by a set of differential equations called replicator equations [1]–[6]. The introduction of payoff matrix in game theory [7] to evolutionary biology [8] allows us to translate the interactions between individuals to the selection rules among species. It is important to point out that the replicator equations, though powerful with rather general applicability, is limited to the well-mixed populations in the infinite population limit. However, real ecological systems are neither spatially well-mixed nor infinitely large in population size. Many biological effects might arise when finite-size fluctuations and spatial structure are considered. In consequence, the studies of the evolution in finite-size populations and social networks in various ecological systems are elaborated for both theoretical and practical interests [9]–[25]. Although some analytical approaches are able to include the stochasticity and the spatial degrees of freedom, the need of stochastic dynamics and local interaction make numerical simulation a powerful tool to explore the population dynamics and the important quantities to characterize ecological systems. The population dynamics generated by frequency-dependent selection are usually simulated by Moran process [26], [27] and its generalized versions [18], [28], [29]. A common feature of these evolutionary algorithms is the prior knowledge of fitness for each individuals in advance for the two-body interaction. However, the need of fitness, a global property beyond the encountering two individuals in interaction, is unreasonable in local competitions and might cost more numerical efforts in large populations and large connections limits. To avoid the disadvantages mentioned above, we introduce a local third-party algorithm, adding in a local reference to participate in the local death-birth updating processes. This three-party Reference-Gamble-Birth (RGB) algorithm is designed to improve the disadvantage in Moran process for frequency selection in finite populations with different spatial structures. In the paper, we first review the Moran process briefly, then introduce the RGB algorithm in details. Next, we write down the mean-filed dynamics for a single update in RGB algorithm in the well-mixed populations and verify that the dynamics is equivalent to the replicator equations. At the end, we take the rock-paper-scissors game to demonstrate the standard procedure to handle arbitrary payoff matrix in RGB algorithm. By applying the rock-paper-scissors game on different spatial networks, we find that the numerical results agree to the experimental results in bacterial games in literature, and therefore echoes the importance to include both spatial structure and finite-population effects properly in evolutionary dynamics.

II. Moran process

Numerical simulations are widely used in the investigation of evolutionary dynamics in finite populations. The effects of stochasticity and fluctuation in finite populations are naturally included in the evolutionary algorithms. Among numerous algorithms, Moran process is the most well-known stochastic model to deal with the selection driven dynamics in finite populations. In each update, two individuals are evolved, one for reproduction and another for death, and therefore the population size remains constant in time. Among these two individuals, one is randomly chosen and the other is chosen depending on the fitness. Take Death-Birth update as example, one individual is randomly chosen to be eliminated first and then one of its neighbors is chosen for reproduction according to a probability proportional to fitness. However, fitness is a state variable depending on the configuration of populations. It might causes numerical loads when the the size of populations or the number of neighbors increases. Besides, fitness is a global property which includes all information about all neighbors. Thus, it is unreasonable to introduce the global property into the local competition between two individuals. In order to reduce numerical costs and make the algorithm closer to the competition among individuals, we propose the Reference-Gamble-Birth (RGB) algorithm for simulating the stochastic dynamics in finite populations.

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III. Reference-Gamble-Birth (RGB) algorithm

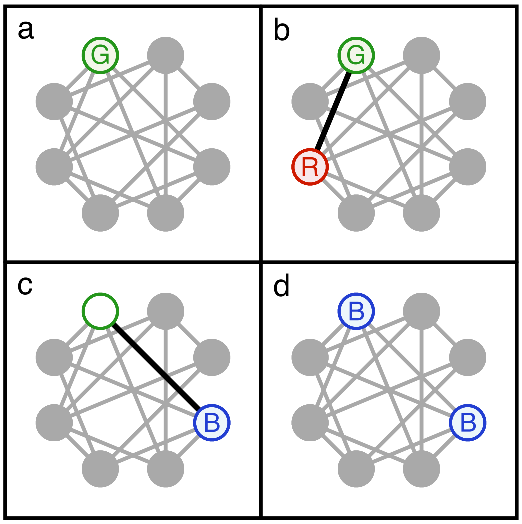

Fig. 1. **Reference-Gamble-Birth (RGB) algorithm.** Individuals are represented by grey filled circles and social networks which describes possible interaction among individuals are shown as grey lines. There are three highlighted individuals and two highlighted links, which interprets that three parties interaction is used to mimic the selection process between two individuals in RGB algorithm.

