Emergence of cooperation in phenotypically heterogeneous populations: a replicator dynamics analysis

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Abstract. The emergence of cooperation is analyzed in heterogeneous populations where two kinds of individuals exist 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. Individuals thus behave under partial information conditions. The interactions between individuals are described by the snowdrift game, where individuals can either cooperate or defect. The evolution of such populations is studied in the framework of evolutionary game theory by means of the replicator dynamics. Overlapping generations are considered, so the replicator equations are

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formulated in discrete-time form. 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 the four monomorphic states are unstable and that a polymorphic state exists which is a global attractor for non-degenerate initial states of the population. The result for the discrete-time replicator coincides with the one of the continuous case.

Keywords: game-theory (theory), applications to game theory and mathematical economics, critical phenomena of socio-economic systems, nonlinear dynamics

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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 1982). Nowak (2006a) 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 and Sigmund 1998), (4) reciprocity in networks in not well-mixed populations (Veloz et al. 2014) 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 channelled towards individuals that carry the same tag, i.e. that have a sufficiently similar phenotype. 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 phenotypic difference between neighbor individuals. The aim of the present article is to study the emergence of cooperation when individuals are unable to recognize their own tag but perceive the tag of their opponent.

The motivation is twofold. 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. With such marking, individuals know whether their opponents are marked or not but do not know whether themselves are marked or not7. Nevertheless, Dennis et al (2008) observed that marked fowls suffer more aggressive events and have less body mass than their unmarked pen mates. Iñarra and Laruelle (2012) propose a model for the experiment, a variation of the hawk-dove game with finite heterogeneous population and incomplete information. Types are payoff irrelevant. The present paper can be seen as an extension from the static analysis of the problem to a dynamic one by using the replicator dynamics. An alternative motivation for our study can be found in the evolution of emotions: in certain situations, individuals may decide to act differently depending on whether the opponent looks angry, cooperative, etc. When players meet, they perceive the emotion on the opponent but do not know how they are perceived (Frank 2011).

More precisely, the present paper studies the emergence of cooperation in snowdrift games where individuals have two types. Individuals are unable to recognize their own type but perceive their opponent’s type. There are four pure strategies: (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. 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 and Sigmund (1998) and Albuszta and Miękisz (2004).

Previously, Weibull (1995) studies the replicator dynamics in homogeneous populations and with players having complete information. The first contribution of this paper is the extension to the case of heterogeneous populations of individuals with incomplete information and with overlapping and non-overlapping generations, therefore presenting both the continuous and discrete-time formulations of the replicator dynamics. Weibull (1995) assumes either positive payoffs and/or a high enough positive background birthrate constant $\beta$ to ensure the well-posedness of the discrete replicator dynamics. By contrast we focus on the size of the discrete time-step $\delta$, i.e. we derive

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7 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).
alternative restrictions on the minimum number of overlapping generations that still ensure mathematical well-posedness. In fact, our result for an upper bound for $\delta$ (i.e. a minimum number of overlapping generations) is equivalent to finding a lower bound for the parameter $\beta$ added by Weibull.

While our analytical model keeps some important similarities with Riolo et al. (2001)'s numerical model such as (i) the establishment of rules for the emergence of type based cooperation without relying on direct or indirect reciprocity and (ii) the dependence of the frequency of cooperation on the cost-to-benefit ratio, we introduce some important differences. The first is that, as already mentioned, individuals do not know their own type. A second important difference regards the fact that type is not heritable but introduced artificially, so that offspring inherit strategies but not necessarily the type of their parents. Despite not knowing their own type, we show that the emergence of cooperation among individuals is still feasible and sustainable.

It should be emphasized that we work in the context of a very large population whose evolution relies on deterministic selection, in which the fittest strategies always survive and coexist in the steady-state, thus pushing the less fit strategies to extinction. When there is one single fittest strategy, the population becomes monomorphic. This approach has some important differences when compared with microscopic processes taking place in a finite well-mixed population as studied in Nowak et al. (2004), Nowak (2006b), Traulsen et al. (2006), Wild and Traulsen (2007) and Ji and Xian-Jia (2011), among several other works in the vast literature. Under finite population, evolution is often modelled with a frequency-dependent Moran process (Moran 1958, 1962) in which an individual is randomly selected for reproduction with a probability proportional to her fitness obtained from the game, thus producing one offspring, which then replaces a randomly selected individual (possibly the parent), keeping the population size constant.

The outcome of such a stochastic evolutionary process relies on the interplay between random drift and selection and a less fit mutant might be able to invade and become fixed, thus replacing an incumbent population even in games where the incumbent population strategy is strictly dominant. Coexistence of strategies in the long run is not possible given that one of the two monomorphic absorbing states of the Markovian chain process is eventually reached. Moreover, for a finite population of size $N$ the traditional concept of evolutionarily stable strategy (ESS) defined in Maynard and Price (1973) needs to be extended. The incumbent strategy is ESS if selection opposes: (i) a mutant invasion and (ii) a mutant fixation, i.e. a mutant replacing the incumbent population. When $N = 2$, the game is necessarily played between a mutant and an incumbent and both conditions (i) and (ii) require that the payoff obtained by the latter be larger, thus the condition defined in Maynard and Price (1973) for an ESS is neither necessary nor sufficient. When $N$ becomes large but finite, the traditional ESS condition is necessary but not sufficient.

Regarding variations of the fitness function used in finite populations, Nowak et al. (2004) used a convex combination between a unitary background fitness (neutral drift effect) and the expected payoff from the game in the limit of weak selection, i.e. when the game contributes residually and can be seen as a perturbation to neutral drift. One limitation of such a linear fitness function is that, in order to guarantee positive fitness values, it requires an upper bound for the parameter accounting for the intensity of selection. This issue was overcome by introducing an exponential fitness function as in

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Traulsen et al (2006) where the Fermi function was used with a non-negative temperature parameter in order to control the intensity of selection. In Ji and Xian-Jia (2011) an exponential fitness function is also used and mutations are taken into account.

The rest of the paper is organized as follows. In section 2 we present the snowdrift game, we derive the discrete-time replicator equation for the case of homogeneous populations and we recall the stability results of Weibull. This section serves also as a guide for the more complex case of heterogeneous populations. In section 3, we derive the discrete-time replicator system for heterogeneous populations and we present the numerical simulation of the trajectory of a non-degenerate initial population (all strategies are present in the population). In section 4, we study the stability of fixed points and invariant manifolds of the system, finding that the monomorphic states are unstable and that an invariant manifold exists which corresponds to a polymorphic state and which is a global attractor for non-degenerate populations. Section 5 contains our discussion of the results, a mention of similar results in other games and our conclusions, where we point out to the case of degenerate populations as the immediate further work and we give some insight of the main open problems. An appendix section contains the analysis of eigenvalues for the stability of fixed points.

