

The Polymorphism of Producing Public Goods in an Evolutionary Volunteer's Dilemma Game

Zi-Xuan Guo (✉ guozixian980101@outlook.com)

Northwestern Polytechnical University

Matjaž Perc

University of Maribor

Qing-Ming Li

International Business School, Shaanxi Normal University

Lei Shi

Yunnan University of Finance and Economics

Rui-Wu Wang

Northwestern Polytechnical University

Jun-Zhou He

Northwestern Polytechnical University

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Abstract

There is an inconsistency between theory and observations with regards to the contributions of strong and weak players to the public goods. Theory suggests that contributors are either strong players in asymmetric games or cooperative players in symmetric games, but experiments indicate that the weak players in asymmetric systems also contribute to public goods. To reconciling these conflicts, we here study an evolutionary volunteer's dilemma game by assuming different roles can be interchangeable. In this model, the evolutionary dynamics shows the dynamics of multiple equilibria that depend on initial conditions, which can be interpreted as the production modes of public goods under different circumstances. Precisely, we find that the survival of strong individuals with mixed strategies is associated with two different outcomes. One result is equal to Selten's (1980) model, and public goods are produced by strong players if the defectors are weak players, where strong defectors are scarce in the initial condition. In another result, the weak individuals with mixed strategies produce public goods if the defectors are strong individuals, where the strong cooperators are absent in the initial condition. Concretely, the game degenerates to a mixed population of strong individuals with the weak players going extinct, and the weak defectors are scarce in the initial condition. The studied evolutionary game may help to explain the emergence of diverse forms of cooperation in asymmetric evolutionary games.

1. Introduction

Explaining the existence of cooperation under the threat of defection is one of the greatest challenges for evolutionary biology, as well as for the social science (Axelrod, 1984; Frank, 1998; Rankin et al., 2007; Archetti, 2010). In social groups, cooperators pay a cost by contributing to the public goods, but defectors enjoy the same benefits for free. The question thus is, how can cooperation prevail (Olson, 1965)? Traditionally, the theoretical framework for addressing this puzzle is evolutionary game theory, and social dilemmas in particular. Social dilemmas describe situations where what is best for an individual is at odds with what is best for the group or the society as a whole. Social dilemmas occur at all levels of biological organization, including microbes (Crespi, 2001), vertebrates (Creel, 1997), and human societies, *et al.* (Hardin, 1968).

Previous studies on explaining cooperation behavior are primarily based on the assumption that individuals interact with one another symmetrically (i.e. the individual costs and benefits of cooperation are identical for all individuals) (Axelrod, 1984; Hauert et al., 2006). But in fact, it was shown that individuals interact asymmetrically in almost all the studies concerning inter-specific cooperation (Pellmyr and Leebens-Mack, 2000; Pellmyr and Huth, 1994; Wang et al., 2011) as well as intra-specific cooperation (Reeve, 1992; Ratnieks and Wenseleers, 2007). This asymmetrical interaction could be caused by a variety of factors such as a difference in resource availability to different individuals, a difference amongst individuals in their probability of winning a fight with others (Maynard Smith, 1982; Wang et al., 2011). Indeed, existing game theory shows that players that interact asymmetrically might alter the payoffs and influence cooperative actions during a game (Maynard Smith, 1982; Gaunersdorfer et al., 1991; Nikiforakis et al., 2010; Wang et al., 2010a; He et al., 2015).

The normal form analysis of asymmetric game is a bimatrix game. Based on the bimatrix game, the models of Selten (1980) and Diekmann (1993) predicted that the public goods would be produced only by strong players, and that all players might adopt mixed strategies. These predictions help to explain the producing of public goods in asymmetric systems, but they are difficult to explain the fact that public goods is produced by strong individuals with mixed strategies in some systems, while they are produced by weak individuals with mixed strategies in others. For a bimatrix game, the players in different positions have different strategy sets and payoff matrices in asymmetric games (Hofbauer and Sigmund, 1998). In particular, the players in different positions are distinguished in bimatrix games, which indicates that the asymmetric interactions are not interchangeable. This is appropriate for games aiming to describe parasite-host interactions, but hardly so for games describing owners and intruders, or workers and the queen, or strong players and weak players, or parents and offspring. In these cases, a player can at one point in time be in one position, and at some other time assume the other position (Hofbauer and Sigmund, 1998).

