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# Evolution of cooperation in a multidimensional phenotype space

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ABSTRACT

The emergence of cooperation in populations of selfish individuals is a fascinating topic that has inspired much theoretical work. An important model to study cooperation is the phenotypic model, where individuals are characterized by phenotypic properties that are visible to others. The phenotype of an individual can be represented for instance by a vector $\mathbf{x} = (x_1, \ldots, x_n)$, where $x_1, \ldots, x_n$ are integers. The population can be well mixed in the sense that everyone is equally likely to interact with everyone else, but the behavioral strategies of the individuals can depend on their distance in the phenotype space. A cooperator can choose to help other individuals exhibiting the same phenotype and defects otherwise. Cooperation is said to be favored by selection if it is more abundant than defection in the stationary state. This means that the average frequency of cooperators in the stationary state strictly exceeds $1/2$. Antal et al. (2009c) found conditions that ensure that cooperation is more abundant than defection in a one-dimensional (i.e. $n = 1$) and an infinite-dimensional (i.e. $n = \infty$) phenotype space in the case of the Prisoner's Dilemma under weak selection. However, reality lies between these two limit cases. In this paper, we derive the corresponding condition in the case of a phenotype space of any finite dimension. This is done by applying a perturbation method to study a mutation-selection equilibrium under weak selection. This condition is obtained in the limit of a large population size by using the ancestral process. The best scenario for cooperation to be more likely to evolve is found to be a high population-scaled phenotype mutation rate, a low population-scaled strategy mutation rate and a high phenotype space dimension. The biological intuition is that a high population-scaled phenotype mutation rate reduces the quantity of interactions between cooperators and defectors, while a high population-scaled strategy mutation rate introduces newly mutated defectors that invade groups of cooperators. Finally it is easier for cooperation to evolve in a phenotype space of higher dimension because it becomes more difficult for a defector to migrate to a group of cooperators. The difference is significant from $n = 1$ to $n = 2$ and from $n = 2$ to $n = 3$, but becomes small as soon as $n \geq 3$.

## 1. Introduction

Evolutionary game theory is the study of frequency-dependent selection (Maynard Smith, 1982; Maynard Smith and Price, 1973; Hofbauer and Sigmund, 1988, 2003; Cressman, 2003; Nowak and Sigmund, 2004; Nowak, 2006). The fitness of an individual is not constant, since it depends on the payoff of the strategy used by the individual in interaction with other individuals. It was originally expressed in terms of the replicator equation in the case of pairwise interactions in an infinite well-mixed population, which means that any two individuals interact with the same probability (Taylor and Jonker, 1978; Hofbauer et al., 1979; Zeeman, 1980).

Consider an evolutionary game with $n$ possible strategies, labeled by the integers $i = 1, \ldots, n$. The payoff matrix $A = (a_{i,j})$ is a $n \times n$ matrix, whose entry $a_{i,j}$ represents the payoff received by an individual playing strategy $i$ against an individual playing strategy $j$. The frequency of strategy $i$ is denoted by $x_i$. Then the replicator equation is given by

$$\dot{x}_i = x_i\Big(w_i(\mathbf{x}) - \overline{w}(\mathbf{x})\Big),$$

where $w_i(\mathbf{x})$ and $\overline{w}(\mathbf{x})$ represent the expected payoff to strategy $i$ and the average payoff in the population, respectively, given by

$$w_i(\mathbf{x}) = \sum_{j=1}^{N} a_{i,j} x_j$$

and

$$\overline{w}(\mathbf{x}) = \sum_{i=1}^{N} x_i w_i(\mathbf{x}),$$

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with $\mathbf{x} = (x_1, \ldots, x_n)$. This fundamental equation can be extended to spatial games in a graph-structured population, with every individual occupying a vertex of the graph interacting with its nearest neighbors (Ohtsuki and Nowak, 2006b), or in a group-structured population with groups of interacting individuals randomly chosen in an infinite population (Hilbe, 2011). It can be extended also to games with multiple players in a finite or infinite well-mixed population (Gokhale and Traulsen, 2010).

Infinitely large, well-mixed populations and deterministic dynamics are idealizations. Real populations have a finite number of individuals besides being not perfectly mixed. Linear games have been considered in the context of finite populations. In the absence of mutation, selection can favor or oppose a mutant strategy to replace a resident strategy. This will be the case for instance if the probability of fixation of the mutant is larger or smaller than it would be under neutrality (Rousset and Billiard, 2000; Nowak et al., 2004; Taylor et al., 2004; Lessard, 2005; Imhof and Nowak, 2006; Ladret and Lessard, 2007, 2008). In the presence of symmetric mutation, selection is said to favor a strategy if this strategy is more abundant on average, that is, if its average frequency in the stationary state strictly exceeds what it would be under neutrality (Fudenberg and Imhof, 2006; Antal et al., 2009a,b; Tarnita et al., 2009, 2011; Gokhale and Traulsen, 2011; Kroumi and Lessard, 2014).

Spatial structures have been considered more recently for games in finite populations. The spatial distribution of a population allows interactions between individuals to depend on their locations. In the traditional setting of spatial games, the individuals are arranged on a regular lattice and interactions occur among nearest neighbors (Nowak and May, 1992). A generalization of this structure is the graph structure where individuals occupy the vertices of a graph and the edges indicate who interacts with whom (Lieberman et al., 2005; Ohtsuki and Nowak, 2006a,b; Ohtsuki et al., 2006; Taylor et al., 2007a,b; Santos et al., 2008).

