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**EMERGENCE OF COOPERATION
IN HETEROGENEOUS
POPULATION: A DISCRETE-TIME
REPLICATOR DYNAMICS
ANALYSIS**

by
Ramón Escobedo and Annick Laruelle

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Departamento de Fundamentos del Análisis Económico I
Ekonomi Analisiaren Oinarriak I Saila



University of the Basque Country

Emergence of cooperation in heterogeneous population: a discrete-time replicator dynamics analysis

Ramón Escobedo · Annick Laruelle

Abstract The emergence of cooperation is analyzed in heterogeneous populations where individuals can be classified in two groups according to their phenotypic appearance. Phenotype recognition is assumed for all individuals: individuals are able to identify the type of every other individual, but fail to recognize their own type, and thus behave under partial information conditions. The interactions between individuals are described by 2×2 symmetric games where individuals can either cooperate or defect. The evolution of such populations is studied in the framework of evolutionary game by means of the replicator dynamics. Overlapping generations are considered, so the replicator equations are formulated in discrete-time form. The well-posedness conditions of the system are derived. Depending on the parameters of the game, a restriction may exist for the generation length. The stability analysis of the dynamical system is carried out and a detailed description of the behavior of trajectories starting from the interior of the state-space is given. We find that, provided the conditions of well-posedness are verified, the linear stability of monomorphic states in the discrete-time replicator coincides with the one of the continuous case. Specific from the discrete-time case, a relaxed restriction for the generation length is derived, for which larger time-steps can be used without compromising the well-posedness of the replicator system.

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R. Escobedo
AEPA-Euskadi, Pte. Deusto 7, 48014 Bilbao, Spain.
E-mail: escobedor@gmail.com

A. Laruelle
BRiDGE, Foundation of Economic Analysis I, University of the Basque Country (UPV/EHU) Avenida Lehendakari Aguirre, 83, 48015 Bilbao, Spain.
IKERBASQUE, Basque Foundation of Science, 48011 Bilbao, Spain.
E-mail: a.laruelle@ikerbasque.org

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1 Introduction

Consciously or unconsciously, in humans, animals or microscopic organisms, cooperative behaviors emerge in almost all circumstances of life. Even if it is still difficult to understand how someone can *pay a cost for another individual to receive a benefit*, some light has been shed on the mechanisms of the evolution of cooperation (Maynard Smith 1982). Nowak (2006) reviews five mechanisms that may lead to cooperation: (1) kin selection (Hamilton 1964), where donors and recipients of cooperation are genetically related; (2) direct reciprocity (Trivers 1971), where cooperation occurs between two unrelated individuals or even members of different species along repeated encounters; (3) indirect reciprocity, where individuals who cooperate are more likely to receive cooperation (Nowak 1998), (4) reciprocity in networks in not well-mixed populations (Veloz et al. 2012), and (5) group selection, where cooperators help others in their own group and defectors do not (Wilson and Dugatkin 1997).

These mechanisms often combine each other and give rise to more complex cooperative behaviors. This happens especially when the likelihood of type (kin, species or phenotype) recognition abilities is taken into account, where it is plausible to think that individuals tend to cooperate more frequently with those of the same type than their own, and defect with those of the other type. Riolo et al. (2001) and Traulsen and Schuster (2003) studied the emergence of cooperation based on similarity, when cooperation is channeled towards individuals that are sufficiently similar, i.e., carrying the same tag. Then, *tag-based donation can lead to the emergence of cooperation among agents who have only rudimentary ability to detect environmental signals* (Riolo et al. 2001).

In these models, individuals are assumed to know the tags of other individuals as well as their own tag. However, individuals are not always capable of recognizing their own kin, or even their own species, although they can perceive a phenotypical difference between neighbor individuals. In an experiment in animal welfare in poultry industry carried out by Dennis et al. (2008) with domestic fowls, two types of individuals are generated by artificially marking a given proportion of fowls on the back of their necks. Chickens behave under partial information conditions: they are unable to identify their own type (whether they have a mark or not) but observe their opponent's type. This induces an alternative form of discrimination by tags. Although the marks are clearly visible to our eyes, to what extent they serve chickens to perform morphological differentiation within their conspecifics is out of the scope of this work, but see Vallortigara (2009). Nevertheless, Dennis et al. (2008) observed that marked fowls suffer more aggressive events and have less body mass than their unmarked pen mates.

The above described experiment has been recently analyzed by means of game theory models. The common feature of these models is that individuals fail to recognize their own type, while they are able to recognize their opponents' type. [Iñarra and Laruelle \(2012\)](#) describe the evolutionarily stable strategies for the hawk-dove game. [Barreira da Silva Rocha et al. \(2011\)](#) use the (continuous) replicator dynamics to study the emergence of discriminative behavior in all 2×2 symmetric games. [Barreira da Silva Rocha and Laruelle \(2013\)](#) focus on the snowdrift games to study the emergence of discriminative cooperation also using the (continuous) replicator dynamics.

Here we study the emergence of cooperation in 2×2 symmetric games. Each individual can either cooperate or not. Cooperation is costly but may generate a benefit. If the cost of cooperation is larger than the benefit, cooperation is useless. If cooperation is beneficial (i.e., the benefit is larger than the cost), we distinguish two cases: when full cooperation is required to obtain the benefit and when partial cooperation is sufficient. The population considered is heterogeneous, with two types of individuals. In consequence, individuals can choose different actions for different types of opponents. Four pure strategies exist: 1) cooperate with both types, 2) defect against both types, 3) cooperate with the first type, defect against the second type, and 4) defect against the first type, cooperate with the second type

After a given interval of time during which the encounters take place (a *generation*), each individual of the population is replaced by a number of offspring proportional to the fitness of the progenitor individual. Offspring are identical to their progenitor, i.e., they play the same pure strategy. The dynamics of the entire population along successive generations is then described by a system of equations, each one controlling the time-evolution of the size of each subgroup of the population (one per pure strategy). We focus our interest in the case where population changes in time are not necessarily small (overlapping generations), so we use the discrete-time version of the replicator dynamics, as in [Nowak \(1998\)](#) and [Alboszta and Miękisz \(2004\)](#).

The rest of the paper is organized as follows. In Section 2, we present a taxonomy of all 2×2 symmetric games involving cooperation. In Section 3, we first derive the equations of the discrete-time replicator dynamics for homogeneous populations, and we recall the classical results obtained in the continuous-time case ([Weibull 1995](#)). Then, we derive the discrete-time replicator system for heterogeneous populations, and we also recall the recent results obtained by [Barreira da Silva Rocha et al. \(2011\)](#) in the continuous-time case. In Section 4, we derive the sufficient conditions of well-posedness of the discrete-time replicator model. In Section 5, the stability analysis of the stationary states and invariant manifolds is carried out. The sufficient conditions of stability are derived, and a detailed description of the qualitative behavior of trajectories in the corresponding state-space is presented. In Section 6, we show that for appropriate initial conditions, the sufficient condition of well-posedness and stability can be relaxed for the case where partial cooperation is sufficient. Finally, Section 7 contains our conclusions. We also point out the immediate further work and give some insight of the main open problems.

2 To cooperate or to defect

We are interested in 2×2 games, that is, in games that describe the interactions involving two individuals where each individual has two possible actions: to cooperate (pure strategy s_1) or to defect (pure strategy s_0). The result of an encounter for an individual playing strategy s_i with another individual playing strategy s_j is given by the *individual's utility* $v(s_i, s_j)$. Cooperation has a cost $c > 0$, and may generate a benefit $b > 0$ for both individuals.

The different combinations of strategies and their resulting utilities can be summarized in the following matrix:¹

	s_1	s_0
s_1	$v(s_1, s_1)$	$v(s_1, s_0)$
s_0	$v(s_0, s_1)$	$v(s_0, s_0)$

If both individuals defect, there is no cost nor benefit: $v(s_0, s_0) = 0$. If both individuals cooperate, both bear the cost and receive a benefit: $v(s_1, s_1) = b - c$. If only one individual cooperates, this individual bears the cost, while the opponent does not. For the benefit, two cases are considered, depending on how the benefit is generated. We will say that *full cooperation is required* when the benefit only arises when both players cooperate. In this case, $v(s_1, s_0) = -c$ and $v(s_0, s_1) = 0$. By contrast, we will say that *partial cooperation is sufficient* when the benefit arises as long as at least one player cooperates. In this case, $v(s_1, s_0) = b - c$ and $v(s_0, s_1) = b$.

What matters is the difference of utility between an action and the other. Neither the best responses, nor the Nash equilibrium, are modified by the following transformation of utilities:

$$\begin{aligned} u(s_i, s_0) &= v(s_i, s_0) - v(s_1, s_0), \\ u(s_i, s_1) &= v(s_i, s_1) - v(s_0, s_1). \end{aligned}$$

Denoting $u_i = u(s_i, s_i)$, $i = 0, 1$, the (normalized) matrix of utilities is given by

$$\begin{array}{c|cc} & s_1 & s_0 \\ \hline s_1 & u_1 & 0 \\ s_0 & 0 & u_0 \end{array} \quad (1)$$

$$\text{where } \begin{cases} u_0 = c, & u_1 = b - c, & \text{if } \textit{full cooperation} \text{ is required,} \\ u_0 = c - b, & u_1 = -c, & \text{if } \textit{partial cooperation} \text{ is sufficient.} \end{cases}$$

The benefit b is strictly positive, so $u_1 + u_0 \neq 0$ and it is always possible to define the following parameter $\bar{u} \in \mathbb{R}$ that serves as a cost-benefit ratio:

$$\bar{u} \stackrel{\text{def}}{=} \frac{u_0}{u_0 + u_1} = \begin{cases} \frac{c}{b} & \text{if } \textit{full cooperation} \text{ is required,} \\ 1 - \frac{c}{b} & \text{if } \textit{partial cooperation} \text{ is sufficient.} \end{cases} \quad (2)$$

¹ We consider symmetric games: the opponent's utility for an individual playing strategy s_i while the opponent plays strategy s_j is given by $v(s_j, s_i)$.

The games can be classified into three categories. In the first two categories, cooperation can be beneficial, i.e., $b > c$, while in the third one, cooperation is never beneficial, i.e., $b < c$. We refer to the last category as *useless cooperation*. Then:

- If *full cooperation* is required, then $u_0 > 0$ and $u_1 > 0$. This corresponds to a game of coordination (like the stag-hare game). The cost-benefit ratio is given by $c/b = \bar{u}$, with $0 < \bar{u} < 1$.
- If *partial cooperation* is sufficient, then $u_0 < 0$ and $u_1 < 0$. This corresponds to a game of anticoordination (like the snowdrift game). The cost-benefit ratio is $c/b = 1 - \bar{u}$, with $0 < 1 - \bar{u} < 1$.
- If *cooperation is useless*, then $u_1 < 0 < u_0$. This corresponds to a prisoner's dilemma and "defect" (s_0) is always a dominant strategy. The cost-benefit ratio is greater than one: $c/b = \bar{u} > 1$ if full cooperation is required, and $c/b = 1 - \bar{u} > 1$ (i.e., $\bar{u} < 0$) if partial cooperation is sufficient.

