Cooperation driven by mutations in multi-person Prisoner's Dilemma

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Abstract

The n-person Prisoner's Dilemma is a widely used model for populations where individuals interact in groups. The evolutionary stability of populations has been analysed in the literature for the case where mutations in the population may be considered as isolated events. For this case, and assuming simple trigger strategies and many iterations per game, we analyse the rate of convergence to the evolutionarily stable populations. We find that for some values of the payoff parameters of the Prisoner's Dilemma this rate is so low that the assumption, that mutations in the population are infrequent on that time-scale, is unreasonable. Furthermore, the problem is compounded as the group size is increased. In order to address this issue, we derive a deterministic approximation of the evolutionary dynamics with explicit, stochastic mutation processes, valid when the population size is large. We then analyse how the evolutionary dynamics depends on the following factors: mutation rate, group size, the value of the payoff parameters, and the structure of the initial population. In order to carry out the simulations for groups of more than just a few individuals, we derive an efficient way of calculating the fitness values. We find that when the mutation rate per individual and generation is very low, the dynamics is characterized by populations which are evolutionarily stable. As the mutation rate is increased, other fixed points with a higher degree of cooperation become stable. For some values of the payoff parameters, the system is characterized by (apparently) stable limit cycles dominated by cooperative behaviour. The parameter regions corresponding to high degree of cooperation grow in size with the mutation rate, and in number with the group size. For some parameter values, we find more than one stable fixed point, corresponding to different structures of the initial population.
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1. Introduction

In social and natural systems, the action of an individual often affects a number of other individuals, and there are numerous examples of situations where so-called free riders or defectors take advantage of others cooperating for a common good (Hardin, 1968; Maynard Smith, 1982; Sugden, 1986).

A game-theoretic approach for the study of cooperation can be based on the Prisoner's Dilemma game (Flood, 1958; Rapoport and Chammah, 1965)—a

situation that captures the temptation to act in a selfish way to gain a higher own reward instead of sharing a reward by cooperating. In the game, the players independently choose an action, either to defect or to cooperate.

In the two-person game, the scores are R (reward) for mutual cooperation, T (temptation score) for defection against a cooperator, S (sucker's payoff) for cooperation against a defector, and P (punishment) for mutual defection, with the inequalities $S < P < R < T$ and (usually) $R > (T + S)/2$. We use fixed values on R and S in this study, $R = 1$ and $S = 0$, while $0 < P < 1 < T < 2$. (In the population dynamics we use there are only three independent parameters, the third one being a growth constant.) From theoretic and simulation studies of two-person Prisoner's Dilemma game, it is known under

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which circumstances repeated interactions may allow for a cooperative population to be established that can resist invasion by non-cooperative mutants (see, e.g. Rapoport and Chammah, 1965; Axelrod and Hamilton, 1981; Molander, 1985; Axelrod, 1987; Miller, 1996; Lindgren, 1992; Nowak and Sigmund, 1992).

In the *n*-person Prisoner's Dilemma game, *n* players simultaneously choose an action, whether to cooperate or to defect. In the literature, there are several evolutionary models based on the *n*-person Prisoner's Dilemma using various strategy sets and pairing mechanisms, e.g. where the players are distributed in space. To our knowledge, the first evolutionary models of this type are those by Matsuo (1985) and Adachi and Matsuo (1991, 1992), where individuals simultaneously play on a square lattice. A similar cellular automaton was presented by Albin (1992). In these models, a player performs a certain action every round depending on previous actions of the nearest neighbours. Fitness is given by joint actions of the player and its nearest neighbours. This means that an action at a certain position may influence the play at distant sites in the course of the iterated game. Models based on local groups on a lattice, where each player participates in several overlapping but isolated games (see, e.g. Matsushima and Ikegami, 1998; Lindgren and Johansson, 2001), can much more easily exhibit a high degree of cooperation—the main mechanism being a kind of kin or group selection allowing for the formation of stable cooperative clusters, as has also been observed for the 2-person game (Nowak and May, 1993; Lindgren and Nordahl, 1994). Hauert and Schuster (1997) give a model involving probabilistic strategies with finite memory. They find that an error-correcting strategy type, previously studied in the context of the 2-person Prisoner's Dilemma in (Lindgren, 1992) and under the name 'Pavlov' in (Nowak and Sigmund, 1993), may perform successfully also in the multi-player case. Other extensions of the strategy space introduce longer memory in terms of internal states (see, e.g. Akimov and Soutchanski, 1997; Lindgren and Johansson, 2001).

In this paper, we revisit the classic *n*-person Prisoner's Dilemma. Following Boyd and Richerson (1988) and Molander (1992), the behaviours of the participants are modelled by simple reactive strategies. These authors analyse the stability of stationary populations in the limit where mutations are infrequent: a mutation either is driven to extinction by the selective pressure from the resident population, or leads to a new resident population. The general conclusion from their studies is that cooperation is difficult to obtain when extending the group size beyond the two persons in the original Prisoner's Dilemma game. When mutations are infrequent, we find that for some values of the payoff parameters, the rate of convergence to the evolutionarily stable populations is so low that the assumption that mutations in the population are infrequent on that time-scale is unreasonable. Furthermore, the problem is compounded as the group size is increased. In order to address this issue, we derive a deterministic approximation of the evolutionary dynamics with explicit, stochastic mutation processes, valid when the population size is large. Among the questions we analyse are: How does the evolutionary dynamics, and especially the long-term average degree of cooperation, depend on how frequently mutations occur in the population? To what extent does the choice of parameter values in the Prisoner's Dilemma payoff matrix affect the outcome? How does the evolutionary dynamics depend on the group size?

The paper is organized as follows: In Section 2, we define the multi-person game and the strategy set used in our study. In Section 3, the evolutionary dynamics with an explicit flow of mutations is presented, and we review the evolutionary stability analysis in the case of infrequent mutations. In Section 4, we derive a deterministic approximation to the evolutionary dynamics with mutations, and present the new method for rapid calculation of fitness levels. In Section 5, the results from simulations and numerical analysis of the evolutionary dynamics is presented and discussed. In Section 6 we conclude with a summary and outlook.