Another spatial structure is a population subdivided into two subpopulations with any migration rates (Ladret and Lessard, 2007), or an island model with a large number of islands and uniform or proportional dispersal (Rousset and Billiard, 2000; Ladret and Lessard, 2008; Lessard, 2011a,b). The stepping stone model (see, e.g., Rousset and Billiard, 2000; Rousset, 2006) is a spatial model with local dispersal. Suppose a population subdivided into $d$ demes labeled by the integers $1, \ldots, d$, and a migration matrix $M = (m_{i,j})$, where $m_{i,j}$ is the proportion of offspring in deme $i$ that come from deme $j$. The stepping stone model corresponds to the case where $m_{i,j} = \frac{m}{2}$ if $j = i+1$ or $i-1$, and 0 otherwise, for $i = 2, \ldots, d-1$. For $i = 1$, we have $m_{1,j} = \frac{m}{2}$ if $j = 2$ or $d$, and 0 otherwise. Similarly, we have $m_{d,j} = \frac{m}{2}$ if $j = 1$ or $d-1$, and 0 otherwise.

The geometry of human populations is determined by associations that individuals have with various groups or sets. Each individual may belong to many sets, for example, a student may study several subjects and take different classes. A particular setting is studied in Tarnita et al. (2009): a population of $N$ individuals is distributed over $M$ sets where each individual belongs exactly to $K$ sets. Interactions occur within each given set. For a review of evolutionary dynamics in structured populations, see, e.g., Lehmann and Rousset (2010, 2014) or Nowak et al. (2010).

The Prisoner's Dilemma (Axelrod and Hamilton, 1981; Axelrod, 1984) is a simple game in which there is a tension between individual interests and a common good. It has been studied in economics, philosophy and machine learning. It is crucial for understanding human relations, evolution and morality. In the Prisoner's Dilemma, there are two strategies, $C$ and $D$, which refer to cooperation and defection, respectively. The payoff matrix is given by

$$\begin{array}{c c} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} R & S \\ T & P \end{pmatrix} \end{array}, \tag{1}$$

where $T > R > P > S$. Here, $R$ is the *reward payoff* that each player receives if both cooperate, $P$ is the *punishment payoff* that each player receives if both defect, $T$ is the *temptation payoff* that a player receives if he alone defects and $S$ is the *sucker payoff* that a player receives if he alone cooperates. A simpler form of the Prisoner's Dilemma is the additive model with a payoff matrix in the form

$$\begin{array}{c c} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} b-c & -c \\ b & 0 \end{pmatrix} \end{array}, \tag{2}$$

where $b > 0$ is the benefit gained by the opponent of a cooperator and $c > 0$ is the cost incurred by a cooperator.

Individuals exhibit other phenotypic traits in addition to their behavioral strategies as size, height, or other aspects of physical appearance, which supports the idea that behavioral strategy is triggered by phenotypic similarity. This is known as the green-beard effect which is based on the theory of the selfish gene (Hamilton, 1964a,b; Dawkins, 1976), according to which an individual possesses the gene that creates the incentive to be altruistic toward individuals who also possess this gene. It appears when a gene produces three phenotypic effects: a perceptible characteristic (the hypothetical green beard), a recognition by other individuals of this characteristic and a preferential treatment of those recognized. An individual carrier of this gene recognizes the other porters of this gene and behaves in a way altruistic toward them.

The effect of phenotypic similarity on the evolution of cooperation has been studied in the framework of an infinite structured population (see, e.g., Riolo et al., 2001; Axelrod et al., 2004; Traulsen and Claussen, 2004; Jansen and Van Baalen, 2006; Traulsen and Nowak, 2007). Rousset and Roze (2007) and Lehmann et al. (2009) consider an island model with an infinite number of demes composed of $N$ haploid individuals. There are two loci with two alleles segregating at each locus. The first is the helping locus with a helping allele or a cheating allele. The second is the matching locus with a mutant recognition allele or a wild allele. There are pairwise interactions within demes. An individual $i$ adopts the strategy *cooperation* against an individual $j$ of the same deme if $i$ has the helping allele at the helping locus while $i$ and $j$ have the same allele at the matching locus, otherwise $i$ adopts the strategy *defection* against $j$.

More recently Lehmann et al. (2009) considered a finite well-mixed population according to a Wright–Fisher model. Like in Rousset and Roze (2007), there are two loci, a strategy locus and a matching locus. With two alleles at the matching locus, a wild type and a mutant type, it is a model with a finite phenotype space, actually two phenotypes.

Another setting is the one-dimensional or infinite-dimensional phenotype space with *a priori* infinite possible states which was studied by Antal et al. (2009c). Consider a population of $N$ individuals which follows a Wright–Fisher model. In each generation, every individual produces the same large number of offspring. The next generation of $N$ individuals is sampled from this pool of offspring. Consider a one-dimensional (respectively infinite-dimensional) phenotype space: each individual has a phenotype represented by an integer (respectively an infinite vector of integers) and adopts a strategy among the two strategies of the Prisoner's Dilemma, $C$ and $D$. An individual inherits its parent's phenotype $i$ with probability $1 - v$, or one of the phenotypes $i - 1$ and $i + 1$ with the same probability $v/2$ (respectively with probability $v$ an individual jumps to a new unique phenotype). Similarly an individual inherits its parent's strategy with probability $1 - u$ or adopts a strategy chosen at random among $\{C, D\}$ with probability $u$. Cooperation is conditional on being of the same phenotype. In other words, a $C$-player cooperates if the opponent is of the same phenotype, and defects otherwise. On the other hand, a $D$-player