As the illustration of Reference-Gamble-Birth (RGB) algorithm shown in Fig. 1, the configuration updates are decomposed into four steps. Firstly, a Gamble (G) is randomly picked from the entire populations. Next, a Reference (R), which interacts with Gamble and determines the fate of Gamble, is randomly selected from the neighbors of Gamble. The death probability P_d of Gamble while interacting with Reference is determined only by Gamble and Reference. The release of empty site due to the death of Gamble gives rise to the reproductive competition among neighbors of Gamble to fill up the empty site by its own offspring. At the end, the change of configuration looks like two-body interaction generated by the substitution of Birth for Gamble.

In RGB algorithm, the third party Reference provides information in the surrounding of Gamble and determines the death probability of Gamble. By doing this, we can avoid using global fitness to determine the fate of local competition. But, how could a two-body interaction simulated by three-parties and how do a third individual show up in replicator equations? In the following, we are going to explain the relationship between death probability P_d and payoff matrix and verify that the dynamics of RGB algorithm is the same as replicator dynamics in well-mixed infinite populations.

IV. Replicator equation

The death probability P_d plays an important role in RGB algorithm. Since the death probability is determined by the species of Gamble and Reference, the RGB update only needs the information of the time invariant payoff matrix for species rather than the time dependent fitness for each individuals. By introducing a death matrix D, which has simple relation with death probability $D_{GR} = P_d$, we are able to consider the dynamics of RGB algorithm in well-mixed populations and try to compare it to the replicator dynamics.

For a single update, there are two possible ways to change the composition of populations

$$D_{kj}x_ix_jx_k \quad \text{and} \quad D_{ij}x_ix_jx_k. \tag{1}$$

The first term comes from the process that Gamble belongs to species k, Reference belongs to species j and Birth belongs to species i, and therefore the death probability is D_{kj} and populations change with $\Delta N_i = 1$ when $k \neq i$. The second term describes the opposite process that Gamble belongs to species i, Reference belongs to species j and Birth belongs to species k, and therefore it has D_{ij} and $\Delta N_i = -1$ when $k \neq i$. Thus, the mean field population dynamics generated by RGB algorithm can be written as

$$\begin{aligned}\frac{\langle \Delta N_i \rangle}{\Delta \tau} &= \sum_{k \neq i} \sum_j D_{kj}x_ix_jx_k - \sum_{k \neq i} \sum_j D_{ij}x_ix_jx_k \\ &= \sum_{j,k} \left(D_{kj} - D_{ij}\right) x_ix_jx_k. \end{aligned} \tag{2}$$

The summation over j and k arise naturally since there is no restriction on the species of Reference and Birth. The only term should be taken out happens when both Gamble and Birth belong to the same species because $\langle \Delta N_i \rangle = 0$ in this case. But the exclusion of i from the summation over k is then removed due to the cancelation when both processes are considered simultaneously. By considering the simultaneity of interaction (i.e. $t = \Delta\tau/N$) and taking the continuous-time limit, the left hand side in Eq. (2) can be represented as

$$\frac{\langle \Delta N_i \rangle}{\Delta \tau} = \frac{\langle \Delta x_i \rangle}{\Delta t} = \frac{dx_i}{dt}, \tag{3}$$

where $x_i = N_i/N$ denotes the frequency of species i. By replacing Eq. (3) into Eq. (2), we find that the population dynamics simulated by RGB algorithm agrees with the replicator equations in cubic form.