2. The *n*-person Prisoner's Dilemma game

In this section, we review the *n*-person Prisoner's Dilemma game and define the strategy set used in our study. Each player interacts with $n-1$ other players. Depending on the number k of others cooperating, a player receives the score $V(C|k)$ when cooperating and the higher score $V(D|k)$ when defecting. The scores increase with an increasing number of cooperators, and also the total score given to all players increases if one player switches from defection to cooperation, see, e.g. Boyd and Richerson (1988). Thus

$$\begin{cases} V(D|k) > V(D|k-1) \text{ and } V(C|k) > V(C|k-1), \\ V(D|k) > V(C|k), \\ (k+1)V(C|k) + (n-k-1)V(D|k+1) \\ \quad > kV(C|k-1) + (n-k)V(D|k). \end{cases} \quad (1)$$

In this paper we shall assume that the scores V can be calculated as a linear combination of the scores against the other players in $n-1$ ordinary two-player Prisoner's Dilemma games:

$$V(C|k) = \frac{k}{n-1} \quad \text{and}$$

$$V(D|k) = T\frac{k}{n-1} + P\frac{n-k-1}{n-1}, \quad (2)$$

where we have divided by $n-1$ in order to make it easier to compare results from different group sizes. The parameters P and T obey $0 < P < 1 < T < 2$. Note that this is still an n-person game since the same action is performed simultaneously in all games. This is a more general game than the one studied by Boyd and Richerson (1988), since they assume that $T - P = 1$ (corresponding to a line in our parameter region), but less general than the payoff functions considered in (Molander, 1992). Other score functions that fulfil the conditions in Eq. (1) are expected to yield similar results (cf. Molander, 1992), and it is straightforward to extend the numerical methods in this paper to arbitrary score functions $V(C|k)$ and $V(D|k)$, using the method for evaluating the fitness values presented in Section 4.

It is assumed that the players have no way of coordinating their choices, and that all player wish to maximize their score. Hence, in the single round game, the optimal choice of action is to defect, and this leads to all players in the group defecting and scoring only $P < 1$ instead of 1, which they get if all cooperate. If there is a high probability that the group will play again, we have the iterated n-person Prisoner's Dilemma, and then cooperation may develop under some circumstances.

We focus on the set of trigger strategies (Schelling, 1978) as the strategy space for the evolution, which was also considered by, e.g. Boyd and Richerson (1988) and Molander (1992). A trigger strategy s_k is characterized by the degree of cooperation that it requires in order to continue to cooperate: a player with trigger strategy s_k cooperates if at least k other players cooperate. In a game with n participants, k is in the range $0, \ldots, n$. The strategy s_0 is an unconditional cooperator and s_n is an unconditional defector. Each player decides whether to cooperate or to defect based on the actions of the other players. In the first round after the formation of a group, all players are assumed to cooperate, with the exception of unconditional defectors. Then the players that are unhappy with the number of cooperators switch to defection. This may cause other players to change their action, and this is iterated until a stable configuration has been reached. Note that the number of cooperators may only decrease or be stable, and that this procedure converges to the stable configuration with the maximum number of cooperators. In a repeated game without noise, this implies that a group of players with different trigger levels reaches a certain degree of cooperation, some players may be satisfied and cooperate while the others defect. Despite their simplicity, trigger strategies capture many important aspects of the many-person game, and allow for straight-forward evaluation of the expected score for a player in a group randomly generated from a given population.

It should be noted that some aspects of this game depend very strongly on the expected number of iterations (Boyd and Richerson, 1988); most notably, the ability to defend against pure defectors in large groups requires very long games, to offset the cost of initial cooperative actions when defectors are present in a group. In this article, however, we focus on the role of mutations in the evolutionary dynamics. For simplicity, and in order to treat the fitness values analytically, we limit the study to the simpler situation when the games are infinitely iterated, and we use the average score per player and round as a fitness variable for the selection in the population dynamics. This assumption can also be interpreted as a one-round game with players making binding contracts in a negotiation before the game.

3. Evolutionary dynamics

Consider a population of N individuals. From one generation to the next, a fraction δ of the population is replaced using fitness proportional selection, where the fitness of an individual is proportional to the number of offspring surviving to reproductive age. Throughout this paper, $\delta = 0.1$. If small enough, the value of δ does not influence the structure of the evolving population, but determines the evolutionary time scale. Assuming that the population size is large and constant, the evolutionary dynamics takes the form of

$$x'_l = x_l + \delta \left(\frac{f_l}{\bar{f}} - 1 \right) x_l, \tag{3}$$

where x_l is the fraction of players in the population with trigger level l, x'_l is the value of x_l in the next generation, f_l is the expected fitness for a player with trigger level l, and $\bar{f} = \sum_{l=0}^{n} x_l f_l$ is the average fitness in the population.

The expected fitness f_l for a player with trigger level l is the expected score of the player in a randomly formed group:

$$f_l = \sum_{i_1, \ldots, i_{n-1}=0}^{n} x_{i_1} \cdots x_{i_{n-1}} S(l, i_1, \ldots, i_{n-1}), \tag{4}$$

where $S(l, i_1, \ldots, i_{n-1})$ is the score of a player with strategy s_l in a game with $n-1$ other players, using strategies $s_{i_1}, \ldots, s_{i_{n-1}}$, respectively.

Molander (1992) gives an analysis of the model, with general score functions $V(C|k)$ and $V(D|k)$, when it is assumed that a mutation will either lead to a new resident population, or that the evolutionary dynamics will bring the population back to the situation before the mutation. Molander shows that in each interval $P \in ((k-1)/(n-1), k/(n-1))$, where $k \in \{1, \ldots, n-2\}$, there is either a mixture of strategies s_k and s_n, which is evolutionarily stable, or there is a mixture of strategies $s_0, \ldots, s_{n-1}$ (all cooperating), that resists invasion by strategy s_n, but which is not evolutionarily stable. Finally, there is no other asymptotically stable

population in that interval. In the interval $P \in ((n-2)/(n-1), 1)$, the purely cooperative equilibrium mixture is the only possible asymptotically stable population.