2. Cooperation in homogeneous populations

We are interested in $2 \times 2$ games that describe the interactions between two individuals that have only two possible actions: to cooperate ($s_C$) or to defect ($s_D$). The result of an encounter for an individual playing $s_i$ with another individual playing $s_j$, with $i, j \in \{C, D\}$, is given by the individual’s utility $u(s_i, s_j)$. The different combinations of strategies and their resulting utilities can be summarized in the following matrix:

\[
\begin{array}{cc}
  s_C & s_D \\
  s_C & u(s_C, s_C) & u(s_C, s_D) \\
  s_D & u(s_D, s_C) & u(s_D, s_D) \\
\end{array}
\]

Cooperation has a cost $c > 0$ and may generate a benefit $b > 0$ for both individuals. When both individuals cooperate, both share the cost and receive the benefit: $u(s_C, s_C) = b - c/2$. When both defect, there is no cost nor benefit: $u(s_D, s_D) = 0$. When only one individual cooperates, this individual bears the cost, while the opponent does not; nevertheless the cooperation of one individual is sufficient for both individuals receiving the benefit\(^8\): $u(s_C, s_D) = b - c$ and $u(s_D, s_C) = b$. The matrix of the games of cooperation reduces to the following:

\[
\begin{array}{cc}
  s_C & s_D \\
  s_C & b - c/2 & b - c \\
  s_D & b & 0 \\
\end{array}
\]

\(^8\) We consider symmetric games: the opponent’s utility for an individual playing $s_i$ while the opponent plays $s_j$ is given by $u(s_j, s_i)$.

An alternative situation is when the cooperation of both individuals is necessary to generate the benefit. In this case we would have $u(s_C, s_D) = -c$ and $u(s_D, s_C) = 0$. This would correspond to a game of coordination: the individual obtains more utility when choosing the same action than does the opponent: $u(s_D, s_D) > u(s_C, s_D)$ and $u(s_C, s_C) > u(s_D, s_C)$.

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We are interested in the snowdrift game\textsuperscript{10}, where the benefit of cooperation is larger than its cost, \( b > c \). In the prisoner’s dilemma, \( b < c \) and defect is always a dominant strategy, still both individuals are better off if both cooperate than if both defect: \( c < 2b \).

We define the following parameter \( a \in (0, 1) \), which is the ratio of what a player gets when working alone (numerator) or in cooperation (denominator):

\[
 a = \frac{b - c}{b - c/2}. \tag{2}
\]

Parameter \( a \) is in fact the probability of cooperation in the Nash equilibrium, i.e. in the steady-state of the snowdrift game played by homogeneous populations. It can be also defined as \( a = 1 - \rho \), where \( \rho \) is the cost-to-net benefit ratio (when there is mutual cooperation); see, e.g. caption of figure 2 in \textit{Doebeli and Hauert (2005)}, p. 759.

We consider a homogeneous population of individuals playing game (1). Let \( n^t \) denote the size of the population at time \( t \geq 0 \). When individuals exclusively use pure strategies, the population can be divided into two subgroups of sizes \( n^t_C \) and \( n^t_D \) according to the pure strategy they are programmed to play, \( s_C \) and \( s_D \) respectively.

Denote by \( \theta^t_i = n^t_i/n^t, i = C, D, \) the proportion of individuals of each subgroup at time \( t \). Then, for all \( t \geq 0 \), the absolute and relative population frequencies are respectively such that \( n^t_C + n^t_D = n^t \) and \( \theta^t_C + \theta^t_D = 1 \), so the population state at time \( t \) can be characterized by the scalar value \( \theta^t_c \), in the state-space \([0, 1]\). A state is said to be \textit{monomorphic} if all the individuals use one single strategy (\( \theta^t_C = 0 \) or 1); otherwise, the state is said to be \textit{polymorphic}.

The replicator dynamics describes the time evolution of each subgroup of the population. When the population changes are not necessarily small, the replicator dynamics takes the form of a discrete-time map for the vector \( \theta^t = (\theta^t_C, \theta^t_D) \),

\[
 \theta^{t+\delta} = \mathcal{F}(\theta^t), \tag{3}
\]

where the evolution of the population is described in terms of successive generations.

Here \( \delta \in (0, 1) \) denotes the time elapsed between the overlapping of two consecutive generations. From one generation to another, individuals involved in pairwise encounters are replaced by a number of offspring (identical to their parents in the strategy they are programmed to play) according to the resulting utility of these encounters. We adopt the classical formulation in which the time-step \( \delta \) equals the fraction of the population that is renewed in each generation (\textit{Weibull (1995)}. Thus, in overlapping generations (i.e. not all the individuals are replaced from one generation to the next), only a portion \( \delta \) of the population is subject to potential changes in each iteration.

Denoting by \( u_i(\theta^t_i), i = C, D, \) the utility that individuals from each subgroup obtain when the population is in state \( \theta^t_C \), the size of each subgroup evolves according to the following recurrences:

\[
 n^{t+\delta}_C = (1 - \delta)n^t_C + \delta n^t_C u_C(\theta^t_C)
\]

\[
 n^{t+\delta}_D = (1 - \delta)n^t_D + \delta n^t_D u_D(\theta^t_C).
\]

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 \( \delta \) increases or decreases

\textsuperscript{10}The results obtained in the paper can be easily extended to the whole class of symmetric anti-coordination games, i.e. when \( u(s_D, s_D) < u(s_C, s_D) \) and \( u(s_C, s_C) < u(s_D, s_C) \). An individual obtains more utility if he chooses the action not chosen by her opponent. Here \( u(s_C, s_D) < u(s_C, s_C) \) also holds (an individual gets more if both cooperate than if she cooperates while her opponent defects).

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proportionally to the utility obtained by the subgroup. Note that, in only one generation, not all the population can be renewed ($\delta < 1$), nor remain unchanged ($\delta > 0$).

When the population is in state $\theta^t_C$, the individual has a probability $\theta^t_C$ of meeting an opponent playing $s_C$ and a probability $1 - \theta^t_C$ of meeting an opponent playing $s_D$. Thus, the utilities $u_i(\theta^t_C)$, $i = C, D$, are given by

$$u_C(\theta^t_C) = \theta^t_C \left( b - \frac{c}{2} \right) + (1 - \theta^t_C) (b - c) = b - c + \theta^t_C \frac{c}{2}$$

$$u_D(\theta^t_C) = \theta^t_C b + (1 - \theta^t_C) 0 = \theta^t_C b.$$  

The evolution of the size of each subgroup is then given by

$$n^{t+\delta}_C = n^t_C \left[ 1 - \delta + \delta(b - c) + \delta \theta^t_C \frac{c}{2} \right],$$

$$n^{t+\delta}_D = n^t_D \left[ 1 - \delta + \delta \theta^t_C b \right], \quad \forall t \geq 0,$$

so that the total population $n^{t+\delta} = n^{t+\delta}_C + n^{t+\delta}_D$ evolves as follows:

$$n^{t+\delta} = n^t \left[ 1 - \delta - \delta \left( b - \frac{c}{2} \right) (\theta^t_C)^2 + \delta (2b - c) \theta^t_C \right]$$

$$= g(\theta^t_C)n^t,$$

where we have introduced the function $g(\xi): [0, 1] \rightarrow \mathbb{R}$ defined by

$$g(\xi) \overset{\text{def}}{=} (1 - \delta) + \delta \xi (2 - \xi) \left( b - \frac{c}{2} \right). \quad (4)$$

The function $g(\xi)$ is strictly positive for all $\xi \in [0, 1]$ and $\delta \in (0, 1)$ and can be viewed as the *instantaneous growth factor of the population for a cooperation frequency $\xi \in [0, 1]$*: if $g(\xi) > 1$ (resp. $g(\xi) < 1$), the population size increases (resp. decreases) from time $t$ to time $t + \delta$\textsuperscript{11}.

