Abstract

Cooperation is usually represented as a Prisoner’s Dilemma game. Although individual self-interest may not favour cooperation, cooperation can evolve if, for example, players interact multiple times adjusting their behaviour accordingly to opponent’s previous action. To analyze population dynamics, replicator equation has been widely used under several versions. Although it is usually stated that a strategy called Generous-tit-for-tat is the winner within the reactive strategies set, here we show that this result depends on replicator’s version and on the number of available strategies, stemming from the fact that a dynamics system is also defined by the number of available strategies and not only by the model version. Using computer simulations and analytical arguments, we show that Generous-tit-for-tat victory is found only if the number of strategies available is not too large, with defection winning otherwise.
INTRODUCTION

Cooperation is ubiquitous in nature despite being against individual self-interest [1, 2]. Since cooperators incur a cost on themselves to provide a benefit to others, Darwinian selection seems to oppose the evolution of cooperation. However this apparent difficulty can be overcome provided that positive assortment among cooperators exists, such that cooperators more often interact with other cooperators than with defectors [3]. Positive assortment among cooperators may be the indirect outcome of spatial structure, kin discrimination, or conditional behaviour [9, 10]. The evolution of cooperation can be analyzed in the framework of evolutionary game theory, where individuals are called players, behaviours are called strategies — cooperation (C) or defection (D) — and reproduction rate is equated to the gains given by the prisoner’s dilemma payoff matrix [4–6]. Classical game theory states that defection is the best choice in one-shot games [7]. On the other side, if several rounds are played, conditional behaviour based on direct reciprocity allows the emergence of cooperation [4, 5, 8, 11].

Conditional cooperative behaviour can be represented by the set of reactive strategies, described by the probability to cooperate, \( p \), given that the opponent cooperates in the previous round and by the probability to cooperate, \( q \), given that the opponent defects in the previous round. An individual strategy is defined by the pair \((p, q)\), with both \( p \) and \( q \) in the interval \([0, 1]\). For example \((p, q) = (1, 0)\) characterizes the tit-for-tat strategy (TFT), the winner strategy in the well known Axelrod tournaments [4]. However Nash equilibrium analysis of reactive strategies indicates that in noise environment the strategy characterized by \((p, q) = (1, 1/3)\), also called Generous Tit-for-tat strategy (GTFT), should be the winning strategy [5, 12]. Other studies have investigated evolutionary stable strategies (ESS). They have found that is not clear if an ESS exists neither that it can be achieved [13, 14].

In well-mixed populations the evolution of reactive strategies can be analyzed by numerical analysis of the replicator dynamics: from an initial configuration where a large number of strategies are equally available, first the fraction of unconditional defectors, characterized by \((p, q) = (0, 0)\), usually referred as ALLD strategy, increases; when ALLD decays TFT grows and then is outperformed by GTFT [5, 6, 12, 16]. However results have not been consistently obtained, as some authors use Taylor’s replicator equation while others prefer Maynard Smith’s version of the replicator equation, inadvertently changing from continu-
ous to discrete versions [12]. Indeed one is allowed to choose or even create a microscopic rule that specifies how the strategy update mechanism will occur [18]. Of course different microscopic rules might imply in different replicator equations [6, 18]. Although equilibria solutions are the same for both Taylor’s and Maynard’s continuous models, trajectories starting from an uniform strategy distribution can be quite different depending on the number of available strategies at the beginning. In fact a dynamical system is defined not only by the version of the differential equation, but also by the dimensionally of the problem (the number of available strategies).

As in literature it is not found a study concerning the evolution of reactive strategies depending on the number of such strategies, here we analyze the this evolution in well-mixed populations modelled by different versions of replicator dynamics, namely Taylor’s version, Maynard Smith’s version, considering both continuous and discrete versions of each one. Using analytical arguments and numerical methods to compute an approximated solution to the replicator equation we show that cooperation establishment depends on the number of initial strategies available as well as on the replicator equation version.