Suppose that a population with groups of size n consists of a mixture of strategies s_k and s_n, in fractions x and $1-x$, respectively. Since, in this population, strategy s_k cooperates if and only if there are at least k other players with the same strategy in the group, and since strategy s_n always defects, direct evaluation of Eq. (4) gives

$$f_k(x) = \sum_{i=1}^{k} P \binom{n-1}{i-1} x^{i-1}(1-x)^{n-i}$$
$$+ \sum_{i=k+1}^{n} \frac{i-1}{n-1} \binom{n-1}{i-1}$$
$$\times x^{i-1}(1-x)^{n-i} \qquad (5)$$

for strategy s_k and

$$f_n(x) = \sum_{i=0}^{k} P \binom{n-1}{i} x^i(1-x)^{n-i-1}$$
$$+ \sum_{i=k+1}^{n-1} \left[P + (T-P)\frac{i}{n-1} \right]$$
$$\times \binom{n-1}{i} x^i(1-x)^{n-i-1}, \qquad (6)$$

for strategy s_n. We find the equilibrium by setting $f_k(x) = f_n(x)$ and then solving for x, with the requirement $0 < x < 1$. Existence and uniqueness of this equilibrium is guaranteed by the result of Molander (1992). In Fig. 1 we show how the equilibrium fitness depends on P for $T = 1.2$, for group size $n \in \{2, \dots, 10\}$. Note that the fitness at the asymptotically stable population approaches $f = P$ as n increases, indicating a decreasing degree of cooperation. From the existence and uniqueness of the asymptotically stable populations of this form, and from a Taylor expansion of f_k and f_n to the order x^{k+1}, follows that $x \sim 1/n$ at the asymptotically stable population, for $T > 1$.

Consider a small perturbation of one of the evolutionarily stable populations constituted by the strategies s_k and s_n. The long-term response by the evolutionary dynamics to the perturbation is given by the eigenvalues λ of the Jacobian of $x' - x$ at the evolutionarily stable population. We find that the rate of convergence to the evolutionarily stable state approaches zero, as P approaches $k/(n-1)$, for $k \in \{1, \dots, n-2\}$. This is illustrated in Fig. 2 for $n = 4$ and $P \in (0, 1/3)$. Thus, if P is close enough to $k/(n-1)$, the evolutionary dynamics does not relax to the stationary population between mutations even for the case when each perturbation is very small, provided that they occur frequently enough. Since the selective forces are so weak, it takes very long time to drive a mutation to extinction, and we conclude that it is insufficient to analyse the evolutionary properties in the limit of
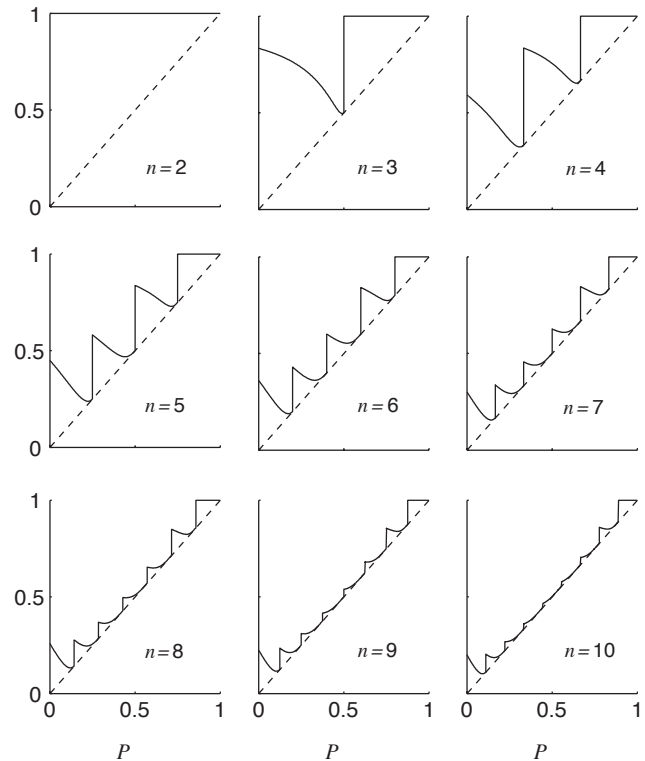

Fig. 1. The payoff at equilibrium as a function of P (thick line), for $T = 1.2$ and group size $n \in \{2, \dots, 10\}$. Also shown is the payoff P (dashed line) for a population of pure all-defect.
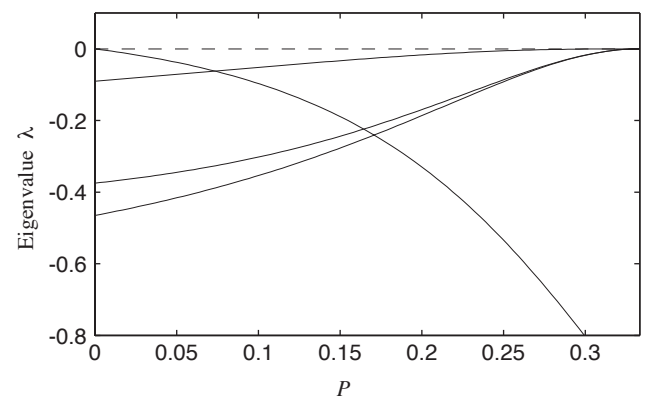

Fig. 2. Eigenvalues λ of the Jacobian for the replicator dynamics [cf. (9)], at the evolutionarily stable population, in the limit of infrequent mutations. After a small perturbation, the dynamics eventually returns to the evolutionarily stable state, but the time it takes to do so [characterized by $-(\ln 2)/\lambda$], diverges as P approaches $\frac{1}{3}$. The Jacobian, with elements $J_{ij} = \partial/\partial x_j(f_i - \bar{f})$, is evaluated at the stationary population, was obtained from explicit expressions of f_i and $\bar{f}$. These in turn were calculated using (10) and Theorem 1.

infrequent mutations. In the following, we extend the evolutionary dynamics Eq. (3) to explicitly include the mutation process, and analyse how the evolutionary dynamics is influenced by this process.