Then, the proportion of individuals $\theta^{t+\delta}_C$ playing $s_C$ evolves as described by the following equation,

$$\theta^{t+\delta}_C = \frac{\theta^t_C}{g(\theta^t_C)} \left[ 1 - \delta + \delta(b - c) + \delta \theta^t_C \frac{c}{2} \right], \quad (5)$$

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

$$\theta^{t+\delta}_C - \theta^t_C = \frac{\delta \theta^t_C}{g(\theta^t_C)} \left( \theta^t_C - 1 \right) \left( b - \frac{c}{2} \right) (\theta^t_C - a). \quad (6)$$

Equation (5) is the discrete-time replicator equation for a homogeneous population of individuals playing the game defined in (1). The evolution of the population is thus determined by (5) and appropriate initial conditions for $n^0_C$ and $n^0_D$. As the growth rates can be smaller than 1, we will assume that initial populations are large enough to prevent them from extinction (that is, $n^0$ is large enough so that $n^t \gg 1 \forall t < t_L$, for a large enough value of $t_L$).

We now study the stability properties of the dynamical system given by equation (5). The fixed points $\theta^*_C$ of (5) are those where $\theta^{t+\delta}_C = \theta^t_C = 0$, that is, $\theta^*_C = 0$, $\theta^*_C = 1$ and $\theta^*_C = a$. Their stability is given by the classical result of Weibull for the continuous-time model: the monomorphic states are unstable and the polymorphic state is asymptotically

\textsuperscript{11} In the case of the prisoner dilemma and coordination games, a more restrictive condition is required on $\delta$ in order to guarantee that $g(\xi)$ is positive. This was already pointed out by Weibull (1995) (p 125), which added a positive ‘background birthrate’ $\beta$ to the growth factor to prevent it from being negative. Similarly, Hofbauer and Sigmund (2003) added a constant $c$ as a ‘background payoff’.

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stable. As reported by Weibull (1995), ‘[...] the discrete-time orbits essentially make straight-line jumps in the direction of the tangent of the continuous-time orbit (p. 125), so it suffices to verify two conditions: first, discrete trajectories do not leave the domain [0, 1] and second, they do not jump successively around the fixed point $a$ (although the jumps are in the direction of the asymptotically stable point $a$, the distance $|\theta^t_C - a|$ has to decrease monotonically to zero).

Trajectories are confined to [0, 1] for all $\delta \in (0, 1]$ because, on the one hand, the replicator equation preserves the condition $\theta^t_D + \theta^t_C = 1$ for all $t \geq 0$ (just by summing the equations of $\theta^t_C + \delta \theta^t_C$ and $\theta^t_D + \delta \theta^t_D$) and on the other hand, $\theta^t_C$ and $\theta^t_D$ are positive because the expression between brackets in (5) is the sum of positive terms for all $\theta^t_C, D \in (0, 1)$.

To show that trajectories are prevented from jumping over the fixed point $a$ for all $\delta \in (0, 1]$, we observe that a jump takes place if and only if the sign of $\theta^t_C - a$ is not equal to the sign of $\theta^0_C - a$. From (6), we have:

$$\theta^t_C - a = \theta^0_C - a + \frac{\delta \theta^0_C}{g(\theta^0_C)} (\theta^t_C - 1) \left( b - \frac{c}{2} \right) (\theta^0_C - a)$$

$$= (\theta^0_C - a) \left[ 1 + \frac{\delta \theta^0_C}{g(\theta^0_C)} (\theta^t_C - 1) \left( b - \frac{c}{2} \right) \right]$$

$$= \frac{\theta^0_C - a}{g(\theta^0_C)} \left[ 1 - \delta + \delta \theta^0_C \left( b - \frac{c}{2} \right) \right],$$

where the term between brackets is always strictly positive, thus preventing sign changes.

3. Replicator system in heterogeneous populations

We now consider a heterogeneous population where two types of individuals coexist: individuals of type $I$ and individuals of type $II$. We denote by $x$ the proportion of individuals of type $I$, that is, each individual has a probability $x$ of meeting an individual of type $I$ and a probability $1 - x$ of meeting an individual of type $II$. We assume that $x$ is constant; in the population dynamic process this corresponds to assume 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, as in the experimental case described in the introduction (Dennis et al. 2008).

Such random allocation of type would suggest a stochastic process with type fluctuation. As we work in the context of very large populations, the effect of stochasticity disappears and the proportion of each type can be assumed to remain constant. We leave for future research the study of the evolution of strategies in finite heterogeneous populations by means of a genetic algorithm.

Individuals are programmed to play a pure strategy. A pure strategy specifies one of the two possible action ($s_C$ or $s_D$) for each type of opponent ($I$ or $II$). As individuals recognize their opponent’s type but fail to recognize their own type, there are four pure strategies that we respectively denote by $s_{CC}$, $s_{DC}$, $s_{CD}$ and $s_{DD}$, where $s_{ij}$, for $ij \in \mathcal{I} = \{CC, DC, CD, DD\}$, denotes the strategy of playing $s_i$ against an opponent of type $I$ and $s_j$ against an opponent of type $II$\footnote{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.}.
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Dividing the population into as many subgroups as there are pure strategies, i.e. four subgroups, \( n^t = n^t_{CD} + n^t_{DC} + n^t_{CC} + n^t_{DD} \), where \( n^t_{ij} \) denotes the number of individuals that at time \( t \geq 0 \) are programmed to play the pure strategy \( s_i \) for \( ij \in \mathcal{I} \) and denoting by \( \theta^t_{ij} \) the proportion of individuals at time \( t \geq 0 \) in the subgroup \( ij \), we have, for \( ij \in \mathcal{I} \),

\[
\theta^t_{DD} = 1 - \theta^t_{CD} - \theta^t_{DC} - \theta^t_{CC}, \quad \forall t \geq 0.
\]

(7)

Then, the state of the population is characterized by the three-dimensional vector \( \theta^t = (\theta^t_{CD}, \theta^t_{DC}, \theta^t_{CC}) \) in the state-space \( \Omega \), which is the unit tetrahedron:

\[
\Omega = \{ \theta \in [0, 1]^3 : \theta_{CD} + \theta_{DC} + \theta_{CC} \leq 1 \}.
\]

Monomorphic states are those where \( \theta^t_{ij} = 1 \) for some \( ij \in \mathcal{I} \) and a polymorphic state is such that \( \theta^t_{ij} < 1 \) for all \( ij \in \mathcal{I} \).