Next, we try to figure out the link which leads the RGB dynamics to be equivalent to the replicator dynamics by choosing the proper relationship between the death matrix D_{ij} and the element of payoff matrix P_{ij}. Start from cubic-form replicator equations

$$\begin{aligned}\frac{dx_i}{dt} &= x_i\left(f_i - \phi\right) = x_i\left(\sum_j P_{ij}x_j - \phi\right) \\ &= \sum_{j,k} (P_{ij} - P_{kj})x_ix_jx_k, \end{aligned} \tag{4}$$

where fitness is given by $f_i = \sum_j P_{ij}x_j$ since specie i gets payoff P_{ij} when interacting with species j and the probability of interacting with species j is x_j. The average fitness of entire populations $\phi = \sum_k f_kx_k$ keeps the total populations as a constant. Now, consider a canonical payoff matrix C with matrix elements determined by $C_{ij} = -D_{ij}$, and therefore $-1 \leqslant C_{ij} \leqslant 0$ for all types of interactions. Then replicator equation can be rewritten as

$$\begin{aligned}\frac{dx_i}{dt} &= \sum_{j,k}(C_{ij} - C_{kj})x_i x_j x_k \\ &= \sum_{j,k}\left(D_{kj} - D_{ij}\right)x_i x_j x_k. \end{aligned} \quad (5)$$

By comparing Eq. (2) to Eq. (5), we find that the population dynamics simulated by RGB algorithm is the same as the replicator dynamics when the canonical payoff matrix D in RGB algorithm follows the relation $D_{ij} = -C_{ij}$ where C is the canonical payoff matrix in replicator equation. That means we can use RGB algorithm to simulate the evolution of ecological systems when its payoff matrix is satisfied the definition of canonical payoff matrix C, where $-1 \leqslant C_{ij} \leqslant 0$ for all elements. Thus, the next question is how to construct canonical payoff matrix C from arbitrary payoff matrix P.

Before digging into details, we first revisit an important property of replicator equations: they remain unchanged if an arbitrary constant is added to all elements in a single column in payoff matrix. Consider the situation that adding a constant a_n to all elements in the n-th column in payoff matrix P, then new payoff matrix $P^{'}$ can be written as

$$P^{'}_{ij} = P_{ij} + a_n \delta_{nj}. \quad (6)$$

Since $\sum_i x_i = 1$, fitness $f_i^{'}$ and average fitness $\phi^{'}$ are

$$f_i^{'} = \sum_j P^{'}_{ij} x_j = f_i + a_n x_n \text{ and } \phi^{'} = \sum_i f_i^{'} x_i = \phi + a_n x_n. \quad (7)$$

Two additional terms in $f_i^{'}$ and $\phi^{'}$ are identical, and therefore their contributions to population dynamics are canceled out directly. By simple algebra, we verify that columnwise adding a constant indeed make no change on the replicator equation. This idea can be generalized to add different constants on different columns simultaneously since the cancelation of $\sum_n a_n x_n$ terms in fitness $f_i^{'}$ and average fitness $\phi^{'}$. Thus, we can use this trick to simplify the payoff matrix without changing the replicator dynamics.

Back to our original question about how to construct canonical payoff matrix C from general payoff matrix P. It turns out the method is quite simple and the only consequence we need to deal with is a time rescaling as explain in the following. General speaking, there is no restriction on the elements of payoff matrix, so P_{ij} could be positive or negative depending on the interaction between species. But, we can subtract the largest elements in each column from all elements in the same column and make the entire payoff matrix $P_{ij} \leqslant 0$. Next, introduce a rescaling time scale s to transform payoff matrix P to canonical payoff matrix C. The canonical transformation of payoff matrix is defined as

$$C_{ij} = P_{ij}/s, \quad (8)$$

where choice of the rescaling time scale s must have a lower bound $s_m = -\min(P_{ij})$ so that $-1 \leqslant C_{ij} \leqslant 0$ is easily satisfied. Any larger s is acceptable and the only influence shows up in the numerical efficiency since the death matrix in RGB algorithm is defined as $D_{ij} = -C_{ij}$. Next, we need to check the influence of canonical transformation on replicator equation. Applying Eq. (8) into replicator equation

$$\begin{aligned}\frac{dx_i}{dt} &= x_i\left(f_i - \phi\right) \\ &= s x_i \left(\sum_j C_{ij}x_j - \sum_{j,k} C_{kj}x_j x_k\right) \\ &= s x_i \left(\tilde{f}_i - \tilde{\phi}\right) \\ &= s\frac{dx_i}{d\tilde{t}}, \end{aligned} \quad (9)$$