4. Evolutionary dynamics with mutations

We now introduce mutations as an explicit part of the evolutionary dynamics. The population is subject to selection as in Eq. (3). In addition, a number $\mathcal{M}_{l \to j}$ of individuals per generation switch from strategy s_l to strategy s_j due to mutations. The mutations are assumed to be generated by stochastic events, e.g. by a Poisson process, in the process of reproduction. We assume that the probability of surviving to reproductive age does not depend on the offspring's strategy, but only on that of the parent. Hence, our measure of fitness comprises factors such as parental care, as well as vying for resources. It follows that the evolutionary dynamics takes the form

$$x'_l = x_l + \delta\left(\frac{f_l}{\bar{f}} - 1\right)x_l + \frac{1}{N}\sum_{j=0}^{n}(\mathcal{M}_{j \to l} - \mathcal{M}_{l \to j}). \quad (7)$$

In a single generation, each player with strategy s_l has an expected number $\delta f_l x_l / \bar{f}$ of offspring surviving to reproductive age. Mutations occur independently in the creation of each offspring, with a probability of $\mu \ll 1$ per offspring per generation, and the strategy of the mutated offspring is chosen randomly among the $n+1$ strategies (strategies $s_0, \ldots, s_n$), with equal probability. The expected number of mutations per generation in the whole population is then μN. Since the population size is assumed to be large, by the law of large numbers (see, e.g. Rice, 1995) the number $\mathcal{M}_{l \to j}$ of mutated offspring is approximately equal to its expected value, given by

$$\mathcal{M}_{l \to j} \approx \frac{\mu \delta N f_l x_l}{(n+1)\bar{f}}. \quad (8)$$

Note that this approximation is valid for all fitness values. Inserting Eq. (8) into Eq. (7), we obtain the following expression for the evolutionary dynamics:

$$x'_l = x_l + \delta\left(\frac{f_l}{\bar{f}} - 1\right)x_l + \delta\mu\left(\frac{1}{n+1} - \frac{f_l}{\bar{f}}x_l\right). \quad (9)$$

This equation is similar to the population dynamics introduced by Eigen (1971) in the study of quasi-species (see also, e.g. Eigen and Schuster, 1977; Schuster and Sigmund, 1985). Since $\mu \ll 1$, the mutation process is only expected to have a significant impact on the evolutionary dynamics when the fitness values for all players are close to the average fitness in the population, i.e. when the population is close to equilibrium.

We expect that the impact of a finite mutation rate on the evolutionary dynamics is increasing with the population size. Hence, the evolutionary dynamics of large groups are of special interest. When the group size is small, or when only a couple of strategies are present in the population (as in Section 3), f_l may be evaluated from Eq. (4) by direct summation. For larger group sizes, and when many strategies are present in the population, this becomes impractical due to the rapid growth of the number of terms in the sum, as shown in Table 1. Thus, in order to investigate the evolutionary dynamics of larger groups, we need a way to evaluate the fitness values of players in groups of more than just a few players.

The population is characterized by the probability P_i^l that the number of cooperating players equals i, in a group with one player using strategy s_l and the $n-1$ other players chosen randomly from the population. Since strategy s_l cooperates if $i > l$ we have

$$f_l = \sum_{i=0}^{l} P_i^l V(\text{D}|i) + \sum_{i=l+1}^{n} P_i^l V(\text{C}|i-1). \quad (10)$$

Thus, efficient calculation of the P_i^l allows for the study of the evolutionary dynamics in larger groups. We derive a method for calculating P_i^l, for arbitrary population compositions, that avoids the rapid growth of the number of terms in Eq. (4). Note that since P_i^l only depends on the distribution of trigger levels in the population, this method may be applied for any payoff functions $V(\text{C}|i)$ and $V(\text{D}|i)$. Using a simple observation on the number of cooperating players in a group, we obtain:

Theorem 1. *In a population of trigger strategies, the probability P_i^l that the number of cooperating players equals i, in a group with one player using strategy s_l and the $n-1$ other players chosen randomly from the population, is*

$$P_i^l = \begin{cases} 0 \\ \quad \text{whenever } i = l, \\ D_{n-1}^{l,0} \\ \quad \text{when } i = 0, \\ (x_0 + \cdots + x_{n-1})^{n-1} \\ \quad \text{when } i = n, \\ \binom{n-1}{i - \mathbf{1}_{(l<i)}}(x_0 + \cdots + x_{i-1})^{i - \mathbf{1}_{(l<i)}} D_{n-1-i+\mathbf{1}_{(l<i)}}^{l,i} \\ \quad \text{otherwise,} \end{cases} \quad (11)$$

where $\mathbf{1}_{(l<i)}$ is one if $l < i$ and zero otherwise, and $D_m^{l,i}$ is given by the recursive formula

$$D_m^{l,i} = \begin{cases} x_n^m & \text{when } i = n-1, \\ \sum_{j=0}^{M}\binom{m}{j}x_{i+1}^j D_{m-j}^{l,i+1} & \text{otherwise,} \end{cases} \quad (12)$$

where $M = m + i + 2 - \mathbf{1}_{(l<i)} - n$.

Table 1
The number of terms in a direct evaluation of f_l from (4) for all l, for $n = 2 \ldots 10$. The number grows very rapidly with n

n	Number of terms
2	9
3	64
4	625
5	7776
6	117649
7	2097152
8	43046721
9	1000000000
10	25937424601

The proof is in the appendix. Note that whenever $l < i$ and $l' < i$, $P_i^l = P_i^{l'}$, so if $l < i$ then $P_i^l = P_i^0$. Using tables to store evaluated values of $D_m^{l,i}$, it is possible to evaluate the values of P_i^l for all l and i in $\sim n^4$ operations. It may be possible to reduce this to $\sim n^3$ operations through further exploitations of the recursive structure of $D_m^{l,i}$.

5. Results

Armed with an efficient method for evaluating the fitness values, we proceed to the results from our simulations. We have investigated how the evolutionary dynamics [cf. (9)] depends on different factors: the payoff parameters P and T, the initial population, group size and mutation rate.

5.1. Dependency on the payoff parameters

We have measured the long-term degree of cooperation, over the parameter region of P and T, for various choices of group size n. The initial state of the population is the always defecting strategy s_n.

The long-term degree of cooperation is quantified by the time-average and standard deviation of the average score in the population, estimated from long simulations of the system, with the initial transients removed. The standard deviation of $\bar{f}(t)$ is defined as $\langle \bar{f}(t)^2 \rangle - \langle \bar{f}(t) \rangle^2$, where $\langle \cdot \rangle$ denotes time average.