As in the homogeneous case, we denote by \( U_{ij}(\theta^t) : \Omega \subset \mathbb{R}^3 \rightarrow \mathbb{R} \) the utility that an individual can expect when playing strategy \( ij \) in state \( \theta^t \). Then, the size of each subgroup \( ij \in \mathcal{I} \) evolves according to the following equation,

\[
n^t_{ij} = (1 - \delta)n^t_{ij} + \delta n^t_{ij} U_{ij}(\theta^t),
\]

(8)

with \( 0 < \delta < 1 \). In the heterogeneous case, the utility \( U_{ij}(\theta^t) \) depends on the individual’s type: denoting by \( U_{ij}^t(\theta^t) \) [resp. \( U_{ij}^{II}(\theta^t) \)] the utility of an individual of type \( I \) (resp. \( II \)) at time \( t \), the expected utility \( U_{ij}(\theta^t) \) can be decomposed as follows:

\[
U_{ij}(\theta^t) = x U_{ij}^I(\theta^t) + (1 - x) U_{ij}^{II}(\theta^t).
\]

(9)

To compute \( U_{ij}^I(\theta^t) \) and \( U_{ij}^{II}(\theta^t) \), 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 \( s_C \) or \( s_D \) and the state of the population \( \theta^t \) determines the opponent’s action, which is \( s_i \) with probability \( \theta^t_{ij} \). Thus, we have:

\[
U_{ij}^I(\theta^t) = x \left[ \theta^t_{CD} u(s_i, s_C) + \theta^t_{DC} u(s_j, s_D) + \theta^t_{CC} u(s_i, s_C) + \theta^t_{DD} u(s_i, s_D) \right] + (1 - x) \left[ \theta^t_{CD} u(s_j, s_C) + \theta^t_{DC} u(s_j, s_D) + \theta^t_{CC} u(s_i, s_C) + \theta^t_{DD} u(s_i, s_D) \right]
\]

\[
U_{ij}^{II}(\theta^t) = x \left[ \theta^t_{CD} u(s_i, s_D) + \theta^t_{DC} u(s_i, s_C) + \theta^t_{CC} u(s_i, s_C) + \theta^t_{DD} u(s_i, s_D) \right] + (1 - x) \left[ \theta^t_{CD} u(s_j, s_D) + \theta^t_{DC} u(s_j, s_C) + \theta^t_{CC} u(s_j, s_C) + \theta^t_{DD} u(s_j, s_D) \right].
\]

Defining the frequency of cooperation \( f : \Omega \subset \mathbb{R}^3 \rightarrow \mathbb{R} \) when population is in state \( \theta \) by

\[
f(\theta) = \theta_{CC} + x \theta_{CD} + (1 - x) \theta_{DC},
\]

and denoting by \( f^t_{ij} \) the frequency of cooperation in the four monomorphic states, i.e.

\[
f^t_{CC} = 1, \quad f^t_{CD} = x, \quad f^t_{DC} = 1 - x, \quad f^t_{DD} = 0,
\]

we can substitute the expressions of \( U_{ij}^I(\theta^t) \) and \( U_{ij}^{II}(\theta^t) \) into (9) to obtain

\[
U_{ij}(\theta^t) = x u(s_i, s_C) f(\theta^t) + x u(s_i, s_D)[1 - f(\theta^t)]
\]

\[
+ (1 - x) u(s_j, s_C) f(\theta^t) + (1 - x) u(s_j, s_D)[1 - f(\theta^t)].
\]

(10)

Plugging (10) into (8) and using \( n^t_{ij} = n^t_{ij} \theta^t_{ij} \), we find that the evolution of each subpopulation size is given by

\[
n^t_{ij} = n^t_{ij} \left[ 1 - \delta + \delta f(\theta^t) [f_{ij} u(s_C, s_C) + (1 - f_{ij}) u(s_D, s_C)] + \delta[1 - f(\theta^t)] [f_{ij} u(s_C, s_D) + (1 - f_{ij}) u(s_D, s_D)] \right]
\]

\[
= n^t_{ij} \left[ 1 - \delta + \delta f_{ij}(b - c) + \delta f(\theta^t) \left[ (1 - f_{ij}) b + \frac{c}{2} f_{ij} \right] \right], \quad t \geq 0.
\]
Then, using the instantaneous growth factor \( g(\xi) \) defined in (4), the evolution of the total population size \( n^{t+\delta} = n^{t+\delta}_{CD} + n^{t+\delta}_{DC} + n^{t+\delta}_{CC} + n^{t+\delta}_{DD} \) is given by
\[
n^{t+\delta} = g(f(\theta^t)) n^t,
\]
so that the proportion of individuals playing \( s_{ij} \) at time \( t + \delta \) is, for all \( ij \in \mathcal{I} \),
\[
\theta_{ij}^{t+\delta} = \frac{\theta_{ij}^t}{g(f(\theta^t))} \left\{ 1 - \delta + \delta f_{ij} (b-c) + \delta f(\theta^t) \left[ (1-f_{ij})b + \frac{c}{2} f_{ij} \right] \right\} \\
= \theta_{ij}^t \left[ 1 + \delta \left( b - \frac{c}{2} \right) \left( \frac{f(\theta^t) - f_{ij}}{g(f(\theta^t))} \right) \right],
\]
and the growth rate of the subgroup \( ij \in \mathcal{I} \) is
\[
\theta_{ij}^{t+\delta} - \theta_{ij}^t = \frac{\delta \theta_{ij}^t}{g(f(\theta^t))} \left( b - \frac{c}{2} \right) \left( f(\theta^t) - f_{ij} \right) (f(\theta^t) - a).
\]
We recall here that \( g(f(\theta)) \) is strictly positive for all \( \theta \in \Omega \), given that \( f(\theta) \in [0, 1] \).

Equations (11) constitute a system of four equations (in fact three, as one of them is redundant with relation (7), which must be solved together with initial conditions, given by the coordinates of the initial point \( \theta^0 = (\theta^0_{CD}, \theta^0_{DC}, \theta^0_{CC}) \) in the state-space \( \Omega \). The function \( \mathcal{F} \) of map (3) is the vector \((F_{CD}(\theta^t), F_{DC}(\theta^t), F_{CC}(\theta^t))\), where the functions \( F_{ij}(\theta): \Omega \to \mathbb{R} \) are defined by the right hand side of (11). The evolution of a population is then given by (11) and an initial condition for each subgroup, \( n^{0}_{ij}, \ ij \in \mathcal{I} \).

The expression of the homogeneous case (6) is recovered by doing the following respective replacements in (12): \( \theta_{ij}^{t+\delta} \) and \( \theta_{ij}^t \) are replaced by \( \theta_{ij}^{t+\delta} \) and \( \theta_{ij}^t \), \( f(\theta^t) \) is replaced by \( \theta_{ij}^t \) and \( f_{ij} \) by 1, \( ij \in \mathcal{I} \).

Figures 1 and 2 show the numerical simulation of the time-evolution of the discrete-time replicator system for \( x = 0.4, b = 0.5, c = 0.1 \) (so \( a = 0.89 \)) and \( \delta = 0.6 \), with the initial condition \( \theta^0 = (0.3, 0.2, 0.01) \), for which \( f(\theta^0) = 0.25 \).

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 spatial steps decrease along the orbit.