The game in which players can condition their strategies on their own position is called the role game (Gaunersdorfer et al., 1991; Hofbauer and Sigmund, 1998; Cressman et al., 1996; Berger, 2001). In the role game, there are several roles (or positions), and each role possesses several strategies (Gaunersdorfer et al., 1991). In addition, each individual will find itself with a certain probability in a particular role. Importantly, the opponents always have different roles in bimatrix games and role games (Gaunersdorfer et al., 1991; Hofbauer and Sigmund, 1998), which in turn implies that both the bimatrix games and the role games only focus on asymmetric interactions. However, the interactions between players can be either asymmetric or symmetrical (i.e., different or same roles) in an asymmetric game system. Examples include worker confronts worker in a worker-queen system, strong (or weak) player confronts a strong (or weak) player in a strong-weak system.

In this study, combining symmetric and asymmetric interaction (He et al., 2013), we developed an asymmetric volunteer's dilemma game with four strategy types by taking into account the assumption that different positions can be interchangeable in role games (Gaunersdorfer et al., 1991). Viewing this asymmetric game as an evolutionary game, we find that it possesses multiple equilibria which depend on different initial condition. That means which individuals would pay the extra cost to voluntarily produce the public goods depends on the initial condition. In what follows, we present the model in more detail, and we present results that may help to explain the emergence of diverse forms of cooperation in asymmetric evolutionary games.

2. Model

2.1 Model Assumption

The volunteer's dilemma (VOD) is a step-level public good game where only one actor's cooperation is necessary and sufficient to produce the public good (Diekmann, 1985; Diekmann and Przepiorka, 2016). And the 2-Person VOD game can be described as the following: two individuals are engaged in a pairwise

interaction and each can volunteer (i.e., cooperate, denoted C) or freeriding (i.e., defect, denoted D); the cost paid by a volunteer is c , and when the public goods is produced, each individuals obtain benefit $b > c$; if no individuals volunteer, the public goods is not produced and there is no cost and no benefit for mutual interaction individuals (Diekmann, 1985).

In this study, we would like to exploit how asymmetric interactions between the recipient and cooperative donor affect the cooperative behavior. We assume that the benefits is equal but the costs is unequal for co-players. That is, there are two types of volunteers with different cost (c_s, c_w) , here $c_w \geq c_s$. Used as a form of addressed for "strong" player and "weak" player of volunteer with low cost (c_s) and volunteer with high cost (c_w), respectively. According to the above assumptions, the payoff matrix of this asymmetric game can be described in Table 1.

Table 1 Payoff matrices for the asymmetric VOD

		"Weak" Player	
		Cooperation (C)	Defection (D)
"Strong" Player	Cooperation (C)	$(b - c_s, b - c_w)$	$(b - c_s, b)$
	Defection (D)	$(b, b - c_w)$	$(0, 0)$

Based on this structure, the asymmetric volunteer's dilemma game has two efficient and strict equilibria with exactly one "volunteer" and one "free-riders". Moreover, an additional equilibrium point in mixed strategies exist (Diekmann, 1993). But the mixed strategies are not an evolutionary stable strategy, and all orbits converge to one or the other of two opposite pure strict equilibria in the evolutionary process (He et al., 2014; Hofbauer and Sigmund, 1998). These evolutionary results for asymmetric systems are based on the assumption that the different positions are solidified for two populations. This assumption is hardly appropriate for games where one individual is sometimes in one position and sometimes in the other. It is also hardly possible that for male-female or worker-queen conflicts, the genetic programs for the roles are linked in the form of conditional strategies (Hofbauer and Sigmund, 1998).

Furthermore, both asymmetry and symmetry interaction between the opponent individuals might exist in an actuality asymmetric system. For reconcile model with the actuality, we assume the position is interchangeability (Gaunersdorfer et al., 1991) and the asymmetric interaction and symmetric interaction of opponent individuals all exist. Then we develop an asymmetric game with four strategy types for public goods (He et al. 2013). Therefore, the two strategies are also present for the two positions in the previous game (see Table 1). The population will consist of four behavioral types: S^C (i.e. play

cooperation if the player is "strong"), S^D (i.e. play defection if the player is "strong"), W^C (i.e. play cooperation if the player is "weak"), W^D (i.e. play defection if the player is "weak"). Symmetrizing this asymmetric game, the payoff matrices can be described in Table 2 based on Table 1.