In the top diagram of Fig. 3, the result for $n = 4$ is shown. For a large part of the domain, cooperation is high, while there are two regions, D_1 and D_2, with significantly lower payoffs. These two areas are characterized by fixed points in the dynamics, dominated by strategy pairs (s_1, s_4) and (s_2, s_4), respectively. These correspond to the fixed points given by the evolutionary stability analysis, discussed in Section 3 and illustrated in Fig. 1. The other strategies are also present, albeit at a much lower level (of the order of μ): the abundance of such a strategy is determined by a balance between the
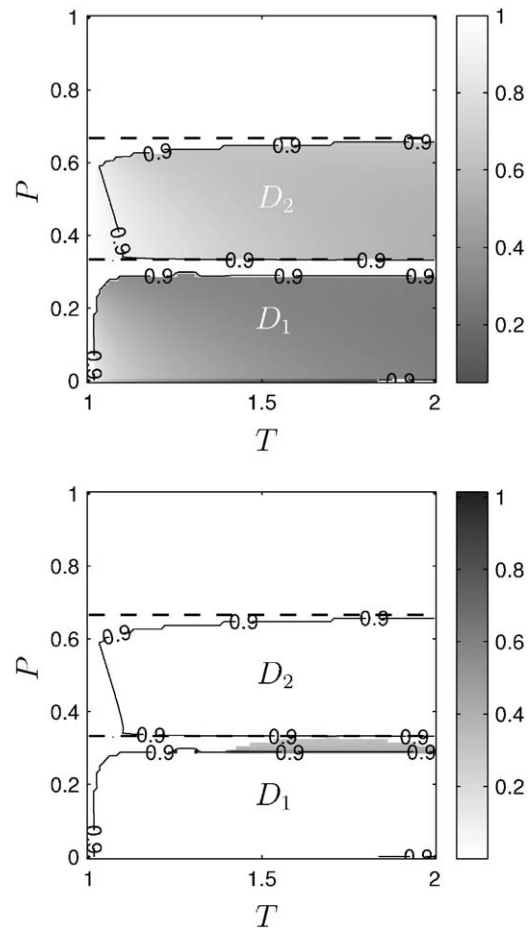

Fig. 3. *Top*: Asymptotic time-average of the average payoff in the population (represented by the grey value, as indicated in the scale to the right of the figure), as a function of the parameters T and P, for $n = 4$ and $\mu = 10^{-4}$. *Bottom*: Asymptotic standard deviation of the average payoff in the population (represented by the grey value, as indicated in the scale to the right of the figure), as a function of the parameters T and P. The averages and standard deviations were estimated from long simulations of the system, with the initial transients removed. The line where the average payoff equals 0.9 is shown in both panels. Also shown in both panels are the borders at $P = \frac{1}{3}$ and $P = \frac{2}{3}$ between the different asymptotically stable populations, in the limit of infrequent mutations (dashed lines).

net flow of mutations to the strategy, and the selective pressure on the strategy from the population. In the limit $\mu \to 0$, D_1 and D_2 corresponds to $0 < P < 1/3$ and $1/3 < P < 2/3$, respectively, with $1 < T < 2$ in both cases.

In the lower part of Fig. 3, we give the standard deviation of the average score (the transient excluded). A value significantly above zero indicates a varying average fitness, such as caused by the presence of oscillatory dynamics. Note that most of the parameter region is dominated by stable fixed points, corresponding to the fixed points of the dynamics in the limit $\mu \to 0$. In the cooperative region, the fixed points are given by a mixture of cooperating strategies dominated by strategy s_{n-1}. An exception is the ridge between region

D_1 and D_2. In this region, stable fixed points are characterized by a mixture of all strategies but the always defecting strategy s_n, and thus a high level of cooperation, contrary to what is expected from the stationary population in the limit $\mu \to 0$. Furthermore, part of this area is characterized by oscillating dynamics (as indicated by a non-zero variance in the lower part of Fig. 3), between cooperative and defecting strategies.

5.2. Dependency on the initial population

When the system is initialized with a population of s_3 strategies, in the case of group size $n = 4$, we find that in some parts of the parameter region, there exist other stable fixed points, see Fig. 4. Most of region D_2 in Fig. 3 has been replaced by a cooperative fixed point dominated by strategy s_3, and parts of region D_1 in Fig. 3 has been affected in a similar way. In this case, cooperation is established and kept stable in the major part of the parameter region.

In our model we have assumed that mutations are frequent in the population, which alters the conclusions by Molander as discussed in Section 3 in two ways: First, the cooperative region we observe for $P > 2/3$, is now a stable fixed point, while there is no stable fixed point in that region in the absence of mutations. Second, in the cooperative region between regions D_1 and D_2, the flow of mutations destabilizes the fixed point given by the analysis of Molander discussed above, resulting in either an oscillating distribution of strategies, or a fixed point involving more than two strategies.

5.3. Dependency on the mutation rate

A more detailed numerical investigation for group size $n = 6$ is shown in Fig. 5, where the average payoffs are calculated as functions of P for $T = 1.6$. When increasing the mutation rate (from 10^{-5} to 10^{-3}), less of the fixed points characterized by strategy pairs (s_k, s_n) remains. Each interval $((k-1)/(n-1), k/(n-1))$ of P is characterized by two regimes: At the lower end and in the middle, the population is given by the (s_k, s_n) equilibrium, indicated by a thick line. At the higher end, the dynamics is either in a stable limit cycle (see Fig. 6) or in an equilibrium involving more than two strategies, resulting in a higher average score. In the higher end of these intervals, the fraction of cooperating strategies vanish in the infinitesimal mutation limit, so the effect of the finite mutation flow is that cooperating strategies here gets an advantage. From the figure it is clear that the regime for which the degree of cooperation is high, grows with increased mutation rate. The oscillatory dynamics (cf. Fig. 6) is characterized by a period where the population is dominated by cooperating strategies in the absence of the unconditional defector, but a slow drift due to the mutation flow
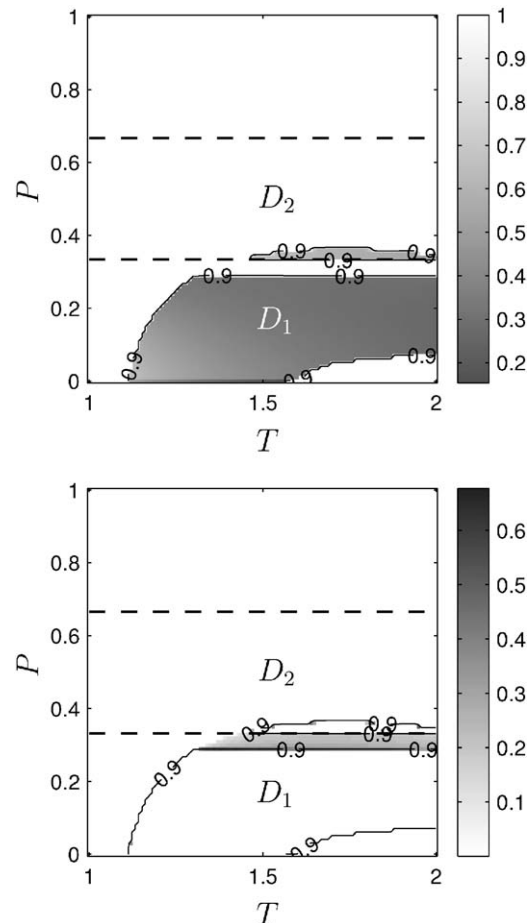