Figure 1. Three views of the trajectory in the \((\theta_{CD}, \theta_{DC}, \theta_{CC})\)-space. We have used \( x = 0.4, b = 0.5, c = 0.1 \) (so \( a = 0.89 \)) and \( \delta = 0.6 \). Circles denote the successive values of \( \theta^t \) in each time-iteration, starting from \( \theta^0 = (0.3, 0.2, 0.01) \) in the lower region of \( \Omega \). The trajectory goes upwards decelerating and converging asymptotically to \( \theta^\infty = (0.038, 0.22, 0.74) \).

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Figure 2. Two views of the phase plane $\Omega$, showing the trajectory detailed in figure 1. The plane $\theta_{DD} = 0$ (black) is intersected by the three parallel planes $P_a$ (upper), $P_{1-x}$ (middle) and $P_x$ (lower). The trajectory starts from below $P_x$, crosses successively $P_x$ and $P_{1-x}$ and, while approaching $\theta_{00} = 0$, converges asymptotically to $P_a$. Here, $|f(\theta^w) - a|/a < 10^{-14}$.

The trajectory converges asymptotically to a point located in the upper region of $\Omega$, $\theta^w = (0.038, 0.22, 0.74)$, where $|f(\theta^w) - a|/a < 10^{-14}$ after $10^3$ time-iterations.

This simulation corresponds to a relatively large value of $\delta = 0.6$. For small values of $\delta$, the trajectory approximately follows the same path and tends to the continuous orbit corresponding to the continuous-time replicator system ($\delta = 0$). For larger values of $\delta$, the separation between circles increases because the time-steps of the trajectory are larger, so that the trajectory separates from the orbit of the continuous-time case.

For very large values of $\delta$, we must check that trajectories remain in the tetrahedron along all successive generations and this, for all initial condition. To prove that, we note that a point $\theta \in \mathbb{R}$ is in $\Omega$ if and only if its components $\theta_{ij}$, $ij \in \mathcal{I}$, are positive or zero. The factor of $\theta_{ij}^t$ in the first row of (11) is the sum of three positive terms, so that, if $\theta_{ij}^t \in \Omega$, then $\theta_{ij}^{t+\delta}$ is positive $\forall t \geq 0$, $\forall ij \in \mathcal{I}$ and $\forall \delta \in [0, 1]$. Summing up the four equations in (11) for $ij \in \mathcal{I}$, we see that the replicator system preserves the condition $\theta^0_{CD} + \theta^0_{DC} + \theta^0_{CC} = 1 - \theta^0_{DD} \leq 1$, so that $\theta_{ij}^{t+\delta} \in \Omega$ $\forall t \geq 0$, $\forall ij \in \mathcal{I}$ and $\forall \delta \in [0, 1]$.

4. Stability in heterogeneous populations

In this section we study the stability of the equilibria of the replicator system (fixed points and invariant manifolds), which turn out to be the monomorphic and polymorphic states of the population. The (un)stability of the fixed points is determined by a linear analysis based on the first method of Lyapunov (eigenvalues of the linearized equations), while an internal manifold is shown to be a global attractor of the interior of the tetrahedron, by means of a qualitative analysis of the evolution of the trajectories.

Our study is limited to the trajectories starting from the interior of $\Omega$. The study of trajectories living in the boundary of $\Omega$, 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 \(a\) with respect to \(x\) and \(1 - x\) and would be of considerable length. Our study is thus limited to the case of nondegenerate populations.

Let us find the elements of the phase plane: fixed points and invariant manifolds.

Fixed points \(\theta^* \in \Omega\) of the system (11) are such that \(\mathcal{F}(\theta^*) = \theta^*\), that is, the points \((\theta_{CD}^*, \theta_{DC}^*, \theta_{CC}^*)\) such that the right hand side of (12) is zero for all \(ij \in I\) simultaneously. The four vertices \((\theta_{CD}, \theta_{DC}, \theta_{CC}) = (0, 0, 0), (0, 1, 0), (0, 0, 1)\) and \((1, 0, 0)\) are isolated fixed points: when \(\theta_{ij}^* = 0\) then \(\theta_{ij}^{t+\delta} = 0\) and when \(\theta_{ij}^* = 1\), the factor \(f_{ij} - f(\theta^t)\) in (12) is zero so \(\theta_{ij}^{t+\delta} = 1\)

Denote by \(\mathcal{P}_a, \mathcal{P}_1, \mathcal{P}_x\) and \(\mathcal{P}_{1-x}\) the four planes defined by the equations
\[
\mathcal{P}_a : f(\theta) = a, \quad \mathcal{P}_1 : f(\theta) = 1, \quad \mathcal{P}_x : f(\theta) = x, \quad \mathcal{P}_{1-x} : f(\theta) = 1 - x.
\]
Figure 2 shows the three planes \(\mathcal{P}_a, \mathcal{P}_x\) and \(\mathcal{P}_{1-x}\) for \(x = 0.4\) and \(a = 0.89\).

The plane \(\mathcal{P}_{1-x}\) appears above \(\mathcal{P}_x\) because here \(x < 1/2\) and we have chosen \(\theta_{CC}\) as the vertical coordinate. The plane \(\mathcal{P}_1\) (not shown) is located above \(\Omega\) and intersects \(\Omega\) at \((0, 0, 1)\), while \(\mathcal{P}_a\), which is not empty because \(a \in (0, 1)\), is below \(\mathcal{P}_1\) and above \(\mathcal{P}_{1-x}\), because \(a > 1 - x\). The value of \(a\), \(x\) and \(1 - x\) can in fact be observed in the figure as the intersections of the respective plane with the vertical axis \(\theta_{CD} = \theta_{DC} = 0\).

Note also that \((1, 0, 0) \in \mathcal{P}_x, (0, 1, 0) \in \mathcal{P}_{1-x}\) and that \(\mathcal{P}_a\) intersects the plane \(\theta_{DD} = 0\) (which is the face of \(\Omega\) towards which the trajectory seems to converge), but not the plane \(\theta_{CC} = 0\) (the basis of the tetrahedron). The plane \(\mathcal{P}_a\) intersects the tetrahedron; otherwise, the intersection is empty. When \(a \in (0, 1)\), the factor \(f(\theta^t) - a\) in (12) is zero for all \(\theta \in \mathcal{P}_a\), so \(\theta_{ij}^{t+\delta} = \theta_{ij}^t\) for all \(ij \in I\), showing that every point of \(\mathcal{P}_a\) is a fixed point. Finally, as the four planes are parallel, no other fixed point can exist.

An invariant manifold \(\mathcal{M}\) is a subset of \(\Omega\) such that if the initial condition of a trajectory is in \(\mathcal{M}\), then the whole trajectory is in \(\mathcal{M}\). Continuous trajectories cannot cross, depart from or arrive to, invariant manifolds, but discrete trajectories can jump over them. Thus, confinement of trajectories to specific regions or to the whole domain \(\Omega\) must be made evident explicitly.