When cooperation can be beneficial, we will refer to *large benefits of cooperation* if the ratio cost-benefit is smaller than $1/2$ (if $0 < u_1 < u_0$ or $u_0 < u_1 < 0$). Otherwise, we will refer to *small benefits of cooperation* (if $0 < u_0 < u_1$ or $u_1 < u_0 < 0$).

We now derive the system of ordinary differential equations describing the dynamics of a population of individuals which play the above defined games, i.e., the *replicator dynamics*.

3 Discrete-time replicator system

Let us first recall the replicator dynamics in homogeneous populations.

3.1 Homogeneous populations

We consider a homogeneous population of individuals playing the above defined games. Let n^t denote the size of the population at time t . If individuals exclusively use pure strategies, the population can be divided into two subgroups of sizes n_0^t and n_1^t according to the pure strategy they are programmed to play, s_0 and s_1 respectively. Denote by $\theta_i^t = n_i^t/n^t$ the proportion of individuals playing the strategy s_i ($i = 0, 1$) at time t . Then, we have $n_0^t + n_1^t = n^t$ and $\theta_0^t + \theta_1^t = 1$ for all $t \geq 0$. The population state at time t can thus be characterized by the scalar value θ_1^t in the state-space $[0, 1]$. A state is said to be *monomorphic* if all the individuals uses one single strategy ($\theta_1^t = 0$ or 1); otherwise, the state is said to be *polymorphic*.

The replicator dynamics describes the time evolution of each subgroup of the population. In the continuous-time case, it consists in a system of ordinary

differential equations for the vector $\boldsymbol{\theta}(t) = (\theta_0(t), \theta_1(t))$:

$$\frac{d\boldsymbol{\theta}(t)}{dt} = \mathcal{F}(\boldsymbol{\theta}).$$

When the population changes are not necessarily small, the replicator dynamics takes the form of a discrete-time map for the vector $\boldsymbol{\theta}^t = (\theta_0^t, \theta_1^t)$,

$$\boldsymbol{\theta}^{t+\delta} = \mathcal{F}(\boldsymbol{\theta}^t), \quad (3)$$

where the evolution of the population is described in terms of successive generations. Here $\delta \in (0, 1]$ denotes the duration of one generation. From one generation to the other, individuals involved in pairwise encounters are replaced by a number of offsprings (identical to their parents in the strategy they are programmed to play) according to the resulting utility of these encounters.

We are interested in the discrete-time case in which generations overlap, that is, not all the individuals are replaced from one generation to the next. As in the classical formulation, we let the time-step δ of the map (3) equal the fraction of the population that is renewed in each generation (Weibull 1995). Thus, in one time-step, only a portion δ of the population is subject to potential changes.

Let us denote by $u_i(\theta_1^t)$, $i = 0, 1$, the utility that individuals from each subgroup obtain when the population is in state θ_1^t . Then, the size of each subgroup evolves according to the following recurrences:

$$\begin{aligned} n_0^{t+\delta} &= (1 - \delta)n_0^t + \delta n_0^t u_0(\theta_1^t), \\ n_1^{t+\delta} &= (1 - \delta)n_1^t + \delta n_1^t u_1(\theta_1^t). \end{aligned}$$

These equations mean that, from one generation (at time t) to the next (at time $t + \delta$), a fraction $1 - \delta$ of individuals remains unchanged, and a fraction δ increases or decreases proportionally to the utility obtained by the subgroup.

When the population is in state θ_1^t , the individual has a probability θ_1^t of meeting an opponent playing s_1 and a probability $1 - \theta_1^t$ of meeting an opponent playing s_0 . Thus, the utilities $u_i(\theta_1^t)$, $i = 0, 1$, are given by

$$\begin{aligned} u_0(\theta_1^t) &= \theta_1^t u(s_0, s_1) + (1 - \theta_1^t) u(s_0, s_0) = (1 - \theta_1^t) u_0, \\ u_1(\theta_1^t) &= \theta_1^t u(s_1, s_1) + (1 - \theta_1^t) u(s_1, s_0) = \theta_1^t u_1, \end{aligned}$$

where u_0 and u_1 have been defined in (1), and the evolution of the size of each subgroup of the population can be written as

$$\begin{aligned} n_0^{t+\delta} &= n_0^t [(1 - \delta) + \delta(1 - \theta_1^t) u_0], \\ n_1^{t+\delta} &= n_1^t [(1 - \delta) + \delta \theta_1^t u_1]. \end{aligned}$$

Then, the total population $n^{t+\delta} = n_1^{t+\delta} + n_0^{t+\delta}$ evolves as follows:

$$n^{t+\delta} = n^t \left[1 - \delta + \delta [(1 - \theta_1^t)^2 u_0 + (\theta_1^t)^2 u_1] \right].$$

The proportion of individuals $\theta_1^{t+\delta} = n_1^{t+\delta}/n^{t+\delta}$ playing s_1 is thus given by

$$\theta_1^{t+\delta} = \frac{(1-\delta)\theta_1^t + \delta(\theta_1^t)^2 u_1}{1-\delta + \delta(1-\theta_1^t)^2 u_0 + \delta(\theta_1^t)^2 u_1}, \quad (4)$$

and the growth rate of this subgroup of the population is given by

$$\theta_1^{t+\delta} - \theta_1^t = \frac{n_1^{t+\delta} - n^{t+\delta}\theta_1^t}{n^{t+\delta}} = \delta\theta_1^t \frac{(u_0 + u_1)(\theta_1^t - \bar{u})(1 - \theta_1^t)}{1 - \delta + \delta(1 - \theta_1^t)^2 u_0 + \delta(\theta_1^t)^2 u_1}, \quad (5)$$

where \bar{u} was defined in (2).

Equation (4) is the discrete-time replicator equation for a homogeneous population of individuals playing the game defined in (1).

Dividing by δ at both sides of Eq. (5) and taking the limit $\delta \rightarrow 0$, we obtain the continuous-time replicator equation,

$$\lim_{\delta \rightarrow 0} \frac{\theta_1^{t+\delta} - \theta_1^t}{\delta} = \theta_1^t (u_0 + u_1) (\theta_1^t - \bar{u}) (1 - \theta_1^t).$$

The following result of stability holds (Weibull 1995):

- (i) If full cooperation is required ($u_0 > 0$, $u_1 > 0$), there are two stationary states, $\theta_1^* = 0$ and $\theta_1^* = 1$, both monomorphic and asymptotically stable.
- (ii) If partial cooperation is sufficient ($u_0 < 0$, $u_1 < 0$), the stationary state is polymorphic, $\theta_1^* = \bar{u} = 1 - c/b$ (i.e., $\theta_0^* = 1 - \bar{u}$), and asymptotically stable.
- (iii) If cooperation is useless ($u_1 < 0 < u_0$), there is a unique stationary state, $\theta_1^* = 0$, and it is monomorphic and asymptotically stable.

We now use this derivation as a guide to obtain the discrete-time replicator system in the case of heterogeneous populations.

3.2 Heterogeneous populations

Consider a heterogeneous population where two types of individuals coexist: individuals of type I and individuals of type II . Let us denote by x the proportion of individuals of type I , i.e., each individual has a probability x of meeting an individual of type I and a probability $1 - x$ of meeting an individual of type II .² We assume that x is constant.³

Individuals are programmed to play a pure strategy. A pure strategy specifies one of the two possible action (s_0 or s_1) for each type of opponent (I or II). Here we assume that individuals recognize their opponent's type but fail to recognize their own type. There are then four pure strategies s_{10} , s_{01} , s_{11} and s_{00} ,

² We assume that the population is sufficiently large to approximate the proportion and the probability.

³ In the population dynamic process this corresponds to assuming that each new offspring is randomly assigned a type in such a way that x does not change. The allocation of type is completely independent of the strategy the offspring is programmed to play.

where s_{ij} , $ij \in \mathcal{I} = \{10, 01, 11, 00\}$, denotes the strategy of playing s_i against an opponent of type I and s_j against an opponent of type II .⁴

To derive the replicator equations, the population is divided into as many subgroups as there are pure strategies, that is, four subgroups.

Let n_{ij}^t (resp. θ_{ij}^t) denote the number (resp. proportion) of individuals at time $t \geq 0$ programmed to play the pure strategy s_{ij} , for $ij \in \mathcal{I}$.

Then,

$$\theta_{00}^t = 1 - \theta_{10}^t - \theta_{01}^t - \theta_{11}^t \quad \forall t \geq 0, \quad (6)$$

so the state of the population can be characterized by the three-dimensional vector $\boldsymbol{\theta}^t = (\theta_{10}^t, \theta_{01}^t, \theta_{11}^t)$ in the state-space Ω , which is the unit tetrahedron:

$$\Omega = \{\boldsymbol{\theta} \in [0, 1]^3 : \theta_{10} + \theta_{01} + \theta_{11} \leq 1\}.$$

The state is said to be *monomorphic* if all the individuals use one single strategy ($\theta_{ij}^t = 1$ for some $ij \in \mathcal{I}$); otherwise, the state is said to be *polymorphic*.