where $\tilde{f}_i = \sum_j C_{ij}x_j$ and $\tilde{\phi} = \sum_k \tilde{f}_k x_k$ are the fitness and average fitness for canonical payoff matrix C. We find that the time rescaling on payoff matrix does not change the structure of replicator equation. However, the unit of time is reduced by factor of s since the change in populations is s-time smaller then the original one after canonical transformation. All time scales after canonical transformation are enhanced by factor of s, and therefore it should be transformed back to real time used in original replicator equation for further comparison and interpretation by

$$t = \tilde{t}/s. \quad (10)$$

This matches our intuition that time is increased by factor of s when we decrease the reaction rate by factor of s, so the original time scale can be easily calculated by Eq. (10). Thus, canonical payoff matrix C can be constructed from any payoff matrix P by a smart choice of s in canonical transformation in Eq. (8) and the tiny price we need to pay for the canonical transformation is the rescaling of time in Eq. (10).

V. Rock-Paper-Scissors game

Rock-paper-scissors game is one of the common paradigms in evolutionary game theory. The non-transitive cyclic interaction provides the potential robustness of biodiversity in rock-paper-scissors system. Thus, lots of theoretical attentions focus on the properties of rock-paper-scissors game to understanding the mechanism account biodiversity [30]–[47]. Recently, empirical investigations have identified several ecological systems as the rock-paper-scissores system including the coral reef invertebrates [48], the mating strategies of lizards in California [49], the bacterial game in vitro and in vivo [50]–[52], the vertebrate community in the high-Arctic tundra in Greenland [53] and the plant communities [54], [55]. These findings in nature make rock-paper-scissors game not only a theoretically interesting model but also a practical system to study. In particular, Kerr et al. [50] pointed out the influence of noise and spatial degrees of freedom to the ecological stability. Motivated by the experimental results, theoretical studies focus on the emergence of spatial pattern and the interplay with mobility in rock-paper-scissors game [31], [34], [36], [38], [39], [41]–[45]. In the following, we briefly review the properties of payoff matrix and its connection to ecological stability in well-mixed populations and then numerically study the extinction time in rock-paper-scissors systems by Reference-Gamble-Birth algorithm to address the influence of network structures on ecological stability.

The general rock-paper-scissors game can be described by a 3×3 matrix in the evolutionary game theory. According to phase-plane analysis, the population dynamics in replicator equations can be categorized into three types by the determinant of payoff matrices. When the determinant is positive, a unique global stable fixed point is located inside the simplex, and therefore all initial configurations will converge to the stable fixed point. The stable fixed point attracts population configuration and guarantees the maintenance of biodiversity in ecological systems. On the other hands, the unique interior fixed point is unstable when the determinant is negative. The unstable fixed point will push the population configuration toward the boundaries of the simplex and make the extinction of species. A special case happens when the determinant is equals to zero. The interior fixed point is the center of the population dynamics, and therefore leads to the neutral oscillation in population dynamics.

While in numerical simulation, we need another method to identify the stability of ecological systems. Based on the previous works in literatures, the ecological stability can be differentiated by the scaling forms of extinction time in numerical simulation. In well-mixed finite populations, there are two driving forces to determined to population dynamics. One is the replicator dynamics mentioned above and another is the finite size fluctuation which will lead to the dissipation in biodiversity. When the determinant is positive, the replicator dynamics against the finite size fluctuation toward extinction causes the extinction time to be an exponential function in population size. When the determinant is negative, both the replicator dynamics and the finite size fluctuation drive population configuration toward extinction, and therefore the extinction time then becomes a logarithmic function in population size. As for the neutral case, the extinction time is expected to be a power law in population size due to the biased random walk generated by the finite size fluctuation. Combine both analytical and numerical approaches, the properties of rock-paper-scissors games is be summarized in Table I.

TABLE I. PROPERTIES OF RPS GAME IN WELL-MIXED POPULATIONS.

determinant	ecological stability	fixed point	scaling form
positive	biodiversity	stable	$T_{ex} \sim e^{N/N^*}$
0	neutral	center	$T_{ex} \sim N$
negative	extinction	unstable	$T_{ex} \sim \log N$