Table 2 Payoff matrices for the symmetrizing asymmetric VOD

		Player B			
		S^C	S^D	W^C	W^D
Player A	S^C	$b - c_s$	$b - c_s$	$b - c_s$	$b - c_s$
	S^D	b	0	b	0
	W^C	$b - c_w$	$b - c_w$	$b - c_w$	$b - c_w$
	W^D	b	0	b	0

Note: Payoff is same to the classic VOD model when strong counter strong players or weak counter weak players, viz. the payoff of both players is symmetric.

2.2. Evolutionary Stability of Asymmetric Volunteer's Dilemma Game

Evolutionary game theory applies to study the robustness of strategy profiles and sets of strategy profiles with respect to evolutionary forces in games played repeatedly in large populations of boundedly rational agents (Weibull, 1996). In this section, we present an evolutionary game dynamic which describes how the frequencies of strategies within a population change in time according to the strategies' success (Maynard Smith, 1982; Hofbauer and Sigmund, 1998), and explore which equilibrium will survive in evolutionary refinement.

Combining the assumptions of the asymmetric volunteer's dilemma game model with the theory of replicator dynamics (Taylor and Jonker, 1978; Hofbauer and Sigmund, 1998), we can establish the replicator equation about the asymmetric volunteer's dilemma game as follows:

$$\begin{cases} dx_1/dt = x_1(E_S^C - E) \\ dx_2/dt = x_2(E_S^D - E) \\ dx_3/dt = x_3(E_W^C - E) \\ dx_4/dt = x_4(E_W^D - E) \end{cases} \quad (2.1)$$

Where x_1, x_2, x_3 and x_4 are respectively the probabilities of four behavioral types S^C, S^D, W^C, W^D , and $E_S^D/E_W^D, E_S^C/E_W^C$ and E are respectively the payoff of the four behavioral types and the average payoffs.

Then, we can obtain two point equilibriums A ('black point') and B ('red point'), and two line of the equilibriums EF ('green dash line') and AB ('blue solid line') (see Figure 1). The solution trajectories will converge to the point equilibriums A and B if the initial values of the system fall in the hyperplanes $S^C-W^C-W^D$ ('black solid cures with arrow') and $S^C-W^C-S^D$ ('red dash cures with arrow'), respectively (Figure 1-3). Moreover, the solution trajectories will converge to the line of equilibrium EF if the initial values of the system fall in the hyperplanes $S^D-W^C-W^D$ ('green dash cures with arrow') while they will converge to the line of equilibrium AB if the initial values of the system fall in the interior ('blue dash lines with arrow') or the hyperplanes

$S^C-S^D-W^D$ ('blue solid cures with arrow') (see Figures 1). Here, we denote the equilibria of the system by $A(x_1^*, 0, 0, x_4^*)$, $B(x_1^{**}, x_2^{**}, 0, 0)$, $E(0, 0, \bar{x}_3, \bar{x}_4)$, $F(0, \bar{\bar{x}}_2, \bar{\bar{x}}_3, 0)$, where the elements of a vector $(\cdot, \cdot, \cdot, \cdot)$ respectively represent the probabilities of four strategic types S^C, S^D, W^C, W^D , and $x_1^* = 1 - x_4^*$, $x_4^* = c_s/b = x_2^{**}$, $x_1^{**} = 1 - x_2^{**}$ and $\bar{x}_3 = 1 - \bar{x}_4$, $\bar{x}_4 = c_w/b = \bar{\bar{x}}_2$, $\bar{\bar{x}}_3 = 1 - \bar{\bar{x}}_2$. Then the hyperlines AB and EF imply that $\theta_1 = 1 - c_s/b$, $\theta_2 + \theta_4 = c_s/b$, $\theta_3 = 0$ and $\theta_3 = 1 - c_w/b$, $\theta_2 + \theta_4 = c_w/b$, $\theta_1 = 0$, respectively.