The plane \(\mathcal{P}_a\) is a connected set of fixed points and is therefore an invariant manifold (fixed points are invariant manifolds, so each vertex of \(\Omega\) is an invariant manifold, but we will refer to them as fixed points). The four planes \(\theta_{ij} = 0, ij \in I\) and the six edges \(\theta_{ij} = \theta_{kl} = 0, ij, kl \in I, kl \neq ij\), are invariant manifolds, because \(\theta_{ij}^0 = 0 \Rightarrow \theta_{ij}^t = 0\) for all \(t \geq 0\) and all \(ij \in I\).

The rest of the section is devoted to characterize the concept of stability we use in this study and to prove the following theorem of stability:

**Theorem 1.**

(a) All vertices of \(\Omega\) for the heterogeneous replicator system are unstable.

(b) The invariant manifold \(\mathcal{P}_a\) is a global attractor of the interior of \(\Omega\).

**Proof.** of (a): The fixed points of the system (11) are located in the boundary of \(\Omega\), so no open set containing a fixed point can be contained in \(\Omega\). 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 \(\Omega\).
A fixed point \( \theta^* \in \Omega \) is *Lyapunov stable* if for all neighborhood \( V \) of \( \theta^* \), there exists a neighborhood \( U \) of \( \theta^* \) such that \( U \subset V \) and

\[
\forall \theta^0 \in U \cap \Omega, \quad \theta^t \in V \cap \Omega.
\]

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

\[
\forall \theta^0 \in U \cap \Omega, \quad \lim_{t \to +\infty} \theta^t = \theta^*.
\]

Assume that a trajectory starts nearby the fixed point \( \theta^* \), that is, \( \theta^0 = \theta^* + \epsilon^0 \), where \( \epsilon^0 = (\epsilon^0_{CD}, \epsilon^0_{DC}, \epsilon^0_{CC}) \in \mathbb{R}^3 \) is a small perturbation. The linear stability of \( \theta^* \) is given by the time evolution of \( \epsilon^t \): if \( \|\epsilon^t\| \to 0 \), then \( \theta^t \to \theta^* = 0 \) and \( \theta^* \) is asymptotically stable; if \( \|\epsilon^t\| \) grows, then \( \theta^* \) is unstable (first method of Lyapunov).

The time evolution of the perturbation is given by

\[
\epsilon^t = \theta^t - (\theta^* + \epsilon^t)^t = \theta^t - \theta^*.
\]

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

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

where \( J \mathcal{F}(\theta^*) \) denotes the Jacobian matrix of the vector function \( \mathcal{F}(\theta) \) evaluated in \( \theta^* \) (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 \( \epsilon^{t+k\delta} = J \mathcal{F}(\theta^*) \cdot \epsilon^{t+(k-1)\delta} \), i.e.

\[
\epsilon^{t+k\delta} = J \mathcal{F}(\theta^*) \cdot [J \mathcal{F}(\theta^*) \cdot \epsilon^{t+(k-2)\delta}] = \ldots = [J \mathcal{F}(\theta^*)]^k \cdot \epsilon^t.
\]

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. We show in the detailed appendix (Jacobian matrices, eigenvalues) that all vertices have at least one eigenvalue larger than 1. \( \square \)

**Proof** of (b): The proof consists of two parts: first we prove that trajectories starting from the interior of \( \Omega \) move towards (but not necessarily converge to) \( \mathcal{P}_a \) and second, we prove that trajectories can not jump over \( \mathcal{P}_a \). This would prevent the case in which a trajectory jumps successively around \( \mathcal{P}_a \) in such a way that the distance from the trajectory to \( \mathcal{P}_a \) does not necessarily decrease, thus compromising the convergence.

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.

\[
B_M = \left\{ \theta^0 \in \Omega : \exists t_0 \geq 0 \text{ such that } t > t_0 \Rightarrow \theta^t \in M \right\}. \tag{13}
\]

When \( B_M \) is a neighborhood of \( M \), \( M \) is called an *attractor*. As \( B_M \) is not necessarily an open set, we relax this definition and we will say that \( M \) is an attractor if \( M \subseteq B_M \).

The study of the trajectories living in the boundary of \( \Omega \) is rich and would deserve a proper analysis (to be done). When \( \mathcal{P}_a \) doesn’t cross the planes \( \theta_{CC} = 0 \) or \( \theta_{DD} = 0 \), trajectories living in these planes cannot converge asymptotically to \( \mathcal{P}_a \), so \( \mathcal{P}_a \) cannot

\[ \text{Note that these expressions are also valid for the continuous model.} \]
be considered a global attractor of $\Omega$. When $x < a < 1 - x$, then $P_a$ intersects all the faces of $\Omega$, but, still, not all the edges of $\Omega$ can be intersected by $P_a$, so, in some edges, trajectories exist which cannot arrive to $P_a$. Thus, $P_a$ is not a global attractor of the whole $\Omega$, but we prove here that it is a global attractor of the interior of $\Omega$.

Simple phase plane considerations allow us to describe the general behavior of trajectories in the interior of the tetrahedron.

The direction in which orbits are travelled is determined by the variation of each coordinate $\theta_{ij}$, i.e. by the sign of $\theta'_{ij} - \theta_{ij}$ in expression (12). As $b > c/2$ and $g(f(\theta'))$ is positive, this means that the variation of $\theta_{ij}$ is given by the sign of the product\(^{14}\)

\[(f(\theta') - f_{ij})(f(\theta') - a),\]

that is, according to the relative position of the point $\theta'$ with respect to the planes $P_{aij}$.

Let us consider a trajectory starting from below $P_{aij}$, i.e. $f(\theta') - a < 0$. As $f_{CC} = 1$, $f(\theta') - f_{CC} < 0$, so $\theta'^{DC} - \theta'_{CD} > 0$ in (12) and the trajectory moves upwards. This is what happens in figures 1 and 2, where the orbit starts from below the planes $P_x$, $P_{1-x}$ and $P_a$, with a small value of $f(\theta')$ (but from the interior of $\Omega$, i.e. out of the planes $\theta_{11} = 0$ and $\theta_{00} = 0$), so that $f(\theta') - f_{ij} < 0$ for $ij \in \mathcal{I} - \{DD\}$ (but $f(\theta') > f_{DD} = 0$).

Below $P_a$, trajectories grow, eventually cross $P_x$ and $P_{1-x}$ and move towards $P_a$. Above $P_a$, $f(\theta') - a > 0$ and $\theta'^{CC} - \theta_{CC}$ is negative, so the trajectories decrease towards $P_a$ (this is the reason why we put $\theta_{CC}$ in the vertical coordinate).

In figure 2(a), the orbit exhibits a change of variation in $\theta'^{CD}$ when the plane $P_x$ is crossed. This corresponds to the instant of time in which $\theta'^{CD} - \theta_{CD} = 0$ in (12) for $ij = CD$. Similarly, figure 2(b) shows a change of variation in $\theta'^{DC}$ when the trajectory crosses $P_{1-x}$, i.e. when $\theta'^{DC} - \theta_{DC} = 0$ in (12) for $ij = DC$.

