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LETTER TO THE EDITOR

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Olaf Stenull† and Heinz G Schuster

Institut für Theoretische Physik, Christian-Albrechts-Universität zu Kiel, Leibnizstraße 15, D-24098 Kiel, Germany

Abstract. We present a soluble variant of the replicator model well established in theoretical biology and game theory. By using methods of statistical physics we derive an analytical solution to our model which becomes exact in the long time limit. We apply our model to the iterated prisoner's dilemma game and compare our results to numerical simulations.

The replicator model describes the evolution of self-replicating entities, replicators, in different areas of biological sciences, for example sociobiology, ecology, prebiotic evolution and genetics [1, 2]. While it finds increasing interest, in particular in the context of dynamical game theory, most investigations still essentially rely on numerical simulations [3, 5, 6]. Here we introduce a diluted version of the replicator dynamics and present an analytic solution to our model.

As the original replicator model, our model describes the time evolution of a population by a set of so-called game dynamical equations. The population consists of n species, each adopting a certain strategy i. The state of the population at time step (generation) t is characterized by a vector $x^t = (x_0^t, \ldots, x_{n-1}^t)$ with x_i^t being the fraction of the population which belongs to species i ($x_i^t \geqslant 0$, $\sum_{i=0}^{n-1} x_i^t = 1$). A pay-off matrix $\mathbf{A} = (A_{ij})_{ij=0}^{n-1}$ encodes the interactions between the species.

In the original replicator model each species interacts with all members of the population in every time step. In our diluted annealed [7] model we draw in each generation one specific species $j(t)$ randomly with equal probability out of the set $\{0, \ldots, n-1\}$. Then all members of the population interact with $j(t)$. At the next time step a new species is drawn and so on.

The pay-off of species i, $A_{ij(t)}x_{j(t)}^t$, is viewed as a measure of its reproductive success (fitness) [8]. The offspring inherits its species strategy, and hence the growth rate of a species is set proportional to its fitness. Accordingly, the time evolution of the entire population is governed by

$$x_i^{t+1} = \frac{x_i^t A_{ij(t)} x_{j(t)}^t}{\sum_{i=0}^{n-1} x_i^t A_{ij(t)} x_{j(t)}^t} \qquad i = 0, \ldots, n-1. \qquad (1)$$

Since the iterated prisoner's dilemma has become the leading paradigm for the emergence of cooperation in biological societies, we are in particular interested in the

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† Present address: Institut für Theoretische Physik III, Heinrich-Heine-Universität zu Düsseldorf, Universitätsstaße 1, D-40225 Düsseldorf, Germany.

situation where the members of the population play this game. The prisoner's dilemma (PD) is a two-player game [9, 10]. The players have to opt simultaneously for one of the two strategies C (cooperate) or D (defect). If both players cooperate they receive a pay-off of R points. The pay-off for joint defection is P points. An unilaterally defecting player obtains T points while his opponent ends up with S points. Because $T > R > P > S$ and $R > (T + S)/2$ (we use $T = 5$, $R = 3$, $P = 1$ and $S = 0$) a rational player will choose D since this yields the higher pay-off no matter whether the opponent opts for C or D. However, if there is a sufficiently high probability that the players will meet again there is no longer a single best strategy for the iterated prisoner's dilemma (IPD).

We consider a simple version of the IPD where strategies are entirely specified by the outcome of the previous round. Such strategies are said to have one-step memory and can be described by a quadruple $p^i := (p_1^i, p_2^i, p_3^i, p_4^i)$, where the components denote the probabilities of cooperating after the outcome of the previous round was R, S, T or P, respectively. If all components are either 0 or 1 such a strategy is deterministic. There are 16 deterministic strategies with one-step memory (which we label by $i = 0, \ldots, 15$, with the ith quadruple being the binary representation for i).

We take uncertainty into account by introducing a small probability ϵ to misimplement a move and replacing 1 by $1 - \epsilon$ and 0 by ϵ in the deterministic strategies [11]. If $\epsilon > 0$ (we use $\epsilon = 10^{-5}$) the game between two strategies i and j can be modelled as a Markov process with fully ranked transition matrix

$$
\begin{pmatrix}
p_1^i p_1^j & p_1^i(1 - p_1^j) & (1 - p_1^i)p_1^j & (1 - p_1^i)(1 - p_1^j) \\
p_2^i p_3^j & p_2^i(1 - p_3^j) & (1 - p_2^i)p_3^j & (1 - p_2^i)(1 - p_3^j) \\
p_3^i p_2^j & p_3^i(1 - p_2^j) & (1 - p_3^i)p_2^j & (1 - p_3^i)(1 - p_2^j) \\
p_4^i p_4^j & p_4^i(1 - p_4^j) & (1 - p_4^i)p_4^j & (1 - p_4^i)(1 - p_4^j)
\end{pmatrix}.
$$