3. Discussion

Traditionally, research on public goods assumes that the interactions among opponents are symmetric, such that for example the resources are equally divided among individuals, or each player possesses the same competitive capacity. In the symmetric equilibrium of the volunteer dilemma with symmetric costs, each player has an equal probability of cooperation (Diekmann, 1985; Maynard Smith, 1982; Hofbauer and Sigmund, 1998). However, in real social dilemmas, costs may be asymmetric, and the payoffs might therefore be unequal (Binmore and Samuelson, 2001; Wang et al., 2011; 2010a). Selten (1980) first proposed and studied an asymmetric model, which assumed that the distribution of payoffs is unequal between players. Using an evolutionary two-person game, the model predicted that the public goods would only be produced by the so-called strong player, i.e., the one with lower costs. However, these theoretical results are not easily reconciled with experimental observations that the public goods are almost exclusively produced by the so-called weak players, i.e., those with high costs (e.g., Ratnieks and Wenseleers, 2007).

Another asymmetric game was developed by Diekmann (1993), who introduced an unequal distribution of costs and interests among different players. Diekmann's model showed that players might adopt mixed strategies, and players with lower costs (i.e., strong players) will contribute less frequently than players with high costs (i.e., weak player). This result leads to a puzzling paradox when looking at empirical observations (Diekmann, 1993). Later on, He et al. (2014) generalized results of Diekmann (1993) for the case of genetically related individuals in a simplified version in which there is one strong player and $N-1$ weak players with different benefits and costs, which showed that the mixed equilibrium identified by Diekmann (1993) is not evolutionary stable. However, the existence of two other evolutionary stable states (ESSs) was revealed, namely i) the collective good is produced by the strong player while weak players defect, and ii) the strong player always defects while the weak player cooperates with a certain probability. Moreover, He et al. (2014) showed that the former equilibrium has a larger domain of attraction and might therefore be biologically more relevant (He et al., 2014; Gavrillets, 2015).

It is important to note that the models of Selten (1980), Diekmann (1993) and He et al. (2014) all boil down to a bimatrix game (Mangasarian, 1964; Savani and Stengel, 2006; Shokrollahi, 2017). However, these games including role games (Gaunersdorfer et al., 1991) concentrate on asymmetric interactions between opponents but neglect symmetric interactions in asymmetric cooperation systems. The asymmetric game model for public goods we present here brings together both the asymmetric interactions and symmetric interactions. Besides, this model provides a better agreement between theory and real-life observations. In particular, symmetrizing the asymmetric public goods game with four strategy types and using evolutionary game theory, we show two types of equilibria in this dynamics. One type implies that the public good is produced by strong players with mixed strategies while weak players always defect for almost all initial values (AB). The other type, implies that the weak player with mixed strategies cooperate while strong players always defect (EF). The different initial conditions correspond to the initial states of individual strategies, and they might stem from differences in inheritance and habitat (He et al., 2014). Since the strategy is able to succeed via inheritance (Maynard Smith & Price,

1973; Maynard Smith, 1982), the initial states of individual strategies might be inherited from its parents. For instance, the hierarchy of the offspring of the spotted hyena greatly depends on the hierarchy of their mothers (Kruuk, 1972; Holekamp and Smale, 1991; Engh et al., 2000; Van Horn et al., 2004). Furthermore, study of Frankino and Pfenning (2001) showed that the phenotype of gene expression depends on both the individual's internal state and the larval environmental conditions (Frankino and Pfenning, 2001).

In Figure 1, the domain of attraction of the equilibrium (AB) includes almost all initial values (Figures 1 & 2), implying that the "strong" players produce public goods in almost all the asymmetric systems. This prediction is consistent with observed features of many societies, such as group movement (Couzin et al., 2005; Guttal and Couzin, 2010; Barta and Giraldeau, 1998; Mathot and Giraldeau, 2010), resource/food acquisition (Smith et al. 2015), punishment free-riding (Hooper et al., 2010; O'Gorman et al., 2009), managing within-group conflicts (Mesterton-Gibbons et al., 2011; Bisonnette et al., 2015; Frank, 1996; Ruttan and Borgerhoff Mulder, 1999) or resolving between-group interactions (Gavrilets and Fortunato, 2014; Gavrilets, 2015).