Fig. 4. *Top*: Asymptotic time-average of the average payoff in the population (represented by the grey value, as indicated in the scale to the right of the figure), as a function of the parameters T and P, when the population is initialized with a population of s_3 strategies, in the case of group size $n = 4$ and $\mu = 10^{-4}$. *Bottom*: Asymptotic standard deviation of the average payoff in the population (represented by the grey value, as indicated in the scale to the right of the figure), as a function of the parameters T and P. The line where the average payoff equals 0.9 is shown in both panels. Also shown in both panels are the borders at $P = \frac{1}{3}$ and $P = \frac{2}{3}$ between the different asymptotically stable populations, in the limit of infrequent mutations (dashed lines).

destabilizes that state. After a short interval in which the defector enters but quickly disappears, the period starts again with the cooperating strategies. The period of the oscillations is approximately proportional to $(\delta\mu)^{-1}$.

5.4. Dependency on the group size

In Fig. 7, the average payoff as function of P is shown for four different group sizes, for $T = 1.2$. The mutation rate is very low, $\mu = 10^{-7}$, and for group size $n = 3$, the results are indistinguishable from the evolutionary stability analysis based on fixed points involving only two strategies. As the group size increases, we find that even for this low mutation rate, there are significant differences compared with the case of infinitesimal
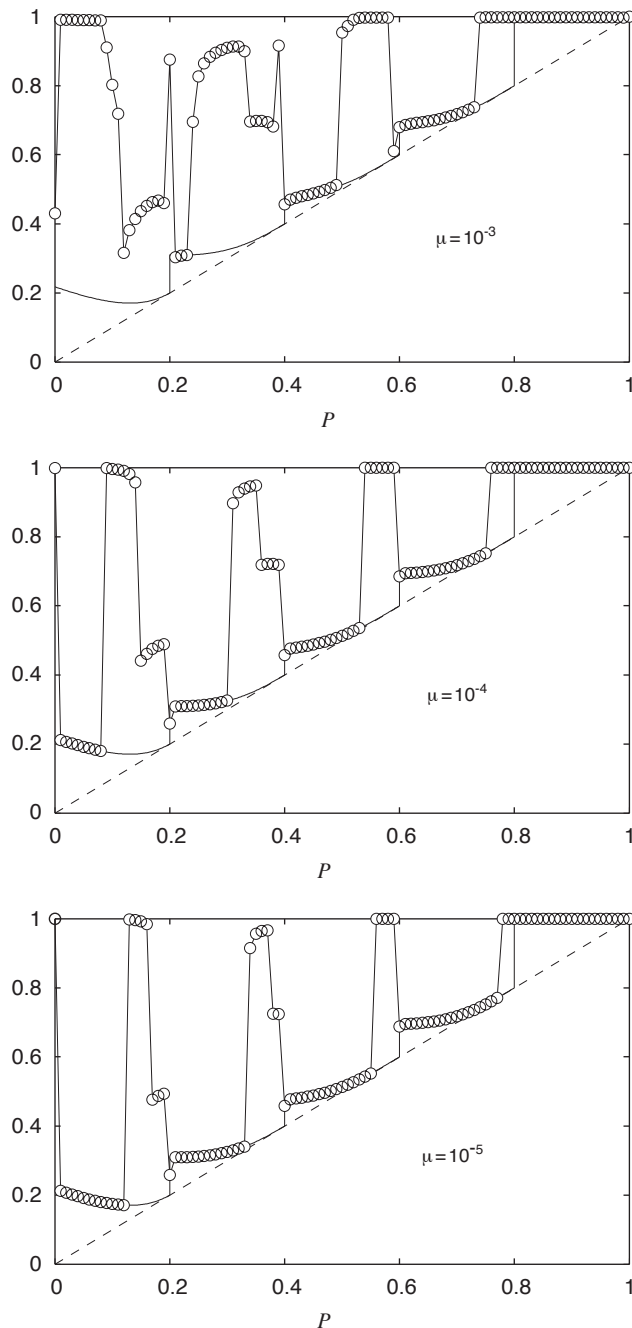
Fig. 5. The time-averaged average payoff in the population as a function of P, for $n = 6$ and $T = 1.6$, for $\mu = 10^{-3}$ (top), $\mu = 10^{-4}$ (middle), and $\mu = 10^{-5}$ (bottom). Also shown is the payoff in the limit of infinitesimal μ (thick line) and the payoff P for a population of pure all-defect (dashed line).

mutation flow. As the group size gets larger, we get both an increasing number and size of cooperative regions, with the exception of the original cooperative region for $P > (n - 2)/(n - 1)$. This illustrates that we can get a higher degree of cooperation when group size is increased for some parameter values, while for other values cooperation decreases.

As expected, the evolutionarily stable states are increasingly sensitive to the rate of mutations, as the group size increases. Also for very low rates of mutations, the average degree of cooperation remains high as the group size increases, even though the corresponding degree in the limit of infrequent mutations converges to the payoff for a population of all-defect players.