Based on the knowledge mentioned above, we want to use Reference-Gamble-Birth algorithm to investigate the spatial effect on the ecological stability in rock-paper-scissors systems. In numerical simulation, we know the payoff matrix first and then try to simulate the dynamics generated from this particular payoff matrix. Thus, the standard procedure for setting up the parameters in RGB algorithm should be starting from the payoff matrix P and then constructing the canonical payoff matrix C and then choosing the proper rescale time scale to determine the death matrix D. Now, we take the most simplest rock-paper-scissors model as paradigm to show the corresponding death matrix D for RGB algorithm and the numerical results in different social networks. The payoff matrix for the non-transitive cyclic interaction in rock-paper-scissors system is

$$P = \begin{pmatrix} 0 & -1 & 1 \\ 1 & 0 & -1 \\ -1 & 1 & 0 \end{pmatrix}. \tag{11}$$

By subtracting the largest element from all matrix elements and choosing the rescaling time scale $s = 2$ for maximizing the simulating efficiency, then death matrix is

$$D = \begin{pmatrix} 1/2 & 1 & 0 \\ 0 & 1/2 & 1 \\ 1 & 0 & 1/2 \end{pmatrix}. \tag{12}$$

The element of the death matrix can be interpreted as the following. Since the interaction is symmetry in rock-paper-scissors game, the encountering with others could only have three possible conditions: encounters a prey, a predator and the same species. In RGB language, the Reference could be a prey or a predator or the same species form the viewpoint of Gamble. Thus, the elements of death matrix should be pinned down as three different values. The dominant species has no chance to die when interacting with its prey. On the other hand, the prey is threatened and has certain chance to die. However, this non-zero death probability is enhance to 1 due to the time scale s we choose to improve simulating efficiency. As for the self-interacting case, the death probability is 0.5 since the self-interacting payoff is in the middle of the rest two cases. Once we have the death probabilities for all possible interactions, we can use RGB algorithm to simulate the frequency dependent population dynamics between species.

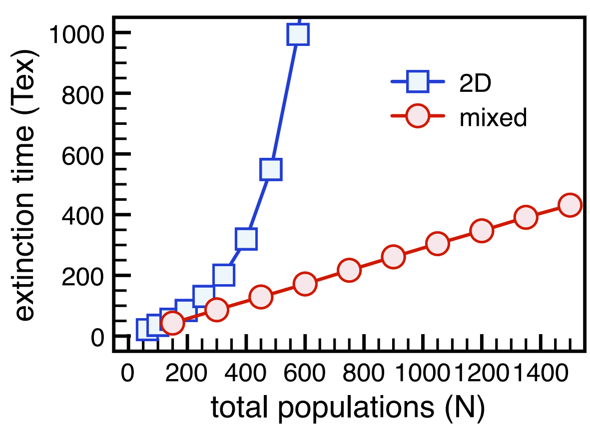

Fig. 2. **Extinction time for rock-paper-scissors game.** The extinction time is an important indicator for characterizing ecological stability in finite populations. The numerical results show that the extinction time T scales differently with the population size N in different social networks. The scaling function changes from linear to exponential indicates that the ecological stability is enhanced due to the local interaction in two-dimensional network.

The simulating results as shown in Fig. 2 agrees to the experimental results in bacterial game. From the phase-plane analysis of replicator equation, we know the deterministic dynamics is neutral in stability. In well-mixed populations, the extinction time T is expected to scale linearly with the population size N due to the finite size fluctuation. On the other hand, two-dimensional network enhances the ecological stability, and therefore the scaling function gets modified from power laws to exponential.

VI. CONCLUSION

In order to reduce numerical costs and to make the algorithm closer to the competition among individuals, we design the Reference-Gamble-Birth (RGB) algorithm for simulating the stochastic dynamics in finite populations. Unlike Moran process and it generations, the RGB algorithm involves three individuals (i.e. Reference, Gamble and Birth) in a single update. A third party called Reference is introduced to provide the information of surrounding for Gamble, and therefore the death probability is independent of the fitness of Gamble. We also prove that the dynamics of three body RGB algorithm is equivalent to the replicator dynamics in large N limit. By considering the rock-paper-scissors in different networks, we show the numerical results agree with the experimental results in the spatial influence on the stability in bacterial community. We believe that the RGB algorithm is a useful numerical tool to deal with the population dynamics and other dynamical quantities from the fundamental interaction among species in all kinds of ecological systems. For further extension of RGB algorithm, it can be easily combined with the other important factors (mobility, density and etc.) to simulate the evolutionary dynamics under various social networks.

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