Outside the plane $\theta_{DD} = 0$, $\theta'^{DD} - \theta_{DD}$ is negative so the trajectory moves also toward the plane $\theta_{DD} = 0$. Above $P_x$, $\theta'^{CD} - \theta_{CD}$ becomes negative and above $P_{1-x}$, it is $\theta'^{DC} - \theta_{DC}$ which becomes negative, so that in this upper region, both $\theta'^{CD}$ and $\theta'^{DC}$ decrease. However, the variation of the trajectory with respect to $P_a$ is still given by the sign of $f(\theta') - a$, so that trajectories starting from between $P_x$ and $P_{1-x}$ or from above $P_{1-x}$ follow the same scenario with respect to $P_a$ and therefore move towards $P_a$.

In the continuous-time case, such a behavior would mean that the plane $P_a$ is an attractor (and this would therefore ends the corresponding proof). However, in the discrete-time case, trajectories can jump over $P_a$ and can eventually oscillate around $P_a$, not necessarily converging (i.e. reducing the distance) to $P_a$. It is then not possible to already classify $P_a$ as an attractor; this is done in the next step of the proof.

The second part of the proof of (b) in theorem 1 consists in showing that trajectories can not jump over $P_a$. We will need the following

**Lemma 1.** The function $P: \mathbb{R}^3 \to \mathbb{R}$ given by $P(\theta) = \theta_{CC} + x^2\theta_{CD} + (1 - x)^2\theta_{DC} - [f(\theta)]^2$ verifies the following properties:

(a) $P(\theta) \geq 0$ for all $\theta \in \Omega$,

(b) If $\theta$ is a vertex of $\Omega$ then $P(\theta) = 0$,

(c) $P(\theta) \leq f(\theta) - [f(\theta)]^2$ for all $\theta \in \Omega$.

\(^{14}\)This product determines also the sign of $d\theta_{ij}/dt$ in the continuous case, so that both the continuous and discrete-time trajectories have the same variation in a given point $\theta \in \Omega$. 

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Proof of lemma 1. 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 \(\alpha_1 = \sqrt{\theta_{CC}}, \alpha_2 = x\sqrt{\theta_{CD}}, \alpha_3 = (1 - x)\sqrt{\theta_{DC}}, \beta_1 = \sqrt{\theta_{CC}}, \beta_2 = \sqrt{\theta_{CD}}\) and \(\beta_3 = \sqrt{\theta_{DC}}\). Then, \((\theta_{CC} + x\theta_{CD} + (1 - x)\theta_{DC})^2\) is smaller or equal to

\[(\theta_{CC} + x^2\theta_{CD} + (1 - x)^2\theta_{DC})(\theta_{CC} + \theta_{CD} + \theta_{DC}),\]

so \([f(\theta)]^2 \leq \theta_{CC} + x^2\theta_{CD} + (1 - x)^2\theta_{DC}\) for all \(\theta \in \Omega\) and (a) is proved.

Part (b) is obvious and so is (c), by noting that \(x < 1\) and \(1 - x < 1\), so

\[P(\theta) \leq \theta_{CC} + x\theta_{CD} + (1 - x)\theta_{DC} - [f(\theta)]^2 = f(\theta) - [f(\theta)]^2.\]

We are now ready to prove part (b) of theorem 1:

A trajectory starting from a point \(\theta^0\) will jump from one side of \(P_a\) to the other in the next iteration if and only if there is a change of sign from \(f(\theta^0) - a\) to \(f(\theta^0) - a\).

Expanding \(f(\theta^0)\) according to the replicator system equations (11), we have

\[f(\theta^0) = \theta_{CC}^0 + x\theta_{CD}^0 + (1 - x)\theta_{DC}^0\]

\[= \theta_{CC}^0 \left[1 + \delta \left(b - \frac{c}{2}\right) \frac{f(\theta^0) - 1)(f(\theta^0) - \theta)}{g(f(\theta^0))}\right] + x\theta_{CD}^0 \left[1 + \delta \left(b - \frac{c}{2}\right) \frac{f(\theta^0) - \theta)(f(\theta^0) - a)}{g(f(\theta^0))}\right] + (1 - x)\theta_{DC}^0 \left[1 + \delta \left(b - \frac{c}{2}\right) \frac{f(\theta^0) - (1 - x)(f(\theta^0) - a)}{g(f(\theta^0))}\right]
\]

\[= f(\theta^0) - \delta \left(b - \frac{c}{2}\right) \frac{f(\theta^0) - \theta}{g(f(\theta^0))} \left[\theta_{CC}^0 + x^2\theta_{CD}^0 + (1 - x)^2\theta_{DC}^0 - [f(\theta^0)]^2\right]
\]

\[= f(\theta^0) - \delta \left(b - \frac{c}{2}\right) \frac{f(\theta^0) - \theta}{g(f(\theta^0))} P(\theta^0).
\]

Substracting \(a\) at both sides and dividing by \(f(\theta^0) - a\), we have:

\[
\frac{f(\theta^0) - \theta}{f(\theta^0) - a} = 1 - \delta \left(b - \frac{c}{2}\right) \frac{P(\theta^0)}{g(f(\theta^0))} = \frac{1}{g(f(\theta^0))} \left[g(f(\theta^0)) - \delta \left(b - \frac{c}{2}\right) P(\theta^0)\right].
\]

The numerator (between brackets) of the right hand side of this last expression is

\[1 - \delta - \delta \left(b - \frac{c}{2}\right) [f(\theta^0)]^2 + \delta(2b - c)f(\theta^0) - \delta \left(b - \frac{c}{2}\right) P(\theta^0),\]

which, with lemma 1 in mind, can be written as the following sum of positive terms,

\[1 - \delta + \delta \left(b - \frac{c}{2}\right) [2f(\theta^0) - [f(\theta^0)]^2 - P(\theta^0)],\]

so that \(f(\theta^0) - a\) and \(f(\theta^0) - a\) have the same sign, thus preventing jumps over \(P_a\). \(\square\)
Emergence of cooperation in phenotypically heterogeneous populations

5. Discussion

We have studied the conditions under which cooperation can emerge in the snowdrift game in heterogeneous populations. Individuals ignore if they are interacting with an individual of their own type as they recognize their opponent’s type but do not known their own type. We have proposed a model to describe the evolution of such populations in the framework of evolutionary game theory. 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 with 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 essentially consists in establishing the conditions under which the discrete trajectories, which evolve by jumps, follow the continuous ones, paying special attention to prevent the trajectories from leaving the state-space $\Omega$ and from jumping over internal invariant manifolds. We have shown that the four monomorphic states are unstable and that the population evolves towards a polymorphic state where the frequency of cooperation is given by the ratio $a$. The stability of the invariant manifold $P_a$ has been studied specifically after giving a detailed description of the behavior of trajectories starting from the interior of $\Omega$. The reason of this specific study is that the discrete trajectories can 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 $P_a$.

The result is that $P_a$ is a global attractor for the interior of the tetrahedron, that is, whatever the distribution of the initial population, provided the population is nondegenerate (i.e. $\theta_{ij} \neq 0$ for all $ij \in I$), the population adjusts itself to reach the cooperation frequency given by $a$. This happens unconditionally for all values of the time-step $\delta$ in $(0, 1)$.