As in the homogeneous case, we denote by $U_{ij}(\boldsymbol{\theta}^t): \Omega \rightarrow \mathbb{R}$ the utility an individual can expect when playing strategy s_{ij} in state $\boldsymbol{\theta}^t$. Then, the size of each subgroup $ij \in \mathcal{I}$ evolves according to the following equation:

$$n_{ij}^{t+\delta} = (1 - \delta)n_{ij}^t + \delta n_{ij}^t U_{ij}(\boldsymbol{\theta}^t). \quad (7)$$

In the heterogeneous case, the utility $U_{ij}(\boldsymbol{\theta}^t)$ depends on the individual's type. If $U_{ij}^I(\boldsymbol{\theta}^t)$ [resp. $U_{ij}^{II}(\boldsymbol{\theta}^t)$] is the utility of an individual of type I (resp. II) at time t , the expected utility $U_{ij}(\boldsymbol{\theta}^t)$ can be decomposed as follows:

$$U_{ij}(\boldsymbol{\theta}^t) = xU_{ij}^I(\boldsymbol{\theta}^t) + (1 - x)U_{ij}^{II}(\boldsymbol{\theta}^t). \quad (8)$$

To compute $U_{ij}^I(\boldsymbol{\theta}^t)$ and $U_{ij}^{II}(\boldsymbol{\theta}^t)$, note that these utilities depend on the opponent's type and on the state of the population. The opponent's type determines the individual's action s_1 or s_0 , and the state of the population $\boldsymbol{\theta}^t$ determines the opponent's action, which is s_{ij} with probability θ_{ij}^t . Thus, we have:

$$\begin{aligned} U_{ij}^I(\boldsymbol{\theta}^t) &= x [\theta_{10}^t u(s_i, s_1) + \theta_{01}^t u(s_i, s_0) + \theta_{11}^t u(s_i, s_1) + \theta_{00}^t u(s_i, s_0)] \\ &\quad + (1 - x) [\theta_{10}^t u(s_j, s_1) + \theta_{01}^t u(s_j, s_0) + \theta_{11}^t u(s_j, s_1) + \theta_{00}^t u(s_j, s_0)] \\ U_{ij}^{II}(\boldsymbol{\theta}^t) &= x [\theta_{10}^t u(s_i, s_0) + \theta_{01}^t u(s_i, s_1) + \theta_{11}^t u(s_i, s_1) + \theta_{00}^t u(s_i, s_0)] \\ &\quad + (1 - x) [\theta_{10}^t u(s_j, s_0) + \theta_{01}^t u(s_j, s_1) + \theta_{11}^t u(s_j, s_1) + \theta_{00}^t u(s_j, s_0)]. \end{aligned}$$

We now introduce the following

Definition 1 The function $f(\boldsymbol{\theta}): \Omega \rightarrow \mathbb{R}$ given by

$$f(\boldsymbol{\theta}) \stackrel{def}{=} \theta_{11} + x\theta_{10} + (1 - x)\theta_{01}$$

is the frequency of cooperation when the population is in state $\boldsymbol{\theta}^t$. Accordingly, we denote by f_{ij} the frequency of cooperation in the four monomorphic states. That is:

$$f_{11} = 1, \quad f_{10} = x, \quad f_{01} = 1 - x, \quad f_{00} = 0. \quad (9)$$

⁴ If individuals recognized their own type, they would behave differently according to their own type, so that the number of pure strategies would be eight.

Then, substituting the expressions of $U_{ij}^I(\boldsymbol{\theta}^t)$ and $U_{ij}^{II}(\boldsymbol{\theta}^t)$ into (8), we obtain

$$U_{ij}(\boldsymbol{\theta}^t) = xu(s_i, s_1)f(\boldsymbol{\theta}^t) + xu(s_i, s_0)(1 - f(\boldsymbol{\theta}^t)) \\ + (1 - x)u(s_j, s_1)f(\boldsymbol{\theta}^t) + (1 - x)u(s_j, s_0)(1 - f(\boldsymbol{\theta}^t)),$$

which, by using the basic matrix (1) and the frequencies of the monomorphic states (9), can be simplified into

$$U_{ij}(\boldsymbol{\theta}^t) = f(\boldsymbol{\theta}^t)f_{ij}u_1 + [1 - f(\boldsymbol{\theta}^t)](1 - f_{ij})u_0, \quad \forall ij \in \mathcal{I}. \quad (10)$$

Plugging (10) into (7) and using $n_{ij}^{t+\delta} = n^t \theta_{ij}^t$, we obtain that the evolution of each subpopulation size is given by

$$n_{ij}^{t+\delta} = n^t \theta_{ij}^t \left[1 - \delta + \delta [f(\boldsymbol{\theta}^t)f_{ij}u_1 + [1 - f(\boldsymbol{\theta}^t)](1 - f_{ij})u_0] \right].$$

The total population size $n^{t+\delta} = n_{10}^{t+\delta} + n_{01}^{t+\delta} + n_{11}^{t+\delta} + n_{00}^{t+\delta}$ then evolves as

$$n^{t+\delta} = n^t \left[1 - \delta + \delta [f(\boldsymbol{\theta}^t)^2 u_1 + [1 - f(\boldsymbol{\theta}^t)]^2 u_0] \right].$$

The proportion of individuals playing s_{ij} at time $t + \delta$ is $\theta_{ij}^{t+\delta} = n_{ij}^{t+\delta} / n^{t+\delta}$, so the discrete-time replicator equation for the population subgroup $ij \in \mathcal{I}$ is

$$\theta_{ij}^{t+\delta} = \theta_{ij}^t \frac{1 - \delta + \delta [f(\boldsymbol{\theta}^t)f_{ij}u_1 + [1 - f(\boldsymbol{\theta}^t)](1 - f_{ij})u_0]}{1 - \delta + \delta [f(\boldsymbol{\theta}^t)]^2 u_1 + \delta [1 - f(\boldsymbol{\theta}^t)]^2 u_0} \quad (11)$$

$$= \theta_{ij}^t \left[1 + \delta \frac{(u_0 + u_1) [f_{ij} - f(\boldsymbol{\theta}^t)] [f(\boldsymbol{\theta}^t) - \bar{u}]}{1 - \delta + \delta [f(\boldsymbol{\theta}^t)]^2 u_1 + \delta [1 - f(\boldsymbol{\theta}^t)]^2 u_0} \right] \quad (12)$$

Equations (11) constitute a system of four equations which can be reduced to three equations as one of them is redundant with relation (6). The function \mathcal{F} of map (3) is the vector $(F_{10}(\boldsymbol{\theta}^t), F_{01}(\boldsymbol{\theta}^t), F_{11}(\boldsymbol{\theta}^t))$, where the functions $F_{ij}(\boldsymbol{\theta}): \Omega \rightarrow \mathbb{R}$ are defined by the right hand side of (11). The system of equations (11) must be solved together with initial conditions, which are given by the coordinates of the initial point $\boldsymbol{\theta}^0 = (\theta_{10}^0, \theta_{01}^0, \theta_{11}^0)$ in the state-space Ω .

Remark 1 The homogeneous case is recovered by replacing $\theta_{ij}^{t+\delta}$ and $f(\boldsymbol{\theta}^t)$ by θ_{11}^t and f_{ij} by 1 (cooperation frequency when using strategy s_1) in Eq. (11).

Fig. 1 shows a numerical simulation of the time-evolution of the replicator system for $x = 0.4$, $u_0 = -0.4$, $u_1 = -0.05$ (so $\bar{u} = 0.88$) and $\delta = 0.6$, with the initial condition $\boldsymbol{\theta}^0 = (0.3, 0.2, 0.01)$, for which $f(\boldsymbol{\theta}^0) = 0.25$.

The successive positions of the trajectory in each generation are represented by circles in equispaced intervals of time, thus emphasizing the discrete character of the model. In these figures, the separation between circles corresponds exactly to one single time-step, so that it can be observed that the initial steps are large and then decrease along the trajectory. The trajectory converges asymptotically to a point located in the upper region of Ω , with coordinates $\boldsymbol{\theta}^w = (0.038, 0.22, 0.74)$, where $f(\boldsymbol{\theta}^w)$ is such that $|f(\boldsymbol{\theta}^w) - \bar{u}|/\bar{u} < 10^{-14}$ after 10^3 time-iterations.

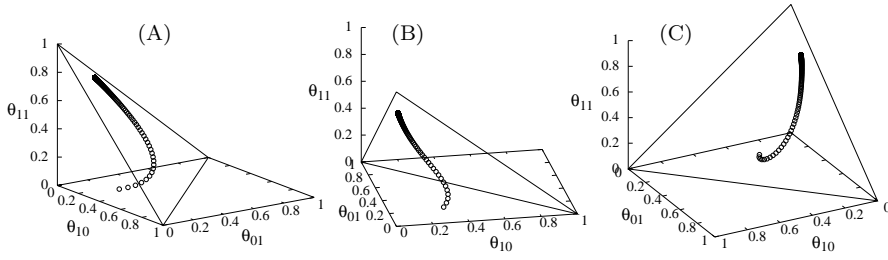


Fig. 1 Three views of the unit tetrahedron Ω in the $(\theta_{10}, \theta_{01}, \theta_{11})$ -space. We used $x = 0.4$, $u_0 = -0.4$, $u_1 = -0.05$ (so $\bar{u} = 0.88$) and $\delta = 0.6$. Circles denote the successive values of θ^t in each time-iteration, starting from $\theta^0 = (0.3, 0.2, 0.01)$ in the lower region of Ω . The trajectory grows decelerating and converging asymptotically to $\theta^w = (0.038, 0.22, 0.74)$.

This simulation corresponds to a relatively large value of $\delta = 0.6$. For small values of δ , the trajectory approximately follows the same path and tends to the continuous line corresponding to the continuous-time replicator system. For larger values of δ , the separation between circles increases because the time-steps of the trajectory are larger, so that the trajectory separates from the path of the continuous case. For very large values of δ , the trajectory can eventually jump outside the tetrahedron, as described by Weibull in a similar situation (Weibull 1995).

Our interest is thus in finding the upper bound for δ guaranteeing that, for all initial conditions, trajectories remain in the tetrahedron for all successive generations. Then, we will describe the stable population states and convergent interior solution trajectories, which, as underlined by Weibull, do not necessarily coincide with those of the continuous-time model (Weibull 1995).

Relation with the continuous-time case. As we did in the homogeneous case, using (11), the growth rate of the subgroup $ij \in \mathcal{I}$ can be written as follows:

$$\theta_{ij}^{t+\delta} - \theta_{ij}^t = \delta \theta_{ij}^t \frac{(u_0 + u_1)[f(\theta^t) - \bar{u}][f_{ij} - f(\theta^t)]}{1 - \delta + \delta[f(\theta^t)]^2 u_1 + [1 - f(\theta^t)]^2 u_0}. \quad (13)$$

Dividing by δ at both sides of and taking the limit $\delta \rightarrow 0$, we obtain the continuous-time replicator dynamics,

$$\dot{\theta}_{ij}^t = \theta_{ij}^t (u_0 + u_1) (f(\theta^t) - \bar{u}) [f_{ij} - f(\theta^t)], \quad ij \in \mathcal{I},$$

for which Barreira da Silva Rocha et al. (2011) obtained the following result:

- (i) If full cooperation is required, there are two stationary states $\theta_{00}^* = 1$ and $\theta_{11}^* = 1$, and both are monomorphic and asymptotically stable. Thus, the system converges to a monomorphic state where the entire population either cooperates or defects.
- (ii) If partial cooperation is sufficient, the monomorphic states are unstable and there is a set of neutrally stable points $\mathcal{P}_{\bar{u}} = \{\theta \in \Omega : f(\theta) = \bar{u}\}$. Thus, the system converges to a polymorphic state where the frequency of cooperation is $\bar{u} = 1 - b/c$.

- (iii) If cooperation is useless, there is a unique stationary state $\theta_{00}^* = 1$, which is monomorphic and asymptotically stable. Thus, the system converges to a monomorphic state where the entire population defects.

Let us now study the stability of the discrete-time replicator system for heterogeneous populations. As reported in Weibull (1995) (p. 125),

[...] convergence and stability in continuous-time dynamics do not imply convergence and stability in corresponding discrete-time dynamics. [...] the discrete-time orbits essentially make straight-line jumps in the direction of the tangent of the continuous-time orbit.