MODEL

The prisoner’s dilemma is a two-player game, where each player may choose between cooperation (C) or defection (D). Depending on the opponent’s strategy, the focal player obtains $R$ if both cooperate; $P$ if both defect; $S$ if the focal cooperates and the opponent defects; and $T$ if the focal defects and the opponent cooperates, where $T \geq R > P > S$ and $R > \frac{T+P}{2}$. Here we use Axelrod’s payoff values [4],

$$
\begin{pmatrix}
C & D \\
3 & 0 \\
5 & 1
\end{pmatrix}
$$

In the repeated prisoner’s dilemma the one-shot game is played several times by the same two players. If the strategy in round $n$ is based on the opponent decision in round $n-1$, the set of probabilistic reactive strategies can be defined by the probability $p$ that the player cooperates in round $n$ given that the opponent cooperated in round $n-1$ and by the probability $q$ that the player cooperates in round $n$ given that the opponent defected in
round \( n - 1 \). Of course one has a continuous space of available strategies. For each pair of reactive strategies, \( s_1 = (p_1, q_1) \) and \( s_2 = (p_2, q_2) \), the sequence of decisions made by both players is a Markov chain. The stationary probabilities of cooperation \([5, 6]\), \( m_1 \) and \( m_2 \), considering an infinitely repeated game, are given by

\[
m_1 = \frac{q_2(p_1 - q_1) + q_1}{1 - (p_1 - q_1)(p_2 - q_2)}, \tag{2}
\]

\[
m_2 = \frac{q_1(p_2 - q_2) + q_2}{1 - (p_1 - q_1)(p_2 - q_2)}. \tag{3}
\]

The average payoff \( E(s_1, s_2) \) of strategy \( s_1 \) playing against \( s_2 \) can then be written as

\[
E(s_1, s_2) = Rm_1m_2 + Sm_1(1 - m_2) + T(1 - m_1)m_2 + P(1 - m_1)(1 - m_2). \tag{4}
\]

In an infinite well-mixed population with \( n \) strategies available, let \( x_i \) be the fraction of individuals adopting strategy \( s_i = (p_i, q_i) \). The average payoff of strategy \( i \) is given by

\[
f_i = \sum_{j=1}^{n} x_j E(s_i, s_j).
\]

The evolution of the fraction of each strategy can be described by Taylor’s replicator equation

\[
\dot{x}_i = x_i (f_i - \phi), \tag{5}
\]

or by Maynard Smith’s replicator equation

\[
\dot{x}_i = x_i \frac{(f_i - \phi)}{\phi}, \tag{6}
\]

where \( \phi = \sum_{i=1}^{n} x_i f_i \) is the average payoff of the population. Taylor’s equation is a mean field equation of a birth-death process, while Maynard’s equation, also called adjusted replicator equation, is a mean field equation of an imitation process \([15, 18]\). Although equations \((5)\) and \((6)\) have the same fixed points, their fluxes are different. It is worth mentioning that different values of \( n \) define distinct non-linear dynamical systems, with different behaviors.

The discrete form of Taylor’s replication equation is given by

\[
x_i(t+1) = x_i(t) + x_i(t)[f_i(t) - \phi(t)], \tag{7}
\]

and the discrete form of Maynard’s replication equation is given by

\[
x_i(t+1) = \frac{x_i(t)f_i(t)}{\phi(t)}, \tag{8}
\]

where \( t \) is a discrete variable assuming integer values.
We are going to study the trajectories of initial strategies of Taylor continuous, Maynard continuous, Taylor discrete, and Maynard discrete versions of the replicator equation. The initial strategies are defined on a grid as
\[ (p_i, q_j) = \left( \epsilon + \frac{i}{d}(1 - 2\epsilon), \epsilon + \frac{j}{d}(1 - 2\epsilon) \right) \]
with \(0 \leq i, j \leq d\) and \(n = (d + 2)^2\). We are dividing the continuous space of strategy and turning it in a space that has a finite number of strategies available. As \(d\) goes to infinity, the continuous strategy space is recovered. Note that \(\epsilon \leq p, q \leq 1 - \epsilon\). The continuous versions are solved by the Runge-Kutta-Fehlberg with precision \(10^{-5}\), which is a method that furnishes an approximation for the exact solution.