More precisely, the solution trajectories will converge to the locally stable point A and B if the initial values of the system lie in the hyperplanes $S^C - W^C - W^D$ and $S^C - W^C - S^D$, respectively (Figure 1 and Figure 2a,d). It is important to point out that the equilibrium point A in Figure 1 corresponds to the equilibrium of Selten's (1980) model that "strong" populations will adopt the volunteer strategy, while the opponents adopt free-riding (Figure 3b). And the equilibrium point B means that the asymmetric system will evolve to a symmetric system with a mixed "strong" population, that is, the population with higher costs (c_w) goes extinct (Figure 3d). These two equilibria are consistent with predictions of general theory that in public goods games contributors are either strong players in the asymmetric system (Selten 1980; Smith et al. 2015) or each individual with equal probability in the symmetric system (Diekmann, 1985; Hauert et al., 2004; Archetti, 2009; Archetti and Scheuring, 2010).

If the initial values of the system fall in the hyperplanes $S^D - W^C - W^D$, the asymmetric dynamic system (2.1) will converge to the line of equilibrium EF (Figures 2, 3 & 4). The EF predicts that the "strong" population adopts the free-rider strategy while the "weak" population adopts volunteering to produce the public goods. It is worth noting that the provider of the public goods in the "weak" population are also free-riders on the lines of the EF equilibrium (Figure 3a and Figure 4a). This result is biologically relevant, for example in social insect colonies some public goods (e.g., foraging, building and brood care) are produced by workers, but a proportion of the colony's workers appear to spend their time being completely inactive (Dornhaus, 2008; Duarte et al., 2011; Charbonneau and Dornhaus, 2015; Ratnieks and Wenseleers, 2007). Similar phenomena also exist in vertebrates (Reeve, 1992; Singh et al., 2006), or human societies (Hardin, 1968). Meanwhile, our results also show that the extent of the free-rider fraction depends on the initial values of the system and on the cost-benefit ratio of producing public goods c_W/b (Figure 3 and Figure 4).

A slight inconsistency of our results is that the equilibrium line EF is a generalized saddle point with its own basin of attraction, given by the hyperplanes $S^D - W^C - W^D$ (Figure 1 and Figure 2b,c). On the contrary, the equilibrium line AB (including A and B) is locally stable. In effect, the solution trajectories will converge to the EF line if the initial values of the system fall in the hyperplanes $S^D - W^C - W^D$ (Figure 2c, Figure 3a and Figure 4a). That is, the model we developed predicts that "weak" players might also produce public goods with mixed strategies under some initial conditions, but this EF equilibrium is unstable. In the future, this could be

remedied by taking other important factor of asymmetric systems that we did not consider here into account, such as stochastic effects of the environment, effects of time delay, and effects of self-feedback. In addition, it is possible to argue that the unstable *EF* equilibrium might have evolved due to specialization and division of labor in the worker class. Indeed, the ecological success of social insects is often attributed to efficient work specialization and a functioning division of labor (Oster and Willson, 1978; Willson, 1991; Charbonneau and Dornhaus, 2015). Finally, we note that moving towards a saddle point in a population was also observed experimentally in *Tribolium* (Cushing et al., 1998).

In conclusion, this research will contribute to a better understanding of the emergence of diverse forms of cooperation in asymmetric evolutionary games and applying these insights to real-life populations.

Declarations

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Statement:

This is a statement to confirm that all methods were carried out in accordance with relevant guidelines and regulations and all experimental protocols were approved by a named institutional and/or licensing committee/s, and informed consent was obtained from all subjects and/or their legal guardian(s).