Thus, the first step in the next section consists in establishing the sufficient conditions for the well-posedness of the system.

4 Well-posedness of the discrete-time replicator system

The dynamical system defined by equations (11) and an initial condition $\theta^0 \in \Omega$ is said to be well-posed if the denominator of these equations is never zero and the successive values of θ^t remain in Ω for all $t > 0$. Well-posedness thus consists in restricting the value of δ to those which prevent the denominator from being zero and the trajectories from jumping outside Ω .

The system is always well-posed if full cooperation is required. If cooperation is useless or if partial cooperation is sufficient there is a condition on the value of δ . We have the following

Theorem 1 *Let $\bar{\delta}$ be the following critical value of $\delta \in [0, 1]$:*

$$\bar{\delta} = \frac{1}{1 - \min\{u_0, u_1\}}.$$

The conditions for δ guaranteeing the well-posedness of the replicator system (11) are as follows:

- (i) *If $u_0 > 0$ and $u_1 > 0$, the system is well-posed for all $\delta \in [0, 1]$.*
- (ii) *If $u_1 < 0$, δ has the upper bound $\delta < \bar{\delta}$.*

A point θ^0 is in Ω if and only if its components θ_{ij}^0 , $ij \in \mathcal{I} - \{00\}$, are positive or zero and verify $\theta_{10}^0 + \theta_{01}^0 + \theta_{11}^0 = 1 - \theta_{00}^0 \leq 1$. The replicator system preserves this last condition; this is shown by summing up the four equations in (11) for $ij \in \mathcal{I}$. Thus, after one iteration, the point θ^δ will be in Ω provided its components are positive or zero.

The following lemmas are devoted to the study of the sign of the denominator and the numerator in equation (11).

Lemma 1 *The sign of the denominator of expression (11) is as follows:*

- (i) *If $u_1 > 0$ and $u_0 > 0$, the denominator is strictly positive for all $\theta \in \Omega$.*
- (ii) *If $u_1 < 0$ and $\delta < \bar{\delta}$, the denominator is strictly positive for all $\theta \in \Omega$.*

(iii) If $u_1 < 0$, $u_0 < 0$ and $\delta > 1/(1 - \bar{u}u_1)$, the denominator is strictly negative for all $\boldsymbol{\theta} \in \Omega$.

Proof The denominator of expression (11) is $1 - \delta + \delta[f(\boldsymbol{\theta}^t)]^2 u_1 + \delta[1 - f(\boldsymbol{\theta}^t)]^2 u_0$. Part (i) is obvious because $1 - \delta > 0$. To prove part (ii), we observe that the denominator of (11) can be viewed as a concave quadratic function of $f(\boldsymbol{\theta})$ which reaches its absolute maximum in $[0, 1]$ at $f(\boldsymbol{\theta}) = \bar{u}$ and its minima at the boundary of $[0, 1]$. There, the values of the denominator are $1 - \delta + \delta u_0$ for $f(\boldsymbol{\theta}) = 0$ and $1 - \delta + \delta u_1$ for $f(\boldsymbol{\theta}) = 1$. Thus, the minimum of the denominator in $[0, \bar{u}]$ is $1 - \delta + \delta u_0$, and in $[\bar{u}, 1]$, $1 - \delta + \delta u_1$ (one is a relative minimum and the other is the absolute minimum, depending on the relative value of u_0 and u_1). The absolute minimum is thus $1 - \delta + \delta \min\{u_0, u_1\}$, which is strictly positive when $\delta < \bar{\delta}$, so the denominator is strictly positive for all $\boldsymbol{\theta} \in \Omega$.

To prove part (iii), note that, as $u_0 + u_1 < 0$, we have the inequality

$$[f(\boldsymbol{\theta})]^2 u_1 + [1 - f(\boldsymbol{\theta})]^2 u_0 = (u_0 + u_1)[f(\boldsymbol{\theta}) - \bar{u}]^2 + \bar{u}u_1 < \bar{u}u_1.$$

Then, for all $\boldsymbol{\theta} \in \Omega$, the denominator is smaller than $1 - \delta + \delta \bar{u}u_1$, which is negative if $\delta > 1/(1 - \bar{u}u_1)$. \square

Corollary 1 *Under the conditions of Lemma 1, the denominator of expression (11) is never zero for all $\boldsymbol{\theta} \in \Omega$.*

Proof Lemma 1 shows that the denominator of expression (11) is either strictly positive or strictly negative for all $\boldsymbol{\theta} \in \Omega$. \square

Lemma 2 *Under the conditions (i) and (ii) of Lemma 1, the numerator of expression (11) is strictly positive for all $\boldsymbol{\theta} \in \Omega$.*

Proof The numerator of expression (11) can be viewed as a function of two variables $(f(\boldsymbol{\theta}), f_{ij}) \in [0, 1]^2$ which is linear in each variable, so its absolute extrema are reached at the vertices of $[0, 1]^2$. The values obtained there are:

$$1 - \delta + \delta u_0, \quad 1 - \delta + \delta u_1 \quad \text{and} \quad 1 - \delta.$$

Then:

- (i) If $u_1 > 0$ and $u_0 > 0$, all values are strictly positive because $\delta \in (0, 1)$.
- (ii) If $\delta < \bar{\delta}$, then $1 - \delta + \delta \min\{u_0, u_1\} > 0$ and all values are strictly positive. \square

We are now ready to prove the theorem:

Proof of Theorem 1: The sign of θ_{ij}^δ is given by the sign of the numerator and the denominator of expression (11) which, by Lemmas 1 and 2, are both strictly positive under conditions (i) and (ii) of Theorem 1, so that the replicator system is well-posed in these cases. In case (iii), Lemma 1 shows that the denominator is negative; however, for $\boldsymbol{\theta}^0 \in \Omega$ such that $f(\boldsymbol{\theta}^0) = 0$ and $ij = 11$ such that $f_{ij} = 1$, the numerator is positive, so $\theta_{11}^\delta < 0$ and the trajectory has left the tetrahedron Ω . \square

In the next section, we describe the general behavior of the trajectories of the discrete-time replicator system.

5 Behavior of the discrete-time replicator dynamics

This section is devoted to describe the general behavior of trajectories obeying the equations of the discrete-time replicator system (11) and starting from the interior of Ω . After identifying the stationary states of the dynamical system, we obtain their stability properties, and we describe how trajectories evolve.

The casuistry of trajectories living in the boundary of Ω , that is, in the faces and edges of the tetrahedron, is very rich. These trajectories correspond to degenerate populations where one or more strategies are not present. As shown later, the analysis would require to take into account the relative value of \bar{u} with respect to x and $1 - x$ and would be of considerable length. Here we limit our study to nondegenerate populations.

5.1 Fixed points and invariant manifolds

5.1.1 Fixed points

The fixed points $\theta^* \in \Omega$ of the discrete-time replicator system (11) are such that $\mathcal{F}(\theta^*) = \theta^*$, that is, $(\theta_{ij}^*)^{t+\delta} = (\theta_{ij}^*)^t$ for all $ij \in \mathcal{I}$ simultaneously. The four vertices of Ω , i.e., $(\theta_{10}, \theta_{01}, \theta_{11}) = (0, 0, 0)$, $(0, 1, 0)$, $(0, 0, 1)$ and $(1, 0, 0)$, are isolated fixed points: when $\theta_{ij}^t = 0$ then $\theta_{ij}^{t+\delta} = 0$, and when $\theta_{ij}^t = 1$, the factor $f_{ij} - f(\theta^t)$ in (12) is zero, so $\theta_{ij}^{t+\delta} = 1$.

Denote by $\mathcal{P}_{\bar{u}}$, \mathcal{P}_1 , \mathcal{P}_x and \mathcal{P}_{1-x} the four planes defined by the equations

$$\mathcal{P}_{\bar{u}} : f(\theta) = \bar{u}, \quad \mathcal{P}_1 : f(\theta) = 1, \quad \mathcal{P}_x : f(\theta) = x, \quad \mathcal{P}_{1-x} : f(\theta) = 1 - x.$$

If u_0 and u_1 have the same sign, then $\bar{u} \in (0, 1)$ and the plane $\mathcal{P}_{\bar{u}}$ intersects the tetrahedron; otherwise, the intersection is empty. If $\bar{u} \in (0, 1)$, then for all $\theta \in \mathcal{P}_{\bar{u}}$, the factor $f(\theta^t) - \bar{u}$ in (12) is zero so $F_{ij} = \theta_{ij}^*$ for all $ij \in \mathcal{I}$, showing that every point of $\mathcal{P}_{\bar{u}}$ is a fixed point. Finally, as the four planes are parallel, no other fixed point can exist.

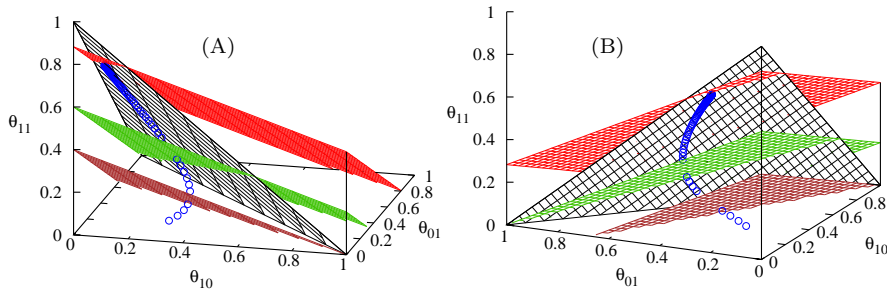


Fig. 2 Two views of the trajectory of Fig. 1 with the plane $\theta_{00} = 0$ (black), intersected by the three parallel planes $\mathcal{P}_{\bar{u}}$ (upper), \mathcal{P}_{1-x} (middle) and \mathcal{P}_x (lower). The trajectory starts from below \mathcal{P}_x , crosses successively \mathcal{P}_x and \mathcal{P}_{1-x} , and, while approaching $\theta_{00} = 0$, converges asymptotically to $\mathcal{P}_{\bar{u}}$. Here, $|f(\theta^w) - \bar{u}|/\bar{u} < 10^{-14}$.

Fig. 2 shows the three planes $\mathcal{P}_{\bar{u}}$, \mathcal{P}_x and \mathcal{P}_{1-x} for $x = 0.4$ and $\bar{u} = 0.88$. The plane \mathcal{P}_{1-x} appears above \mathcal{P}_x because here $x < 1/2$ and we have chosen θ_{11} as the vertical coordinate. The plane \mathcal{P}_1 (not shown) is located above Ω and intersects Ω at $(0, 0, 1)$, while $\mathcal{P}_{\bar{u}}$, which is not empty because $\bar{u} \in (0, 1)$, is below \mathcal{P}_1 and above \mathcal{P}_{1-x} , because $\bar{u} > 1 - x$. The value of \bar{u} , x and $1 - x$ can in fact be observed in the figure as the intersection of the respective plane with the vertical axis $\theta_{10} = \theta_{01} = 0$.