RESULTS

The population starts with \(n\) strategies, defined on the grid \(d \times d\), equally distributed among individuals, i.e. \(x_i(0) = 1/n\). Depending on the dynamical system the population evolves towards either a defective state, with strategies similar to ALLD, or towards a cooperative state, with strategies similar to GTFT \((p, q) = (1, 1/3)\), according to Axelrod’s payoff values), as shown in Figure 1. Cooperation survives in the continuous version of the Maynard only up to \(d = 6\), after which ALLD takes over. For both continuous Taylor and discrete Maynard replicator equations cooperation survives up to \(d = 13\). The discrete Taylor equation has non-physical behaviour, as the fractions diverge. When GTFT wins the typical trajectory in the simplex \(S_n\) is that initially the fraction of the ALLD-like strategy increases, followed by an increasing of the TFT-like strategy, which are finally replaced by the GTFT-like strategy. The crucial transition is from the nearest strategy of ALLD (nALLD) to the nearest strategy of TFT (nTFT). The payoff structure of a game between nALLD and nTFT is such that the best strategy is to play the same strategy of the opponent, i.e., nTFT. In a population of nALLD and nTFT, nTFT can spread only if there is enough individuals adopting nTFT. In order to understand how such transition happens a quantity interpreted as the center of mass of the \(pq\)-plan is studied. The position of the center of mass is calculated by the expressions
\[ p_{cm} = \frac{\sum_{i=1}^{N} x_i p_i}{\sum_{i=1}^{N} x_i} \]
FIG. 1. Winner strategy for different versions of replicator equation and for different numbers of initial available strategies. Cooperation wins under both Taylor continuous and Maynard discrete if $d \geq 14$ and wins under Maynard continuous in $d \geq 7$, where $d$ represents the grid subdivisions defining the available strategies (the larger $d$ is, the large the number of available strategies).

$$q_{cm} = \frac{\sum_{i=1}^{N} x_i q_i}{\sum_{i=1}^{N} x_i}$$

(11)

Roughly the transition takes place along the line $(p, \epsilon)$, where $\epsilon$ is the smallest available $q$. To illustrate the effect of increasing the number of available strategies – increasing $d$ – we can look at the payoff structure of the game between $A = (p, \epsilon)$ and $A' = (p + \Delta p, \epsilon)$. Here $\Delta p$ is related to the density of strategies in the grid. A small (large) $\Delta p$ implies that there is a large (small) number of strategies available. The expected payoffs up to first order in $\epsilon$ are given by

$$E(A, A) = 1 + \frac{3\epsilon}{1 - p},$$

(12)

$$E(A', A') = 1 + \frac{3\epsilon}{1 - (p + \Delta p)},$$

(13)

$$E(A, A') = 1 + \frac{\epsilon (3 + 3p + 4\Delta p)}{1 - p(p + \Delta p)},$$

(14)

$$E(A', A) = 1 + \frac{\epsilon (3 + 3p - \Delta p)}{1 - p(p + \Delta p)}.$$  

(15)

To have the transition from ALLD to TFT, strategy $A'$ must be able to invade a population of $A$ individuals. This condition is satisfied if

$$E(A', A) > E(A, A),$$

(16)
that is, if $p > 1/4$. So as long as some strategies with $p > 1/4$ remain, population configuration can move toward higher $p$ values. On the other side a population of $A'$ individuals can be invaded by type $A$ if

$$E(A', A') < E(A, A'),$$

that is, if $p + \Delta p < 1/4$. If $\Delta p$ is small, equation (17) is easier to be satisfied. Therefore strategy $A'$ is more favoured if $\Delta p$ is large, as long as $p > 1/4$. Hence if the number of available strategies increases, it gets harder for TFT-like strategies to establish in a less cooperative environment. The explanation is summarized in Figure 2.