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Figures

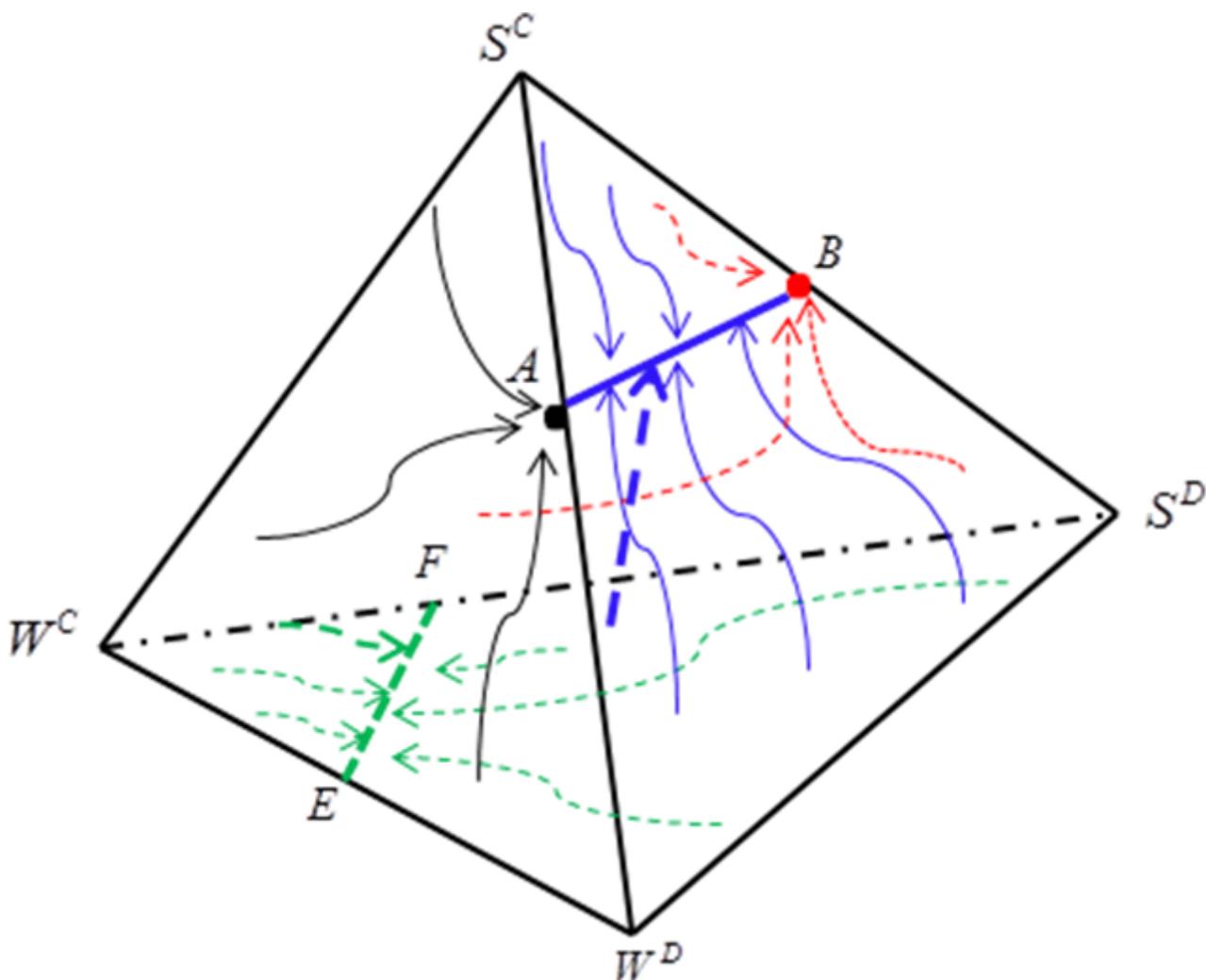


Figure 1

The simplex, divided into four basins of attraction. See the main text for an explanation of the symbols and for further details.