Note also that $(1, 0, 0) \in \mathcal{P}_x$, $(0, 1, 0) \in \mathcal{P}_{1-x}$, and that $\mathcal{P}_{\bar{u}}$ intersects the plane $\theta_{00} = 0$ (which is the face of Ω towards which the trajectory seems to converge), but not the plane $\theta_{11} = 0$ (which is the basis of the tetrahedron).

5.1.2 Invariant manifold

An invariant manifold \mathcal{M} is a subset of Ω such that if the initial condition of a trajectory is in \mathcal{M} , then the whole trajectory is in \mathcal{M} . Thus, trajectories cannot cross, depart from or arrive to, invariant manifolds. Fixed points are invariant manifolds, so each isolated vertex of Ω is an invariant manifold, and, when u_0 and u_1 have the same sign, so is the plane $\mathcal{P}_{\bar{u}}$.

The four planes $\theta_{ij} = 0$, $ij \in \mathcal{I}$ delimiting the tetrahedron Ω are invariant manifolds, because $\theta_{ij}^0 = 0 \Rightarrow \theta_{ij}^t = 0$ for all $t \geq 0$ and all $ij \in \mathcal{I}$. The six edges $\theta_{ij} = \theta_{kl} = 0$, $ij, kl \in \mathcal{I}$, $kl \neq ij$, are also invariant manifolds.

In the continuous case, the fact that the four faces of the tetrahedron are invariant manifolds suffices to say that trajectories starting from inside Ω are confined to Ω for all successive times $t \geq 0$. However, as already mentioned, the essential feature of discrete-time dynamics is that trajectories evolve by jumps and can traverse invariant manifolds. Thus, the confinement of trajectories to specific regions (or to the whole domain Ω , as shown in the previous section) must be made evident explicitly.

5.2 Linear stability of fixed points

First let us define the concept of asymptotic stability.⁵

Definition 1 A fixed point $\theta^* \in \Omega$ is Lyapunov stable if for all neighborhood V of θ^* , there exists a neighborhood U of θ^* such that $U \subset V$ and

$$\forall \theta^0 \in U \cap \Omega, \theta^t \in V \cap \Omega.$$

A fixed point $\theta^* \in \Omega$ is asymptotically stable if it is Lyapunov stable and there exists a neighborhood U of θ^* such that

$$\forall \theta^0 \in U \cap \Omega, \lim_{t \rightarrow +\infty} \theta^t = \theta^*.$$

⁵ The fixed points of the system (11) are located in the boundary of Ω , so no open set containing a fixed point can be contained in Ω . We thus relax the classical definition of stability (see, e.g., Strogatz (1994); Weibull (1995)) and we consider the neighborhoods of the fixed points intersected with the domain Ω .

We now use the first method of Lyapunov for discrete-time systems to establish the (linear) stability of the four vertices of Ω . The fixed points of the discrete-time replicator dynamics coincide with those of the continuous replicator, provided the conditions of well-posedness are verified. That is:

Theorem 2 *Provided the conditions of well-posedness are verified, we have:*

- If $u_1 < 0 < u_0$, then the vertex $(0, 0, 0)$ is asymptotically stable and the other vertices are unstable.
- If $u_0 > 0$ and $u_1 > 0$, then $(0, 0, 0)$ and $(0, 0, 1)$ are asymptotically stable and $(1, 0, 0)$ and $(0, 1, 0)$ are unstable.
- If $u_0 < 0$ and $u_1 < 0$, then all the vertices of Ω are unstable.

Proof of Theorem 2: Assume that a trajectory starts nearby the fixed point θ^* : $\theta^0 = \theta^* + \epsilon^0$, where $\epsilon^0 = (\epsilon_{10}^0, \epsilon_{01}^0, \epsilon_{11}^0)$ is a small perturbation. The linear stability of θ^* is given by the time evolution of ϵ^t : if $\|\epsilon^t\| \rightarrow 0$, then $\theta^t \rightarrow \theta^*$ and θ^* is asymptotically stable; if the perturbation grows, then θ^* is unstable.

The time evolution of the perturbation is given by $\epsilon^t = \theta^t - (\theta^*)^t$, that is, by $\epsilon^t = \theta^t - \theta^*$, so, using the expression of the map (3), we have:

$$\begin{aligned} \epsilon^{t+\delta} &= \theta^{t+\delta} - \theta^* = \mathcal{F}(\theta^t) - \theta^* \\ &= \mathcal{F}(\theta^* + \epsilon^t) - \theta^*. \end{aligned}$$

If $\|\epsilon^0\|$ is sufficiently small, it is possible to find a neighborhood of θ^* where $\mathcal{F}(\theta^* + \epsilon^t)$ can be approximated by the (first two terms of the) Taylor expansion of \mathcal{F} centered in θ^* :

$$\mathcal{F}(\theta^* + \epsilon^t) = \mathcal{F}(\theta^*) + J\mathcal{F}(\theta^*) \cdot \epsilon^t + O(\|\epsilon^t\|^2),$$

where $J\mathcal{F}(\theta^*)$ denotes the Jacobian matrix of the vector function $\mathcal{F}(\theta)$ evaluated in θ^* (see Appendix), and the central dot denotes matrix multiplication. We thus have a linear approximation of $\epsilon^{t+\delta}$,

$$\epsilon^{t+\delta} = J\mathcal{F}(\theta^*) \cdot \epsilon^t,$$

which in the k th iteration yields

$$\begin{aligned} \epsilon^{t+k\delta} &= J\mathcal{F}(\theta^*) \cdot \epsilon^{t+(k-1)\delta} = J\mathcal{F}(\theta^*) \cdot \left[J\mathcal{F}(\theta^*) \cdot \epsilon^{t+(k-2)\delta} \right] \\ &= [J\mathcal{F}(\theta^*)]^k \cdot \epsilon^t. \end{aligned}$$

This means that the size of the perturbation $\|\epsilon^t\|$ will tend to zero if and only if all the eigenvalues of $J\mathcal{F}(\theta^*)$ are smaller than 1.

The detailed study (Jacobian matrices and eigenvalues) shown in the Appendix ends the proof. \square

In words, the result is as follows:

- The monomorphic state $\theta_{00} = 1$ (always defect) is stable if cooperation is useless or full cooperation is required, and unstable if partial cooperation is sufficient.

- The monomorphic state $\theta_{11} = 1$ (always cooperate) is stable if full cooperation is required and unstable otherwise.
- The monomorphic states $\theta_{01} = 1$ and $\theta_{10} = 1$ (cooperate against one type, defect against the other) are always unstable.

5.3 Behavior of trajectories in the interior of Ω

The previous analysis of the linear stability of fixed points helps us to describe the general behavior of trajectories in the interior of the tetrahedron.

The direction toward which a trajectory evolves is determined by the variation of each coordinate θ_{ij} , i.e., by the sign of $\theta_{ij}^{t+\delta} - \theta_{ij}^t$ in expression (13). Provided the well-posedness conditions are verified, this means that θ_{ij}^t varies according to the sign of the product

$$(u_0 + u_1)(f(\boldsymbol{\theta}^t) - \bar{u})[f_{ij} - f(\boldsymbol{\theta}^t)],$$

which is precisely what determines the sign of $d\theta_{ij}/dt$ in the continuous-time case. Then, intuition can be gained from both the continuous case and the numerical simulations with relatively small values of δ .

Fig. 2 shows the growing trajectory depicted in Fig. 1 which successively crosses the three planes \mathcal{P}_x , \mathcal{P}_{1-x} and $\mathcal{P}_{\bar{u}}$. This trajectory will serve us to draw the orbits (*paths*) travelled by trajectories for different values of u_0 and u_1 .

In Fig. 2(A), the orbit exhibits a change of variation in θ_{10}^t when the plane \mathcal{P}_{1-x} is crossed. This corresponds to the *instant of time* in which $\theta_{10}^{t+\delta} - \theta_{10}^t = 0$ in Eq. (13) for $ij = 10$. Similarly, Fig. 2(B) shows a change of variation in θ_{01} when the trajectory crosses \mathcal{P}_x , i.e. when $\theta_{01}^{t+\delta} - \theta_{01}^t = 0$ in Eq. (13) for $ij = 01$. Meanwhile, θ_{11} does not change its variation because $\theta_{11}^{t+\delta} - \theta_{11}^t \neq 0$ under \mathcal{P}_1 in Eq. (13) for $ij = 11$ (this is precisely the reason why θ_{11} has been chosen as the vertical coordinate).

If $u_1 < 0 < u_0$, then \bar{u} is either smaller than 0 (if $u_0 + u_1 < 0$) or larger than 1 (if $u_0 + u_1 > 0$). In consequence, the expression $(u_0 + u_1)(f(\boldsymbol{\theta}^t) - \bar{u})$ is always negative. If u_0 and u_1 have the same sign, then $0 < \bar{u} < 1$ and $(u_0 + u_1)(f(\boldsymbol{\theta}^t) - \bar{u})$ has a different sign at each side of the plane $\mathcal{P}_{\bar{u}}$.

In Figs. 1 and 2, the trajectory starts from below \mathcal{P}_x and close to $(0, 0, 0)$, that is, with a small value of $f(\boldsymbol{\theta}^0)$, and from the interior of Ω , i.e., out of the planes $\theta_{11} = 0$ and $\theta_{00} = 0$.

Assume that $(u_0 + u_1)(f(\boldsymbol{\theta}^t) - \bar{u})$ here. Then, Eq. (13) shows that $\theta_{11}^{t+\delta} - \theta_{11}^t$ is always positive so the trajectory always moves upwards, away from the plane $\theta_{11} = 0$, and is thus forced to cross successively the planes \mathcal{P}_x and \mathcal{P}_{1-x} . Outside the plane $\theta_{00} = 0$, $\theta_{00}^{t+\delta} - \theta_{00}^t$ is always negative so the trajectory moves also toward the plane $\theta_{00} = 0$. Above \mathcal{P}_x , $\theta_{10}^{t+\delta} - \theta_{10}^t$ becomes negative, and above \mathcal{P}_{1-x} , it is $\theta_{01}^{t+\delta} - \theta_{01}^t$ which becomes negative, so that in this upper region, both θ_{10}^t and θ_{01}^t decrease, while θ_{11}^t increases, in such a way that $\boldsymbol{\theta}^t$ necessarily converges to $(0, 0, 1)$. Trajectories starting directly from between \mathcal{P}_x and \mathcal{P}_{1-x} or from above \mathcal{P}_{1-x} are subject to the same scenario and therefore converge to $(0, 0, 1)$.