Of course the transition from nALLD to nTFT does not occur by increasing the frequency of the strategy with slightly higher $p$ value while the frequency of the lower $p$ one gets smaller. This is just a way to try to explain what it is happening concerning the position of the center of mass. The figure shows the evolution of center of mass position. Initially it is localized in the center of the $pq$-plan, since at $t = 0$ the strategies are equally populated. As time passes the center of mass goes toward nALLD. Note that the dynamics is now restricted to the $(p, \epsilon)$ line. If the number of strategies is not too large the center of mass goes toward nTFT and it ends up at nGTFT point.
As the evolutionary trajectory of cooperation includes as major turning points strategies similar to $ALLC = (1,1)$, $ALLD = (0,0)$, $TFT = (1,0)$ and $GTFT = (1, 1/3)$, it is worthwhile to compare the dynamics of these strategies with the equivalent perturbed versions, namely $PALLD = (0.1,0.1)$, $PALLC = (0.9,0.9)$, $PTFT = (0.9,0.1)$, and $PTFT = (0.9,0.3)$. The continuous replicator equation in both Taylor and Maynard’s version has similar dynamics if unperturbed strategies are available. There is no fixed point interior to the simplex $x_{ALLD} + x_{ALLC} + x_{TFT} + x_{GTFT} = 1$. Hence all fixed points, if there is any, must be located on the simplex boundary. The orbits on the four triangular boundaries are shown in figure 4a. All initial conditions converges to a point in the plan in which $x_{ALLD} = 0$. In contrast if the perturbed strategies are available, the replicator dynamics exhibits more complex behaviour, figure 4b. On the boundary $x_{PALLC} + x_{PTFT} + x_{PGTFT} = 1$ instead of drifting there is a stable coexistence of $PALLC$ and $PGTFT$, while on the boundary $x_{PALLD} + x_{PALLC} + x_{PTFT} = 1$, there is one stable equilibrium point surrounded by periodic orbits. Approximately 82\% of the initial conditions converges to the equilibrium given by $x_{PALLC} = 0.13$ and $x_{PGTFT} = 0.87$, while the remaining converges to the equilibrium $x_{PALLD} = 1$. Again, small modifications in the initial conditions have a strong impact on the evolutionary outcome.
In order to test the robustness of \textit{PGTFT} when new strategies are added, we add to the previous perturbed system with \textit{PALLD}, \textit{PALLC}, \textit{PTFT}, and \textit{PGTFT} a fifth strategy, \(s_5 = (p, q)\). In most cases the \textit{PGTFT} strategy is the ultimate winner, as shown in figure 3, but sometimes the winner is the fifth strategy that was added. In a few cases, \textit{PALLD} strategy is able to exploit the cooperators and establishes itself as the winner.

\section*{Conclusions}

Replicator dynamics can be represented by different versions resulting in different outcomes. Not only different versions define different dynamical systems, but also the number of initial strategies defines different dynamical systems. Therefore it is important to study the effect of the number of available strategies. For example, in adaptive dynamics the fact that only the resident and the mutant strategies are present restrict the study to invasion analysis, what potentially leaves a huge part of the phenotype space unexplored [17]. Here, in the context of replicator dynamics, considering the infinitely repeated game case, we showed that if the initial quantity of strategies is small, cooperation can easily dominate the scenario, except in a few cases, where defection is favoured. However, if the number of initial strategies is larger, ALLD-like individuals are more able to perform exploitation and to become more successful. Cooperation is able to establish only if the quantity of initial strategies is below a limit value, depending on the version of the replicator equation (\(d \leq 6\), for continuous version of Maynard Smith and \(d \leq 13\) for both continuous version of Taylor and discrete version of Maynard Smith). Therefore attention must be given to potential effects of the number of available strategies alongside with the choice of evolution equations used to model the population dynamics.

The authors acknowledge helpful discussions with T. Feltrin and M. A. Amaral, and support from the following Brazilian agencies, CAPES, CNPq and FAPEMIG, and Foundational Questions in Evolutionary 258 Biology Fund (FQEB), grant RFP-12-10.

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FIG. 4. Evolutionary trajectories on the faces of the simplex $S_4$. The trajectories of \textit{ALLC}, \textit{ALLD}, \textit{TFT}, and \textit{GTFT} are shown in (a) and the trajectories of the perturbed versions \textit{PALLC}, \textit{PALLD}, \textit{PTFT}, and \textit{PGTFT} are shown in (b).
FIG. 5. Fraction of $PGTFT$ if a fifth reactive strategy defined by $(p,q)$ is made available along with $PALLC$, $PALLD$, $PTFT$, and $PGTFT$ strategies.