6. Summary and outlook

The *n*-person Prisoner's Dilemma game is generally assumed to be characterized by a lower degree of cooperation than the two-person game, when the players are confined to trigger strategies. We have shown that this result is weakened when mutations occur frequently in the population, even though the mutation rate per individual per generation is low, and that it is due to the long relaxation times of the evolutionary dynamics in certain areas of the parameter region. This effect is increasing with group size, since the number of different fixed point regions increases with number of players. From this, we conclude that an analysis of the evolutionary stability is not sufficient in order to achieve an understanding of the long-term evolutionary dynamics.

In order to address this issue, we have derived a deterministic approximation of the evolutionary dynamics with explicit, stochastic mutation processes, valid when the population size is large. We then analysed how the evolutionary dynamics depends on the following factors: mutation rate, group size, the value of the payoff parameters, and on the initial population. In order to carry out the simulations for more than just a few individuals, we have derived an efficient way of calculating the fitness values.

Our results may be summarized as follows: When the mutation rate per individual and generation is very low, the dynamics is characterized by populations that are evolutionarily stable. As the mutation rate is increased, other fixed points with a higher degree of cooperation become stable. For some values of the payoff parameters, the system is characterized by (apparently) stable limit cycles dominated by cooperative behaviour. The parameter regions corresponding to high degree of cooperation grow in size with the mutation rate and in number with the group size. For some parameter values, there are more than one stable fixed point, corresponding to different structures of the initial population. When the group size is increased, the average degree of cooperation in the population may increase or decrease depending on exact payoff parameters and groups size.

The main limitation of this study is that the groups are assumed to persist for a very long time. It is known that, e.g. the ability to defend against pure defectors in large groups requires very long games, to offset the cost of initial cooperative actions when defectors are present
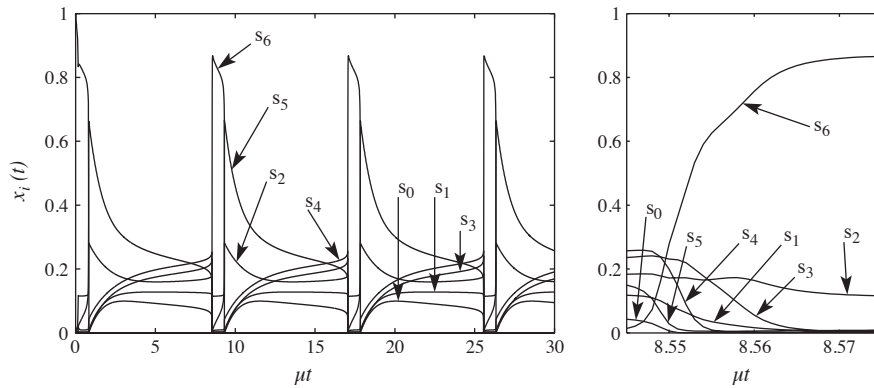
Fig. 6. Time evolution of the population when $n = 6$, $\mu = 10^{-4}$, $T = 1.6$ and $P = 0.33$. The left panel shows the initial transient, and two cycles of the attractor. The right panel shows the breakdown of cooperation, within a cycle, where strategy s_6 comes to dominate the population for a period of time. During the part of the cycle where strategy s_6 is prominent, the system approaches the population mixture which is evolutionarily stable when mutations are infrequent. For the value of P used here, it corresponds to a mixture of strategies s_2 and s_6. For a period of time, this mixture of strategies dominates the population. After a while, however, x_5 starts to grow at the expense of x_6, and after a while there is another sharp transition where x_5 and x_2 grow and x_6 decay to very low levels. The period of the oscillations is approximately proportional to $(\delta\mu)^{-1}$.

in a group (Boyd and Richerson, 1988). It is thus of interest to extend the analysis of this paper to investigate how the evolutionary dynamics is affected when the expected number of iterations is varied.

In this article, we have assumed that all groups are of the same size. In many situations, however, the group size can be expected to vary from one group to another within the population. Our results then indicate that a stable degree of cooperation would be difficult to attain. However, if group size preferences would be part of the players strategies, one could imagine that for certain choices of parameters, the evolutionary dynamics may lead to the formation of groups of certain sizes optimal for a high degree of cooperation. In a forthcoming study, an analysis of dynamic group formation in the n-person Prisoner's Dilemma will be presented.

Acknowledgements

Appendix A. Proof of Theorem 1

We begin with a simple observation on the number of players that cooperate in the iterated game, when no player is unsatisfied with the number of cooperators in the group. This is then exploited to yield an efficient method of evaluating the probabilities P_i^l.

Let k_j denote the number of players with trigger level j in a given group. Assume that strategies $s_0, \ldots, s_{i-1}$ cooperates, that strategies $s_i, \ldots, s_n$ defect, and that no player will switch to defection in the next round. Since strategy s_{i-1} requires at least $i - 1$ other players to

cooperate in the group, it cooperates in the next round if and only if $\sum_{j=0}^{i-1} k_j \geq i$. Strategy s_i defects in the next round provided $\sum_{j=0}^{i-1} k_j \leq i$. Thus, in a stable configuration with i cooperators, $\sum_{j=0}^{i-1} k_j = i$ and $k_i = 0$. From this follows:

Observation A.1. *Assuming that all players cooperate in the first round, except those with strategy s_n, the number i of players that cooperate in the stable configuration is determined by*: (a) *no player has strategy s_i*, (b) *i players have a trigger level less than i, and* (c) *for the group there is no trigger level larger than i for which properties* (a) *and* (b) *hold.*

A randomly composed group with $n - 1$ players contains $k_0 \cdots k_n$ players, with trigger levels $0 \cdots n$ respectively, with probability

$$(n-1)! \frac{x_0^{k_0}}{k_0!} \cdots \frac{x_n^{k_n}}{k_n!}, \quad \text{where} \quad \sum_{i=0}^{n} k_i = n - 1.$$