The above description defines the orbits of the dynamical system (11); a change in the sign of $(u_0 + u_1)(f(\boldsymbol{\theta}^t) - \bar{u})$ leads simply to a change of direction in which the orbits are travelled. Thus, the general behavior is as follows:

- If $u_1 < 0 < u_0$, the orbits are travelled downwards, i.e., in the direction in which θ_{11}^t decreases. Once the trajectory is below \mathcal{P}_x , θ_{10}^t and θ_{01}^t decrease, so the trajectory necessarily converge to the unique asymptotically stable point $(0, 0, 0)$.

When u_0 and u_1 have the same sign, the direction with which orbits are travelled is determined by the sign of $(u_0 + u_1)$ and the relative position of the initial condition $\boldsymbol{\theta}^0$ with respect to the (now non-empty) plane $\mathcal{P}_{\bar{u}}$:

- If $u_0 < 0$ and $u_1 < 0$, the trajectories starting from below $\mathcal{P}_{\bar{u}}$ are such that $f(\boldsymbol{\theta}^t) - \bar{u} < 0$ so $\theta_{11}^{t+\delta} - \theta_{11}^t$ is positive and the orbits are travelled in the direction in which θ_{11}^t increases, i.e., towards $\mathcal{P}_{\bar{u}}$. In turn, trajectories starting from above $\mathcal{P}_{\bar{u}}$ are such that $f(\boldsymbol{\theta}^t) - \bar{u} < 0$ and thus travel the orbits in the direction of decreasing θ_{11}^t , again towards $\mathcal{P}_{\bar{u}}$. In the continuous-time case, such a behavior would mean that the plane $\mathcal{P}_{\bar{u}}$ is an attractor. However, in the discrete-time case, trajectories can jump over $\mathcal{P}_{\bar{u}}$, and can eventually oscillate around $\mathcal{P}_{\bar{u}}$, not necessarily converging (i.e., reducing the distance) to $\mathcal{P}_{\bar{u}}$. It is then not possible to classify $\mathcal{P}_{\bar{u}}$ as an attractor; this is in fact the aim of the next Sec. 5.4. It is nevertheless possible to say, in both the continuous and the discrete cases, that the four vertices of Ω are unstable.
- If $u_0 > 0$ and $u_1 > 0$, the travelling direction is reversed with respect to the previous case so trajectories move away from $\mathcal{P}_{\bar{u}}$: trajectories starting from above $\mathcal{P}_{\bar{u}}$ converge to $(0, 0, 1)$, and those starting from below $\mathcal{P}_{\bar{u}}$ converge to $(0, 0, 0)$, so that these two points are asymptotically stable, while $(1, 0, 0)$ and $(0, 1, 0)$ are unstable. Here yes, $\mathcal{P}_{\bar{u}}$ can be classified as a repeller.

5.4 Stability of the invariant manifold $\mathcal{P}_{\bar{u}}$

In this Section, we show that, when $u_0 < 0$ and $u_1 < 0$, then $\mathcal{P}_{\bar{u}}$ is an attractor, i.e., trajectories move towards $\mathcal{P}_{\bar{u}}$, while when $u_0 > 0$ and $u_1 > 0$, $\mathcal{P}_{\bar{u}}$ is a repeller, i.e., trajectories move away from $\mathcal{P}_{\bar{u}}$ and converge to the respective asymptotically stable vertex located in the same side of $\mathcal{P}_{\bar{u}}$ where the trajectory started.

Definition 2 *The basin of attraction of a closed set $M \subset \Omega$ is the set $B_M \subset \Omega$ of points whose trajectories converge to M , i.e.*

$$B_M = \{ \boldsymbol{\theta}^0 \in \Omega : \exists t_0 \geq 0 \text{ such that } t > t_0 \Rightarrow \boldsymbol{\theta}^t \in M \}. \quad (14)$$

When B_M is a neighborhood of M , M is called an attractor.⁶

⁶ Again, as B_M is not necessarily an open set, we relax this definition and we will say that M is an attractor if $M \subseteq B_M$.

We prove the following result: If cooperation is not useless, there are polymorphic states where the frequency of cooperation $f(\boldsymbol{\theta})$ is \bar{u} . If partial cooperation is sufficient, the population tends to evolve toward one of these polymorphic state. By contrast, if full cooperation is required, the population tends to converge to one of the two monomorphic asymptotically stable states: “always defect” if the initial frequency of cooperation is smaller than \bar{u} , or “always cooperate” if it is larger than \bar{u} .

Theorem 3 *When $\bar{u} \in (0, 1)$, the invariant manifold $\mathcal{P}_{\bar{u}}$ is not empty. Then:*

- *If $u_0 < 0$ and $u_1 < 0$, the sufficient condition of well-posedness of the replicator system (11) for $\delta \in [0, 1]$ is a sufficient condition for $\mathcal{P}_{\bar{u}}$ to be an attractor of the interior of Ω .*
- *If $u_0 > 0$ and $u_1 > 0$, trajectories starting from the interior of Ω move away from $\mathcal{P}_{\bar{u}}$ and converge to the asymptotically stable vertex located in the same side of $\mathcal{P}_{\bar{u}}$ than their initial condition.*

Again, trajectories living in the boundary of Ω have a rich casuistry and will be studied elsewhere; when $\mathcal{P}_{\bar{u}}$ doesn't cross the planes $\theta_{11} = 0$ or $\theta_{00} = 0$, trajectories living in these planes cannot converge asymptotically to $\mathcal{P}_{\bar{u}}$, so $\mathcal{P}_{\bar{u}}$ cannot be considered a global attractor. If $x < c < 1 - x$, then $\mathcal{P}_{\bar{u}}$ intersects all the faces of Ω , but, still, not all the edges of Ω can be intersected by $\mathcal{P}_{\bar{u}}$, so, in some edges, trajectories exist which cannot arrive to $\mathcal{P}_{\bar{u}}$. Thus, $\mathcal{P}_{\bar{u}}$ is a global attractor of the interior of Ω , but *not* of the whole Ω .

The qualitative description of the behavior of inner trajectories given in Sec. 5.3 shows that, when $u_0 < 0$ and $u_1 < 0$, trajectories always move towards $\mathcal{P}_{\bar{u}}$. However, in the discrete-time case, trajectories can jump over manifolds, so, despite the fact that the trajectory travels the orbit in the direction of approaching $\mathcal{P}_{\bar{u}}$, the distance from the trajectory to $\mathcal{P}_{\bar{u}}$ does not necessarily decrease. Although the evolution of this distance can be studied numerically, it suffices to our proof to find conditions for δ such that trajectories are not allowed to jump over $\mathcal{P}_{\bar{u}}$.

Lemma 3 *The function $P(\boldsymbol{\theta}) = \theta_{11} + x^2\theta_{10} + (1-x)^2\theta_{01} - [f(\boldsymbol{\theta})]^2$ verifies*

- (i) $P(\boldsymbol{\theta}) \geq 0$ for all $\boldsymbol{\theta} \in \Omega$,
- (ii) If $\boldsymbol{\theta}$ is a vertex of Ω then $P(\boldsymbol{\theta}) = 0$,
- (iii) $P(\boldsymbol{\theta}) \leq f(\boldsymbol{\theta}) - [f(\boldsymbol{\theta})]^2$ for all $\boldsymbol{\theta} \in \Omega$.

Proof Let us consider the Cauchy-Schwartz inequality

$$(\alpha_1\beta_1 + \alpha_2\beta_2 + \alpha_3\beta_3)^2 \leq (\alpha_1^2 + \alpha_2^2 + \alpha_3^2)(\beta_1^2 + \beta_2^2 + \beta_3^2)$$

with $\alpha_1 = \sqrt{\theta_{11}}$, $\alpha_2 = x\sqrt{\theta_{10}}$, $\alpha_3 = (1-x)\sqrt{\theta_{01}}$, $\beta_1 = \sqrt{\theta_{11}}$, $\beta_2 = \sqrt{\theta_{10}}$ and $\beta_3 = \sqrt{\theta_{01}}$. Then,

$$(\theta_{11} + x\theta_{10} + (1-x)\theta_{01})^2 \leq (\theta_{11} + x^2\theta_{10} + (1-x)^2\theta_{01})(\theta_{11} + \theta_{10} + \theta_{01}),$$

so $[f(\boldsymbol{\theta})]^2 \leq \theta_{11} + x^2\theta_{10} + (1-x)^2\theta_{01}$ for all $\boldsymbol{\theta} \in \Omega$ and (i) is proved.

Part (ii) is obvious, and so is (iii), by noting that $x < 1$ and $1-x < 1$, so

$$P(\boldsymbol{\theta}) \leq \theta_{11} + x\theta_{10} + (1-x)\theta_{01} - [f(\boldsymbol{\theta})]^2 = f(\boldsymbol{\theta}) - [f(\boldsymbol{\theta})]^2. \quad \square$$

Proof of Theorem 3. A trajectory starting from a point $\boldsymbol{\theta}^0$ will jump from one side of $\mathcal{P}_{\bar{u}}$ to the other in one single iteration if and only if

$$\operatorname{sgn}\{f(\boldsymbol{\theta}^\delta) - \bar{u}\} \neq \operatorname{sgn}\{f(\boldsymbol{\theta}^0) - \bar{u}\}.$$

Expanding $f(\boldsymbol{\theta}^\delta)$ according to the replicator system equations (11), we have

$$\begin{aligned} f(\boldsymbol{\theta}^\delta) &= f(\boldsymbol{\theta}^0) + \delta \frac{(u_0 + u_1) [f(\boldsymbol{\theta}^0) - \bar{u}] [\theta_{11}^0 + x^2 \theta_{10}^0 + (1-x)^2 \theta_{01}^0 - [f(\boldsymbol{\theta}^0)]^2]}{1 - \delta + \delta [f(\boldsymbol{\theta}^0)]^2 u_1 + \delta [1 - f(\boldsymbol{\theta}^0)]^2 u_0} \\ &= f(\boldsymbol{\theta}^0) + \delta \frac{(u_0 + u_1) [f(\boldsymbol{\theta}^0) - \bar{u}] P(\boldsymbol{\theta}^0)}{1 - \delta + \delta [f(\boldsymbol{\theta}^0)]^2 u_1 + \delta [1 - f(\boldsymbol{\theta}^0)]^2 u_0}, \end{aligned}$$

where we have used the function $P(\boldsymbol{\theta})$ defined in Lemma 3. Then,

$$\begin{aligned} f(\boldsymbol{\theta}^\delta) - \bar{u} &= (f(\boldsymbol{\theta}^0) - \bar{u}) \left[1 + \frac{\delta (u_0 + u_1) P(\boldsymbol{\theta}^0)}{1 - \delta + \delta [f(\boldsymbol{\theta}^0)]^2 u_1 + \delta [1 - f(\boldsymbol{\theta}^0)]^2 u_0} \right] \\ &= (f(\boldsymbol{\theta}^0) - \bar{u}) \left[\frac{1 - \delta + \delta [f(\boldsymbol{\theta}^0)]^2 u_1 + [1 - f(\boldsymbol{\theta}^0)]^2 u_0 + (u_0 + u_1) P(\boldsymbol{\theta}^0)}{1 - \delta + \delta [f(\boldsymbol{\theta}^0)]^2 u_1 + \delta [1 - f(\boldsymbol{\theta}^0)]^2 u_0} \right] \end{aligned} \quad (15)$$