The stationary distribution $\pi := (\pi_1, \pi_2, \pi_3, \pi_4)$ corresponds to the left-hand eigenvector of the transition matrix with eigenvalue 1. The mean pay-off for i against j can be calculated as

$$
A_{ij} = R\pi_1 + S\pi_2 + T\pi_3 + P\pi_4.
$$

The diluted model can be solved by iteration of equation (1) which yields

$$
x_i^t = \frac{x_i^0 \prod_{\tau=0}^{t-1} A_{ij(\tau)}}{\sum_{i=0}^{n-1} x_i^0 \prod_{\tau=0}^{t-1} A_{ij(\tau)}}
$$

where x_i^0 is the initial frequency of species i. Next we average over all possible realizations of the sequence $\{j(\tau)\}_{\tau=0}^{t-1}$ and obtain

$$
\langle x_i^t \rangle = \frac{1}{n} \sum_{j(0)=0}^{n-1} \cdots \frac{1}{n} \sum_{j(t-1)=0}^{n-1} \frac{x_i^0 \prod_{\tau=0}^{t-1} A_{ij(\tau)}}{\sum_{i=0}^{n-1} x_i^0 \prod_{\tau=0}^{t-1} A_{ij(\tau)}}. \tag{2}
$$

To perform the average it is convenient to introduce new summation variables $m_i = \sum_{\tau=0}^{t-1} \delta_{ij(\tau)}$, which count how often $j(\tau)$ is equal to i for $\tau = 0, \ldots, t - 1$. With these new variables equation (2) reads

$$
\langle x_i^t \rangle = \sum_{m_1} \cdots \sum_{m_n} \frac{x_i^0 \prod_{k=0}^{n-1} A_{ik}^{m_k}}{\sum_{i=0}^{n-1} x_i^0 \prod_{k=0}^{n-1} A_{ik}^{m_k}} P^t(m_0, \ldots, m_{n-1}). \tag{3}
$$

where $P^t(m_0, \ldots, m_{n-1})$ is the multinomial distribution

$$
P^t(m_0, \ldots, m_{n-1}) = \frac{t!}{m_0! \ldots m_{n-1}!} \left(\frac{1}{n}\right)^t
$$

and the sum has to be taken over all combinations of the m_i's such that $\sum_i m_i = t$. In order to eliminate the denominator, we rewrite equation (3) as

$$\langle x_i^t \rangle = x_i^0 \frac{\partial}{\partial x_i^0} \sum_{m_0} \cdots \sum_{m_{n-1}} \ln \left(\sum_{j=0}^{n-1} x_j^0 \prod_{k=0}^{n-1} A_{jk}^{m_k} \right) P^t(m_0, \ldots, m_{n-1}).$$

With the replica trick [12], which is based on the identity

$$\ln Z = \lim_{l \to 0} \frac{Z^l - 1}{l}$$

the average can be expressed as

$$\langle x_i^t \rangle = x_i^0 \frac{\partial}{\partial x_i^0} \lim_{l \to 0} \frac{\langle Z^l \rangle - 1}{l} \tag{4}$$

with

$$\langle Z^l \rangle = \sum_{m_0} \cdots \sum_{m_{n-1}} \frac{t!}{m_0! \ldots m_{n-1}!} \left(\frac{1}{n} \right)^t \left(\sum_{j=0}^{n-1} x_j^0 \sum_{k=0}^{n-1} A_{jk}^{m_k} \right)^l$$

$$= \sum_{m_0} \cdots \sum_{m_{n-1}} \sum_{l_0} \cdots \sum_{l_{n-1}} \frac{t!}{m_0! \ldots m_{n-1}!} \frac{l!}{l_0! \ldots l_{n-1}!} \left(\frac{1}{n} \right)^t \prod_{j=0}^{n-1} x_j^{0 l_j} \prod_{k=0}^{n-1} A_{jk}^{m_k l_j} \tag{5}$$

where $\sum_j l_j = l$. Equation (5) holds for real l if the factorials are interpreted as gamma functions. It can be rearranged to

$$\langle Z^l \rangle = \sum_{l_0} \cdots \sum_{l_{n-1}} \frac{l!}{l_0! \ldots l_{n-1}!} \left(\frac{1}{n} \right)^t \left(\prod_{j=0}^{n-1} x_j^{0 l_j} \right) \left(\sum_{k=0}^{n-1} \prod_{j=0}^{n-1} A_{jk}^{l_j} \right)^t. \tag{6}$$

At large times the average behaviour of our diluted model cannot be distinguished from the situation that the strategies are chosen in a cyclic fashion. Hence the geometric mean enters and we can rewrite equation (6) as

$$\langle Z^l \rangle = \sum_{l_0} \cdots \sum_{l_{n-1}} \frac{l!}{l_0! \ldots l_{n-1}!} \left(\prod_{j=0}^{n-1} x_j^{0 l_j} \right) \left(\sum_{k=0}^{n-1} \prod_{j=0}^{n-1} A_{jk}^{l_j} \right)^{t/n}$$

which leads to

$$\langle Z^l \rangle = \left(\sum_{j=0}^{n-1} x_j^0 \prod_{k=0}^{n-1} A_{jk}^{t/n} \right)^l. \tag{7}$$