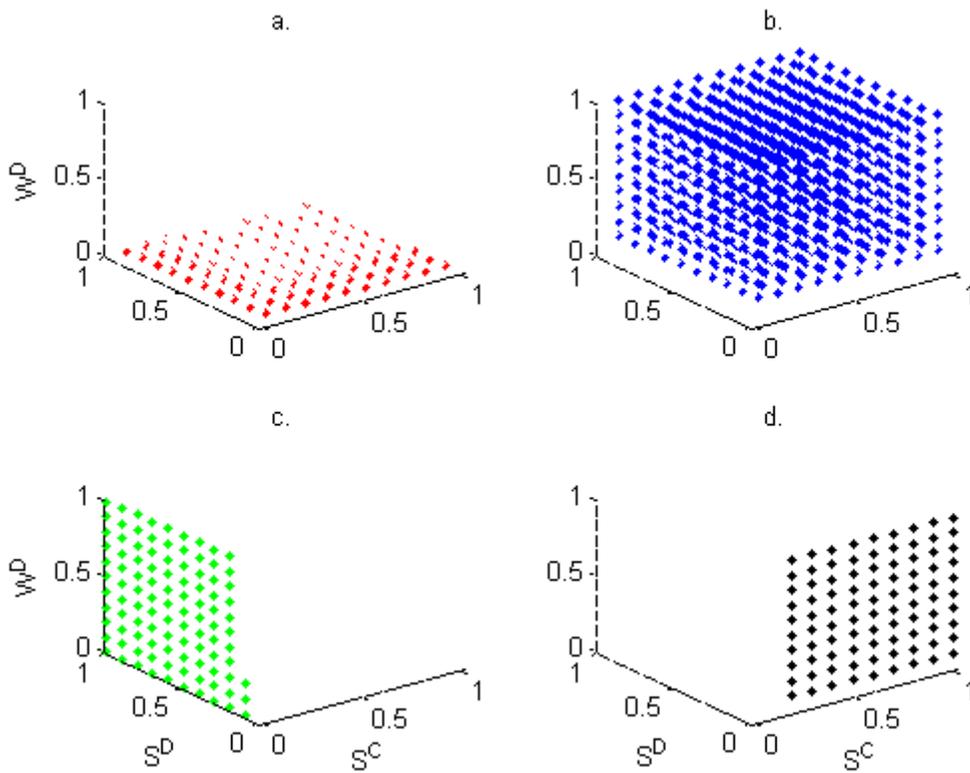


Figure 2

The projection of the basin of attraction of the four different equilibria of the replicator dynamics (2.1) in three-dimensions S^C - S^D - W^D . Parameter values used are $b_s=1$, $b_w=1$, $c_s=0.1$, $c_w=0.2$.