We have:

- If $u_0 < 0$ and $u_1 < 0$, the denominator of (15), which is precisely the denominator of expression (11), is strictly positive by (ii) in Lemma 1 because $\delta < \bar{\delta}$. Using (iii) from Lemma 3 and noting that $u_0 + u_1 < 0$, we see that the numerator of (15) is larger than

$$\begin{aligned} &1 - \delta + \delta \left[[f(\boldsymbol{\theta}^0)]^2 u_1 + [1 - f(\boldsymbol{\theta}^0)]^2 u_0 + (u_0 + u_1) [f(\boldsymbol{\theta}^0) - [f(\boldsymbol{\theta}^0)]^2] \right] \\ &= 1 - \delta + \delta [f(\boldsymbol{\theta}^0) u_1 + [1 - f(\boldsymbol{\theta}^0)] u_0]. \end{aligned}$$

As $f(\boldsymbol{\theta}^0) \in [0, 1]$, we have $f(\boldsymbol{\theta}^0) u_1 + [1 - f(\boldsymbol{\theta}^0)] u_0 \geq \min\{u_0, u_1\}$, so the numerator of (15) is larger than $1 - \delta + \delta \min\{u_0, u_1\}$, which is strictly positive when condition $\delta < \bar{\delta}$ is verified. Then the factor of $f(\boldsymbol{\theta}^0) - \bar{u}$ in (15) is strictly positive and trajectories are not allowed to jump over $\mathcal{P}_{\bar{u}}$.

- If $u_1 > 0$ and $u_0 > 0$, then, by (i) in Lemma 1, the denominator of expression (15) is strictly positive for all $\boldsymbol{\theta}^0 \in \Omega$, and, by (i) in Lemma 3 and noting that $u_0 + u_1 > 0$, so is the numerator of expression (15). Again, trajectories are not allowed to jump over $\mathcal{P}_{\bar{u}}$. \square

6 Relaxation of condition $\delta < \bar{\delta}$ when u_0 and u_1 are negative

When u_0 and u_1 are negative, the tetrahedron Ω is divided in two regions by the plane $\mathcal{P}_{\bar{u}}$: the upper region, where $f(\boldsymbol{\theta}) \geq \bar{u}$, contains the vertex $(0, 0, 1)$, and the lower region, where $f(\boldsymbol{\theta}) \leq \bar{u}$, contains the vertex $(0, 0, 0)$. From (ii) in Lemmas 1 and 2, it turns out that, for trajectories starting from the upper region, the condition preventing them from leaving Ω in a single iteration

is $\delta < 1/(1 - u_1)$, while for trajectories starting from the lower region, the condition is $\delta < 1/(1 - u_0)$. As $u_0 \neq u_1$, one of these conditions is less restrictive than the other, so that, at least for one single iteration, the general well-posedness condition $\delta < \bar{\delta}$ can be relaxed for trajectories starting from the region where the condition is less restrictive.

Denote by $\Omega_{\bar{u}} \subset \Omega$ the region where the condition is less restrictive; when $u_1 > u_0$, $\Omega_{\bar{u}}$ is the upper region, and when $u_1 < u_0$, $\Omega_{\bar{u}}$ is the lower region. Then, we have the following

Theorem 4 *Let δ_J be the following critical value of $\delta \in [0, 1]$:*

$$\delta_J = \frac{u_0 + u_1}{u_0 + u_1 - 2u_0u_1}.$$

Then, the restriction $\delta < \delta_J$ is a sufficient condition for the well-posedness of the discrete-time replicator system in the region $\Omega_{\bar{u}}$.

Recall that we refer to large benefits of cooperation if the ratio cost-benefit is larger than $1/2$ ($u_0 < u_1 < 0$) and to small benefits of cooperation if the ratio cost-benefit is smaller than $1/2$. The theorem provides the optimal bound for δ so that, when partial cooperation is sufficient, the system is well posed for games with large (respectively small) benefits of cooperation, as long as the initial condition is such that the frequency of defection $1 - f(\boldsymbol{\theta})$ is smaller (respectively larger) than the cost-benefit ratio $1 - \bar{u}$.

The proof of Theorem 4 consists in showing that the condition $\delta < \delta_J$ is sufficient to prevent trajectories from jumping over $\mathcal{P}_{\bar{u}}$. It is easy to show that δ_J is smaller than the less restrictive bound $1/(1 - \max\{u_0, u_1\})$. Then, if $\delta < \delta_J$, trajectories starting from $\Omega_{\bar{u}}$ will not leave Ω in a single iteration, and will not jump over $\mathcal{P}_{\bar{u}}$, therefore being confined to $\Omega_{\bar{u}}$ for all successive iterations.

Proof The proof is done for the case $u_1 > u_0$. We are then in the upper region $\Omega_{\bar{u}} = \{\boldsymbol{\theta} \in \Omega: f(\boldsymbol{\theta}) > \bar{u}\}$. For the case $u_1 < u_0$, the proof is identical by simply changing to the lower region and swapping u_1 and u_0 in all the expressions (note that δ_J remains unchanged).

As shown in the proof of Theorem 3, jumps over $\mathcal{P}_{\bar{u}}$ are prevented if the factor of $f(\boldsymbol{\theta}^0) - \bar{u}$ in (15) is positive. When $\delta < \delta_J$, trajectories starting from $\Omega_{\bar{u}}$ are prevented from leaving Ω in one iteration. This means that the denominator of expression (15), which is precisely the denominator of expression (11), is strictly positive for all $\boldsymbol{\theta} \in \Omega$.

On the other hand, as shown also in the proof of Theorem 3, the numerator of (15) is larger or equal to the following expression for all $\boldsymbol{\theta} \in \Omega$:

$$1 - \delta + \delta u_0 + \delta(u_1 - u_0)f(\boldsymbol{\theta}^t).$$

For trajectories starting from $\Omega_{\bar{u}}$, this expression can be viewed as a linearly increasing function of $f(\boldsymbol{\theta})$ in $[\bar{u}, 1]$ (recall that $u_1 > u_0$ and that we are in

the upper region of the tetrahedron). The minimum of this function is thus reached at the left boundary of the interval $[\bar{u}, 1]$. There, its value is

$$1 - \delta + 2\delta \frac{u_0 u_1}{u_0 + u_1},$$

which is strictly positive if and only if $\delta < (u_0 + u_1)/(u_0 + u_1 - 2u_0 u_1)$, which equivals to the condition $\delta < \delta_J$. Then, the numerator of (15) in $\Omega_{\bar{u}}$ is strictly positive for all $\theta \in \Omega$. Moreover, as the numerator reaches this value when $\theta = (0, 0, \bar{u}) \in \Omega_{\bar{u}}$, the bound δ_J can not be refined. \square

7 Conclusion

A taxonomy of 2×2 symmetric games involving cooperation has been proposed. When cooperation is beneficial, two cases have been considered: when full cooperation is required to obtain the benefit and when partial cooperation is sufficient. A third case has been added, that occurs when the cost is larger than the benefit so that cooperation is useless.

We have studied the conditions under which cooperation can emerge in heterogeneous populations where individuals ignore if they are interacting with an individual of their own type. They recognize their opponent's type but do not know their own type. We have proposed a model to describe the evolution of such populations in the framework of evolutionary game theory. To do that, the population has been divided in four subgroups, according to the four pure strategies that an individual can display in an encounter with another individual: to cooperate or to defect which each of both types of individual. We have used the replicator dynamics to follow the variation in size of each subgroup of the population. As we have considered the case where generations overlap, we have used the discrete-time formulation of the replicator system.

The study of the discrete-time formulation of the replicator dynamics is closely related to the continuous-time case. As noted by Weibull, such a study consists essentially in establishing the conditions under which the discrete trajectories, which evolve by jumps, follow the continuous ones, paying especial attention to prevent the trajectories from jumping outside the state-space Ω . The fundamental parameter is thus the size of the jumps, i.e., δ , the time-step of the time evolution, which in this model coincides with the population fraction subject to changes in each generation.

We have thus obtained the restrictions acting upon δ to prevent trajectories from jumping outside Ω . It turned out, not surprisingly, that these conditions guarantee the well-posedness of the system, and that, under these conditions, the discrete trajectories follow the path of the continuous ones (Theorem 1). The result is that in games where full cooperation is required, there is no restrictions for δ , while in games where partial cooperation is sufficient or cooperation is useless, δ must be such that $\delta < \bar{\delta} = 1/(1 - \min\{u_0, u_1\})$.

This relation shows that, for example, in games where partial cooperation is sufficient, the larger is the absolute difference between the utilities of each option (cooperate or defect), i.e., $|u_0|$ or $|u_1|$, the shorter δ must be, i.e., the slower the population must evolve. Reciprocally, the smaller is the difference between both options, the faster the population can evolve.

Then, we have performed the stability analysis of the dynamical system, finding the same result than in the continuous case. The asymptotical stability of the monomorphic states has been established by means of the analysis of the time evolution of a perturbation of these states and the corresponding study of the eigenvalues for each kind of game (Theorem 2):

- (i) If full cooperation is required, the population evolves towards one of the two monomorphic states, where all individuals always cooperate ($\theta_{11} = 1$) or always defect ($\theta_{00} = 1$).
- (ii) If cooperation is useless, the population evolves towards the state where all individuals are defectors ($\theta_{00} = 1$).

If partial cooperation is sufficient, the population evolves towards a polymorphic state where the frequency of defection is given by the cost-benefit ratio $1 - \bar{u}$. The stability of the invariant manifold $\mathcal{P}_{\bar{u}}$ has been studied specifically after giving a detailed description of the behavior of trajectories starting from the interior of Ω . The reason of this specific study is that the jumps of the discrete-time case trajectories can make trajectories to traverse not only the invariant manifolds located in the boundary of the state-space, but also those located in the interior of the state-space, as it is the case of $\mathcal{P}_{\bar{u}}$. We have then derived the conditions for δ under which trajectories cannot cross the stable set $\mathcal{P}_{\bar{u}}$, finding that the conditions precisely coincide with the well-posedness conditions. This proves, consequently, that $\mathcal{P}_{\bar{u}}$ has the same status than in the continuous-time case: $\mathcal{P}_{\bar{u}}$ is an attractor in games where partial cooperation is sufficient, and a repeller in games where cooperation is useless (Theorem 3).