We now consider groups of size n where one player has trigger level l and $n - 1$ players are chosen randomly from the population. Assume that strategies $s_0, \ldots, s_i$ cooperates, and that strategies $s_{i+1}, \ldots, s_n$ defects. Then, in the next round

$$\begin{cases} 0 \ldots i & \text{cooperates} \Leftrightarrow \sum_{j=0}^{i} k_j + \mathbf{1}_{(l \leq i)} \geq i + 1, \\ i + 1 \ldots n & \text{defects} \Leftrightarrow \sum_{j=0}^{i+1} k_j + \mathbf{1}_{(l \leq i+1)} \leq i + 1, \end{cases}$$

where $\mathbf{1}_{(C)}$ is one if the condition C is true and zero otherwise. We cannot have $l = i + 1$ in a stable configuration, since it would contradict Observation A.1, so $P_l^l = 0$ and we have
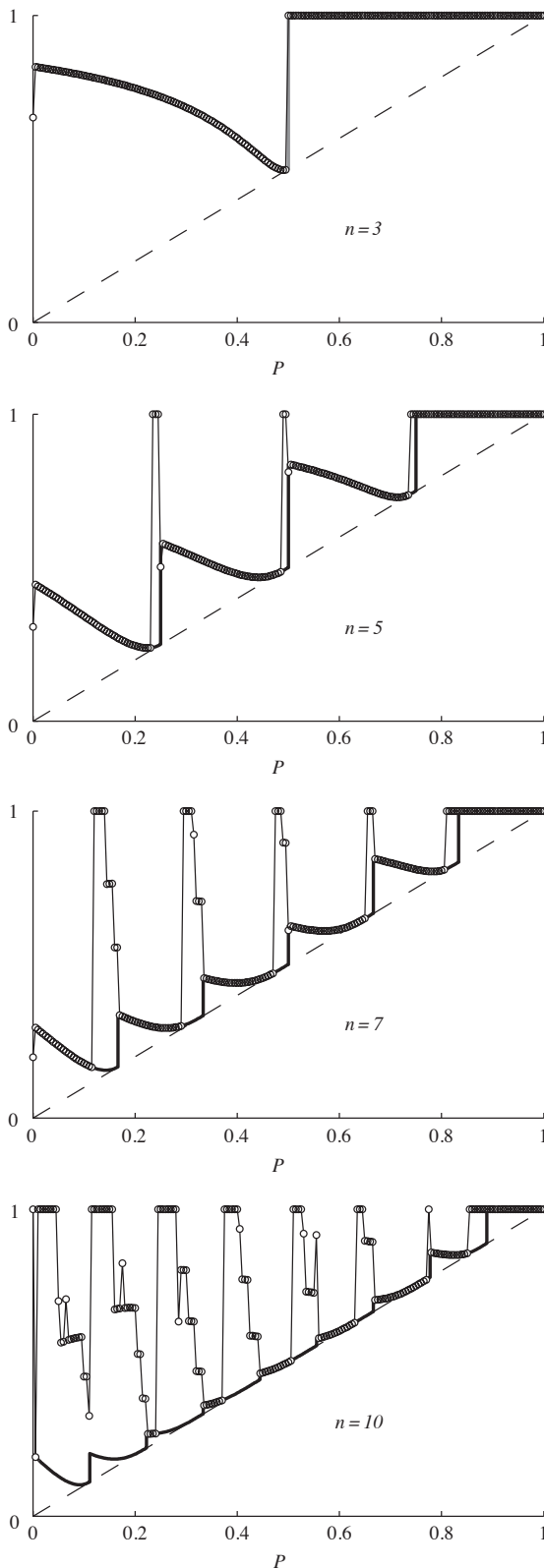
Fig. 7. The time-averaged average payoff in the population for $n \in \{3, 5, 7, 10\}$ (top to bottom), for $T = 1.2$. Circles correspond to simulations with $\mu = 10^{-7}$. Also shown is the payoff in the limit of infinitesimal μ (thick line) and the payoff P for a population of pure all-defect (dashed line).

i is a stable configuration

$$\Rightarrow \sum_{j=0}^{i-1} k_j + \mathbf{1}_{(l<i)} = i \text{ and } k_i = 0. \qquad (A.1)$$

This allows us to write P_i^l as the product of two independent sums:

$$P_i^l = \sum_{\substack{k_0, \ldots, k_{i-1} \text{ s.t.} \\ i \text{ is a stable conf.}}} \quad \sum_{\substack{k_{i+1}, \ldots, k_n \text{ s.t.} \\ k_0 + \cdots + k_n = n \text{ and} \\ \text{strategies } s_i, \ldots, s_n \text{ defects}}} \frac{n!}{k_0! \cdots k_n!} x_0^{k_0} \cdots x_n^{k_n}.$$

The sum over $k_0 \cdots k_{i-1}$ evaluates to

$$\sum_{\substack{k_0, \ldots, k_{i-1} \text{ s.t.} \\ k_0 + \cdots + k_{i-1} = i - \mathbf{1}_{(l<i)}}} \frac{x_0^{k_0}}{k_0!} \cdots \frac{x_{i-1}^{k_{i-1}}}{k_{i-1}!}$$

$$= \frac{1}{(i - \mathbf{1}_{(l<i)})!} (x_0 + \cdots + x_{i-1})^{i - \mathbf{1}_{(l<i)}}.$$

Unfortunately, the sum over $k_{i+1} \cdots k_n$ is not as simple to evaluate. In order to evaluate it, we define D_m^i to be the sum over all groups where m players with a trigger level greater than i is defecting (weighted by $m!$ to give a nicer result):

$$D_m^{l,i} = \sum_{\substack{k_{i+1}, \ldots, k_n \text{ s.t.} \\ k_{i+1} + \cdots + k_n = m, \text{ and} \\ \text{strategies } s_i, \ldots, s_n \text{ defects given } l}} m! \frac{x_{i+1}^{k_{i+1}}}{k_{i+1}!} \cdots \frac{x_n^{k_n}}{k_n!}.$$

By applying (A.1) to $i \cdots n - 1$ we see that

$$D_m^{l,i} = \sum_{\substack{k_{i+1}, \ldots, k_n \text{ s.t.} \\ k_{i+1} + \cdots + k_n = m, \text{ and} \\ k_{j+1} + \cdots + k_n \geqslant n - j + \mathbf{1}_{(l<i)} \text{ for} \\ i \leqslant j \leqslant n-1}} m! \frac{x_{i+1}^{k_{i+1}}}{k_{i+1}!} \cdots \frac{x_n^{k_n}}{k_n!}.$$

The structure of the conditions on the sum allows us to express $D_m^{l,i}$ recursively in terms of $D_m^{l,i+1}$, and we arrive at (11) and (12). □

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