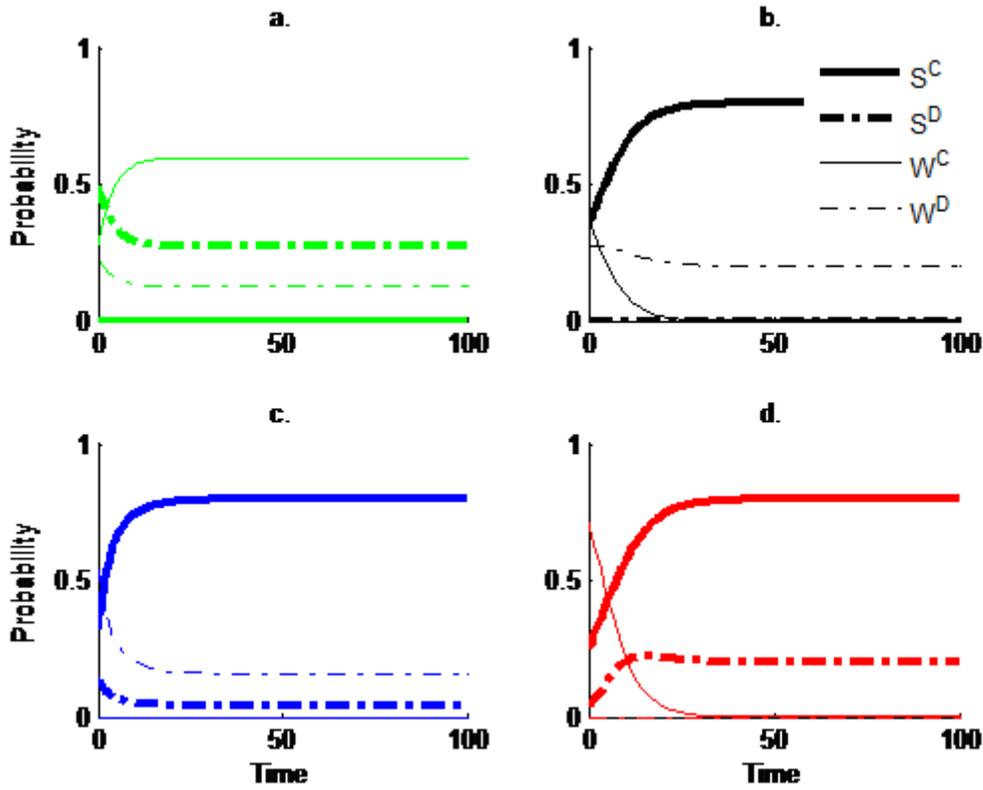


Figure 3

Probability of the four different equilibria of the replicator dynamics, as obtained for the initial values in different hyperplanes. Thick lines and thin lines represent two positions (i.e., "strong" and "weak"), and the solid lines and dash-dotted lines represent two strategies (i.e., cooperation and defection). Here the initial values $a(0, 0.4951, 0.2787, 0.2262)$, $b(0.3474, 0, 0.3835, 0.2691)$, $c(0.3208, 0.1384, 0, 0.5408)$ and $d(0.2469, 0.0419, 0.7112, 0)$ fall in the hyperplanes $SD-WC-WD$, $SC-WC-WD$, $SC-SD-WD$, $SC-SD-WC$ respectively. Parameter values used are $bs=1$, $bw=1$, $cs=0.2$, $cw=0.4$.

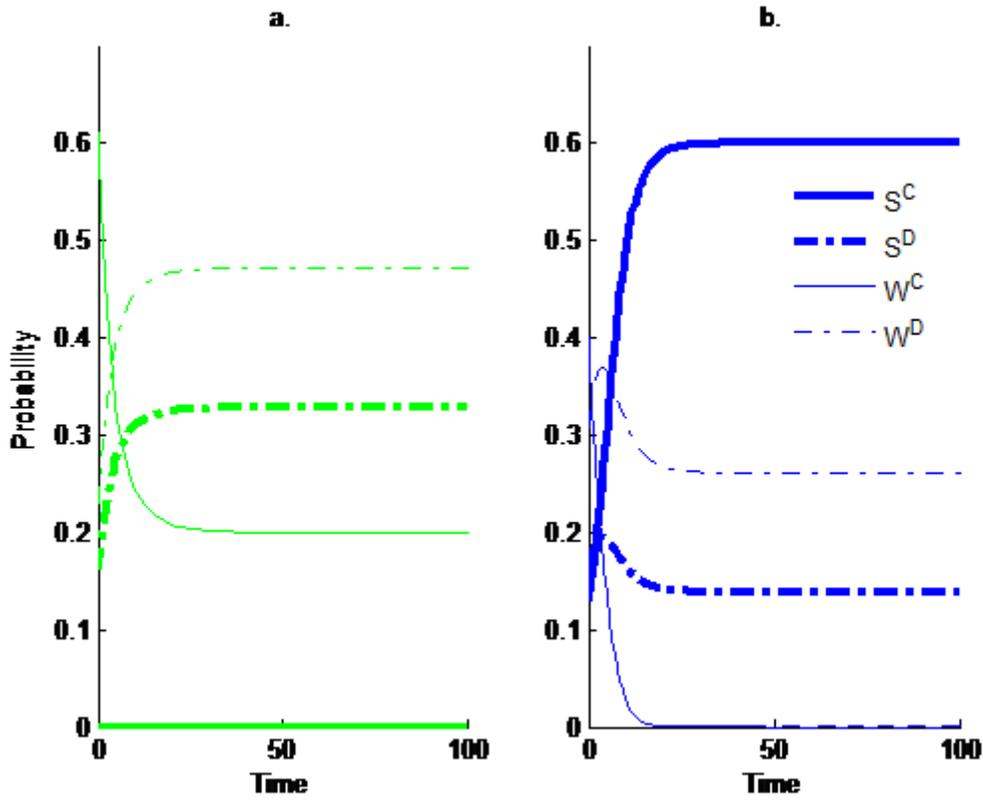


Figure 4

Probability of the four different equilibria of the replicator dynamics for different initial values. Here the initial values $a(0, 0.1599, 0.6102, 0.2298)$ and $b(0.1279, 0.1634, 0.4008, 0.3079)$ fall in the hyperplanes $S^D-W^C-W^D$ and in the inner part of the replicator dynamics (2.1), respectively. Parameter values used are $b_s=1, b_w=1, c_s=0.4, c_w=0.8$.