The calculations carried out to show that $\mathcal{P}_{\bar{u}}$ is an attractor in games where partial cooperation is sufficient have suggested us the possibility of relaxing the restriction on δ when the initial condition of the trajectory can be selected appropriately. We have found the conditions under which a trajectory starting from the appropriate side of the state-space with respect to $\mathcal{P}_{\bar{u}}$ will remain indefinitely in the same side of $\mathcal{P}_{\bar{u}}$. The result is that a larger value of δ can be used which prevents trajectories from leaving the region from which they depart (Theorem 4): if a trajectory starts from the interior of $\Omega_{\bar{u}}$, then the sufficient condition for δ to prevent the trajectory from leaving $\Omega_{\bar{u}}$ is $\delta < \delta_J = (u_0 + u_1)/(u_0 + u_1 - 2u_0u_1)$.

The condition is effectively a relaxation because $\bar{\delta} < \delta_J$, so that δ can be choosed larger than $\bar{\delta}$. This is especially interesting for the case in which the configuration of the initial condition can be selected arbitrarily. By choosing θ^0 in $\Omega_{\bar{u}}$, it is possible to use a larger value of $\delta > \bar{\delta}$ so that the time-steps of the discrete-time trajectories along the orbits of the continuous case are larger, thus accelerating the convergence of the population to the corresponding asymptotically stable state. This can be interesting for populations where,

for example, partial cooperation is sufficient and cooperation frequency has to be maximized. Then, if the initial condition is below $\mathcal{P}_{\bar{u}}$ (where the frequency of cooperation is smaller than \bar{u}), the largest time-step δ_J will allow the population to reach the optimal frequency of cooperation as fast as possible. This last result is specific to the discrete-time case.

Immediate further works should start with the extension of this work to trajectories which can start in the boundary of Ω , that is, in faces and edges of the tetrahedron. This is especially interesting for studying degenerate populations where one of the pure strategies is not present. In particular, the face $\theta_{11} = 0$ corresponds to populations where individuals cooperate with only one type of individuals and discrimination towards the most or least frequent type can take place. Although it is presumable that the stability analysis will yield similar results than in the continuous case, the casuistry of how the invariant manifold $\mathcal{P}_{\bar{u}}$ intersects faces and edges for different values of \bar{u} with respect to the proportion of individuals of each type x and $1 - x$ is very rich and novel results are to be expected.

The values of δ considered in this work have been focussed on general properties of all the trajectories starting in Ω . However, particular initial conditions (corresponding to particular populations) can allow the use of larger values of δ . Our numerical simulations have revealed the existence of trajectories that, for some values of δ , jump over $\mathcal{P}_{\bar{u}}$ more than once. We thus plan to explore the possibility of finding stable oscillatory trajectories which indefinitely jump over $\mathcal{P}_{\bar{u}}$ from one point in one region of Ω to another point in the other region of Ω and *vice versa*. Potential routes to chaos should not be discarded if trajectories jump over $\mathcal{P}_{\bar{u}}$ from different points in each region.

Appendix

Proof of Theorem 2: The general expression of the Jacobian matrix $J\mathcal{F}(\boldsymbol{\theta})$ of the vector function $\mathcal{F}(\boldsymbol{\theta})$, where $\boldsymbol{\theta} = (\theta_{10}, \theta_{01}, \theta_{11})$, is given by

$$J\mathcal{F}(\boldsymbol{\theta}) = \begin{pmatrix} \frac{\partial F_{10}}{\partial \theta_{10}} & \frac{\partial F_{10}}{\partial \theta_{01}} & \frac{\partial F_{10}}{\partial \theta_{11}} \\ \frac{\partial F_{01}}{\partial \theta_{10}} & \frac{\partial F_{01}}{\partial \theta_{01}} & \frac{\partial F_{01}}{\partial \theta_{11}} \\ \frac{\partial F_{11}}{\partial \theta_{10}} & \frac{\partial F_{11}}{\partial \theta_{01}} & \frac{\partial F_{11}}{\partial \theta_{11}} \end{pmatrix},$$

which must be evaluated on the vertices of Ω . Recall, from (12), that

$$F_{ij}(\boldsymbol{\theta}) = \theta_{ij} \left[1 + \delta \frac{(u_0 + u_1) [f_{ij} - f(\boldsymbol{\theta})] [f(\boldsymbol{\theta}) - \bar{u}]}{1 - \delta + \delta [f(\boldsymbol{\theta})]^2 u_1 + \delta [1 - f(\boldsymbol{\theta})]^2 u_0} \right].$$

Defining the function $R(\xi): [0, 1] \rightarrow \mathbb{R}$ as follows,

$$R(\xi) \stackrel{def}{=} \frac{(u_0 + u_1)(\xi - \bar{u})}{1 - \delta + \delta \xi^2 u_1 + \delta (1 - \xi)^2 u_0},$$

we have

$$F_{ij}(\boldsymbol{\theta}) = \theta_{ij} \left[1 + \delta [f_{ij} - f(\boldsymbol{\theta})] R(f(\boldsymbol{\theta})) \right],$$

so the ij - kl -element of $J\mathcal{F}(\boldsymbol{\theta})$, for $kl = ij$ or not, is

$$\begin{aligned} \frac{\partial F_{ij}(\boldsymbol{\theta})}{\partial \theta_{kl}} &= \frac{\partial \theta_{ij}}{\partial \theta_{kl}} \left[1 + \delta [f_{ij} - f(\boldsymbol{\theta})] R(f(\boldsymbol{\theta})) \right] \\ &\quad + \delta \theta_{ij} \frac{\partial f(\boldsymbol{\theta})}{\partial \theta_{kl}} \left[\frac{\partial R(f(\boldsymbol{\theta}))}{\partial f(\boldsymbol{\theta})} [f_{ij} - f(\boldsymbol{\theta})] - R(f(\boldsymbol{\theta})) \right]. \end{aligned} \quad (16)$$

If $\boldsymbol{\theta}^*$ is a vertex of Ω , there exists a unique label $pq \in \mathcal{I}$ such that $\theta_{pq}^* = 1$, i.e., $\theta_{ij}^* = 0$ for all $ij \in \mathcal{I}$, $ij \neq pq$. Then, $f(\boldsymbol{\theta}^*) = f_{pq}\theta_{pq}^* = f_{pq}$. Then:

(i) If $ij = pq$, then $f_{ij} - f(\boldsymbol{\theta}^*) = f_{ij} - f_{pq} = 0$, so

$$\frac{\partial F_{ij}(\boldsymbol{\theta}^*)}{\partial \theta_{kl}} = \frac{\partial \theta_{ij}}{\partial \theta_{kl}} - \delta f_{kl} R(f_{pq}).$$

(ii) If $ij \neq pq$, then $\theta_{ij} = 0$ and the second term in (16) vanishes. Thus:

- If $ij = kl$, $\partial F_{ij}(\boldsymbol{\theta}^*)/\partial \theta_{kl} = 1 + \delta(f_{ij} - f_{pq})R(f_{pq})$
- If $ij \neq kl$, $\partial F_{ij}(\boldsymbol{\theta}^*)/\partial \theta_{kl} = 0$.

The Jacobian matrices and the corresponding eigenvalues are then as follows:

- For $\boldsymbol{\theta}^* = (0, 0, 0)$, we have $R(0) = -u_0/(1 - \delta + \delta u_0)$, so

$$J\mathcal{F}(0, 0, 0) = \frac{1}{1 - \delta + \delta u_0} \begin{pmatrix} 1 - \delta + \delta u_0(1 - x) & 0 & 0 \\ 0 & 1 - \delta + \delta u_0 x & 0 \\ 0 & 0 & 1 - \delta \end{pmatrix}.$$

The eigenvalues are given by the roots of the determinant $|J\mathcal{F}(\boldsymbol{\theta}^*) - \lambda \mathbb{I}|$, where \mathbb{I} is the identity matrix, so

$$\lambda_1 = \frac{1 - \delta + \delta u_0(1 - x)}{1 - \delta + \delta u_0}, \quad \lambda_2 = \frac{1 - \delta + \delta u_0 x}{1 - \delta + \delta u_0} \quad \text{and} \quad \lambda_3 = \frac{1 - \delta}{1 - \delta + \delta u_0}.$$

The condition for asymptotic stability is $|\lambda_i| < 1 \forall i = 1, 2, 3$, which happens if and only if $u_0 > 0$. Thus, $(0, 0, 0)$ is asymptotically stable if and only if $u_0 > 0$.

- For $\boldsymbol{\theta}^* = (0, 0, 1)$, we have $R(1) = u_1/(1 - \delta + \delta u_1)$ so

$$J\mathcal{F}(0, 0, 1) = \begin{pmatrix} 1 - \delta + \delta u_1 x & 0 & 0 \\ 0 & 1 - \delta + \delta u_1(1 - x) & 0 \\ -\delta u_1 x & -\delta u_1(1 - x) & 1 - \delta \end{pmatrix}.$$

The eigenvalues are

$$\lambda_1 = \frac{1 - \delta + \delta u_1 x}{1 - \delta + \delta u_1}, \quad \lambda_2 = \frac{1 - \delta + \delta u_1(1 - x)}{1 - \delta + \delta u_1} \quad \text{and} \quad \lambda_3 = \frac{1 - \delta}{1 - \delta + \delta u_1},$$

which are such that $|\lambda_i| < 1 \forall i = 1, 2, 3$, provided $u_1 > 0$. Then, $(0, 0, 1)$ is asymptotically stable if and only if $u_1 > 0$.

- For $\theta^* = (1, 0, 0)$, we have $f(\theta^*) = x$, so

$$J\mathcal{F}(1, 0, 0) = \begin{pmatrix} 1 - \delta x R(x) & -\delta(1-x)R(x) & -\delta R(x) \\ 0 & 1 + \delta(1-2x)R(x) & 0 \\ 0 & 0 & 1 + \delta(1-x)R(x) \end{pmatrix},$$

whose first two eigenvalues are $\lambda_1 = 1 - \delta x R(x)$ and $\lambda_2 = 1 + \delta(1-2x)R(x)$. Now: $\lambda_1 < 1 \Rightarrow R(x) > 0$ and $\lambda_2 < 1 \Rightarrow R(x) < 0$, which cannot be simultaneously verified, so $(1, 0, 0)$ is unstable for all values of u_0 and u_1 .

- For $\theta^* = (0, 1, 0)$, we have $f(\theta^*) = 1 - x$, so $J\mathcal{F}(0, 1, 0) =$

$$\begin{pmatrix} 1 - \delta(1-2x)R(1-x) & 0 & 0 \\ -\delta x R(1-x) & 1 - \delta(1-x)R(1-x) & -\delta R(1-x) \\ 0 & 0 & 1 + \delta x R(1-x) \end{pmatrix}.$$

Here $\lambda_1 = 1 - \delta(1-2x)R(1-x)$ and $\lambda_3 = 1 + \delta x R(1-x)$, for which $\lambda_1 < 1$ and $\lambda_3 < 1$ are incompatible conditions, so $(0, 1, 0)$ is unstable for all cases. \square

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