Thus, the results show that the frequency of cooperation is identical in both kinds of populations: in the homogeneous case, $\theta^*_C = a$ and in the heterogeneous case, $f(\theta^*) = a$, $\forall \theta^* \in P_a$. The result is similar to what is obtained with the Nash equilibrium. In the homogeneous case, the parameter $a$ is the frequency of cooperation at equilibrium, while in the heterogeneous case, $a$ is the frequency of cooperation in all equilibria.

In consequence, cooperation is not favored by introducing heterogeneity. Moreover, the level of cooperation does not depend on the level of heterogeneity $x$. What depends on $x$, not surprisingly, is the type of individuals towards which cooperation is more frequent: writing the frequency as $f(\theta) = x(\theta_{CC} + \theta_{CD}) + (1-x)(\theta_{CC} + \theta_{DC})$, we see that when $x$ is close to zero or one, almost all the cooperation events take place between those who always cooperate with the majoritarian type and when $x$ is close to $1/2$, then cooperation comes half from each part. This would not be the case in degenerate populations, where $\theta_{ij} = 0$ for at least one $ij \in I$.

Noticeably, it could be shown that in games of cooperation the population evolves towards one of the two monomorphic states where all individuals always cooperate or
always defect, the vertices $\theta_{CC} = 1$ and $\theta_{DD} = 1$ and in the prisoner’s dilemma, the population evolves towards the state where all individuals are defectors, $\theta_{DD} = 1$, but this behavior is conditional on that the time-step is shorter than a critical size $\delta = 1/(1-(b-c))$, required by the fact that trajectories must remain in $\Omega$ and can not jump over $\mathcal{P}_a$ (when $\mathcal{P}_a \cap \Omega \neq \emptyset$).

Trajectories which start in the boundary of $\Omega$, that is, in faces and edges of the tetrahedron would be worth being studied. This is especially interesting for studying degenerate populations where one of the pure strategies is not present. In particular, the face $\theta_{CC} = 0$ 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 to those in the continuous case, the question of how the invariant manifold $\mathcal{P}_a$ intersects faces and edges for different values of $a$ with respect to the proportion of individuals of each type $x$ and $1-x$ is complex and novel results are to be expected. This is left for further research. For a first step in this direction see Barreira da Silva Rocha and Laruelle (2013).

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Appendix

Proof. of theorem 1: The general expression of the Jacobian matrix $J\mathcal{F}(\theta)$ of the vector function $\mathcal{F}(\theta)$, where $\theta = (\theta_{CD}, \theta_{DC}, \theta_{CC})$, is given by

$$J\mathcal{F}(\theta) = \begin{pmatrix} \frac{\partial F_{CD}}{\partial \theta_{CD}} & \frac{\partial F_{CD}}{\partial \theta_{DC}} & \frac{\partial F_{CD}}{\partial \theta_{CC}} \\ \frac{\partial F_{DC}}{\partial \theta_{CD}} & \frac{\partial F_{DC}}{\partial \theta_{DC}} & \frac{\partial F_{DC}}{\partial \theta_{CC}} \\ \frac{\partial F_{CC}}{\partial \theta_{CD}} & \frac{\partial F_{CC}}{\partial \theta_{DC}} & \frac{\partial F_{CC}}{\partial \theta_{CC}} \end{pmatrix},$$

which must be evaluated on the vertices of $\Omega$. Recall, from (11), that

$$F_{ij}(\theta) = \theta_{ij} \left[ 1 + \delta \left( b - \frac{c}{2} \right) \frac{(f(\theta) - f_{ij})(f(\theta) - a)}{g(f(\theta))} \right].$$

Let us define the function $R(\xi) : [0, 1] \to \mathbb{R}$ as follows:

$$R(\xi) = - \left( b - \frac{c}{2} \right) \frac{\xi - a}{g(\xi)}.$$
As eigenvalues must be smaller than 1, the role of \( g(f(\theta)) \) is relevant so the proof is done for the discrete-time case.

Then, we have

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

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

\[
\frac{\partial F_{ij}(\theta)}{\partial \theta_{kl}} = \frac{\partial \theta_{ij}}{\partial \theta_{kl}} \left[ 1 + \delta \left[ f_{ij} - f(\theta) \right] R(f(\theta)) \right] + \delta \frac{\partial f(\theta)}{\partial \theta_{kl}} \left[ \frac{\partial R(f(\theta))}{\partial f(\theta)} \left( f_{ij} - f(\theta) \right) - R(f(\theta)) \right].
\]

(14)

If \( \theta^* \) is a vertex of \( \Omega \), 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, \( f(\theta^*) = f_{pq} \theta^*_{pq} = f_{pq} \). Then:

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

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

(b) If \( ij \neq pq \), then \( \theta_{ij} = 0 \) and the second term in (14) vanishes. Thus:

- If \( ij = kl \), \( \frac{\partial F_{ij}(\theta^*)}{\partial \theta_{kl}} = 1 + \delta (f_{ij} - f_{pq}) R(f_{pq}) \)

- If \( ij \neq kl \), \( \frac{\partial F_{ij}(\theta^*)}{\partial \theta_{kl}} = 0. \)

The eigenvalues of the matrix \( J \mathcal{F}(\theta^*) \) are given by the roots of the determinant \( |J \mathcal{F}(\theta^*) - \lambda I| \), where \( I \) is the identity matrix. Due to the structure of the matrices (two zeroes in at least two rows), the eigenvalues \( \{\lambda_i\}_{i=1}^3 \) are the elements of the diagonal. The condition for asymptotic stability is \( |\lambda_i| < 1 \) for all \( i = 1, 2, 3 \) simultaneously.

For each vertex, we find (at least) one eigenvalue larger than one:

- For \( \theta^* = (0, 0, 0) \), we have \( pq = DD \), so \( f_{pq} = 0 \). Thus:

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

Here \( R(0) = a(b - c/2)/g(0) > 0 \), so \( \lambda_3 = 1 + \delta R(0) > 1 \) and \((0, 0, 0)\) is unstable.
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• For $\theta^* = (0, 0, 1)$, we have $pq = CC$, so $f_{pq} = 1$. Thus:

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

Here $R(1) = -(b - c/2)(1 - a)/g(1) < 0$, so $\lambda_3 = 1 - \delta R(1) > 1$: $(0, 0, 1)$ is unstable.

• For $\theta^* = (1, 0, 0)$, we have $pq = CD$, so $f_{pq} = x$. Thus:

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

Here $\lambda_1 = 1 - \delta xR(x)$ and $\lambda_3 = 1 + \delta (1 - x)R(x)$, for which we observe that $\lambda_1 < 1 \Rightarrow R(x) > 0$ and $\lambda_3 < 1 \Rightarrow R(x) < 0$ cannot be simultaneously verified, so $(1, 0, 0)$ is unstable.

• For $\theta^* = (0, 1, 0)$, we have $pq = DC$, so $f_{pq} = 1 - x$. Thus,

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

Here $\lambda_2 = 1 - \delta (1 - x)R(1 - x)$ and $\lambda_3 = 1 + \delta xR(1 - x)$, for which $\lambda_2 < 1$ and $\lambda_3 < 1$ are incompatible, so $(0, 1, 0)$ is unstable.

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