By substitution of equation (7) into (4) one obtains

$$\langle x_i^t \rangle = \frac{x_i^0 (\prod_{k=0}^{n-1} A_{ik})^{t/n}}{\sum_{i=0}^{n-1} x_i^0 (\prod_{k=0}^{n-1} A_{ik})^{t/n}}. \tag{8}$$

It is important to note that equation (8) is exact in the long time limit for arbitrary A by virtue of the law of large numbers which implies $\lim_{t \to \infty} \langle m_i \rangle = t/n$ for all i. For small times how well the system is described by equation (8) it depends on the nature of A. If the matrix elements are distributed with small fluctuations around an average value, our solution will well describe the short time behaviour. For the IPD though, there are significant deviations during equilibration (see figure 1).

From equation (8) it can be deduced that the strategy which corresponds to the largest row product of A dominates the asymptotic behaviour. It eventually takes over the population for all possible initial conditions in which it is present. Hence our model has a
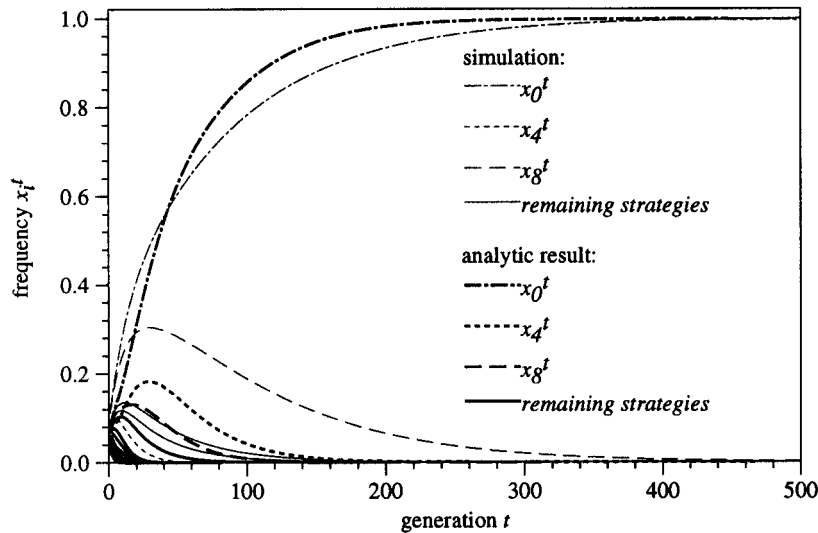
Figure 1. Plot of x_i^t, equation (8), for the IPD (bold curves). The thin curves are obtained by averaging over 10^5 simulations based on equation (1) with $x_i^0 = 1/16$ for all i.

very low intrinsic cooperation pressure [13, 14] that drives the dynamics towards an edge of the simplex on which it is defined. In the IPD the strategy AllD, which plays defect no matter what the opponent does, takes over the population (see figure 1). The original replicator dynamics on the other hand, admits a more complex asymptotic behaviour, including limit cycles [4] and asymptotically stable populations of cooperative strategies.

Chance plays an important role in evolution. Our results indicate that randomness can be incorporated into evolutionary models via dilution. Moreover, dilution may cast an evolutionary model in a form that fosters an investigation by analytical means.

References

[1] Hofbauer J and Sigmund K 1982 *The Theory of Evolution and Dynamical Systems* (Cambridge: Cambridge University Press)
[2] Schuster P and Sigmund K 1983 *Theor. Biol.* **100** 533
[3] Nowak M A and Sigmund K 1990 *Nature* **355** 250–3
[4] Nowak M A, Sigmund K and El-Sedy E 1995 *J. Math. Biol.* **33** 703–23
[5] Lindgren K and Nordahl M G 1994 *Physica* D **75** 292–309
[6] Hauert Ch and Schuster H G 1997 *Proc. R. Soc.* B **264** 513–19
[7] Derrida B, Gardner E and Zippelius A 1987 *Europhys. Lett.* **4** 167–73
[8] Maynard Smith J 1982 *Evolution and the Theory of Games* (Cambridge: Cambridge University Press)
[9] Axelrod R and Hamilton W D 1981 *Science* **211** 1390–6
[10] Axelrod R 1984 *The Evolution of Cooperation* (New York: Basic Books)
[11] Nowak M A and Sigmund K 1993 *Proc. Natl Acad. Sci., USA* **90** 5091–4
[12] Mezard M, Parizi G and Virasoro M A 1987 *Spin Glass Theory and Beyond* (Singapore: World Scientific)
[13] Peschel M and Mende W 1982 *The Predator–Prey Model* (Vienna: Springer)
[14] Opper M and Diederich S 1992 *Phys. Rev. Lett.* **69** 1616–19